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1 **Not all species will migrate poleward as the climate warms:**  
2 **the case of the seven baobab species in Madagascar**

3 **Running head: Baobabs redistribution as climate warms**

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19 **Abstract**

20 It is commonly accepted that species should move toward higher elevations and latitudes to track  
21 shifting isotherms as climate warms. However, temperature might not be the only limiting factor  
22 determining species distribution. Species might move to opposite directions to track changes in other  
23 climatic variables. Here, we used an extensive occurrence dataset and an ensemble modelling  
24 approach to model the climatic niche and to predict the distribution of the seven baobab species  
25 (genus *Adansonia*) present in Madagascar. Using climatic projections from three global circulation  
26 models, we predicted species' future distribution and extinction risk for 2055 and 2085 under two  
27 representative concentration pathways (RCPs) and two dispersal scenarios. We disentangled the role  
28 of each climatic variable in explaining species range shift looking at relative variable importance and  
29 future climatic anomalies. Four baobab species (*A. rubrostipa*, *A. madagascariensis*, *A. perrieri*, and *A.*  
30 *suarezensis*) could experience a severe range contraction in the future (> 70% for year 2085 under RCP  
31 8.5, assuming a zero-dispersal hypothesis). For three out of the four threatened species, range  
32 contraction was mainly explained by an increase in temperature seasonality, especially in the North of  
33 Madagascar, where they are currently distributed. In tropical regions, where species are commonly  
34 adapted to low seasonality, we found that temperature seasonality will generally increase. It is thus  
35 very likely that many species in the tropics will be forced to move equatorward to avoid an increase in  
36 temperature seasonality. Yet, several ecological (e.g. equatorial limit, or unsuitable deforested habitat)  
37 or geographical barriers (absence of lands) could prevent species to move equatorward, thus  
38 increasing the extinction risk of many tropical species, like endemic baobab species in Madagascar.

39 **Key-words:** Baobabs; climatic anomaly; climate change; elevation; extinction risk; latitude;  
40 Madagascar; temperature seasonality; species distribution models, species range shift

## 41 1. Introduction

42 Climate change has already modified the spatial distribution of tropical biodiversity (Chen et al., 2009;  
43 Fadrique et al., 2018; Feeley, Silman, & Duque, 2016). Increasing temperatures, anomalous  
44 precipitation regimes (Anderson-Teixeira et al., 2013) and more frequent and severe extreme events  
45 (e.g. heatwaves, droughts and wildfires; Garcia, Cabeza, Rahbek, & Araújo, 2014) all pose significant  
46 challenges to biodiversity by pushing species towards the limits of their climatic tolerances (Rodríguez-  
47 Castañeda, 2013). Temperature has been the main variable considered when studying biotic responses  
48 to climate change for several reasons. First, it is an easy to measure variable. The first reliable  
49 thermometers have been used to measure air temperature since the beginning of the 18th century  
50 (Fahrenheit, 1724). Second, temperature generally decreases with elevation and latitude and has been  
51 historically used to define habitat types on Earth (FAO, 2010; von Humboldt, 1817; Holdridge, 1947).  
52 Third, temperature is a known determinant of species biology and distribution (Sentinella, Warton,  
53 Sherwin, Offord, & Moles, 2020; Tewksbury, Huey, & Deutsch, 2008). Fourth, temperature is strongly  
54 correlated to CO<sub>2</sub> concentration in the atmosphere and is expected to significantly increase at the  
55 global scale in the future, in association with increasing CO<sub>2</sub> emissions due to human activities (IPCC,  
56 2014). As a consequence, it is commonly accepted that species will move towards higher elevations  
57 (i.e. upslope) and latitudes (i.e. poleward) to track shifting isotherms as the climate warms (Colwell,  
58 Brehm, Cardelús, Gilman, & Longino, 2008; Lenoir, Gégout, Marquet, de Ruffray, & Brisse, 2008; Lenoir  
59 & Svenning, 2015).

60 However, it has also been observed that species may go “*against the flow*” under the effect of climate  
61 change: towards lower elevations (i.e. downslope) and lower latitudes (i.e. equatorward) to find  
62 suitable climate conditions (Lenoir et al., 2010). These unexpected directional range shifts may involve  
63 several potential determinants, e.g. indirect biotic response due to the combined effect of both climate  
64 warming and land-use change; changes in interspecific interactions such as competition release;  
65 sensitivity to other environmental gradients not conforming with upslope and poleward range shifts;  
66 physiological or evolutionary adaptations; and random shifts due to stochastic ecological processes  
67 (Crimmins, Dobrowski, Greenberg, Abatzoglou, & Mynsberge, 2011; Lenoir et al., 2010; Pinsky, Worm,  
68 Fogarty, Sarmiento, & Levin, 2013). Yet, studies reporting species range shifts in response to  
69 anthropogenic climate change usually focus on two geographical dimensions solely – latitude and  
70 elevation (Lenoir & Svenning, 2015) – and one single climatic dimension, namely mean annual  
71 temperature. Hence, these studies disregard other relevant climatic predictors such as changes in  
72 precipitation regime, water balance, or temperature seasonality, which may force species to shift  
73 downward in elevation (Crimmins et al., 2011; Lenoir et al., 2010). Given that, it is extremely important  
74 to account for additional climatic variables different from the mean annual temperature and consider  
75 other potential ecological processes that could explain species range shifts in multiple directions.

76 The most commonly employed tools to predict current and future distribution of species under climate  
77 change from a set of observations and climatic predictors are correlative species distribution models  
78 (SDMs) (Elith & Graham, 2009; Foden et al., 2019; Guisan et al., 2013; Porfirio et al., 2014). The main  
79 outputs of these SDMs are maps of species potential distributions in the present and future. Nowadays,  
80 many easy-to-use softwares (the JAVA Maxent; Phillips, Anderson, & Schapire, 2006) or libraries (e.g.  
81 “*sdm*” and “*biomod2*”; Naimi & Araújo, 2016; Thuiller, Lafourcade, Engler, & Araújo, 2009) have been  
82 made available to easily derive such redistribution maps. Comparing present with future species  
83 distribution maps, one can assess species vulnerability to climate change by looking at species range  
84 shift, contraction, or expansion (Vieilledent, Cornu, Cuní Sanchez, Leong Pock-Tsy, & Danthu, 2013).

85 Surprisingly, conservation studies that employ correlative SDMs to assess species vulnerability to  
86 climate change mostly do not disentangle the respective effect of predictor variables in explaining  
87 species range shift (Fourcade, Besnard, & Secondi, 2018). Thus, they fail at explaining the possible  
88 underlying mechanisms behind such changes. For example, in an article studying the vulnerability of  
89 three baobab species to climate change in Madagascar, Vieilledent et al. (2013) showed that *Adansonia*  
90 *suarezensis* H. Perrier, and *A. perrieri* Capuron, will likely become extinct by 2085. However, the study  
91 does not analyze the respective role of each variable in explaining species range shift and does not  
92 suggest potential mechanisms that could explain the species extinction. In addition, a recent study  
93 assessing the vulnerability of Madagascar endemic baobabs to future climate change also failed to  
94 explore the underlying mechanisms behind expected species range shifts (Wan et al., 2020).

95 To help fill this gap, we investigate here the specific role of a set of climatic variables in explaining shifts  
96 in species distribution associated with climate change. We chose the seven emblematic baobab species  
97 that can be found in Madagascar (*Adansonia* L. genus; Malvaceae family) for this purpose. Six of the  
98 seven species are endemic to Madagascar (*Adansonia grandidieri* Baill., *A. madagascariensis* Baill., *A.*  
99 *perrieri*, *A. rubrostipa* Jum. and Perr., *A. suarezensis*, and *A. za* Baill), while the remaining species also  
100 occurs in the African continent: *A. digitata* L. (Wickens 2008). Each of the seven baobab species are  
101 located in different regions of Madagascar, being adapted to different climates and could potentially  
102 have different responses to climate change. We gathered an extensive and unprecedented occurrence  
103 dataset obtained from more than 15 years of field prospection and photo-interpretation of high-  
104 resolution satellite images. We used an ensemble modelling approach to model the climatic niche and  
105 to predict the distribution of these seven species. Using SDMs and climatic projections, we assessed  
106 whether each species could experience range shift, contraction or expansion, and in which direction.  
107 Looking at the relative climatic variable importance and future climatic anomalies, we disentangled  
108 the role of each climatic variable in explaining species range shift. Based on species' extinction risk, we  
109 made suggestions to update the current baobab species conservation status. Finally, we attempted to  
110 generalize our results to other species in the tropics that should experience similar climatic anomalies  
111 in the future.

## 112 2. Material and methods

### 113 2.1 Presence and pseudo-absence data

114 We used photo-interpretation of very high-resolution QuickBird (61 cm resolution: most of the cases,  
115 especially for baobab identification from the crown or by their projected shadow) and Spot5 (2.5 m  
116 resolution: only in few specific cases, such as dense and homogeneous forests) satellite images  
117 available on Google Earth (<http://www.google.com/earth/index.html>; see Yu & Gong, 2012) to locate  
118 *A. grandidieri* and *A. suarezensis* individual trees in Madagascar. To validate occurrence data from  
119 photo-interpretation, ground-truth verifications were conducted identifying baobabs trees by the  
120 basis of their crown size, shape and color during flowering period (see Vieilledent et al. 2013). Ground-  
121 truth verification was conducted during the flowering period to facilitate species identification and  
122 validation of species occurrence data (see Vieilledent et al., 2013 for further details). For the other five  
123 Malagasy baobab species (*A. digitata*, *A. madagascariensis*, *A. perrieri*, *A. rubrostipa*, and *A. za*) we  
124 used an extensive presence only data-set available thanks to prospective fieldwork (2000 to 2015)  
125 from the Cirad Madagascar team. During fieldwork, baobab trees were identified at the species level  
126 and georeferenced with a GPS to generate a unique occurrence data-set for all Malagasy baobab  
127 species.

128 Our raw data-set contains 137,285 occurrence records encompassing all seven Malagasy baobab  
129 species. First, we removed all points with coordinates outside Madagascar (only for *A. digitata* because  
130 occurrence records were also collected in Comoro islands). Then, for each of the seven species  
131 separately, we created a grid with 1-km<sup>2</sup> cell resolution covering the Madagascar territory and  
132 identified all cells that had at least one occurrence record for the focal baobab species. Finally, we  
133 removed all cells and respective presence observation data with incomplete bioclimatic information.  
134 For instance, the initial set of 1,686 occurrence records available for *A. suarezensis* was reduced to a  
135 total of 170-pixel units of 1-km<sup>2</sup> each (Table S1 for all baobabs species). Our observation sample size  
136 was sufficient to perform SDMs because the recommended minimum sample size (see van Proosdij,  
137 Sosef, Wieringa, & Raes, 2016) for narrow-ranged species (as for *A. perrieri* – 21 1-km<sup>2</sup> grid cells) is as  
138 low as 3 while it is recommended to have at least 13 occurrence points for widespread species (as for  
139 *A. grandidieri* or *A. za* – 3,772 and 460 1-km<sup>2</sup> grid cells, respectively). We randomly sampled 10,000  
140 pseudo-absences (i.e. virtual absence data which are drawn to be representative of the environmental  
141 variability in the study-area; Barbet-Massin, Jiguet, Albert, & Thuiller, 2012) across all Madagascar for  
142 each species to constitute a presence/pseudo-absence data-set. By using pseudo-absences we used  
143 both presence and pseudo-absence information to predict species' habitat suitability and distribution,  
144 optimizing spatial and environmental discrimination (Senay, Worner, & Ikeda, 2013). Consequently,  
145 we aimed to have a good representativity of the climate variability in Madagascar and to be able to  
146 compute a relative probability of presence across the country.

### 147 2.2 Bioclimatic data

148 We used current (~1950-2000) and future (2055 and 2085) climatic data at 30 arc-seconds resolution  
149 (about 1 km at the equator) over the entire spatial extent of Madagascar. This data is freely available  
150 on MadaClim (<https://madaclim.cirad.fr/>). The MadaClim website provides climatic data for  
151 Madagascar obtained from the WorldClim (<http://worldclim.org/bioclim/>) and CGIAR-CCAFS climate  
152 data portal (<http://www.ccafs-climate.org/>). We selected four bioclimatic variables (Hijmans,  
153 Cameron, Parra, Jones, & Jarvis, 2005) to model species distribution which were weakly correlated

154 among each other and easy to interpret with regard to baobab species distribution. Three of them  
155 were previously selected via a principal component analysis among all the 19 WorldClim bioclimatic  
156 variables (following Vieilledent et al. (2013): **(1)** mean annual precipitation – *prec* (mm.y<sup>-1</sup>); **(2)** mean  
157 annual temperature – *tmean* (°C); **(3)** temperature seasonality – *tseas* (sd x 100 °C). In addition, we  
158 included a synthetic variable reflecting **(4)** climatic water deficit – *cwd* (mm). The *cwd* variable was  
159 computed from monthly precipitation (*mcprec*) and potential evapotranspiration (*pet*) using the  
160 following formula (**Equation 1**):

$$161 \quad \textit{cwd} = - \sum_i \min (\textit{mcprec}_i - \textit{pet}_i, 0) \quad (1)$$

162 Potential evapotranspiration is defined as the evaporation amount that would occur if a sufficient  
163 water source was available. We used the Thornthwaite formula (Thornthwaite, 1948) to compute the  
164 monthly potential evapotranspiration. The four selected bioclimatic variables are widely used **(i)** to  
165 define biomes globally, known as Holdridge Life Zones System (Holdridge, 1947) and **(ii)** as proxies for  
166 other bioclimatic variables. For instance, the mean annual temperature (*tmean*) is a proxy for solar  
167 radiation and temperature stress (Haigh, 2007). Additionally, the mean annual temperature may  
168 indicate potential losses of plant productivity (Hatfield & Prueger, 2015). The temperature seasonality  
169 (*tseas*) can be interpreted as a proxy for the growing season (Hatfield & Prueger, 2015) while the  
170 annual precipitation (*prec*) is a proxy for potential water availability (Amisssah, Mohren, Kyereh,  
171 Agyeman, & Poorter, 2018). Finally, the climatic water deficit (*cwd*) can be indicative of water stress  
172 and drought periods (Fayolle et al., 2014; Stephenson, 1990).

173 For future climate data (2055 and 2085) we selected three different global circulation models (GCMs)  
174 from the World Climate Research Programme (CMIP5) (i.e., NorESM1-M, GISS-E2-R, and HadGEM2-ES)  
175 under two representative concentration pathways (RCPs: carbon dioxide emission scenarios) (i.e., RCP  
176 4.5 and 8.5). The RCP 8.5 scenario is characterized by high concentration and increasing CO<sub>2</sub> gas levels  
177 emissions (Riahi, Grübler, & Nakicenovic, 2007; van Vuuren et al. 2011) and can be considered the  
178 most likely emission scenario in the absence of effective mitigation policies regarding CO<sub>2</sub> emissions,  
179 whereas RCP 4.5 is known as the “mitigation scenario” because of projected reduction of CO<sub>2</sub> gas levels  
180 emissions (van Vuuren et al. 2011). A recent discussion has been brought in the literature affirming  
181 that RCP 8.5 is a problematic scenario for near-term (2030-2050) emissions and indicate that RCP 4.5  
182 is more likely than RCP 8.5 (Hausfather & Peters, 2020). Despite this recent discussion, we projected  
183 our main results under RCP 8.5 because: (i) we projected for long-term climate change (i.e. 2085)  
184 where projections presented by RCP 8.5 in 2100 are more probable than RCP 4.5 (Schwalm, Glendo &  
185 Duffy, 2020a); (ii) historical cumulative CO<sub>2</sub> emissions from 2005 to 2020 are more in accordance with  
186 RCP 8.5 than RCP 4.5 (Schwalm, Glendo & Duffy, 2020)b; (iii) RCP 4.5 underestimate biotic feedbacks  
187 (e.g. changes in soil dynamics, forest fires frequency and severity, permafrost thaw) which accelerates  
188 warming, further supporting RCP 8.5 (Schwalm, Glendo & Duffy, 2020b); (iv) in our study we used RCP  
189 8.5 for the sake of risk assessment and not to compare RCPs effectiveness, despite RCP 4.5 projected  
190 temperature by 2100 is 1.7-3.2 °C, whereas for RCP 8.5 is 3.2-5.4 °C (Fuss et al. 2014). As a  
191 consequence, the outputs of RCP 4.5 in our study are presented in the supplementary material.

### 192 **2.3 Species distribution modeling: statistical algorithms, model performance and** 193 **importance of bioclimatic variables**

194 We selected four statistical algorithms to model the bioclimatic niche and distribution of the seven  
195 studied baobab species: generalized linear models (GLMs); generalized additive models (GAMs);  
196 random forests (RF); and Maxent. Algorithms selection included standard regression models, such as

197 the parametric GLM and the non-parametric GAM, classification tree (RF), and maximum entropy  
198 approach (Maxent). We aimed to quantify output uncertainty and generate a gradient from robustness  
199 (GLM and GAM) to complex algorithms, i.e. RF and Maxent (Elith & Graham, 2009). The uncertainty  
200 quantification of predictive modeling follows the premise of the ensemble modelling approach (Araújo  
201 & New, 2007), which enables a consensus identification among all forecasts and the exploration of the  
202 full breadth of intermodal variability (Kujala, Moilanen, Araújo, & Cabeza, 2013).

203 As we used two regression models (GLM and GAM) and two machine learning approaches (RF and  
204 Maxent) to fit SDMs, the inclusion of 10,000 pseudo-absence points (background points for Maxent  
205 algorithm) is advised for better SDM outputs to obtain more accurate results (Barbet-Massin et al.,  
206 2012). We randomly split our presence/pseudo-absence data-set using 70% for model calibration  
207 (training data-subset) and 30% for model validation (testing data-subset) to evaluate the predictive  
208 performances of our SDMs (Hijmans, 2012). We repeated the cross-validation procedure five times.  
209 Model performance in predicting species presence-absence was estimated using four different and  
210 complementary metrics: Area Under the Receiving Operating Characteristics Curve (*AUC*); True Skills  
211 Statistics (*TSS*); Sensitivity (*Sen*); and Specificity (*Spe*; Liu, White, & Newell, 2011). We thus calculated  
212 the mean value of *AUC* and *TSS* metrics across the five testing data-subsets obtained from the cross-  
213 validation procedure for each selected algorithm. By doing this we were able to describe the modelling  
214 performance in predicting species presence-absence. We also computed *AUC* and *TSS* metrics across  
215 the full data-set.

216 The *AUC* computes the model probability to rank a randomly chosen presence site instead of a  
217 randomly absent site (Liu et al., 2011; Pearce & Ferrier, 2000) and is commonly used as an accuracy  
218 index for SDMs using ensemble modelling approaches (Hao, Elith, Guillera-Arroita, & Lahoz-Monfort,  
219 2019). It is a threshold-independent index, and it is also independent to prevalence (Allouche, Tsoar,  
220 & Kadmon, 2006), which is the proportion of samples representing species presence (McPherson, Jetz,  
221 & Rogers, 2004). If *AUC* values are  $\geq 0.9$ , the model is commonly considered as highly accurate  
222 (Thuiller et al., 2009). The *TSS* metric is a threshold-dependent index (Liu et al., 2011) and is computed  
223 with a probability threshold maximizing its values. *TSS* values range from -1 to 1, and accurate models  
224 (correctly predicting both presences and absences) lead to values close to one (Thuiller et al., 2009).  
225 The *TSS* index is equal to Sensitivity + Specificity - 1. Sensitivity is the probability of correctly predicting  
226 a presence while specificity is the probability of correctly predicting an absence (Liu et al. 2011). As  
227 well as the *AUC* index, *TSS* is not sensitive to prevalence (Allouche et al., 2006; Lawson, Hodgson,  
228 Wilson, & Richards, 2014), so we used both accuracy indexes to evaluate SDM outputs for rare (such  
229 as *A. perrieri*) or abundant (such as *A. grandidieri*) baobab species.

230 To evaluate the performance of the ensemble model based on committee averaging we used three  
231 previously mentioned metrics: *TSS*, *Sen*, and *Spe*, following Araújo and New (2007). We previously  
232 defined an evaluation threshold using the accuracy index *TSS* (i.e. minimum score of 0.6 or 60%) in  
233 order to: **(i)** remove “bad algorithms/models”; **(ii)** build our ensemble model; **(iii)** test and evaluate the  
234 ensemble model forecasting capability (i.e. predicting species presence-absence); and **(iv)** make the  
235 binary transformation for the committee averaging computation (Thuiller et al. 2009).

236 For each statistical algorithm, we calculated the relative variable importance among the four studied  
237 bioclimatic variables selected for the SDMs. The computation principle follows the one used for RFs,  
238 where one bioclimatic variable is shuffled over the full data-set or the testing data-subset. To compute  
239 variable importance (*I*), the model prediction is calculated in this shuffled data-set, and a correlation



240 (Pearson's correlation) is computed between baseline predictions (*pred\_ref*) and the shuffled  
241 predictions (*pred\_shuffled*; see Equation 2).

$$242 \quad I = 1 - cor(pred_{ref}, pred_{shuffled}) \quad (2)$$

243 We thus generated a rank according to the variable importance over the four statistical algorithms for  
244 each species. The rank was defined by calculating the mean obtained from 6 model runs (5 runs from  
245 the testing data-subset and 1 run from the full data-set). The rank with higher mean values indicates  
246 which bioclimatic variable is more important to explain the species distribution. We used the Biomod2  
247 R package (Thuiller et al. 2009) to generate the SDMs.

## 248 **2.4 Current species distribution, climatic niche and elevational range**

249 For each species and each modelling algorithm, predicted probabilities of occurrence during the  
250 current period were binary transformed (0 for species absence and 1 for species presence) using the  
251 probability threshold maximizing TSS. Then, the current species distribution area (SDAp in km<sup>2</sup>) was  
252 defined as the set of 1-km<sup>2</sup> pixels where two out of the four modelling algorithms predicted the  
253 presence of the focal species. When only one algorithm out of the four predicted a presence for a given  
254 species, it was considered as uncertain. The species was considered absent when none of the four  
255 algorithms predicted a presence.

256 To characterize each species bioclimatic niche, we randomly sampled 1,000 points in the current  
257 species distribution area and computed the density (i.e. frequency), mean values, and 95% quantiles  
258 for each of the four studied bioclimatic variables, as well as for elevation. Elevation data in Madagascar  
259 was obtained from the SRTM (Shuttle Radar Topography Mission) 90 m Digital Elevation Data available  
260 from the CGIAR-CSI GeoPortal. Elevation data was aggregated at 1 km resolution and is also available  
261 for download on the MadaClim website.

## 262 **2.5 Ensemble forecasting and future species distribution**

263 To predict species distribution area in the future, we used an ensemble forecasting approach (Araujo  
264 & New 2007). For each of the two RCPs separately (RCP 4.5 and RCP 8.5), we combined climatic  
265 projections obtained from the three different GCMs (NorESM1-M, GISS-E2-R, and HadGEM2-ES) and  
266 across the four modelling algorithms (GLM, GAM, Random Forest, and Maxent). We thus obtained, for  
267 each species under each RCP and for each year (2055 and 2085), 12 maps of the future probability of  
268 presence. Again, the probability of presence was converted into binary data (0 for species absence and  
269 1 for species presence) using the same probability threshold which maximizes TSS during current  
270 conditions. Species distribution area in the future (SDAf) was defined as the set of 1-km<sup>2</sup> pixels where  
271 most projections (6 out of 12) predicted the presence of the focal species. When less than 6 models  
272 out of the 12 predicted a presence, the species presence in the future was considered uncertain. The  
273 species was considered absent in the future when none of the 12 projections predicted a presence.

274 When predicting future range maps under each RCP for 2055 and 2085, we also considered two  
275 contrasting dispersal hypotheses, with the reality likely to fall in between. The full-dispersal hypothesis  
276 considers the possibility for all baobab species to colonize new climatically favorable sites outside the  
277 current species distribution range. The zero-dispersal hypothesis considers the impossibility for  
278 baobab species to naturally colonize new climatically favorable sites outside the current species  
279 distribution range. This can be due to unsuitable conditions (other than climate, such as land-use)

280 outside the current species distribution area, or to that baobab species may not be able to disperse  
281 seeds due to geographical barriers or in the absence of animal dispersers (see Vieilledent et al. 2013).

## 282 **2.6. Species range shift and vulnerability to climate change**

283 To evaluate the effect of climate change and the vulnerability of the seven Malagasy baobab species,  
284 we calculated the percentage of area change between the future (SDAf) and present (SDAp)  
285 distribution range (in km<sup>2</sup>). To compute SDAf, SDAP, and mean elevational shifts, we extracted all  
286 presence points indicated as 'presence' by the ensemble modelling and calculated the changes for  
287 each of the investigated future scenarios (mean, 95% quantiles interval, and percentage of area change  
288 in km<sup>2</sup>). Focusing on the year 2085, under RCP 8.5 for the full-dispersal and zero-dispersal scenarios,  
289 we suggested updates for baobabs conservation management strategies given their future distribution  
290 and vulnerability to climate change according to the International Union for Conservation of Nature  
291 Red List (IUCN, 2012a). Finally, we calculated potential latitudinal and elevational species range shifts  
292 by extracting 1,000 random points inside each species distribution range projected for the present and  
293 the future (2055 and 2085), under both RCPs 4.5 and 8.5 scenarios and for the full-dispersal hypothesis.

## 294 **3. Results**

### 295 **3.1 Range contraction and vulnerability of baobab species to climate change**

296 For all seven baobab species we obtained high True Skill Statistics (TSS) values for both the model  
297 cross-validation (Table S2) and the ensemble model (Table S3). For the ensemble model, the TSS was  
298  $\geq 0.83$  for all the species except for *A. za*, for which the TSS was equal to 0.67 due to a relatively lower  
299 specificity (Table S3). High TSS values indicate that the models can then be confidently used to predict  
300 the vulnerability of species to climate change. Four baobab species are expected to be highly  
301 vulnerable to climate change under RCP 8.5, whereas for RCP 4.5 three species are expected to be  
302 highly vulnerable. *Adansonia perrieri* and *A. suarezensis* might experience a complete range loss  
303 modelled by 2085 (under RCPs 4.5 and 8.5), and could face extinction, under both the full and zero -  
304 dispersal hypothesis (Figures 1, S2; Tables 1, S4). Still, under RCP 8.5, *A. madagascariensis* and *A.*  
305 *rubrostipa* could experience a contraction in modelled suitable range by 2085, and thus might be  
306 threatened by extinction, under both the full ( $\geq -32\%$  area) and zero-dispersal hypothesis ( $\geq -71\%$  area).  
307 The three other baobab species modelled under RCP 8.5 (*A. za*, *A. grandidieri* and *A. digitata*), are  
308 expected to be resilient to climate change (Figure S1). These species might experience a small range  
309 contraction (down to -3%) under the zero-dispersal hypothesis and a strong range expansion (from  
310 +118% for *A. za* up to +300% for *A. grandidieri* and *A. digitata*) when modelled under the full-dispersal  
311 hypothesis (Table 1). Under RCP 4.5 and zero-dispersal hypothesis *A. madagascariensis* is predicted to  
312 lose 8% of its current distribution area, indicating that the species might not be threatened (Figure S2).  
313 The projections under RCP 4.5 and full-dispersal hypothesis also indicated a strong range expansion  
314 from +78% for *A. za* up to +268% for *A. grandidieri* and *A. digitata* (Figure S2; Table S4). Among these  
315 three species, only *A. digitata* is expected to contract its modelled suitable range by 2085 under zero-  
316 dispersal hypothesis: -20% (Figure S2). Both *A. grandidieri* and *A. za* might not be affected according  
317 to this predictive scenario.

### 318 **3.2 Baobab species range shift in latitude and elevation**

319 Among the four vulnerable baobab species, *A. suarezensis* and *A. perrieri* are expected to contract their  
320 range equatorward in 2085 under RCP 4.5 and for the full-dispersal hypothesis (both species are  
321 expected to go extinct under RCP 8.5 whatever the dispersal hypothesis). *Adansonia madagascariensis*  
322 is also expected to move equatorward while *A. rubrostipa* is expected to move poleward under RCP  
323 8.5 and full-dispersal hypothesis (Figures 1, 2). For the three resilient species (*A. za*, *A. grandidieri* and  
324 *A. digitata*), their distributional ranges should expand equatorward (*A. za*), poleward (*A. digitata*), or  
325 in both directions for *A. grandidieri* under RCP 8.5 and the full-dispersal hypothesis (Figure S1).  
326 Regarding shifts in elevation, all baobab species are expected to shift upward in the future (from +100  
327 m for *A. za* to +351 m for *A. rubrostipa*; Figures 2 and S3) when considering the full-dispersal hypothesis  
328 and scenario RCP 8.5 (except for *A. perrieri* and *A. suarezensis* where we considered RCP 4.5). When  
329 considering RCP 8.5 and the zero-dispersal hypothesis all threatened baobab species are expected to  
330 shrink their distribution upward (Figure 2; Table 1). Under RCP 4.5 for 2085, baobabs are expected to  
331 remain at current elevational gradient or to move upwards until 2085 (Figure S4). The potential  
332 redistribution of these species in 2085 and RCP 4.5 indicates that the *A. digitata* and *A. rubrostipa*  
333 might move poleward, whereas the other species are expected to remain in similar latitudes in the  
334 future (Figure S4).

### 335 **3.3 Climatic gradients and future climatic anomalies in Madagascar**

336 We identified four main climatic gradients in Madagascar (Figure 3) which are important to  
337 subsequently interpret species distribution on the island. A first gradient shows a decrease of the mean  
338 annual temperature with elevation. A second one shows an increase in temperature seasonality  
339 associated with higher latitude (lower seasonality at the North, toward the Equator, higher seasonality  
340 at the South, toward the South pole). A third gradient shows a decrease in annual precipitation from  
341 East to West associated with dominant Eastern winds and orographic precipitation (higher  
342 precipitation in the East). Finally, a fourth gradient shows an increase of the climatic water deficit from  
343 East to West due to the combining effects of precipitation and temperature. Computation of future  
344 climatic anomalies in 2085 under RCP 8.5 shows a general increase in the mean annual temperature  
345 over the whole Madagascar (from +2.5 to +4.0 °C), with a stronger increase in the inner-land than on  
346 the coast. Temperature seasonality should also generally increase over the whole Madagascar,  
347 especially at the North of the island where the temperature seasonality anomaly should reach up to  
348 +3 °C. Precipitation should generally decrease over the island (from 0 to -300 mm/yr) with a stronger  
349 decrease in the North-East. Associated with the general increase in temperature and decrease in  
350 precipitation, the climatic water deficit should generally increase (from 0 to +1500 mm/yr) over the  
351 island and decrease should be stronger in the Western part of Madagascar (> 500 mm/yr).

### 352 **3.4 Importance of each bioclimatic variable in explaining species redistribution**

353 For *A. madagascariensis*, *A. perrieri*, and *A. suarezensis*, three out of the four potentially threatened  
354 baobab species in 2085 under RCP 8.5, the most important variable for explaining species distribution  
355 and thus redistribution was temperature seasonality (Figure 4 and Table 2). These three species are  
356 currently distributed in the Northern part of Madagascar (Figure 1) and might experience, by 2085  
357 under RCP 8.5, a strong increase in temperature seasonality (from +1,13 to +1,48 °C) inside their  
358 current distribution range (Figures 1 and 4, Table S5). For the fourth threatened species (*A. rubrostipa*),  
359 the most important variable was climatic water deficit (Table 2). This species could experience, by 2085  
360 under RCP 8.5, a strong increase in climatic water deficit inside its current distribution range (+870

361 mm/yr; Figures 1, 3 and 4). The second most important variable for the four threatened species were  
362 either annual mean temperature (*A. madagascariensis*), mean annual precipitation (*A. rubrostipa* and  
363 *A. suarezensis*), or climatic water deficit (*A. perrieri*).

364 For *A. grandidieri*, and *A. za*, two out of the three non-threatened baobab species under RCP 8.5 in  
365 2085, the most important variable for explaining these species distribution and redistribution was  
366 mean annual precipitation (Figure 4 and Table 2). Mean annual precipitation should not significantly  
367 change (from -31 to -70 mm/yr) inside the current distribution range of *A. grandidieri* and *A. za* (Figures  
368 3, 4, and Table S5), which are two species already adapted to dry climate (precipitation < 1000 mm/yr,  
369 Figure S5; Table S5). The second most important variable for these two species was annual mean  
370 temperature which is expected to significantly increase inside the two species' distribution range in  
371 the future (+3.5 °C, Figure 3; Table S5), although not affecting their distribution (Figure 1). For *A.*  
372 *digitata*, the third non-threatened species, the two most important variables were temperature  
373 seasonality (+0,87 °C) and the climatic water deficit (+680 mm/yr). These two variables are expected  
374 to increase inside the species distribution range in the future (Figures 3, 4 and Table S5), although not  
375 affecting its distribution.

## 376 4. Discussion

### 377 4.1 Vulnerability of baobab species to climate change and conservation status

378 We showed that four out of the seven Malagasy baobab species are expected to experience a strong  
379 range contraction under the effect of climate change (> 70% for year 2085 under RCP 8.5 and the zero-  
380 dispersal hypothesis) and could be strongly threatened with extinction according to our predictive  
381 scenarios. These four species are: *A. madagascariensis*, *A. perrieri*, *A. suarezensis*, and *A. rubrostipa*.  
382 Among these four species, *A. perrieri* and *A. suarezensis* could face a complete loss of their habitat by  
383 2085 due in particular to an increase in the temperature seasonality in the future. The three other  
384 Malagasy baobab species, *A. grandidieri*, *A. za*, and *A. digitata* did not indicate any significant range  
385 contraction when modelled under climate change scenarios, except for *A. digitata* which might reduce  
386 its modelled distribution by 20% in 2085 under RCP 4.5 (Figure S2). For *A. grandidieri* and *A. za*, this  
387 resilience can be easily explained. *A. za* is a generalist species that can be found in a large range of  
388 climatic conditions and has a large distribution over Madagascar (Figures S1, S5). For *A. grandidieri*,  
389 while it has a much narrower climatic niche than *A. za* and can be considered as a specialist species, it  
390 is already adapted to hot and dry climates (Figures 4, S1 and S5). Conversely, we did not find a simple  
391 explanation for the resilience of *A. digitata* under RCP 8.5 in 2085. Temperature seasonality and  
392 climatic water deficit (which are expected to increase in the future, Figure 3) were the most important  
393 climatic variables in explaining the distribution of this species (Figure 4). We hypothesize that the  
394 potential combination of the four climatic variables (which are rather close in terms of importance,  
395 Table 2) determines the large suitable habitat for the species in the future and its predicted resilience  
396 to climate change (Figure S1).

397 These results are in line with those obtained by Vieilledent et al. (2013) who have previously  
398 demonstrated, with different statistical models and IPCC climate scenarios, that both *A. perrieri* and *A.*  
399 *suaresensis* should become extinct by 2085 due to climate change, and that *A. grandidieri* should not  
400 be vulnerable to climate change. In a recent study, Wan et al. (2020) found contradictory results to  
401 ours: a resilience of *A. perrieri* and *A. suarezensis*, and a vulnerability of *A. za* to climate change.  
402 However, these conclusions were taken by using a much smaller dataset (245 occurrence points  
403 distributed among the 6 endemic Malagasy baobab species) than ours (4830 in total, see Table S1). In  
404 addition, their statistical approach was very limited in comparison to ours. Wan et al. (2020) used only  
405 one algorithm (Maxent), while we used four algorithms for both the ensemble modelling and the  
406 forecasting approach. In particular, the vulnerability of *A. za* to climate change found by Wan et al.  
407 (2020) seems to be in contradiction with its known biology and distribution as a generalist species  
408 (Figures S1, S2, S5 and Table S5).

409 In light of these results, we recommend updating the IUCN conservation status for the four threatened  
410 baobab species (Table 1) based on the risk assessment under RCP 8.5. We base our recommendations  
411 on the IUCN Red List Categories and Criteria version 3.1 (IUCN, 2012b). We recommend updating *A.*  
412 *madagascariensis* from “Near Threatened” to “Endangered A3c” (population reduction  $\geq$  50% in the  
413 future). For *A. suarezensis*, we recommend updating the conservation status from “Endangered B1ab  
414 + B2ab” to “Critically Endangered B1ab + B2ab” (complete extent of occurrence loss by 2085). For *A.*  
415 *perrieri*, we recommend updating the conservation status from “Critically Endangered C2a(i)” to  
416 “Critically Endangered C2a(i) + A3c” (few mature individuals and potential extinction in the long-term).  
417 Finally, for *A. rubrostipa*, we recommend updating the conservation status from “Least Concern” to  
418 “Endangered A3c” (> 85% habitat loss in 2085). Climate change is not the only threat to Malagasy

419 baobab species. The seven baobab species are also severely threatened by habitat loss associated with  
420 the rampant deforestation in Madagascar (Vieilledent et al., 2018) which prevents species from  
421 regenerating.

## 422 **4.2 Species range shifts in latitude and elevation under climate change**

423 We have shown in our study that temperature seasonality was the most important variable at  
424 explaining species distribution for three out of the four threatened Malagasy baobab species. These  
425 three species (*A. madagascariensis*, *A. perrieri*, and *A. suarezensis*) are currently distributed in the  
426 Northern part of Madagascar, close to the Equator line, where the seasonality is lower. These three  
427 baobab species might experience, by 2085 under RCP 8.5, a strong increase in temperature seasonality.  
428 This strong increase in temperature seasonality is expected to be general to all the Northern region of  
429 Madagascar. To track the change in temperature seasonality, these three species might move  
430 equatorward, where the temperature seasonality is lower. Specifically for *A. madagascariensis*, mean  
431 annual temperature was the second most important variable explaining its distribution, and could also  
432 influence the species redistribution equatorward, thanks to suitable habitats in Northeastern  
433 Madagascar in 2085. Several studies on climate change have considered that the general trend for  
434 species, under the effect of climate change, will be to shift their distribution upward or poleward to  
435 escape from the increasing mean temperature globally (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011;  
436 Lenoir et al., 2008; Parmesan & Yohe, 2003; Pecl et al., 2017; Vanderwal et al., 2013). Using emblematic  
437 Malagasy baobab species as an example, we demonstrate that this might not always be the case.  
438 Depending on both the bioclimatic variables that preferentially determine their distribution (the  
439 temperature seasonality in our study) and the future climatic anomalies (increase in temperature  
440 seasonality in our study), some species are expected to move in the opposite direction under the effect  
441 of climate change, i.e. equatorward.

442 In a review article, Lenoir et al. (2010) have examined the potential mechanisms that could push  
443 species to go “against the flow” under climate change. They underlined the importance of additional  
444 ecological processes, in addition to climate change, to explain observed downslope range shifts in a  
445 warming climate. These mechanisms encompass biotic interactions (release of the competition  
446 associated with species range shift under climate change) and land-use change (new suitable habitats  
447 available downward). In our study, we show that it is not necessary to invoke other processes than  
448 climate change to explain shifts in species distribution in opposite directions. Studying the past range  
449 shift of 464 Australian bird species, VanDerWal et al. (2013), showed that complex interactions  
450 between temperature, precipitation, and species-specific tolerances could result in multi-directional  
451 distribution shifts, including equatorward. In our study, we illustrate one simple climatic mechanism,  
452 based on the change in temperature seasonality, by which species can shift their distribution  
453 equatorward.

454 We have also shown that it is not contradictory for a species to move both equatorward and upward  
455 under climate change, as is the case for *A. perrieri*, *A. suarezensis*, and *A. madagascariensis* (Figure 2).  
456 This counter-intuitive range shift has already been reported for sub-mountainous forest plant species  
457 in France which have shifted their distribution both southward (i.e. equatorward in France) and  
458 upward (Kuhn, Lenoir, Piedallu, & Gégout, 2016). The explanation lies in the presence of mountainous  
459 areas towards the south of the species’ current distribution areas. In Madagascar, the explanation is  
460 different. We have shown that temperature seasonality is much more correlated to latitude than to  
461 elevation and that conversely, mean annual temperature is much more correlated to elevation than  
462 to latitude (Figure S6). Consequently, a species can shift its distribution both equatorward and upward

463 to track changes in both temperature seasonality and mean annual temperature, respectively.  
464 Moreover, assuming that a species moves towards the equator to track changes in temperature  
465 seasonality, it might be that the lands towards the equator are located at higher elevation, thus leading  
466 to an upward shift of the species.

### 467 **4.3 Vulnerability of tropical species to change in temperature seasonality**

468 Our findings could have strong implications regarding species response to climate change in the  
469 tropics. In tropical regions, species are adapted to low temperature seasonality (Hua, 2016; Janzen,  
470 1967; Pacifici et al., 2017; Sheldon, Leaché, & Cruz, 2015). Because sunlight duration (~12 hours a day)  
471 and solar incidence do not change significantly throughout the year, the temperature seasonality in  
472 tropical regions close to the Equator is narrower in comparison with subtropical or temperate regions  
473 (Figure 5a). For instance, temperature seasonality influences plant species biology and traits as it  
474 determines the length of the growing season and their phenology, such as the date of foliation,  
475 flowering and fruiting (Pacifici et al. 2017; Wright, 1996).

476 Here we have shown that an increase in temperature seasonality could force species to shift their  
477 distribution equatorward. Looking at the projected change in temperature seasonality in 2085 under  
478 RCP 8.5, a general increase in temperature seasonality across the tropics is expected (up to +10°C for  
479 the standard deviation of the monthly temperatures), with a particularly marked change in the Amazon  
480 region (Figure 5b). As for *A. perrieri* and *A. suarezensis* in Madagascar, the species redistribution  
481 equatorward to track changes in temperature seasonality might be impeded by several geographic and  
482 climatic barriers. This might also happen through several tropical lands located on islands in the  
483 Caribbean, Indian Ocean, or Southeast Asia for example. On these islands, the absence of land  
484 equatorward could act as a geographical barrier for species moving equatorward due to climate  
485 change. In addition, much of the tropical natural areas have been degraded, largely because of  
486 deforestation (Hansen et al., 2020). This could also prevent species from finding suitable habitats  
487 equatorward in tropical forests. Finally, species already distributed at the equator will not be able to  
488 move toward areas with lower seasonality, in analogy with species already at the top of the mountain  
489 which cannot shift their distribution upward to track temperature changes.

490 To conclude, our study shows that not all species should migrate poleward or upward as the climate  
491 warms, which reinforces the results of previous studies (Kuhn et al. 2016, VanDerWal et al. 2013).  
492 Depending on the relative importance of the bioclimatic variables at explaining species distribution  
493 and regional climatic anomalies, shifts in species distribution can be multi-directional, including  
494 equatorward. We also underline the importance of the increase in temperature seasonality in the  
495 tropics that could potentially drag to extinction a large number of species adapted to low seasonality,  
496 among which three out of the seven emblematic baobab species of Madagascar.



497 **5. Declarations**

498

499 *Data availability* – Data (including the CIRAD baobab occurrence database in Madagascar) and code  
500 used to obtain the results of the present study are available on GitHub

501 ([https://github.com/ghislainv/baobabs\\_mada](https://github.com/ghislainv/baobabs_mada)). The GitHub repository has been permanently

502 archived in the CIRAD Dataverse (<https://doi.org/10.18167/DVN1/LIALRR>).

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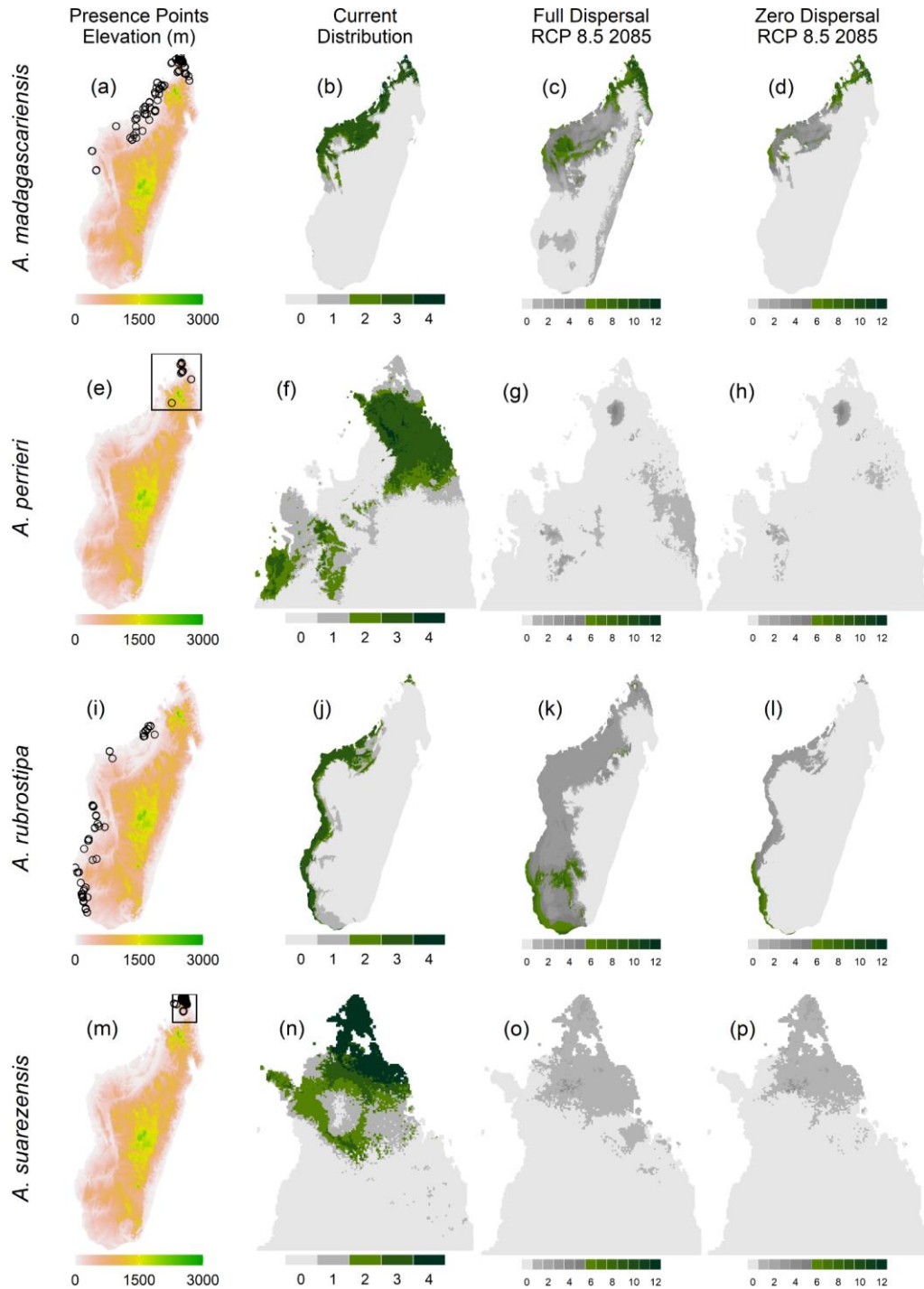
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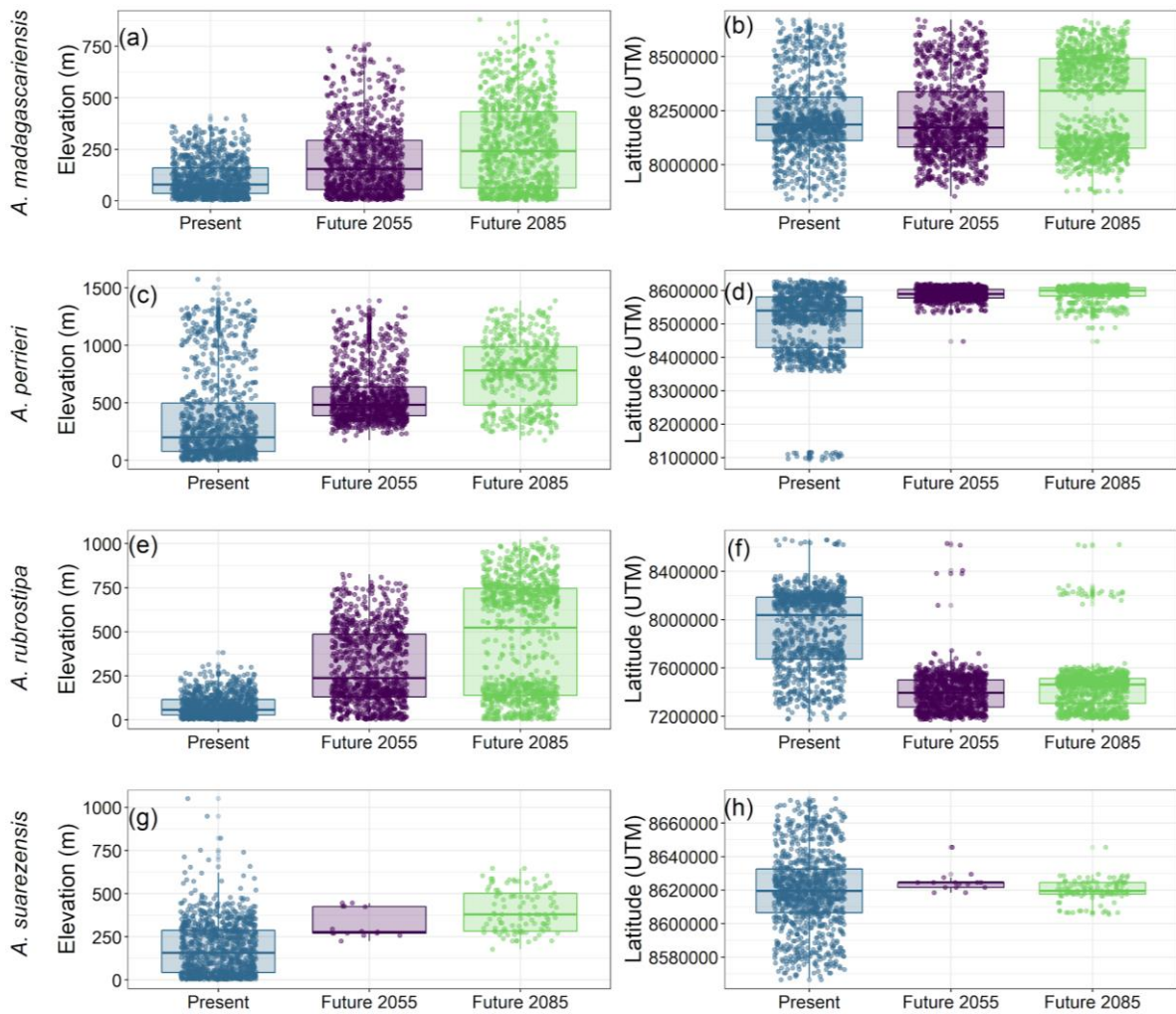


707

708 **Figure 1. Species range contraction under climate change for the four threatened baobab species under RCP**  
 709 **8.5.** The four species are *A. madagascariensis*, *A. perrieri*, *A. rubrostipa*, and *A. suarezensis* (one species per row).  
 710 **(a, e, i, m)** Occurrence points over Madagascar elevation map (elevation in m); **(b, f, j, n)** Current predicted  
 711 species distribution. Legend indicates the number of models (0-4) predicting the species presence; **(c, g, k, o)**  
 712 Projected species distribution in 2085 under scenario RCP 8.5 and the full-dispersal hypothesis. Legend indicates  
 713 the number of models (0-12) predicting the species presence; **(d, h, l, p)** Projected species distribution in 2085  
 714 under scenario RCP 8.5 and the zero-dispersal hypothesis. Legend indicates the number of models (0-12)  
 715 predicting the species presence. For the distribution maps, the species is assumed to be present (green areas)  
 716 when a majority of models predicts a presence (votes  $\geq 2$  in the present, and  $\geq 6$  in the future). The species is  
 717 considered absent (grey areas) when no model (votes = 0), or a minority of models (votes  $< 2$  in the present, and



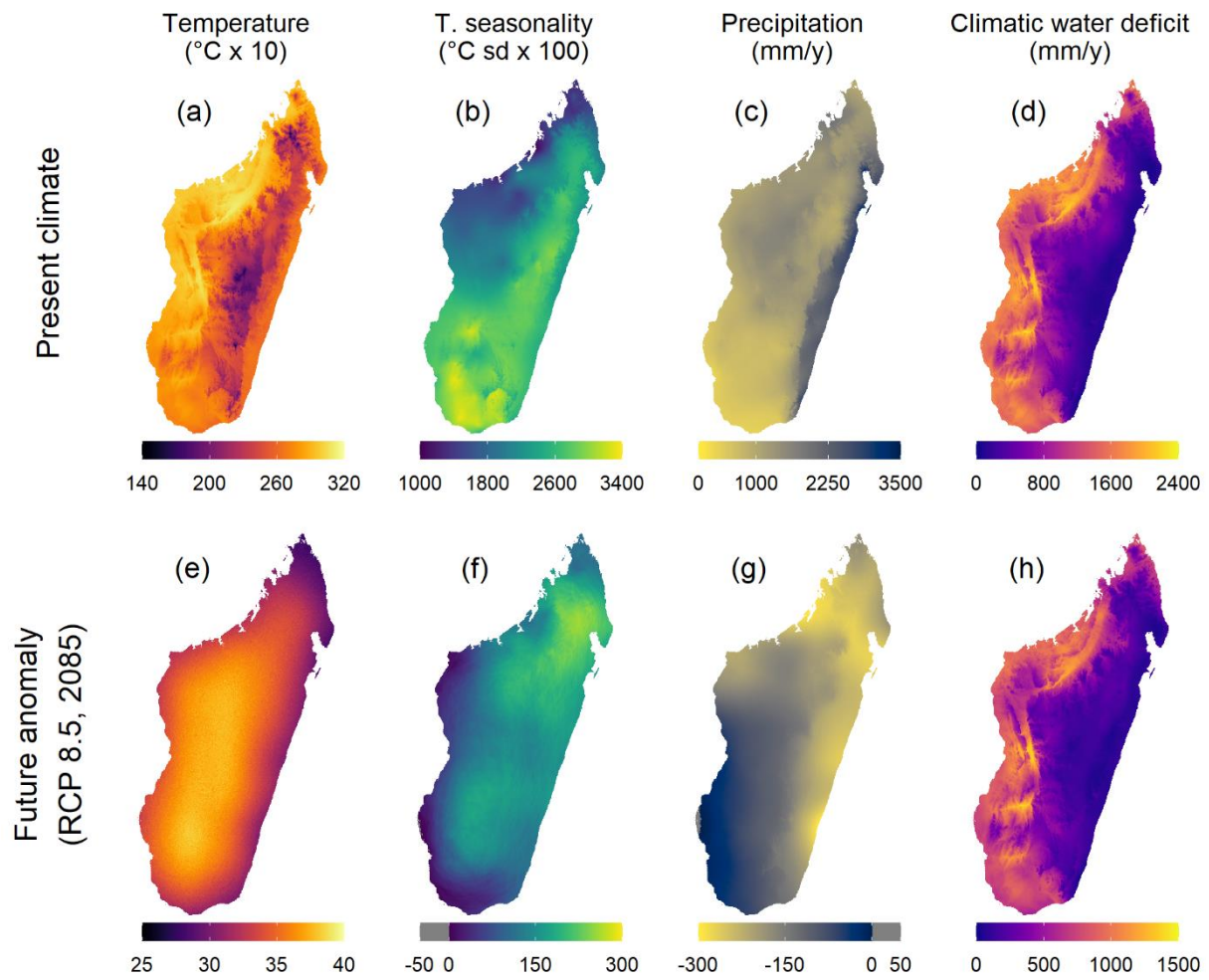
718 < 6 in the future), predicts a presence. Maps for *A. perrieri* and *A. suarezensis*, two species distributed at the  
719 extreme North of Madagascar, have been zoomed in (black squares).



720

721 **Figure 2. Change in elevation and latitude for the most threatened baobab species.** We randomly sampled 1000  
 722 points inside the species predicted occurrence area in the present and in the future (due to the extremely  
 723 reduced distribution area for *A. perrieri* and *A. suarezensis*, we only sampled 416 and 105 points, respectively for  
 724 year 2085, and another 15 points for *A. suarezensis* in 2055). For *A. madagascariensis* and *A. rubrostipa* we  
 725 considered the scenario RCP 8.5 and the full-dispersal hypothesis. Under RCP 8.5, both *A. perrieri* and *A.*  
 726 *suarezensis* became extinct in 2055 and 2085. As a consequence, we used RCP 4.5 to show change in elevation  
 727 and latitude for these two species. **(a, b)** *A. madagascariensis* could migrate to higher elevation under climate  
 728 change scenarios for 2055 and 2085 and also change its latitudinal range to lower latitudes (i.e. equatorward) in  
 729 2085. **(e, f)** *Adansonia rubrostipa* is expected to move to higher elevations and shift its latitudinal range to higher  
 730 latitudes, i.e. poleward. **(c, g)** Both *A. perrieri* and *A. suarezensis* could shift their range to more elevated areas.  
 731 **(d)** *Adansonia perrieri* might shift its range towards lower latitudes, i.e. equatorward. **(h)** *Adansonia suarezensis*  
 732 is expected to retain its niche at lower latitudes

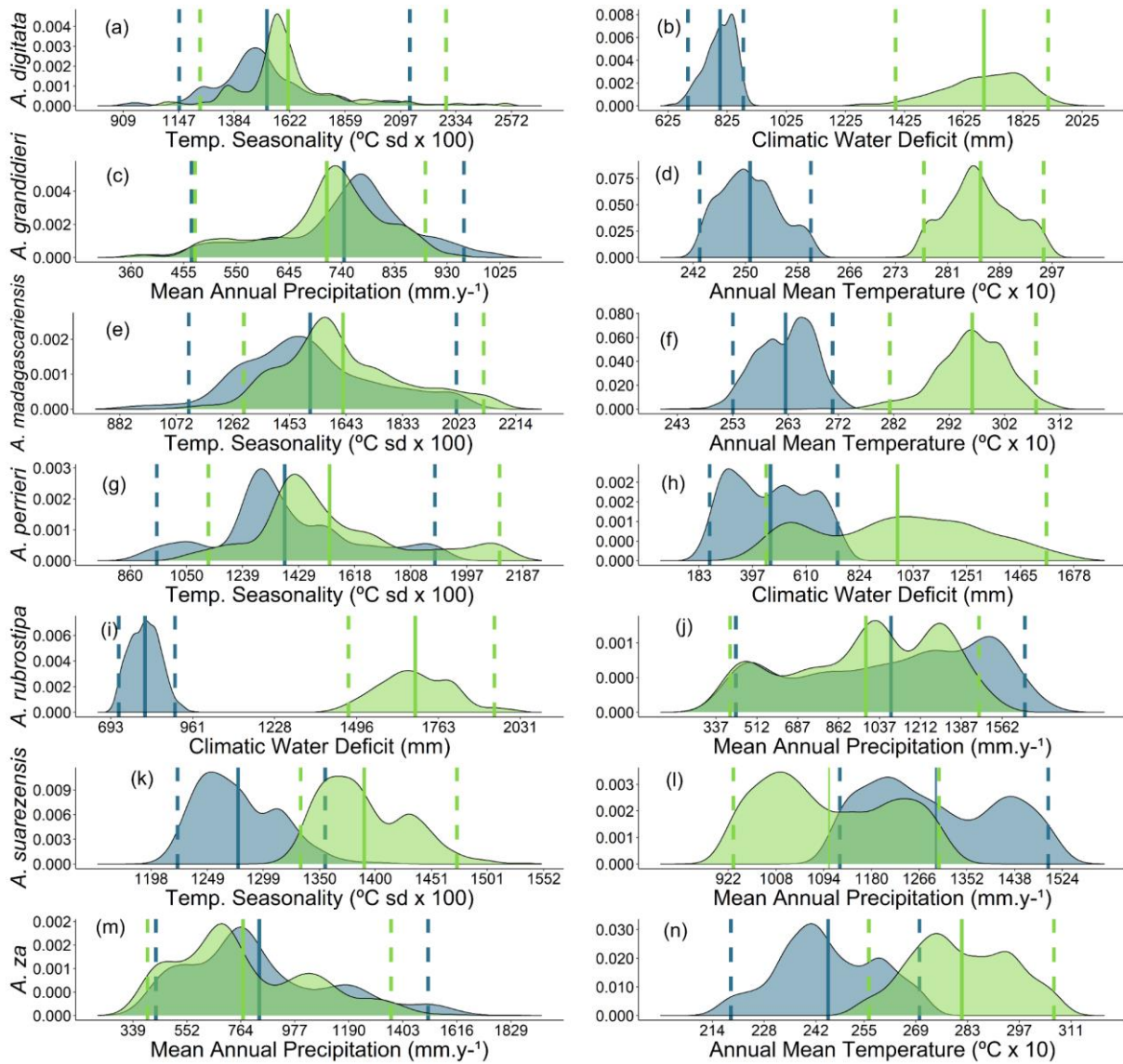
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735 **Figure 3. Spatial variability of the climatic variables in Madagascar and map of the future climatic anomalies.**

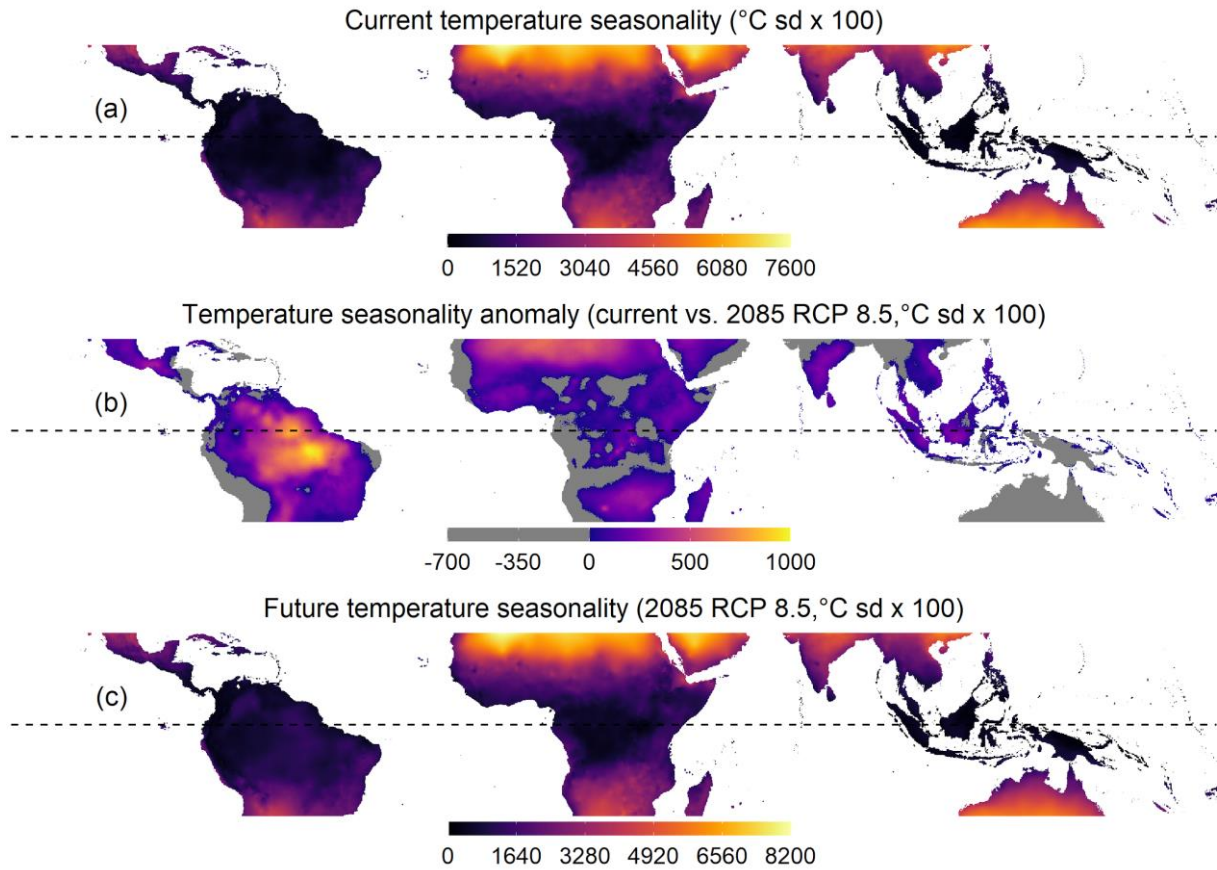
736 The four climatic variables used to perform the SDMs were considered: **(a, e)** annual mean temperature  
 737 (Temperature in  $^{\circ}\text{C} \times 10$ ); **(b, f)** temperature seasonality (T. seasonality, standard deviation of monthly  
 738 temperatures  $\times 100$ ); **(c, g)** annual mean precipitation (Precipitation in  $\text{mm}/\text{y}$ ); **(d, h)** climatic water deficit  
 739 ( $\text{mm}/\text{y}$ ). Climatic anomalies **(e, f, g, h)** were computed as the difference between the mean of future climatic  
 740 data in 2085 (2070-2100) and present (1970-2000) climatic data. Mean future climatic data in 2085 were  
 741 computed from three GCMs (NorESM1-M, GISS-E2-R, and HadGEM2-ES) under RCP 8.5. Four climatic gradients  
 742 are well visible in Madagascar: **(i)** a North-South temperature seasonality gradient associated with latitude (low  
 743 seasonality at the North, equatorward); **(ii)** a decrease in precipitation from East toward West Madagascar due  
 744 to dominant Eastern winds and orographic precipitation (higher precipitation in the East); **(iii)** East-West water  
 745 deficit gradient due to combining effect of both precipitation and temperature; and **(iv)** a decrease in mean  
 746 temperature in more elevated areas. Temperature seasonality should increase for the whole Madagascar. This  
 747 increase will be particularly important in the North of Madagascar ( $> +150$ ) where seasonality is currently low. A  
 748 general increase in temperature ( $> +3^{\circ}\text{C}$ ) is expected in 2085 over Madagascar with climate change, with a higher  
 749 increase in the inner land than on the coast. All Madagascar should experience a decrease in precipitation.  
 750 Decrease in precipitation is expected to be stronger in the East (between  $-150$  and  $-300 \text{ mm}\cdot\text{y}^{-1}$ ). and a strong  
 751 increase in the climatic water deficit.



753

754 **Figure 4. Comparison of current (blue) and future (green) bioclimatic conditions experienced by each species**  
 755 **within the current extent of their respective geographical ranges.** We selected only the two most important  
 756 climatic variables determining species distribution. Left column (panels a, c, e, g, i, k, m) shows the first most  
 757 important variables; Right column (panels b, d, f, h, j, l, n) shows the second most important variables. *Horizontal*  
 758 *axis* represents one of the four bioclimatic variables: mean annual temperature ( $temp - ^\circ C \times 10$ ), temperature  
 759 seasonality ( $^\circ C$ , standard deviation [sd]  $\times 100$ ), mean annual precipitation (mm/y), and climatic water deficit  
 760 (mm). *Vertical axis* shows the distribution of values for that bioclimatic variable. Density plots show current (blue  
 761 density plots) and future (2085, RCP 8.5, mean of 3 GCMs; green density plots). Dark-green shaded areas show  
 762 current and future overlapping values. Bioclimatic envelope (current and future) of each variable was calculated  
 763 within the current species distribution area (1000 random points extracted within occurrence areas indicated by  
 764 the Ensemble approach). Vertical lines: dashed lines represent 95% bioclimatic envelope of future (green) and  
 765 current (blue) variables within each species current distribution area; solid lines represent the computed mean  
 766 value for current (blue) and future (green) bioclimatic data.





768

769 **Figure 5. Map of temperature seasonality and future anomaly in the tropics.** (a) Map of the temperature  
 770 seasonality at 10' resolution across the tropics. Black dashed line represents the equator. Intertropical regions in  
 771 South America, Africa, Southeast Asia, and Oceania have similar low temperature seasonality values and  
 772 temperature seasonality is decreasing from the poles to the equator. (b) Temperature seasonality anomaly  
 773 obtained while comparing future temperature seasonality in 2085 under RCP 8.5 with current temperature  
 774 seasonality. Future temperature seasonality in 2085 under RCP 8.5 is the mean of three GCMs (NorESM1-M,  
 775 GISS-E2-R, and HadGEM2-ES). Temperature seasonality will increase throughout most of the tropics, with a  
 776 particular strong increase in South America. (c) Future temperature seasonality in 2085 under RCP 8.5. (mean of  
 777 the three selected GCMs). Despite changes in temperature seasonality in the future, the gradient of temperature  
 778 seasonality, with a lower temperature seasonality at the equator, will be conserved in the future.

779 **8. Tables**

780 **Table 1. Baobabs' vulnerability to climate change and elevational range shift in 2085 under scenario RCP 8.5.**  
 781 We calculated the species distribution area (km<sup>2</sup>) in the present (SDA<sub>p</sub>) and future (SDA<sub>f</sub>) to describe the change  
 782 in the species distribution area (Change SDA<sub>p</sub> SDA<sub>f</sub> %) according to two dispersal hypotheses (full and zero-  
 783 dispersal). See [IUCN Red List categories and criteria, version 3.1, second edition | IUCN Library System](#) for criteria  
 784 explanation. \*IUCN criteria suggested for Madagascar; \*\* IUCN status defined by populational aspects for the  
 785 referred species once our models did not predict vulnerability for this species.

Baobab species IUCN status	SDA <sub>p</sub> (km <sup>2</sup> )	Current mean elevation (m)	Dispersal hypothesis	SDA <sub>f</sub> (km <sup>2</sup> )	Future mean elevation (m)	Change SDA <sub>p/f</sub> (%)	IUCN Updated Status
<i>Adansonia digitata</i> Not assessed by IUCN	47 872	76	Full	194 447	195	+306	NT*
			Zero	47 017	77	-2	
<i>A. grandidieri</i> Endangered A2c*	27 651	135	Full	118 907	365	+330	EN A2c**
			Zero	27 591	135	0	
<i>A. madagascariensis</i> Near threatened	92 311	105	Full	62 881	263	-32	EN A3c
			Zero	26 878	102	-71	
<i>A. perrieri</i> Critically endangered C2a(i)	14 872	377	Full	0	Extinct	-100	CR C2a(i) + A3C
			Zero	0	Extinct	-100	
<i>A. rubrostipa</i> Least concern	74 194	77	Full	44 833	428	-40	EN A3c
			Zero	11 488	82	-85	
<i>A. suarezensis</i> Endangered B1ab (i,ii,iii,iv,v) + B2ab (i,ii,iii,iv,v)	3347	194	Full	0	Extinct	-100	CR B1ab + B2ab
			Zero	0	Extinct	-100	
<i>A. za</i> Least concern	170 625	265	Full	372 134	365	+118	Least concern
			Zero	166 254	271	-3	

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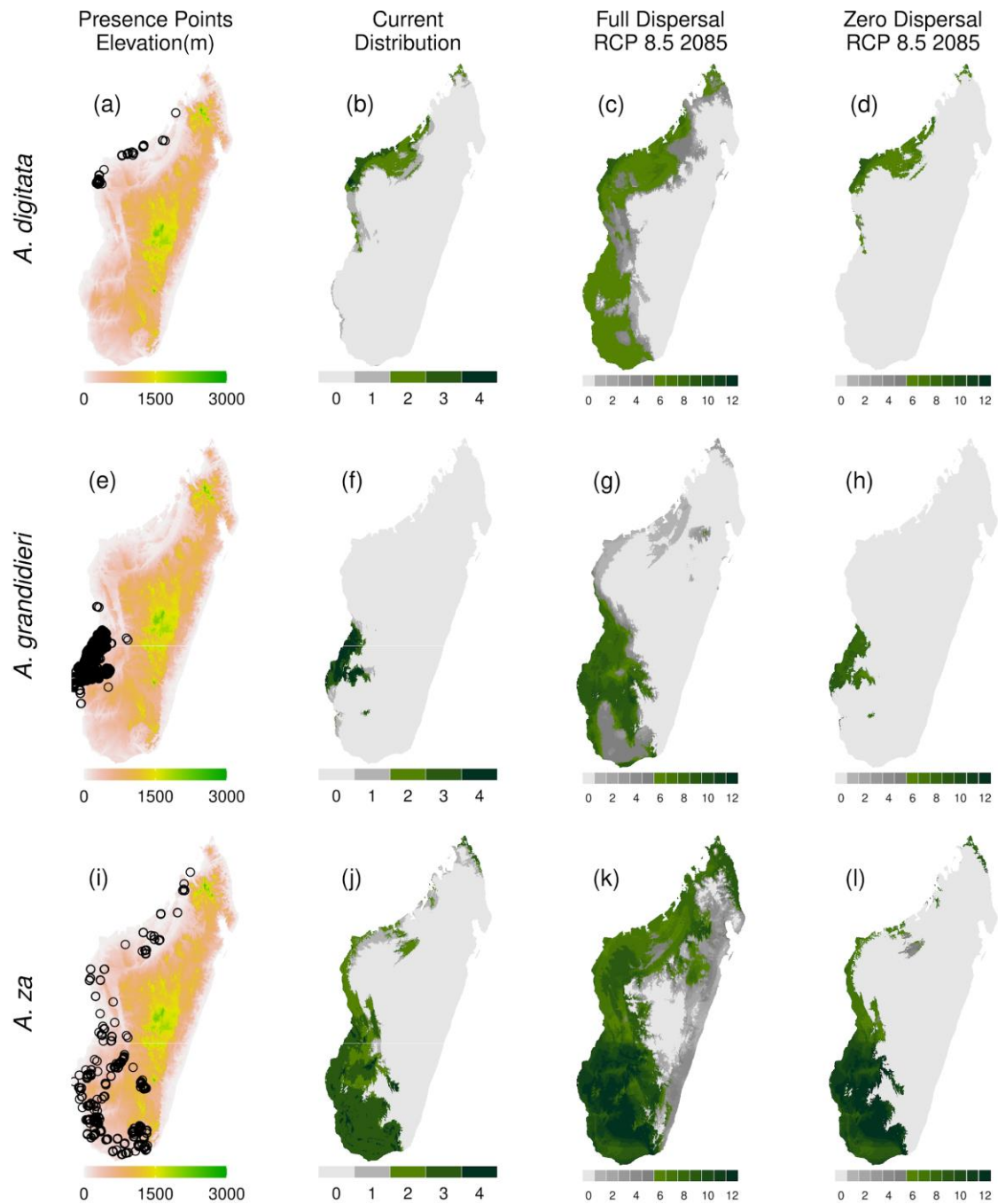
787 **Table 2. Relative importance of the four bioclimatic variables in determining species distribution.** Here we  
 788 present the variable mean rank of importance over the four statistical models for each species. Temperature  
 789 seasonality was the most important variable in determining species distribution for four baobab species: *A.*  
 790 *digitata*, *A. madagascariensis*, *A. perrieri*, and *A. suarezensis*. Precipitation was the most important for *A.*  
 791 *grandidieri* and *A. za*, while climatic water deficit was the most important variable for *A. rubrostipa*.  
 792 Abbreviations: Tmean for mean annual temperature; Tseas for temperature seasonality; Prec for mean annual  
 793 precipitation; Cwd for climatic water deficit. The two most important variables for each species are in bold.

Species	Mean Annual Temperature	Temperature Seasonality	Precipitation	Climatic Water Deficit	Most Important Variables (1st and 2nd)
<i>A. digitata</i>	0.364	<b>0.633</b>	0.372	<b>0.552</b>	Tseas/Cwd
<i>A. grandidieri</i>	<b>0.526</b>	0.239	<b>0.550</b>	0.110	Prec/Tmean
<i>A. madagascariensis</i>	<b>0.651</b>	<b>0.824</b>	0.309	0.153	Tseas/Tmean
<i>A. perrieri</i>	0.369	<b>0.954</b>	0.336	<b>0.518</b>	Tseas/Cwd
<i>A. rubrostipa</i>	0.320	0.330	<b>0.360</b>	<b>0.730</b>	Cwd/Prec
<i>A. suarezensis</i>	0.211	<b>0.987</b>	<b>0.620</b>	0.150	Tseas/Prec
<i>A. za</i>	<b>0.471</b>	0.309	<b>0.625</b>	0.168	Prec/Tmean

794

795 **9. Supporting Information**

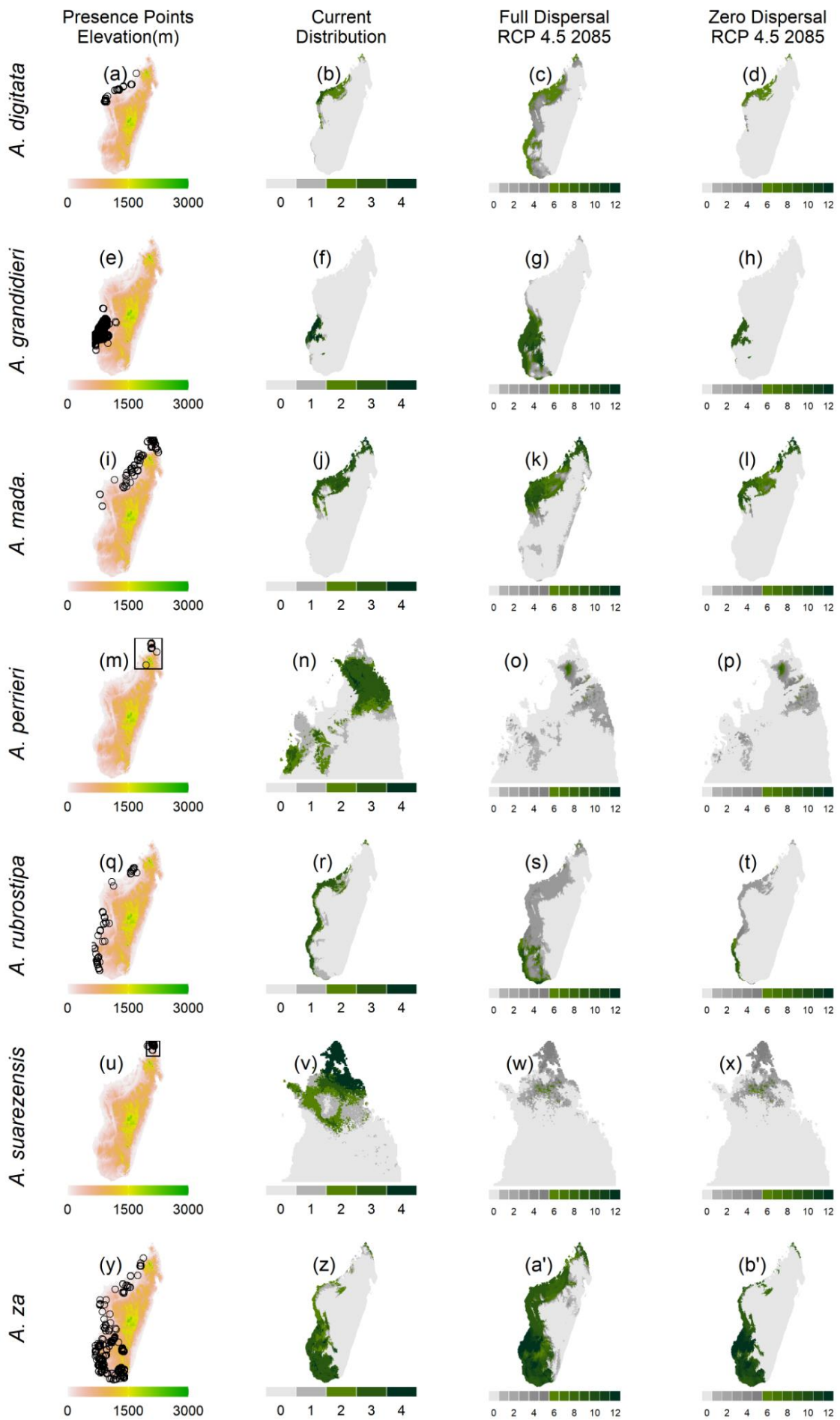
796 **9.1 Supplementary Figures**



797

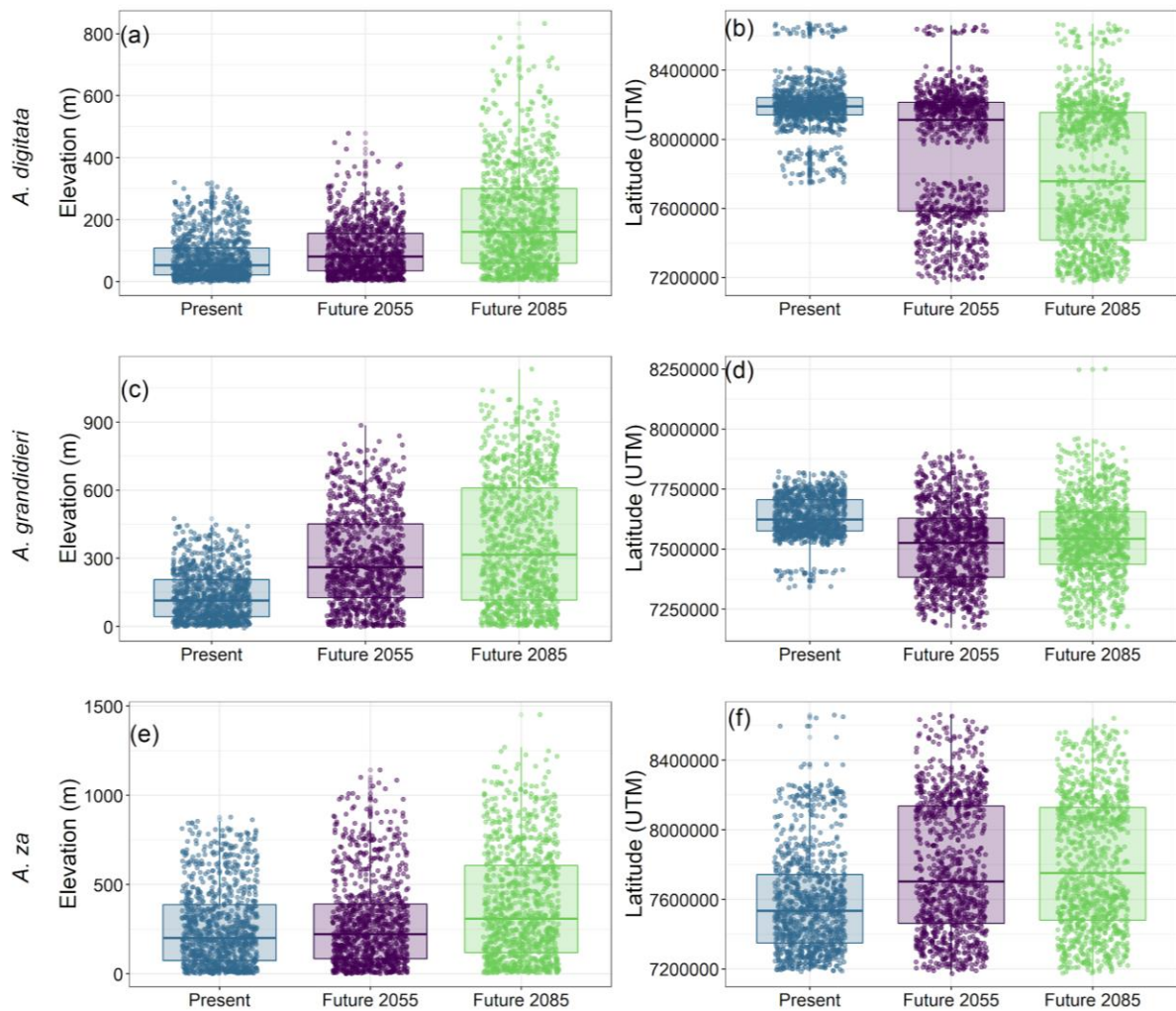
798 **Figure S1. Species range shifts under climate change for the three resilient baobab species under RCP 8.5.** The  
 799 three species are *A. digitata*, *A. grandidieri*, and *A. za* (one species per row). **(a, e, i)** Occurrence points over  
 800 Madagascar elevation map (elevation in m); **(b, f, j)** Current predicted species distribution. Legend indicates the  
 801 number of models (0-4) predicting the species presence **(c, g, k)** Projected species distribution in 2085 under  
 802 scenario RCP 8.5 and the full-dispersal hypothesis. Legend indicates the number of models (0-12) predicting the  
 803 species presence **(d, h, l)** Projected species distribution in 2085 under scenario RCP 8.5 and the zero-dispersal  
 804 hypothesis. Legend indicates the number of models (0-12) predicting the species presence. For the distribution  
 805 maps, the species is assumed to be present (green areas) when a majority of models predicts a presence (votes  
 806  $\geq 2$  in the present, and  $\geq 6$  in the future). The species is considered absent (grey areas) when no model (votes  
 807  $= 0$ ), or a minority of models (votes  $< 2$  in the present, and  $< 6$  in the future), predicts a presence.



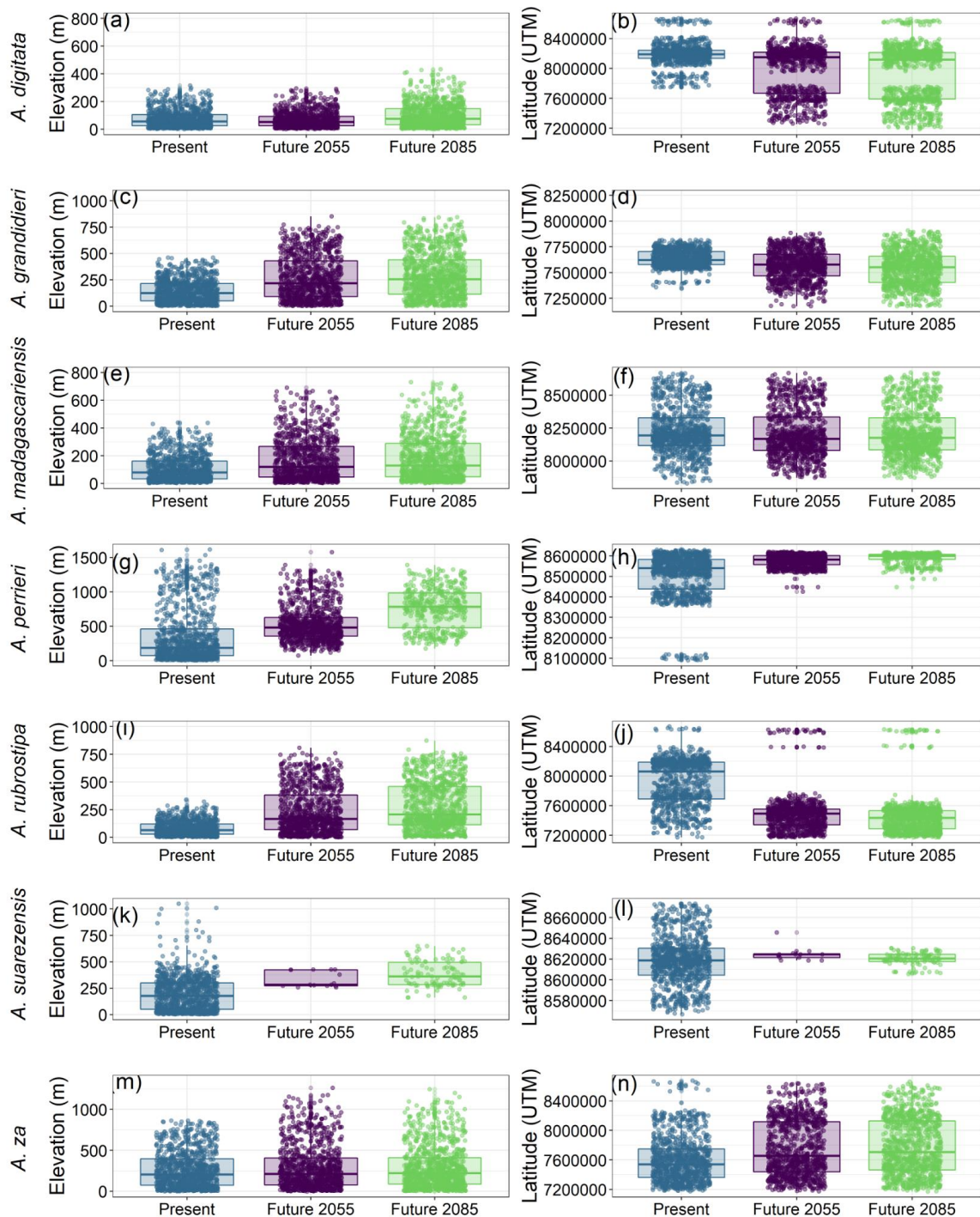


809 **Figure S2. Species range contraction under climate change (RCP 4.5) for all baobab species.** The seven species  
810 are *A. digitata*, *A. grandidieri*, *A. madagascariensis* (*A. mada.*), *A. perrieri*, *A. rubrostipa*, *A. suarezensis*, and *A. za*  
811 (one species per row). **(a, e, i, m, q, u, y)** Occurrence points over Madagascar elevation map (elevation in m); **(b,**  
812 **f, j, n, r, v, z)** Current predicted species distribution. Legend indicates the number of models (0-4) predicting the  
813 species presence; **(c, g, k, o, s, w, a')** Projected species distribution in 2085 under scenario RCP 4.5 and the full-  
814 dispersal hypothesis. Legend indicates the number of models (0-12) predicting the species presence; **(d, h, l, p,**  
815 **t, x, b')** Projected species distribution in 2085 under scenario RCP 4.5 and the zero-dispersal hypothesis. Legend  
816 indicates the number of models (0-12) predicting the species presence. For the distribution maps, the species is  
817 assumed to be present (green areas) when a majority of models predicts a presence (votes  $\geq 2$  in the present,  
818 and  $\geq 6$  in the future). The species is considered absent (grey areas) when no model (votes = 0), or a minority of  
819 models (votes  $< 2$  in the present, and  $< 6$  in the future), predicts a presence. Maps for *A. perrieri* and *A.*  
820 *suaresensis*, two species distributed at the extreme North of Madagascar, have been zoomed in (black squares).

821



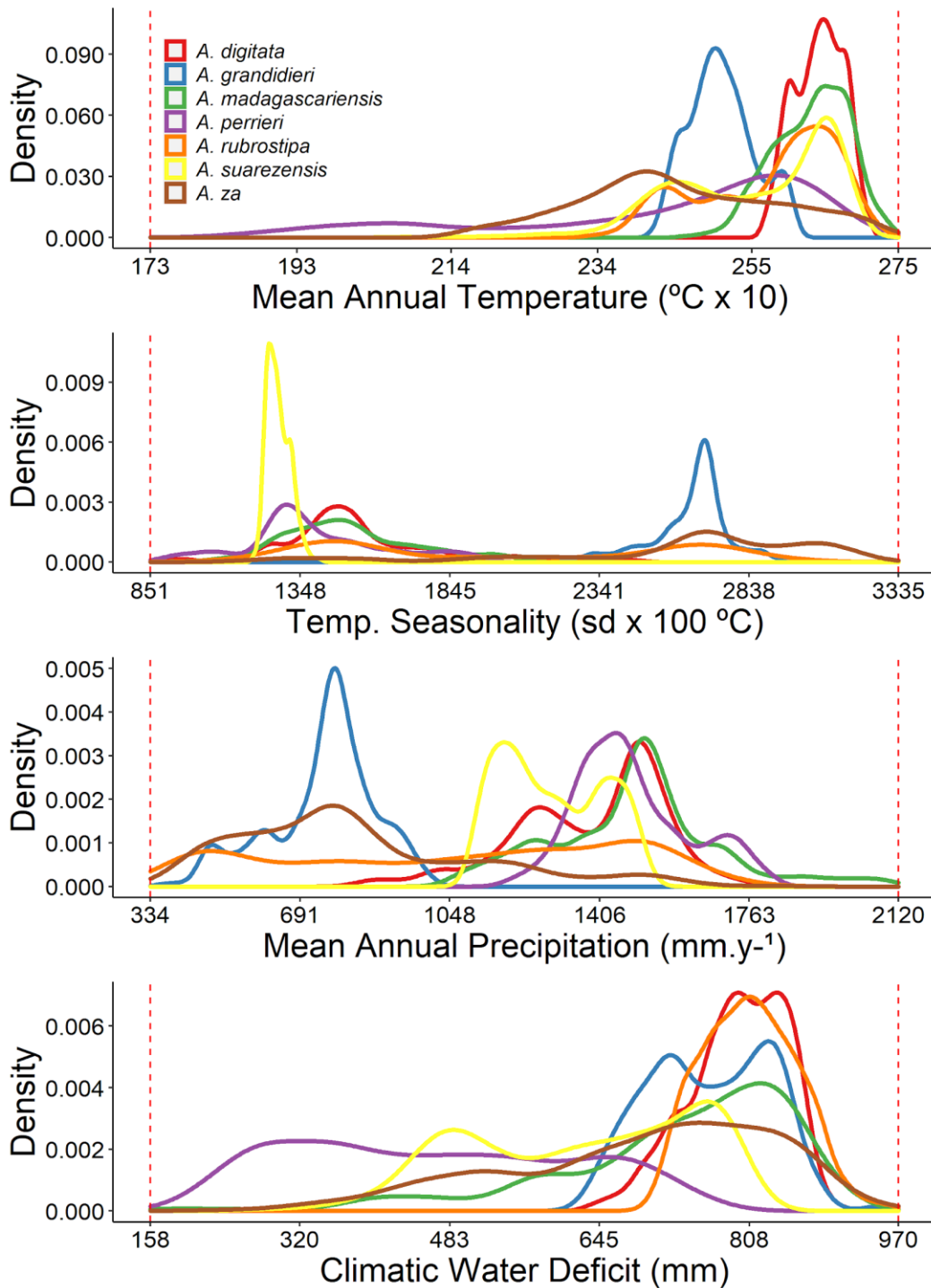
822  
 823 **Figure S3. Change in elevation and latitude for the climate-resilient baobab species.** We randomly sampled  
 824 1000 points inside the species predicted occurrence area in the present and in the future under RCP 8.5 scenario  
 825 and full-dispersal hypothesis. **(a, b)** For *A. digitata*, the species should maintain stable its average elevational and  
 826 latitudinal gradient from the current projection until 2085. **(c, d)** *Adansonia grandidieri* might move to higher  
 827 elevations and shift its latitudinal range to lower latitudes. **(e, f)** *Adansonia za* could slightly shift its elevational  
 828 gradient to more elevated areas in 2085 and higher latitudes, i.e. equatorward, from the present to 2085.



829

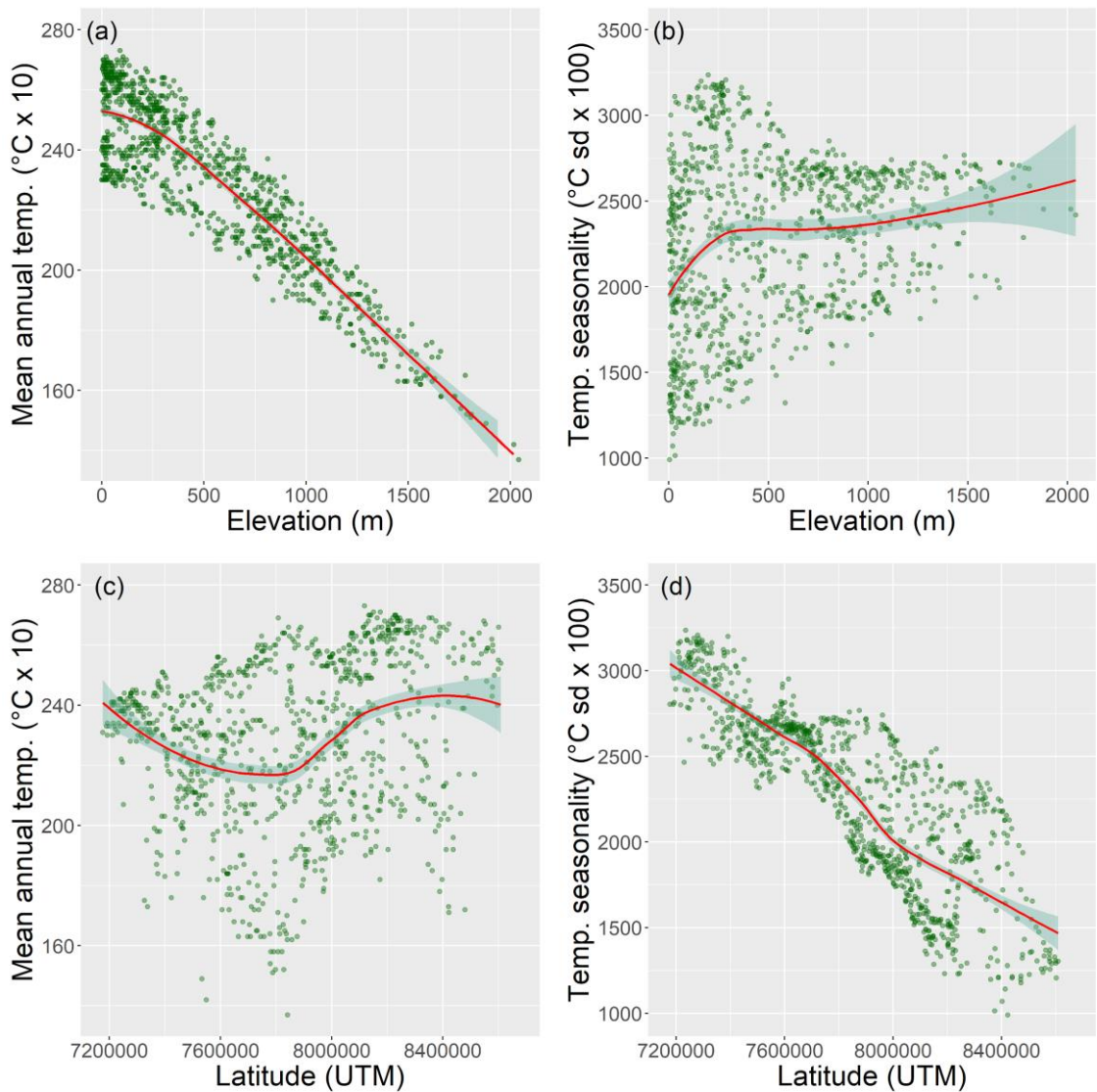
830 **Figure S4. Change in elevation and latitude for the all baobab species under RCP 4.5 in the present and under**  
 831 **two future scenarios (2055 and 2085).** We randomly sampled 1000 points inside the species predicted  
 832 occurrence area in the present and in the future (due to the extremely reduced distribution area for *A. perrieri*  
 833 and *A. suarezensis*, we only sampled 416 and 105 points, respectively for year 2085, and another 15 points for  
 834 *A. suarezensis* in 2055). **(a, c, e, g, i, k, m)** All species showed a tendency to maintain their current elevational  
 835 range in the future or move upwards in 2055 or 2085 considering elevation. **(b, d, j)** Considering latitude  
 836 distributional range, *A. digitata*, *A. grandidieri*, and *A. rubrostipa* are expected to move polewards in the future,  
 837 while **(h, l, m)** *A. perrieri*, *A. suarezensis*, and *A. za* are expected to move equatorward, and **(f)** *A.*  
 838 *madagascariensis* might keep stable its current latitudinal range in 2055 and 2085.





839

840 **Figure S5. Bioclimatic niche of the seven baobabs species found in Madagascar.** We computed species  
 841 bioclimatic niche by randomly sampling 1000 points within each species distribution area for the four climatic  
 842 variables selected in this study: annual mean temperature, temperature seasonality, mean annual precipitation,  
 843 and climatic water deficit. Dashed lines (red) represent the climatic conditions through Madagascar. Baobab  
 844 niche breadth indicates difference between species' climatic niche, with climatic specialist ones (*A. digitata* and  
 845 *A. madagascariensis* – adapted to warmer temperatures –; *A. grandidieri* – adapted to higher seasonality in  
 846 temperature and drier climate –; *A. perrieri* and *A. suarezensis* – adapted to lower seasonality in temperature),  
 847 and generalist/ubiquitous species (*A. rubrostipa* and *A. za*), with a wider climatic niche which encompass almost  
 848 every other baobab species bioclimatic niche.



849

850 **Figure S6. Relationship between climatic, elevational, and latitudinal gradients in Madagascar.** We sampled  
 851 1000 random points through Madagascar extent. **(a)** Mean annual temperature is significantly lower as elevation  
 852 increases. **(b)** Temperature seasonality remains stable as elevation increases, however, as elevation is > 1500 m,  
 853 temperature seasonality might increase. **(c)** The mean annual temperature variation according to latitude in  
 854 Madagascar. Mean annual temperature ranges between 22  $^{\circ}\text{C}$  to 25  $^{\circ}\text{C}$  across the entire country. **(d)** The  
 855 temperature seasonality variation according to latitude in Madagascar. We see a decrease in seasonality from  
 856 South (7200000 UTM) to North Madagascar (8400000 UTM). Shaded area surrounding the red line represents  
 857 the smooth fitting values of the 1000 random points sampled.

858 **9.2 Supplementary Tables**

859

860 **Table S1. Presence data-set used for the species distribution modeling (SDM).** We computed the number  
 861 of presence points with GPS coordinates for each species. Considering a 1-km<sup>2</sup> spatial grid covering  
 862 Madagascar, we identified the cells including at least one presence point for each species independently.  
 863 Doing so we obtained a presence data-set at 1-km<sup>2</sup> resolution for each species. We removed cells with  
 864 incomplete associated bioclimatic data from the presence data-set.

Species	Number of initial presence points with GPS coordinates	Number of 1-km <sup>2</sup> cells with presence data	Number of 1-km <sup>2</sup> cells with presence data in Madagascar and complete bioclimatic data
<i>A. digitata</i>	1854	151	62
<i>A. grandidieri</i>	128 609	3772	3770
<i>A. madagascariensis</i>	1222	159	153
<i>A. perrieri</i>	150	21	21
<i>A. rubrostipa</i>	794	93	90
<i>A. suarezensis</i>	1686	174	170
<i>A. za</i>	2970	460	460

865

866 **Table S2. Performance of the four statistical models in predicting species presence–absence.** AUCc and  
867 TSSc indicate the mean of the Area Under the ROC Curve and the True Skills Statistics respectively after a  
868 5-fold cross-validation procedure (data were split into 70% of the training data and 30% of test data). AUC  
869 full and TSS full indicate the Area Under the ROC Curve and the True Skills Statistics calculated for the full  
870 data-set (100% of the data).

Species	Model	AUC full	AUCc	TSS full	TSSc
<i>A. digitata</i>	GLM	0.972	0.955	0.900	0.903
	GAM	0.989	0.974	0.977	0.949
	Random Forests	1	0.969	0.999	0.927
	Maxent	0.970	0.967	0.859	0.875
<i>A. grandidieri</i>	GLM	0.991	0.991	0.951	0.951
	GAM	0.991	0.990	0.950	0.951
	Random Forests	1	0.994	0.988	0.965
	Maxent	0.989	0.989	0.936	0.936
<i>A. madagascariensis</i>	GLM	0.961	0.958	0.834	0.834
	GAM	0.966	0.963	0.834	0.837
	Random Forests	1	0.964	0.993	0.839
	Maxent	0.959	0.958	0.812	0.819
<i>A. perrieri</i>	GLM	0.993	0.954	0.967	0.913
	GAM	0.991	0.941	0.981	0.887
	Random Forests	1	0.960	1	0.917
	Maxent	0.987	0.987	0.924	0.946
<i>A. rubrostipa</i>	GLM	0.959	0.961	0.839	0.856
	GAM	0.962	0.963	0.831	0.858
	Random Forests	1	0.967	0.999	0.891
	Maxent	0.951	0.953	0.783	0.841
<i>A. suarezensis</i>	GLM	0.998	0.998	0.993	0.991
	GAM	0.999	0.998	0.995	0.993
	Random Forests	1	0.996	0.999	0.989
	Maxent	0.949	0.960	0.992	0.917
<i>A. za</i>	GLM	0.881	0.870	0.631	0.621
	GAM	0.893	0.880	0.676	0.655
	Random Forests	0.999	0.944	0.992	0.742
	Maxent	0.881	0.870	0.638	0.622

871



872 **Table S3. Performance of the ensemble model based on committee averaging.** Values of the threshold-  
873 dependent indices True Skill Statistics (TSS), Sensitivity, and Specificity are described below. Almost all TSS  
874 values were  $\geq 0.83$  except for *A. za*, where the TSS was 0.672 due to a relatively lower specificity. The  
875 performance metrics thus indicate good performance of the ensemble model by correctly predicting  
876 species presence/absence on committee averaging method.

Species	TSS	Sensitivity	Specificity
<i>A. digitata</i>	0.92	1.00	0.92
<i>A. grandidieri</i>	0.95	0.99	0.96
<i>A. madagascariensis</i>	0.83	0.99	0.84
<i>A. perrieri</i>	0.97	1.00	0.97
<i>A. rubrostipa</i>	0.85	0.97	0.87
<i>A. suarezensis</i>	0.99	1.00	0.99
<i>A. za</i>	0.67	0.94	0.72

877

878

879 **Table S4. Baobabs' vulnerability to climate change and elevational range shift in 2085 under scenario**  
 880 **RCP 4.5.** We calculated the species distribution area (km<sup>2</sup>) in the present (SDAp) and future (SDAf) to  
 881 describe the change in the species distribution area (Change SDAp SDAf %) according to two dispersal  
 882 hypotheses (full and zero-dispersal).

Baobab species IUCN status	SDAp (km <sup>2</sup> )	Current mean elevation (m)	Dispersal hypothesis	SDAf (km <sup>2</sup> )	Future mean elevation (m)	Change SDAp f (%)
<i>Adansonia digitata</i> Not assessed by IUCN	47 872	76	Full	91 692	100	+92
			Zero	38 293	68	-20
<i>A. grandidieri</i> Endangered A2c*	27 651	135	Full	101 727	285	+268
			Zero	27 651	135	0
<i>A. madagascariensis</i> Near threatened	92 311	105	Full	123 913	184	+34
			Zero	85 023	108	-8
<i>A. perrieri</i> Critically endangered C2a(i)	14 872	377	Full	427	762	-97
			Zero	427	762	-97
<i>A. rubrostipa</i> Least concern	74 194	77	Full	53 367	283	-28
			Zero	15 636	277	-79
<i>A. suarezensis</i> Endangered B1ab (i,ii,iii,iv,v) + B2ab (i,ii,iii,iv,v)	3347	194	Full	100	393	-97
			Zero	100	393	-97
<i>A. za</i> Least concern	170 625	265	Full	304 482	294	+78
			Zero	170 622	265	0

883

884

885 **Table S5. Climate change within the current species distribution areas.** We computed the climatic  
886 variables' mean and 95% quantiles within the current species distribution areas for the current and future  
887 climates. For the future climate, we considered the mean of the climatic projections of three GCMs (GISS-  
888 E2-R; HadGEM2-ES; NorESM1-M) for the year 2085 under RCP 8.5. Abbreviations: Temp<sub>pf</sub> for mean annual  
889 temperature (in °C x 10); Tseas<sub>pf</sub> for temperature seasonality (in °C sd x 100); Prec<sub>pf</sub> for mean annual  
890 precipitation (in mm.y<sup>-1</sup>); Cwd<sub>pf</sub> for climatic water deficit (in mm) in the present (p) and future (f).

Baobab species	Confidence interval	Temp <sub>p</sub>	Temp <sub>f</sub>	Tseas <sub>p</sub>	Tseas <sub>f</sub>	Prec <sub>p</sub>	Prec <sub>f</sub>	Cwd <sub>p</sub>	Cwd <sub>f</sub>
<i>A. digitata</i>	Mean	264	298	1525	1612	1390	1205	800	1680
	2.5%	258	291	1136	1267	953	937	691	1372
	97.5%	270	306	2246	2208	1665	1454	882	1926
<i>A. grandidieri</i>	Mean	251	286	2649	2729	746	715	764	1670
	2.5%	243	277	2338	2402	467	474	642	1447
	97.5%	260	296	2887	3045	956	895	877	1978
<i>A. madagascariensis</i>	Mean	263	296	1510	1623	1485	1298	724	1546
	2.5%	253	282	1133	1269	1110	986	399	980
	97.5%	272	308	2008	2101	1953	1733	890	1989
<i>A. perrieri</i>	Mean	243	272	1391	1539	1483	1257	465	962
	2.5%	192	223	948	1117	1262	1063	230	436
	97.5%	267	300	1890	2108	1764	1483	738	1563
<i>A. rubrostipa</i>	Mean	258	292	1972	2046	1088	969	808	1678
	2.5%	240	273	1224	1335	413	395	719	1455
	97.5%	270	306	2898	2921	1650	1451	913	1914
<i>A. suarezensis</i>	Mean	255	283	1275	1389	1288	1103	629	1242
	2.5%	233	259	1221	1333	1121	932	402	724
	97.5%	267	295	1357	1479	1498	1303	794	1653
<i>A. za</i>	Mean	245	280	2583	2668	830	760	689	1488
	2.5%	220	256	1282	1406	430	388	378	870
	97.5%	270	307	3183	3229	1524	1363	902	2010