

# Accepted Article

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

3 Running title: Baobabs range shift as climate warms

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

**Running title: Baobabs range shift as climate warms**

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## Abstract

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

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

## 1. Introduction

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

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

important to account for additional climatic variables different from the mean annual temperature and consider other potential ecological processes that could explain species range shifts in multiple directions.

The most commonly employed tools to predict current and future distribution of species under climate change from a set of observations and climatic predictors are correlative species distribution models (SDMs) (Elith & Graham, 2009; Foden et al., 2019; Guisan et al., 2013; Porfirio et al., 2014). The main outputs of these SDMs are maps of species potential distributions in the present and future. Nowadays, many easy-to-use softwares (the JAVA Maxent; Phillips, Anderson, & Schapire, 2006) or libraries (e.g. “*sdm*” and “*biomod2*”; Naimi & Araújo, 2016; Thuiller, Lafourcade, Engler, & Araújo, 2009) have been made available to easily derive such redistribution maps. Comparing present with future species distribution maps, one can assess species vulnerability to climate change by looking at species range shift, contraction, or expansion (Vieilledent, Cornu, Cuní Sanchez, Leong Pock-Tsy, & Danthu, 2013). Surprisingly, conservation studies that employ correlative SDMs to assess species vulnerability to climate change mostly do not disentangle the respective effect of predictor variables in explaining species range shift (Fourcade, Besnard, & Secondi, 2018). Thus, they fail at explaining the possible underlying mechanisms behind such changes. For example, in an article studying the vulnerability of three baobab species to climate change in Madagascar, Vieilledent et al. (2013) showed that *Adansonia suarezensis* H. Perrier, and *A. perrieri* Capuron, will likely become extinct by 2085. However, the study does not analyze the respective role of each variable in explaining species range shift and does not suggest potential mechanisms that could explain the species extinction. In addition, a recent study assessing the vulnerability of Madagascar endemic baobabs to future climate change also failed to explore the underlying mechanisms behind expected species range shifts (Wan et al., 2020).

To help fill this gap, we investigate here the specific role of a set of climatic variables in explaining shifts in species distribution associated with climate change. We chose the seven emblematic baobab species that can be found in Madagascar (*Adansonia* L. genus; Malvaceae family) for this purpose. Six of the seven species are endemic to Madagascar (*Adansonia grandiflora* Baill., *A. madagascariensis* Baill., *A. perrieri*, *A. rubrostipa* Jum. and Perr., *A. suarezensis*, and *A. za* Baill), while the remaining species also occurs in the African continent: *A. digitata* L. (Wickens 2008). Each of the seven baobab species are located in different regions of Madagascar, being adapted to different climates and could potentially have different responses to climate change. We gathered an extensive and unprecedented occurrence dataset obtained from more than 15 years of field prospection and photo-interpretation of high-resolution satellite images. We used an ensemble modelling approach

to model the climatic niche and to predict the distribution of these seven species. Using SDMs and climatic projections, we assessed whether each species could experience range shift, contraction or expansion, and in which direction. Looking at the relative climatic variable importance and future climatic anomalies, we disentangled the role of each climatic variable in explaining species range shift. Based on species' extinction risk, we made suggestions to update the current baobab species conservation status. Finally, we attempted to generalize our results to other species in the tropics that should experience similar climatic anomalies in the future.

## 2. Material and methods

### 2.1 Presence and pseudo-absence data

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

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

information to predict species' habitat suitability and distribution, optimizing spatial and environmental discrimination (Senay, Worner, & Ikeda, 2013). Consequently, we aimed to have a good representativity of the climate variability in Madagascar and to be able to compute a relative probability of presence across the country.

## 2.2 Bioclimatic data

We used current (~1950-2000) and future (2055 and 2085) climatic data at 30 arc-seconds resolution (about 1 km at the equator) over the entire spatial extent of Madagascar. This data is freely available on MadaClim (<https://madaclim.cirad.fr/>). The MadaClim website provides climatic data for Madagascar obtained from the WorldClim (<http://worldclim.org/bioclim/>) and CGIAR-CCAFS climate data portal (<http://www.ccafs-climate.org/>). We selected four bioclimatic variables (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005) to model species distribution which were weakly correlated among each other and easy to interpret with regard to baobab species distribution. Three of them were previously selected via a principal component analysis among all the 19 WorldClim bioclimatic variables (following Vieilledent et al. (2013): **(1)** mean annual precipitation – *prec* (mm.y<sup>-1</sup>); **(2)** mean annual temperature – *tmean* (°C); **(3)** temperature seasonality – *tseas* (sd x 1000 °C). In addition, we included a synthetic variable reflecting **(4)** climatic water deficit – *cwd* (mm). The *cwd* variable was computed from monthly precipitation (*mcpref*) and potential evapotranspiration (*pet*) using the following formula (**Equation 1**):

$$cwd = - \sum_i \min(mcpref_i - pet_i, 0) \quad (1)$$

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

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

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

We selected four statistical algorithms to model the bioclimatic niche and distribution of the seven studied baobab species: generalized linear models (GLMs); generalized additive models (GAMs); random forests (RF); and Maxent. Algorithms’ selection included standard regression models, such as the parametric GLM and the non-parametric GAM, classification tree (RF), and maximum entropy approach (Maxent). We aimed to quantify output uncertainty and generate a gradient from robustness (GLM and GAM) to complex algorithms, i.e. RF and Maxent (Elith & Graham, 2009). The uncertainty quantification of predictive modeling follows the premise of the ensemble modelling approach (Araújo & New, 2007), which enables a consensus identification among all forecasts and the exploration of the full breadth of intermodal variability (Kujala, Moilanen, Araújo, & Cabeza, 2013).

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

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

To evaluate the performance of the ensemble model based on committee averaging we used three previously mentioned metrics: TSS, Sen, and Spe, following Araújo and New (2007). We previously defined an evaluation threshold using the accuracy index TSS (i.e. minimum score of 0.6 or 60%) in order to: **(i)** remove “bad algorithms/models”; **(ii)** build our ensemble model; **(iii)** test and evaluate

the ensemble model forecasting capability (i.e. predicting species presence-absence); and **(iv)** make the binary transformation for the committee averaging computation (Thuiller et al. 2009).

For each statistical algorithm, we calculated the relative variable importance among the four studied bioclimatic variables selected for the SDMs. The computation principle follows the one used for RFs, where one bioclimatic variable is shuffled over the full data-set or the testing data-subset. To compute variable importance (*I*), the model prediction is calculated in this shuffled data-set, and a correlation (Pearson's correlation) is computed between baseline predictions (*pred\_ref*) and the shuffled predictions (*pred\_shuffled*; see Equation 2).

$$I = 1 - \text{cor}(\text{pre}_{\text{ref}}, \text{pred}_{\text{shuffled}}) \quad (2)$$

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

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

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

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

## 2.5 Ensemble forecasting and future species distribution

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

When predicting future range maps under each RCP for 2055 and 2085, we also considered two contrasting dispersal hypotheses, with the reality likely to fall in between. The full-dispersal hypothesis considers the possibility for all baobab species to colonize new climatically favorable sites outside the current species distribution range. The zero-dispersal hypothesis considers the impossibility for baobab species to naturally colonize new climatically favorable sites outside the current species distribution range. This can be due to unsuitable conditions (other than climate, such as land-use) outside the current species distribution area, or to that baobab species may not be able to disperse seeds due to geographical barriers or in the absence of animal dispersers (see Vieilledent et al. 2013).

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

To evaluate the effect of climate change and the vulnerability of the seven Malagasy baobab species, we calculated the percentage of area change between the future (SDAf) and present (SDAp) distribution range (in km<sup>2</sup>). To compute SDAf, SDAp, and mean elevational shifts, we extracted all presence points indicated as ‘presence’ by the ensemble modelling and calculated the changes for each of the investigated future scenarios (mean, 95% quantiles interval, and percentage of area change in km<sup>2</sup>). Focusing on the year 2085, under RCP 8.5 for the full-dispersal and zero-dispersal scenarios, we suggested updates for baobabs conservation management strategies given their future distribution and vulnerability to climate change according to the International Union for Conservation of Nature Red List (IUCN, 2012a). Finally, we calculated potential latitudinal and

elevational species range shifts by extracting 1,000 random points inside each species distribution range projected for the present and the future (2055 and 2085), under both RCPs 4.5 and 8.5 scenarios and for the full-dispersal hypothesis.

### 3. Results

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

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

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

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

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

We identified four main climatic gradients in Madagascar (Figure 3) which are important to subsequently interpret species distribution on the island. A first gradient shows a decrease in the mean annual temperature with elevation. A second one shows an increase in temperature seasonality associated with higher latitude (lower seasonality at the North, toward the Equator, higher seasonality at the South, toward the South pole). A third gradient shows a decrease in annual precipitation from East to West associated with dominant Eastern winds and orographic precipitation (higher precipitation in the East). Finally, a fourth gradient shows an increase in the climatic water deficit from East to West due to the combining effects of precipitation and temperature. Computation of future climatic anomalies in 2085 under RCP 8.5 shows a general increase in the mean annual temperature over the whole Madagascar (from +2.5 to +4.0 °C), with a stronger increase in the inner-land than on the coast. Temperature seasonality should also generally increase over the whole Madagascar, especially at the North of the island where the temperature seasonality anomaly should reach up to +0.3 °C. Precipitation should generally decrease over the island (from 0 to -300 mm/yr) with a stronger decrease in the North-East. Associated with the general increase in temperature and decrease in precipitation, the climatic water deficit should

generally increase (from 0 to +1500 mm/yr) over the island and should be stronger in the Western part of Madagascar (> 500 mm/yr).

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

For *A. madagascariensis*, *A. perrieri*, and *A. suarezensis*, three out of the four potentially threatened baobab species in 2085 under RCP 8.5, the most important variable for explaining species distribution and thus redistribution was temperature seasonality (Figure 4 and Table 2). These three species are currently distributed in the Northern part of Madagascar (Figure 1) and might experience, by 2085 under RCP 8.5, a significant increase in temperature seasonality (from +0.113 to +0.148 °C) inside their current distribution range (Figures 1 and 4, Table S5). For the fourth threatened species (*A. rubrostipa*), the most important variable was climatic water deficit (Table 2). This species could experience, by 2085 under RCP 8.5, a strong increase in climatic water deficit inside its current distribution range (+870 mm/yr; Figures 1, 3, and 4). The second most important variable for the four threatened species were either annual mean temperature (*A. madagascariensis*), mean annual precipitation (*A. rubrostipa* and *A. suarezensis*), or climatic water deficit (*A. perrieri*).

For *A. grandidieri*, and *A. za*, two out of the three non-threatened baobab species under RCP 8.5 in 2085, the most important variable for explaining these species distributions and redistribution was mean annual precipitation (Figure 4 and Table 2). Mean annual precipitation should not significantly change (from -31 to -70 mm/yr) inside the current distribution range of *A. grandidieri* and *A. za* (Figures 3, 4, and Table S5), which are two species already adapted to dry climate (precipitation < 1000 mm/yr, Figure S5; Table S5). The second most important variable for these two species was annual mean temperature which is expected to significantly increase inside the two species' distribution range in the future (+3.5 °C, Figure 3; Table S5), although not affecting their distribution (Figure 1). For *A. digitata*, the third non-threatened species, the two most important variables were temperature seasonality (+0.87 °C) and the climatic water deficit (+680 mm/yr). These two variables are expected to increase inside the species distribution range in the future (Figures 3, 4, and Table S5), although not affecting its distribution.

## 4. Discussion

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

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

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

al. (2020) seems to be in contradiction with its known biology and distribution as a generalist species (Figures S1, S2, S5, and Table S5).

In light of these results, we recommend updating the IUCN conservation status for the four threatened baobab species (Table 1) based on the risk assessment under RCP 8.5. We base our recommendations on the IUCN Red List Categories and Criteria version 3.1 (IUCN, 2012b). We recommend updating *A. madagascariensis* from “Near Threatened” to “Endangered A3c” (population reduction  $\geq 50\%$  in the future). For *A. suarezensis*, we recommend updating the conservation status from “Endangered B1ab + B2ab” to “Critically Endangered B1ab + B2ab” (complete extent of occurrence loss by 2085). For *A. perrieri*, we recommend updating the conservation status from “Critically Endangered C2a(i)” to “Critically Endangered C2a(i) + A3c” (few mature individuals and potential extinction in the long-term). Finally, for *A. rubrostipa*, we recommend updating the conservation status from “Least Concern” to “Endangered A3c” ( $> 85\%$  habitat loss in 2085). Climate change is not the only threat to Malagasy baobab species. The seven baobab species are also severely threatened by habitat loss associated with the rampant deforestation in Madagascar (Vieilledent et al., 2018) which prevents species from regenerating.

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

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

climatic anomalies (increase in temperature seasonality in our study), some species are expected to move in the opposite direction under the effect of climate change, i.e. equatorward.

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

We have also shown that it is not contradictory for a species to move both equatorward and upward under climate change, as is the case for *A. perrieri*, *A. suarezensis*, and *A. madagascariensis* (Figure 2). This counter-intuitive range shift has already been reported for sub-mountainous forest plant species in France which have shifted their distribution both southward (i.e. equatorward in France) and upward (Kuhn, Lenoir, Piedallu, & Gégout, 2016). The explanation lies in the presence of mountainous areas towards the south of the species’ current distribution areas. In Madagascar, the explanation is different. We have shown that temperature seasonality is much more correlated to latitude than to elevation and that conversely, mean annual temperature is much more correlated to elevation than to latitude (Figure S6). Consequently, a species can shift its distribution both equatorward and upward to track changes in both temperature seasonality and mean annual temperature, respectively. Moreover, assuming that a species moves towards the equator to track changes in temperature seasonality, it might be that the lands towards the equator are located at higher elevations, thus leading to an upward shift of the species.

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

Our findings could have strong implications regarding species response to climate change in the tropics. In tropical regions, species are adapted to low temperature seasonality (Hua, 2016; Janzen, 1967; Pacifici et al., 2017; Sheldon, Leaché, & Cruz, 2015). Because sunlight duration (~12 hours a day) and solar incidence do not change significantly throughout the year, the temperature

seasonality in tropical regions close to the Equator is narrower in comparison with subtropical or temperate regions (Figure 5a). For instance, temperature seasonality influences plant species biology and traits as it determines the length of the growing season and their phenology, such as the date of foliation, flowering, and fruiting (Pacifici et al. 2017; Wright, 1996).

Here we have shown that an increase in temperature seasonality could force species to shift their distribution equatorward. Looking at the projected change in temperature seasonality in 2085 under RCP 8.5, a general increase in temperature seasonality across the tropics is expected (up to +1°C for the standard deviation of the monthly temperatures), with a particularly marked change in the Amazon region (Figure 5b). As for *A. perrieri* and *A. suarezensis* in Madagascar, the species redistribution equatorward to track changes in temperature seasonality might be impeded by several geographic and climatic barriers. This might also happen through several tropical lands located on islands in the Caribbean, Indian Ocean, or Southeast Asia for example. On these islands, the absence of land equatorward could act as a geographical barrier for species moving equatorward due to climate change. In addition, much of the tropical natural areas have been degraded, largely because of deforestation (Hansen et al., 2020). This could also prevent species from finding suitable habitats equatorward in tropical forests. Finally, species already distributed at the equator will not be able to move toward areas with lower seasonality, in analogy with species already at the top of the mountain which cannot shift their distribution upward to track temperature changes.

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

## 5. Declarations

*Data availability* – Data (including the CIRAD baobab occurrence database in Madagascar) and code used to obtain the results of the present study are available on GitHub ([https://github.com/ghislainv/baobabs\\_mada](https://github.com/ghislainv/baobabs_mada)). The GitHub repository has been permanently archived in the CIRAD Dataverse (<https://doi.org/10.18167/DVN1/LIALRR>).

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*Conflicts of interest* – The authors declare they have no conflicts of interest.

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## 7. Figures

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

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

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

The four climatic variables used to perform the SDMs were considered: **(a, e)** annual mean temperature (Temperature in °C x 10); **(b, f)** temperature seasonality (T. seasonality, standard deviation of monthly temperatures x 1000); **(c, g)** annual mean precipitation (Precipitation in mm/y); **(d, h)** climatic water deficit (mm/y). Climatic anomalies **(e, f, g, h)** were computed as the difference between the mean of future climatic data in 2085 (2070-2100) and present (1970-2000) climatic data. Mean future climatic data in 2085 were computed from three GCMs (NorESM1-M, GISS-E2-R, and HadGEM2-ES) under RCP 8.5. Four climatic gradients are well visible in Madagascar: **(i)** a North-South temperature seasonality gradient associated with latitude (low seasonality at the North, equatorward); **(ii)** a decrease in precipitation from East toward West Madagascar due to dominant Eastern winds and orographic precipitation (higher precipitation in the East); **(iii)** East-West water deficit gradient due to combining effect of both precipitation and temperature; and **(iv)** a decrease in mean temperature in more elevated areas. Temperature seasonality should increase for the whole Madagascar. This increase will be particularly important in the North of Madagascar ( $> +150$ ) where seasonality is currently low. A general increase in temperature ( $> +3^{\circ}\text{C}$ ) is expected in 2085 over Madagascar with climate change, with a higher increase in the inner land than on the coast. All Madagascar should experience a decrease in precipitation. Decrease in precipitation is expected to be stronger in the East (between -150 and -300 mm.y<sup>-1</sup>). and a strong increase in the climatic water deficit.

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

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

## 8. Tables

**Table 1. Baobabs' vulnerability to climate change and elevational range shift in 2085 under scenario RCP 8.5.**

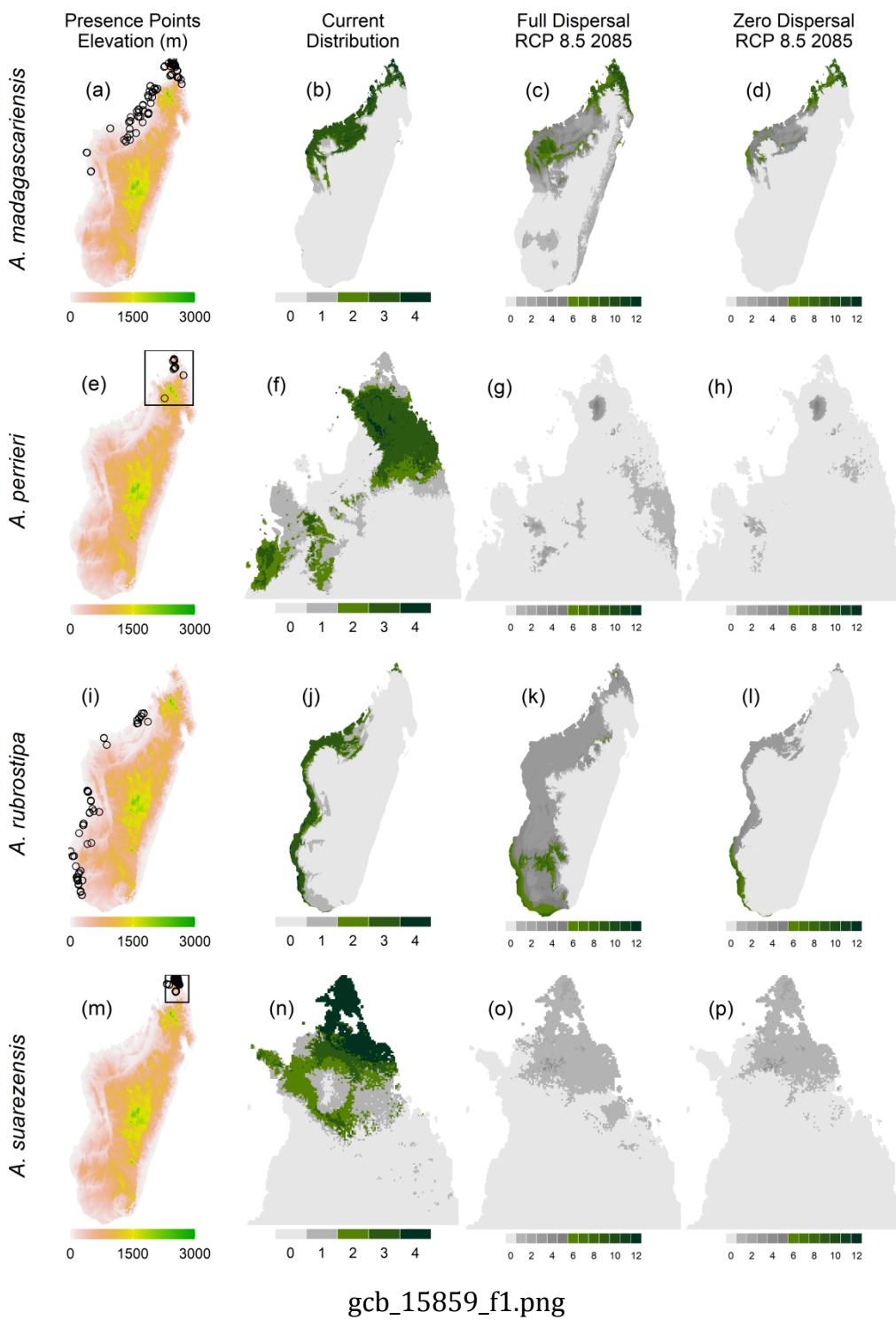
We calculated the species distribution area ( $\text{km}^2$ ) in the present ( $\text{SDA}_p$ ) and future ( $\text{SDA}_f$ ) to describe the change in the species distribution area (Change  $\text{SDA}_p / \text{SDA}_f \%$ ) according to two dispersal hypotheses (full and zero-dispersal). See IUCN Red List categories and criteria, version 3.1, second edition | IUCN Library System for criteria explanation. \*IUCN criteria suggested for Madagascar; \*\* IUCN status defined by populational aspects for the referred species once our models did not predict vulnerability for this species.

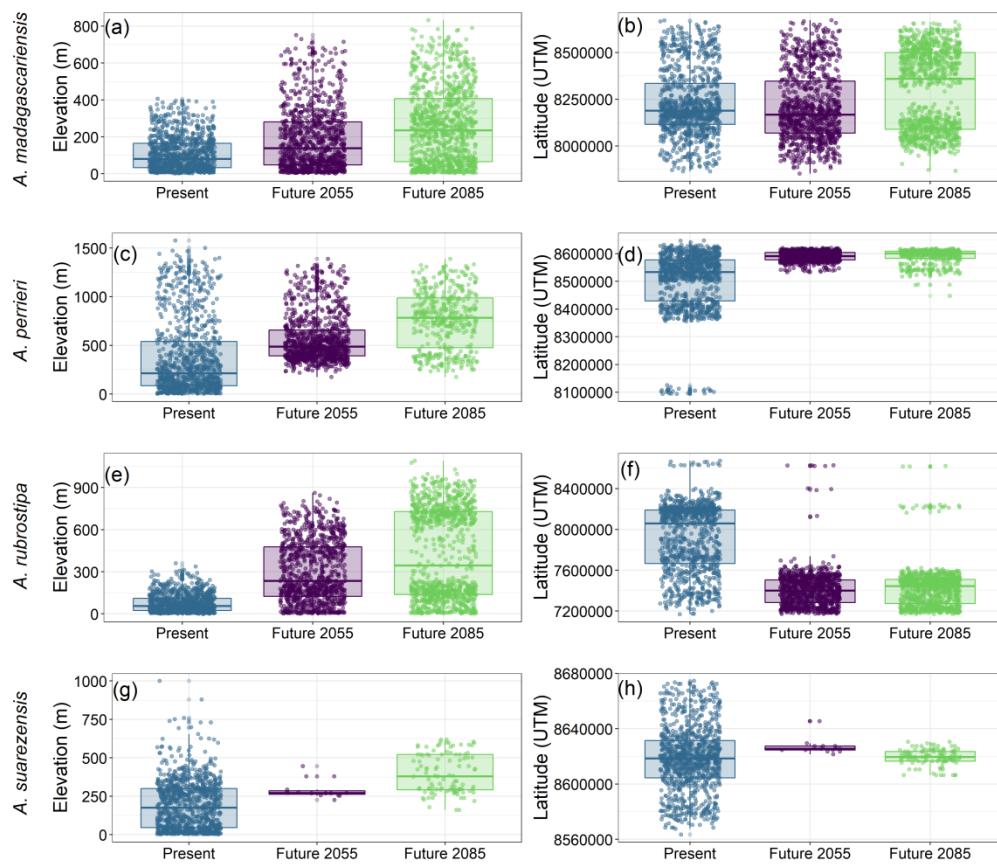
Baobab species IUCN status	<b>Current</b> $\text{SDA}_p$ ( $\text{km}^2$ )	mean elevation (m)	Dispersal hypothesis	<b>Future</b> $\text{SDA}_f$ ( $\text{km}^2$ )	mean elevation (m)	Change $\text{SDA}_{pf}$ (%)	IUCN Updated Status
<i>Adansonia digitata</i> Not assessed by IUCN	47 872	76	Full Zero	194 447 47 017	195 77	+306 -2	NT*
<i>A. grandiflora</i> Endangered A2c*	27 651	135	Full Zero	118 907 27 591	365 135	+330 0	EN A2c**
<i>A. madagascariensis</i> Near threatened	92 311	105	Full Zero	62 881 26 878	263 102	-32 -71	EN A3c
<i>A. perrieri</i> Critically endangered C2a(i)	14 872	377	Full Zero	0 0	<i>Extinct</i> <i>Extinct</i>	-100 -100	CR C2a(i) + A3C

				44			
			Full	833	428	-40	
		74	77				
<i>A. rubrostipa</i>		194					
<b>Least concern</b>				11			EN A3c
			Zero	488	82	-85	
<i>A. suarezensis</i>			Full	0	<i>Extinct</i>	-100	
<b>Endangered</b>	<b>B1ab</b>	3347	194				CR B1ab
(i,ii,iii,iv,v)	+ B2ab			Zero	0	<i>Extinct</i>	+ B2ab
(i,ii,iii,iv,v)						-100	
				372			
			Full	134	365	+118	
<i>A. za</i>		170	265				
<b>Least concern</b>		625		166			Least concern
			Zero	254	271	-3	

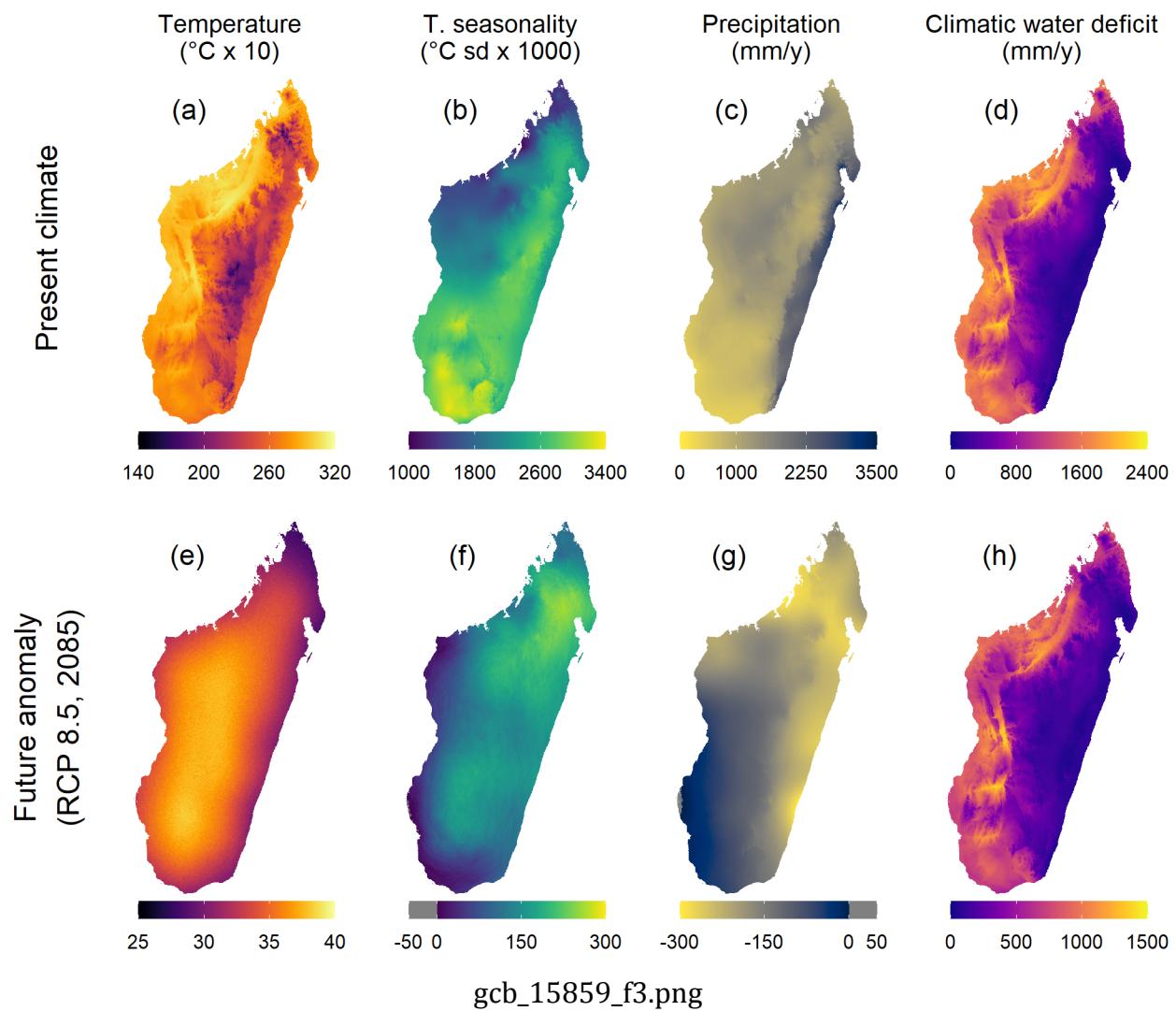
**Table 2. Relative importance of the four bioclimatic variables in determining species distribution.** Here we present the variable mean rank of importance over the four statistical models for each species. Temperature seasonality was the most important variable in determining species distribution for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

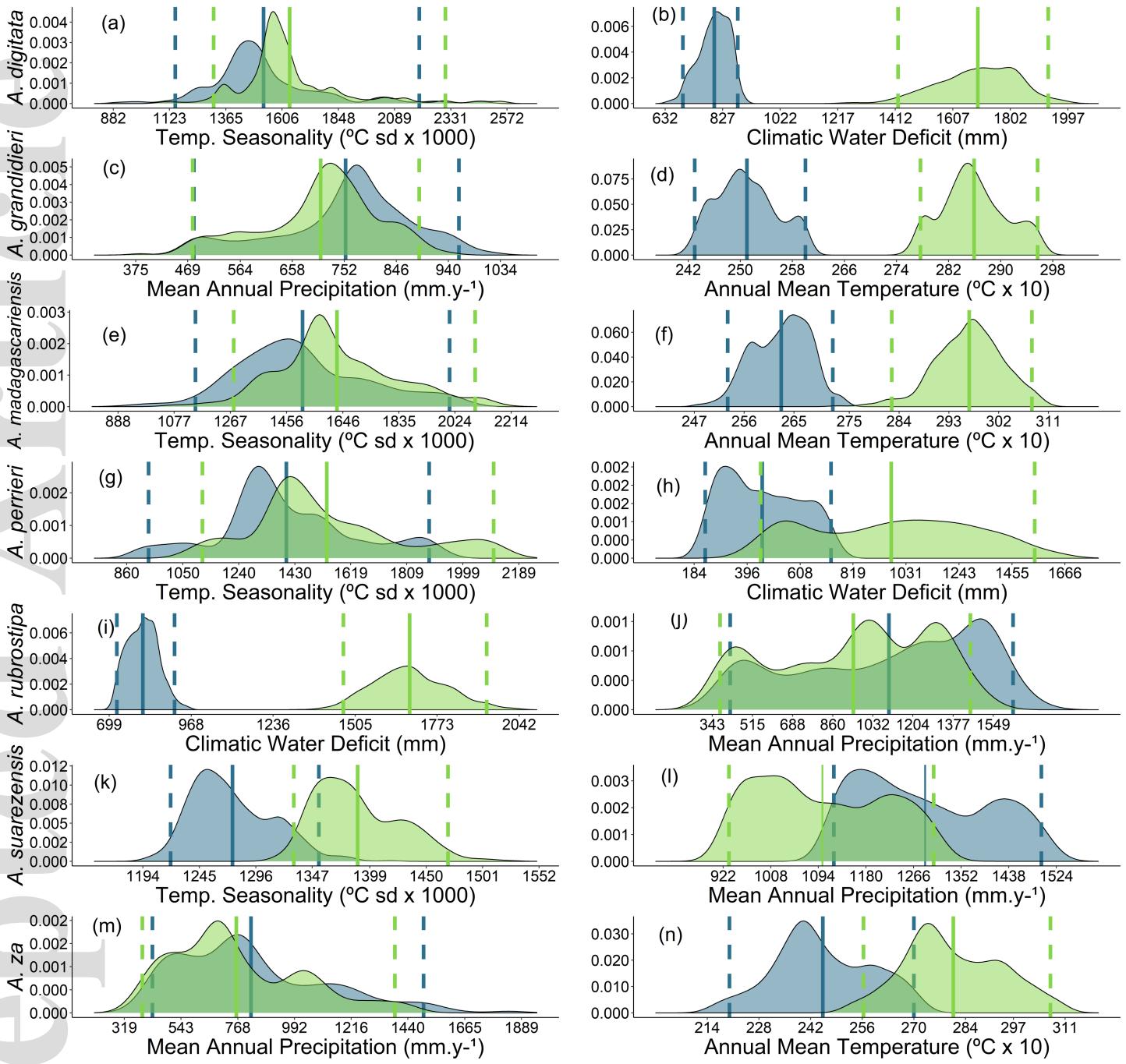
Species	Mean Annual Temperature	Temperature Seasonality	Precipitation	Climatic Water Deficit	Most Important Variables (1st and 2nd)
<i>A. digitata</i>	0.364	<b>0.633</b>	0.372	<b>0.552</b>	Tseas/Cwd
<i>A. grandidieri</i>	<b>0.526</b>	0.239	<b>0.550</b>	0.110	Prec/Tmean
<i>A. madagascariensis</i>	<b>0.651</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





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