



# Vulnerability of baobab species to climate change and effectiveness of the protected area network in Madagascar: Towards new conservation priorities



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## ABSTRACT

Baobab species are representative of the high biodiversity and endemism rates that place Madagascar in the top three of the countries with the highest biodiversity in the world. In this study, we estimated the vulnerability of three endangered Malagasy baobab species (*Adansonia grandidieri* Baill., *Adansonia perrieri* Capuron and *Adansonia suarezensis* H. Perrier) to climate change and the effectiveness of the protected area network (PAN) for the future conservation of these species. To estimate the environmental niche of the species, we used an original data-set based on satellite image analysis to detect species presence and an ensemble modelling approach using three species distribution models (GLM, GAM and MaxEnt). We projected the species distribution in 2050 and 2080 using an ensemble forecasting approach combining the three species distribution models and three global circulation models for climate projections. Measures of connectivity were employed to assess the present and future effectiveness of the existing PAN. Among the three baobab species studied, two are severely threatened by climate change (*A. perrieri* and *A. suarezensis*), in part because the present PAN does not overlap with future species distribution areas. Recently, strong efforts have been made in designing an optimised PAN to conserve Madagascar outstanding biodiversity. Nevertheless, its future effectiveness is questioned by the potential shifts in species distributions due to predicted changes in climate. In the context of climate change, alternative strategies such as ecological restoration would also have to be adopted to conserve biodiversity in Madagascar.

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## 1. Introduction

Madagascar is widely known for its exceptional biodiversity and high endemism rates in many taxonomic groups (Goodman and Benstead, 2005; Kremen et al., 2008), but also for its low percentage of remaining native forest cover and high levels of threat (Harper et al., 2007). As such, the island is universally recognised as a global biodiversity priority (Brooks et al., 2006; Myers et al., 2000). To conserve Madagascar biodiversity, a remarkable work has been done since the Vth IUCN World Parks Congress held in Durban in 2003, in designing an effective protected area network (PAN) integrating present biodiversity hotspots and the existing protected areas at the national level (Kremen et al., 2008).

Nevertheless, in the context of actual fast anthropogenic climate-change (IPCC, 2007; Loarie et al., 2009) producing numerous shifts in the distribution and abundance of species (Lenoir et al., 2008; Parmesan and Yohe, 2003), several authors have warned conservation practitioners of the potential ineffectiveness of fixed protected area networks (Hannah, 2008; Singh and Milner-Gulland, 2011; Pressey et al., 2007; Araujo et al., 2011; Coetzee et al., 2009). Although global warming is expected to be greatest over land and at most high northern latitudes, and least over the Southern Ocean (IPCC, 2007), a pronounced climate change has been predicted for Madagascar during this century, with a mean temperature increase of 1.1–2.68 °C throughout the island from present to 2055 (Tadross et al., 2008; Hannah et al., 2008), leading to estimated biome migration rates of 144–532 m year<sup>−1</sup>, which are significantly higher than average post-glacial rates (100–200 m year<sup>−1</sup>) (Malcolm et al., 2006; Hannah et al., 2008).

To our knowledge, until now, there has been no published work on Madagascar which evaluates species vulnerability to climate

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change and the effectiveness of the PAN for species conservation in the future, although several studies have used climatic data to identify present species distribution areas for conservation purpose (Kremen et al., 2008; Pearson et al., 2007). Through this study, we provide some answers to these two issues focusing on three particular baobab species: *Adansonia grandidieri* Baill., *Adansonia perrieri* Capuron and *Adansonia suarezensis* H. Perrier, for several reasons. First, baobab species are emblematic species of Madagascar biodiversity and endemism (Goodman and Benstead, 2003; Baum, 1995): 6 out of the 8 baobab species existing on Earth are endemic to Madagascar, among which are *A. grandidieri*, *A. perrieri* and *A. suarezensis*. Second, baobab species are of considerable value for Malagasy populations both for practical reasons (use of fruits, seeds, flowers, leaves and bark for food, medicine and construction) and spiritual reasons (sacred tree, “mother of the forest”) (Marie et al., 2009; Wickens and Lowe, 2008). Third, *A. grandidieri*, *A. perrieri* and *A. suarezensis* are the three most threatened baobab species, classified as “endangered” by the International Union for Conservation of Nature (IUCN, 2012a). Fourth, while few data on the distribution of Malagasy baobab species were available in the 1990s (Baum, 1995), we now have a much more precise species presence data-set thanks to the analysis of very-high resolution satellite images to identify trees, complemented by more than 10 years of intensive prospecting work in the field.

Species distribution models (SDM) and global circulation models (GCM) have been widely used to estimate the potential impact of climate change on species distribution (Guisan and Zimmermann, 2000; Araujo et al., 2011; Coetzee et al., 2009). Among the variety of SDM and GCM, the choice of the model accounts for the bulk of the variation in the prediction of species vulnerability to climate change (Buisson et al., 2010). Ensemble forecasting, which combine the predictions of multiple SDM and GCM, can be used to reduce the uncertainty associated to model projections (Coetzee et al., 2009; Araujo and New, 2007). In this study, we first used an ensemble forecasting approach to project the distribution area of the three baobab species in 2050 and 2080. Second, we compared present and future effectiveness of the PAN using measures of connectivity between protected habitat patches. Connectivity is a synthetic index taking into account both the total area of the protected patches and the presence of paths between patches along which movement can occur, thus permitting ecological flows such as genes flow or re-colonisation (Moilanen and Nieminen, 2002; Matisziw and Murray, 2009). On the basis of our results, we discuss the best strategy to conserve biodiversity in Madagascar in the context of climate change.

## 2. Methods

### 2.1. Ecological data

#### 2.1.1. Presence-absence data

*A. grandidieri* and *A. suarezensis* presence data (individual tree or group of neighbouring trees) were obtained through photo-interpretation of very high resolution (VHR) QuickBird satellite images (61 cm resolution). Such VHR images are freely available on GoogleEarth and cover around 70% of *A. grandidieri* prospecting area (Menabe and Atsimo-Andrefana administrative regions) and almost 100% of *A. suarezensis* prospecting area (Diana and Sava regions). In the remaining prospecting area, where QuickBird images were not available, we used high resolutions Spot5 satellite images (2.5 m resolution) also freely available on GoogleEarth. Trees were manually identified on the basis of their crown size, shape and colour and on the basis of the size and shape of the tree shadow projected on the ground (Fig. 1).

We conducted field verification to validate the presence data obtained by photo-interpretation. All the field work was done during the flowering period to facilitate species identification which was performed from the colour of the flower and the appearance of the bark (Baum, 1995). For *A. grandidieri*, along two north-south (Ihotry lake to Kirindy forest) and east-west (along the Mangoky river until Beroroha) transects of 260 and 80 km long respectively and 500 m large, we checked that each *A. grandidieri* tree or group of *A. grandidieri* trees identified by photo-interpretation was present in the field and not confounded with other tree species. Only 2% of the observations were false positives due in part to confusions with trees of *Adansonia za* Baill. or *Adansonia rubrostipa* Jum. & H. Perrier species and also to isolated dead trees no more present in the field. For *A. suarezensis* the field verification was done within two square areas of 20 km side. For this species, 100% of the presence data from photo-interpretation were true positive. To date, no identification method from satellite image is available for *A. perrieri* as the species is characterised by smaller individuals and is often found in closed canopies (A.1). Presence data for *A. perrieri* in this study result from more than 10 years of prospective field work in northern Madagascar.

#### 2.1.2. Environmental data

Current (~1950–2000) and future (2050, 2080) climatic data at 30-s resolution were extracted from the WorldClim data base (Hijmans et al., 2005) (<http://www.worldclim.org>). Climatic variables for Madagascar were resampled at 1-min resolution. Using present monthly data for precipitation (mm), minimal and maximal temperatures (°C), we computed 19 bioclimatic variables (A.2). Because bioclimatic variables were highly correlated, we performed a Principal Component Analysis (PCA) on the bioclimatic variables for each cell of the spatial grid covering Madagascar. We identified the coordinates of each grid cell on the first 6 dominant axis (A.3).

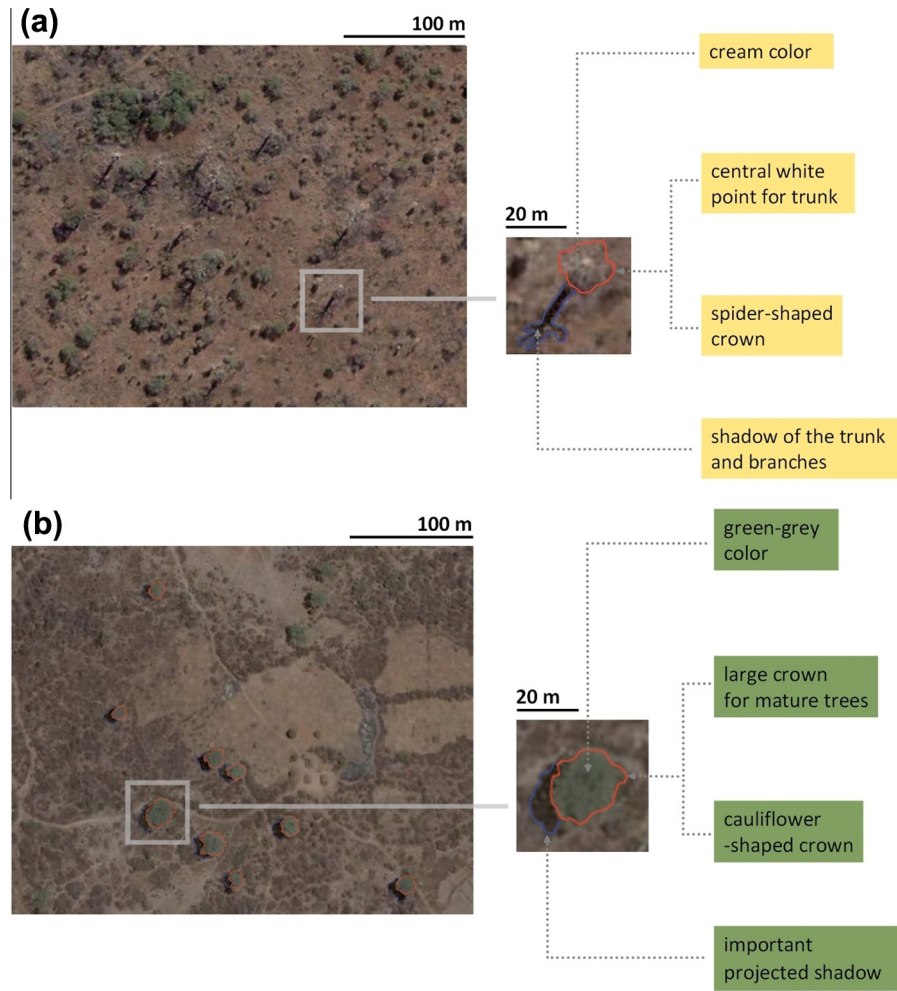
For future climatic data in 2050 and 2080, we used the predictions of three global circulation models (CCCMA, CSIRO and HADCM3) for two contrasted CO<sub>2</sub> emission scenarios: A2a, which assumes a regionally oriented economic development (+2.0 to +5.4 °C of global average surface warming until 2100) and B2a, which assumes local environmental sustainability (+1.4 to +3.8 °C) (IPCC, 2007). For each date (2050, 2080), GCM (CCCMA, CSIRO and HADCM3) and scenario (A2a, B2a), we computed the 19 bioclimatic variables for every grid cell as aforementioned. By projection, we obtained the new grid cell coordinates on the 6 axis of the PCA performed on current climate conditions.

A previous study (Du Puy and Moat, 1996) has demonstrated that geology was a significant factor explaining vegetation type in Madagascar. We then added geological information to climatic data using the simplified geological map provided by the Kew Botanical Garden (Du Puy and Moat, 1996) (<http://www.kew.org/gis/projects/madagascar/download.html>). This map was digitised from the geological map of Madagascar (Besairie, 1964). The 96 original categories were reclassified into predominant rock types. The categories of sedimentary rocks include sandstones, loose (unconsolidated) sands, and two limestone categories of different ages. A broad category of metamorphic rocks (including granites and migmatites), often covered by thick layers of laterites, covers large areas of the central and eastern areas of the island. Lavas and basalts, and several restricted rock types including quartzites, marbles and ultrabasics are also distinguished.

### 2.2. Species distribution modelling

#### 2.2.1. Statistical models

We used three different statistical models commonly used for species distribution modelling (Guisan and Zimmermann, 2000; Elith et al., 2011): Generalised Linear Models (GLM), Generalised



**Fig. 1.** Identification of *A. grandidieri* tree presence from satellite image. Text boxes summarise the rules used to identify trees during (a) the dry season and (b) the rainy season. Analysing high resolution satellite images by photo-interpretation, we were able to identify most of existing *A. grandidieri* and *A. suarezensis* populations in Madagascar.

Additive Models (GAM) and Maximum Entropy models (MaxEnt). For each species, we defined a random variable  $y$  equal to 1 when species was present on the grid cell and to 0 when it was absent. We denoted  $\mathbf{z}$  the vector of environmental covariates (here the geology  $z_0$  and the 6 axis of the PCA for the climate from  $z_1$  to  $z_6$ ).

When using GLM and GAM models, for each grid cell  $i$ ,  $y_i$  is assumed to follow a Bernoulli distribution of parameter  $\theta_i$  (the probability of presence):  $y_i \sim \text{Bernoulli}(\theta_i)$ . Because  $\theta_i$  ranges between 0 and 1, a logit link function is used to link the explicative environmental variables to the probability of presence. For GLM, logit ( $\theta_i$ ) was defined as a linear relationship ( $f$ ) including up to degree three polynomials for climatic factors (Eq. (1)).

$$\text{logit}(\theta_i) = f(z_{0i}) + f(z_{1i} + (z_{1i})^2 + (z_{1i})^3) + \dots + f(z_{6i} + (z_{6i})^2 + (z_{6i})^3) \quad (1)$$

GAM are non-parametric models. They do not require to postulate a specific parametric response function (Thuiller et al., 2009). They use a class of equations called “smoothers” that attempt to locally fit the observations using smooth curves on subsections of the data. GAM are useful when the relationship between the variables are expected to be of a more complex form, not easily fitted by standard linear or non-linear models, or where there is no *a priori* reason for using a particular model. We used cubic spline smoother ( $s$ ) of degree 4 defined on subintervals (Eq. (2)).

$$\text{logit}(\theta_i) = f(z_{0i}) + s(z_{1i}, 4) + \dots + s(z_{6i}, 4) \quad (2)$$

For both GAM and GLM, the likelihood of model  $m$  denoted  $L(\mathbf{y}|m, \mathbf{z})$  depends on presence ( $p$ ) and (pseudo-) absence ( $q$ ) data (Eq. (3)). The model parameters for  $f$  and  $s$  functions were estimated using a maximum likelihood approach. We used a stepwise AIC procedure to identify the most parsimonious GLM and GAM models.

$$\begin{aligned} L(\mathbf{y}|m, \mathbf{z}) &= \prod_{k=1}^p P(y_k = 1|m, z_k) \prod_{l=1}^q P(y_l = 0|m, z_l) \\ &= \prod_{k=1}^p \theta_k \prod_{l=1}^q (1 - \theta_l) \end{aligned} \quad (3)$$

Recently, MaxEnt approach has been intensively used to model species distribution, especially in Madagascar (Kremen et al., 2008; Pearson et al., 2007). This success is partly due to the release of a user-friendly MaxEnt JAVA software (Phillips et al., 2006) and mostly to the fact that the maximum entropy approach provides a consistent mathematical framework to handle presence-only data (Elith et al., 2011). The idea is to maximise the probability (entropy) of observing the species presence given the model and the environmental covariates. This probability has name entropy and can be written  $E(\mathbf{y} = 1|m, \mathbf{z})$ . Denoting  $f_1(\mathbf{z})$  the inverse conditional probability  $P(\mathbf{z}|m, \mathbf{y} = 1)$ ,  $f(\mathbf{z})$  the marginal probability  $P(\mathbf{z})$  and  $g_1(\mathbf{y})$  the



prevalence  $P(\mathbf{y} = 1)$ , the entropy can be decomposed using the Bayes formula (Eq. (4)).

$$E(\mathbf{y} = 1 | m, \mathbf{z}) = [f_1(\mathbf{z})/f(\mathbf{z})]g_1(\mathbf{y}) \quad (4)$$

The prevalence  $g_1(\mathbf{y})$  is a constant, not depending on environmental covariates, so that maximising the entropy of the model given the environmental covariates is equivalent to maximising the ratio  $f_1(\mathbf{z})/f(\mathbf{z})$ . Assuming that  $\log(f_1(\mathbf{z})/f(\mathbf{z})) = \alpha + \beta h(\mathbf{z})$ , several function forms called features ( $h$ ) are tested and several parameters ( $\alpha$  and  $\beta$ ) are estimated to maximise the entropy. We used a logistic output for the predicted probability of presence with MaxEnt model which can be considered an equivalent to the predicted probability using GLM or GAM model (Elith et al., 2011; Roura-Pascual et al., 2009).

Because these three approaches rely on different statistical assumptions and parametrisations, their predictions regarding species probability of presence and species distribution area can be combined in an ensemble modelling approach to estimate an uncertainty associated to the choice of the statistical model (Buisson et al., 2010; Araujo and New, 2007).

### 2.2.2. Model performance

For each model, we randomly selected 10,000 pseudo-absence data (10,000 background points for MaxEnt) that we associated to all presence data to obtain a presence-absence (presence-background for MaxEnt) data-set. We repeated a cross-validation procedure 5 times, randomly splitting the data into 70% of training data and 30% of testing data. We computed the Area Under the Curve (AUC) of the Receiver Operating Characteristic (ROC) on the test data for each repetition. The AUC of a model is a threshold independent measure equivalent to the probability that the model will rank a randomly chosen species presence site higher than a randomly chosen absence site (Liu et al., 2011). The mean  $AUC_{CV}$  of each statistical model for the cross-validation procedure was computed on the basis of the 5 repetitions. We also computed the model AUC on 100% of the presence-absence (presence-background) data. Models for which  $0.9 \leq AUC \leq 1$  are considered to be highly accurate models (Thuiller et al., 2009).

We also computed the True Skill Statistic (TSS = sensitivity + specificity – 1). The sensitivity is the ratio of correctly predicted presences to the total number of presences and the specificity is the ratio of correctly predicted absences to the total number of absences. TSS is a threshold dependent measure (Liu et al., 2011). We thus identified the threshold probability maximising TSS for each model and the corresponding TSS values. When several threshold probabilities led to the same maximum values of TSS, we computed the mean of these probabilities. Models for which  $0.9 \leq TSS \leq 1$  are considered to be highly accurate models (Thuiller et al., 2009).

### 2.2.3. Ensemble modelling, current and future species distribution area

Each statistical model (GLM, GAM and MaxEnt) gave slightly different but nevertheless very good predictions ( $AUC_{CV}$ , AUC and TSS > 0.9). Given the equivalent and high accuracy of each model, we did not reject any of the statistical approach. Using current climate data and geology on each spatial grid cell covering Madagascar, we predicted the mean probability of presence using the three statistical models. We transformed the probability of presence for each spatial grid cell into presence-absence prediction (0 or 1) using the probability threshold maximising TSS. The choice of the threshold dependent index and the identification of the probability threshold is particularly important to set the boundaries of the species distribution area. Several authors advise the use of the TSS rather than alternative threshold dependent measures (e.g. Cohen's Kappa) because TSS is not sensitive to prevalence and is then more adapted to rare species distribution modelling (Thuiller et al., 2009; Liu et al., 2011; Jimenez-Valverde and Lobo, 2007). Follow-

ing the methodology of Araujo and New (2007) for ensemble modelling, we computed the mean of the presence-absence predictions of the three statistical models (we obtained 4 different possible values for the mean prediction: 1, 2/3, 1/3, 0). The set of grid cells for which the mean prediction was superior to 0.5 (two models or more out of three predict a presence) delimited the present species distribution area ( $SDA_p$  in  $km^2$ ). The  $SDA_p$  must be interpreted as the present suitable area of presence of the species regarding climatic and geologic conditions (therefore, biotic interactions such as competition were not considered). The set of grid cells for which only one model out of three predicts a presence defined a buffer zone uncertainty (BZ in  $km^2$ ). The level of uncertainty ( $U$  in %, ranging between 0 and 100) can be defined as  $U = SDA_p / (SDA_p + BZ)$ . Using the computed  $SDA_p$ , we estimated *a posteriori* the climatic and geological niche of each species representing the distribution of the grid cells defining the  $SDA_p$  along the climatic and geological axis.

Using future climatic data predicted by the three different GCM, we computed the future probability of presence using the three statistical models. Therefore, we obtained 9 different probability predictions for each date (2050, 2080) and scenario (A2a, B2a). For each date and scenario, we identified the future species distribution area ( $SDA_f$ ) using the same ensemble modelling approach as the one described to identify the present species distribution area, except that we obtained 10 possible values (1, 8/9, 7/9, ..., 1/9, 0) for the mean prediction. The zone where the mean prediction was inferior to 0.5 included both the uncertainty associated to the choice of the statistical species distribution model and the uncertainty associated to the choice of the global circulation model.

Previous studies (Baum, 1995; Wickens and Lowe, 2008) underlined the difficulty for baobab species in Madagascar to disperse seeds and to regenerate. Dispersal might be limited by the absence of large animals now extinct such as so-called giant lemurs (Mittermeier et al., 2006) and elephant birds (genus *Aepyornis* and *Mullerornis* (Goodman and Benstead, 2003)). The main factor reducing natural regeneration is the conversion of natural habitat into agricultural land and pasture by slash-and-burn (Harper et al., 2007). Due to the difficulty of dispersal and regeneration for baobab species, we assumed a zero-colonisation hypothesis with the impossibility for baobab species to naturally colonise new sites outside the area defined by the present distribution area and the buffer zone, even if climatic and geological conditions are suitable. Thus, the future species distribution area must be interpreted as the future predicted area of presence of the species regarding future climatic and geological conditions and possibility of dispersal and regeneration.

### 2.3. Effectiveness of the protected area network

We considered the last Madagascar Protected Area System ("Système d'Aires Protégées à Madagascar: SAPM") decreed on October, 2008. GIS data regarding the SAPM is available at the Rebioma website (<http://www.rebioma.net>). The SAPM includes what has been historically called "existing protected areas", "temporary protected areas" and "new protected areas" (9.4% of the land surface). For the three baobab species at each date (2010, 2050 and 2080) and under each emission scenario (A2a and B2a), we computed the species distribution area ( $SDA$  in  $km^2$ ), the surface of the SAPM overlapping the species distribution area (protected patches, PPs in  $km^2$ ), and the percentage of PPs relative to present species distribution area  $SDA_p$ .

To assess the effectiveness of the SAPM, we used the graph theory to estimate the connectivity between PPs for each baobab species (Matisziw and Murray, 2009). We used square grid cells of 5-min resolution side covering all the PPs. We defined a graph

with  $N$  nodes located at the centre of each grid cell and arcs connecting nodes. Two nodes  $i$  and  $j$  were connected together with an arc if the distance  $d_{ij}$  between nodes was inferior or equal to  $0.15^\circ$  (with the underlying assumption that each protected cell can be directly connected only to the neighbouring cells). A direct measure of network connectivity is the sum of the total number of arcs between nodes (Eq. (5)). Connectivity is thus a synthetic index taking into account both the total area of the protected patches and the presence of paths between patches along which ecological flows (such as genes flow or re-colonisation) can occur (Moilanen and Nieminen, 2002; Matisziw and Murray, 2009).

$$C = \sum_i \sum_j Z_{ij}, \text{ with } Z_{ij} = 1 \text{ if connectivity between } i \text{ and } j \text{ exists, } 0 \text{ otherwise} \quad (5)$$

In this study, all spatial procedures were implemented in GRASS GIS (Neteler and Mitasova, 2008) and R (Ihaka and Gentleman, 1996) with spatial library “sp”, “maptools”, “spatstat” and “spatgraphs”. Statistical analysis for species distribution models were performed first with R including the BIOMOD library for GLM and GAM approaches (Thuiller et al., 2009) and second with the MaxEnt JAVA application for the MaxEnt approach (Phillips et al., 2006). GRASS GIS, R and MaxEnt scripts are available upon request.

### 3. Results

#### 3.1. Statistical model performance

Using 6 synthetic bioclimatic variables and one geological variable, we obtained accurate species distribution models with AUC and TSS > 0.93 (Table 1). The three statistical approaches were equivalent in terms of performance. The cross-validation approach and the resulting AUCcv values (>0.90, Table 1) indicated that the three statistical models had good predictive capacity and that they can be confidently used to predict future species distribution under the effect of climate change.

#### 3.2. Population size and present species distribution area

We precisely identified 99 *A. perrieri* trees. Because we identified trees or group of trees for *A. grandidieri* and *A. suarezensis* we can only provide a rough estimate of the total population for these two species. We estimated a population of more than one million individuals for *A. grandidieri* and of more than 15,000 individuals for *A. suarezensis*. For the three species, the population size is much bigger than what has been suggested before (Baum, 1995; Wickens and Lowe, 2008).

**Table 1**

Performance of the statistical models in predicting species presence-absence. AUCcv indicates the mean of the Area Under the ROC Curve for the 5 repeated cross-validation procedures (data were splitted into 70% of training data and 30% of test data). AUC indicates the Area Under the ROC Curve for the full data-set (100%). The threshold indicates the probability maximising the True Skill Statistic (TSS).

Species	Model	AUCcv	AUC	TSS	Threshold
<i>A. grandidieri</i>	GLM	0.992	0.992	0.960	0.429
	GAM	0.993	0.993	0.962	0.515
	MaxEnt	0.990	0.995	0.963	0.066
<i>A. perrieri</i>	GLM	0.908	0.993	0.975	0.631
	GAM	0.975	0.976	0.933	0.581
	MaxEnt	0.992	0.996	0.983	0.152
<i>A. suarezensis</i>	GLM	0.999	0.999	0.998	0.485
	GAM	1.000	1.000	0.999	0.490
	MaxEnt	1.000	1.000	0.999	0.056

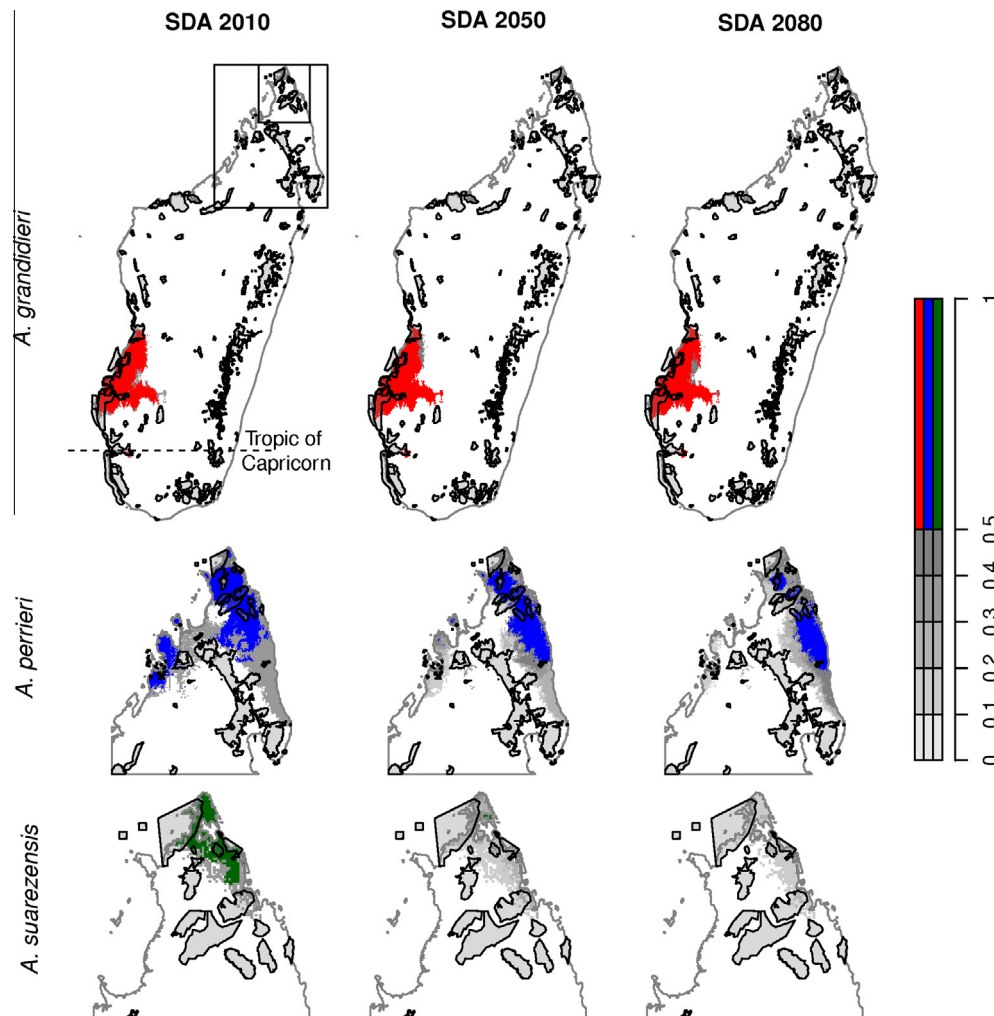
*A. grandidieri* has a wide present distribution area ( $SDA_p = 26,232 \text{ km}^2$ ) located along the Mangoky river and in the West part of the Menabe region and covering about 4.5% of Madagascar area ( $587,040 \text{ km}^2$ ) (Fig. 2). The level of uncertainty regarding *A. grandidieri*  $SDA_p$  is low ( $U = 8\%$ , Fig. 2). *A. grandidieri* is adapted to very dry areas with low annual precipitation ( $<1000 \text{ mm year}^{-1}$ ), high mean annual temperature ( $>23^\circ\text{C}$ ), high precipitation and temperature seasonality ( $>143$  and  $>2.16^\circ\text{C}$ , respectively) (A.4). Geology was not a significant factor explaining the distribution of *A. grandidieri*.

For *A. perrieri*, the number of observations (99 trees distributed in 11 presence pixels of 1-min side) was relatively low and we were able to distinguish two different populations regarding the climatic niche (see bi-modal distributions in A.4). This contributed to a higher uncertainty regarding *A. perrieri* distribution area ( $U = 62\%$ ) compared to the two other species. Current suitable habitat for *A. perrieri* covers a large area ( $SDA_p = 20,956 \text{ km}^2$ ) in the north of Madagascar including Montagne d'Ambre, Ankarana and Daraina regions, Nosy-be island and Anorontany, Ampasindava and Ambolobozo peninsulas (Fig. 2). The species climatic niche seems quite large (A.4). The species is nevertheless not adapted to areas with high precipitations ( $>2150 \text{ mm} \cdot \text{yr}^{-1}$ ), high precipitation seasonality ( $>113$ ) and low mean annual temperature ( $<19^\circ\text{C}$ ) (A.4). MaxEnt identified geology as the second main factor explaining the species distribution. The species is found preferentially on lavas (including basalts and gabbros) and on mesozoic limestones and marls (including “Tsingy”).

*A. suarezensis* has a restricted current distribution area ( $SDA_p = 1200 \text{ km}^2$ ) concentrated around the Diego-Suarez bay and in the Cap d'Ambre at the extreme north of Madagascar (Fig. 2). The level of uncertainty regarding *A. suarezensis* distribution is relatively low ( $U = 39\%$ , Fig. 2). *A. suarezensis* has a very narrow niche regarding climatic variables. The species is adapted to sub-moist areas with annual precipitation between 1100 and  $1300 \text{ mm year}^{-1}$ , very high mean annual temperature between  $24$  and  $27^\circ\text{C}$ , medium precipitation seasonality (between 93 and 113) and low temperature seasonality (between 1.1 and  $1.3^\circ\text{C}$ ) (A.4). Geology was not identified as a significant factor explaining the distribution of *A. suarezensis*.

#### 3.3. Vulnerability of species to climate change

Potential effects of climate change are different depending on the species. For *A. grandidieri*, climate change tends to extend the suitable habitat of the species towards the South of Madagascar (Fig. 3). *A. grandidieri* is adapted to very dry and hot areas with a strong seasonality (A.4). Thus, the predicted increase in precipitation seasonality (0 to  $-100 \text{ mm month}^{-1}$  during the dry season and  $+50$  to  $+100 \text{ mm month}^{-1}$  during the rainy season) and the increase of temperature ( $+1.6$  to  $+2.6^\circ\text{C}$ ) in southern Madagascar in 2055 (Hannah et al., 2008) tends to extend the suitable habitat of this species (Fig. 3). When considering the zero-colonisation hypothesis, (i.e. the impossibility for the species to colonise new sites due to dispersal or regeneration difficulties), the SDA remains constant (between  $26,232$  and  $27,265 \text{ km}^2$ ) (Table 2 and Fig. 2). Contrary to *A. grandidieri*, we observed a displacement and a decrease of the size of the suitable habitat for *A. perrieri* and *A. suarezensis* (Fig. 3). For *A. perrieri*, the potential suitable sites in the west peninsulas disappear and two smaller disconnected suitable sites remain: the Montagne d'Ambre and the region between Daraina and Marojejy national parks (Fig. 2). The SDA for *A. perrieri* drops from  $20,956 \text{ km}^2$  in 2010 to  $6539 \text{ km}^2$  in 2080 (Table 2 and Fig. 2). For *A. suarezensis*, the probability of presence becomes extremely low under the effect of climate change (Fig. 3) and the SDA drops from  $1200 \text{ km}^2$  in 2010 to  $17 \text{ km}^2$  in 2050. The disappearance of the suitable habitat for this species is likely to take



**Fig. 2.** Evolution of the species distribution area (SDA) in the context of climate change (IPCC emission scenario A2a with zero-colonisation hypothesis) and effectiveness of the protected area network. Coloured grid cells, where the majority of the models predicted a presence, define the species distribution area. Grey grid cells, where a minority of the models predicted a presence, define an uncertainty zone regarding the species distribution area. Protected area network is represented with transparent grey areas delimited by plain black lines. *A. grandidieri* seems not vulnerable to climate change, because the SDA is not substantially modified under the effect of climate change and because a large proportion of the SDA is protected. On the contrary, both *A. perrieri* and *A. suarezensis* seems vulnerable to climate change because of a decrease of the SDA and because most of the SDA in the future will not be protected. Moreover, a disappearance of *A. suarezensis* is predicted before 2080 due to loss of suitable habitat for this species. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

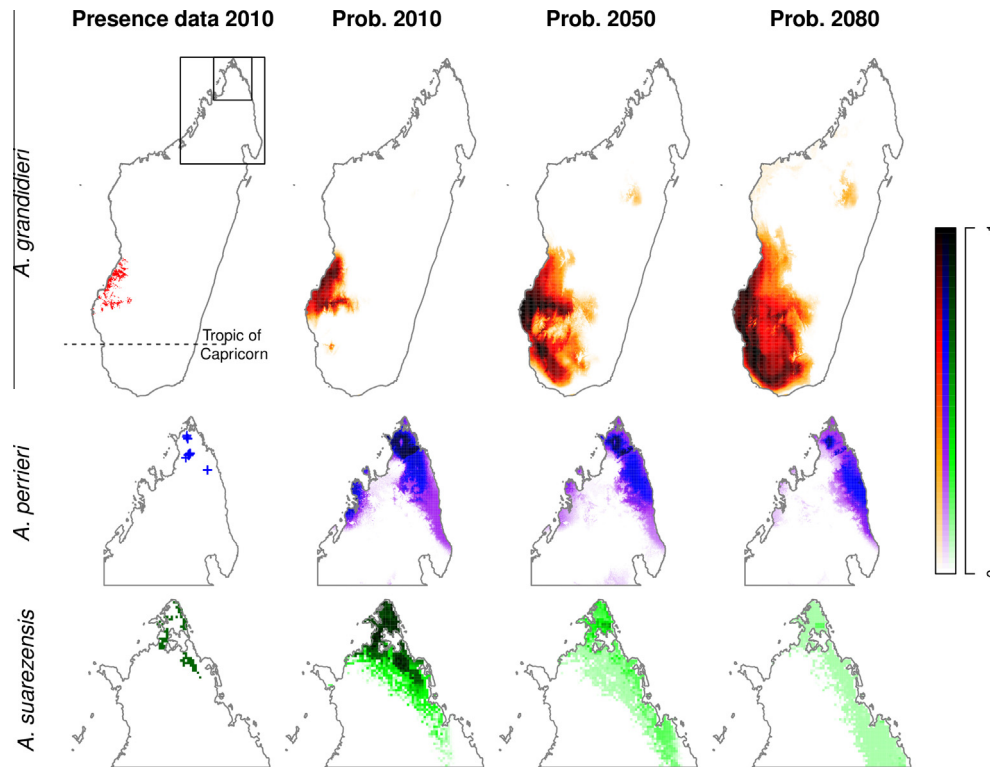
place before 2080 leading to a potential extinction of this species (Fig. 2). Results regarding species vulnerability to climate change were almost independent of the CO<sub>2</sub> emission scenario considered (Fig. 2 compared to Fig. A.5).

### 3.4. Effectiveness of the protected area network

Predicted change in climate is not likely to affect *A. grandidieri* distribution, suggesting that the effectiveness of the protected area network in the future depends only on the overlap between the current SDA and already existing protected areas. The current protected area network can be considered as relatively effective for the conservation of *A. grandidieri* as (i) the protected area network overlaps a part of the SDA (Fig. 2), (ii) PPs have a large surface (6405 km<sup>2</sup> = 24.4% of the SDA in 2010) (Table 2), (iii) PPs include different populations with potential genetic variability (Fig. 2), and (iv) the connectivity between PPs is relatively high ( $C = 378$ ) (Table 2 and Fig. 4). Contrary to *A. grandidieri*, we showed that *A. perrieri* seems to be very vulnerable to climate change (Figs. 2

and 3). If the network of protected areas is regarded as effective at present for the protection of the species (criteria (i) and (ii): existence of large protected areas (PPs surface = 3077 km<sup>2</sup> = 14.7% of the SDA in 2010), (iii) protection of several populations and (iv) rather high connectivity between PPs ( $C = 74$ ), see Table 2 and Fig. 4), this is not the case in the future. Between 2010 and 2080, the PPs surface for *A. perrieri* is likely to drop from 3077 km<sup>2</sup> to 953 km<sup>2</sup> and the connectivity from 74 to 18. We also showed that *A. suarezensis* seems to be vulnerable to climate change (Figs. 2 and 3). Contrary to *A. grandidieri* and *A. perrieri*, the effectiveness of the protected area network for the present conservation of *A. suarezensis* is questionable. Even if it is covering a large percentage of the SDA (25.5%), the surface of the PPs (1200 km<sup>2</sup>) and their connectivity ( $C = 2$ ) are very low compared to the two other species (Fig. 4). Due to the predicted progressive disappearance of the suitable habitat of this species in 2050 and 2080 (Figs. 2 and 3), the protected area network will probably not have any effect on the species conservation in the future, highlighting the need for alternative conservation strategies.





**Fig. 3.** Evolution of the species probability of presence in the context of climate change (IPCC emission scenario A2a). We computed the mean probability of presence using an ensemble forecasting approach including three different statistical species distribution models (SDM) and three different global circulation model (GCM). For *A. grandidieri*, a species adapted to hot and dry climate (see A.4), climate change tends to increase the probability of presence and extend the suitable habitat of the species towards the South of Madagascar. Contrary to *A. grandidieri*, a general decrease of the probability of presence is predicted for *A. perrieri* and *A. suarezensis* with a reduction of the suitable habitat for these two species. For *A. suarezensis*, the probability of presence becomes extremely low under the effect of climate change.

## 4. Discussion

### 4.1. Updating IUCN species conservation status

Conservation status of *A. grandidieri*, *A. perrieri* and *A. suarezensis* were established in 1998 using the 1994 IUCN Red List Categories and Criteria version 2.3 (IUCN, 2012a) and should be actualised in view of the results we obtained in our study regarding population size and species vulnerability to climate change. We used the current IUCN Red List Categories and Criteria version 3.1 (IUCN, 2012b) to suggest new conservation status for the three baobab species we studied.

In 1952, French botanist Perrier de la Bâthie (Perrier de la Bâthie, 1952) estimated that *A. grandidieri* was represented “by only a few individuals” and that the species would have

disappeared before the end of the 20<sup>th</sup> century. As described in the IUCN Red List, *A. grandidieri* was observed in five locations only in 1998 and classified as endangered species (EN) based on IUCN criteria A1c (population reduction of at least 50% over the last 10 years or three generations, see IUCN (2012a) for more details on classification criteria) and A2c (population reduction of at least 50% within the next 10 years or three generations). Our results puts into perspective the endangered status regarding criteria A1c: *A. grandidieri* populations include more than 1 million mature individuals in an area larger than 25,000 km<sup>2</sup>. Nevertheless, a decline of 50% of the population within the next three generations due to regeneration difficulties associated to change in land use is highly probable and justifies the endangered status of the species regarding criteria A2c.

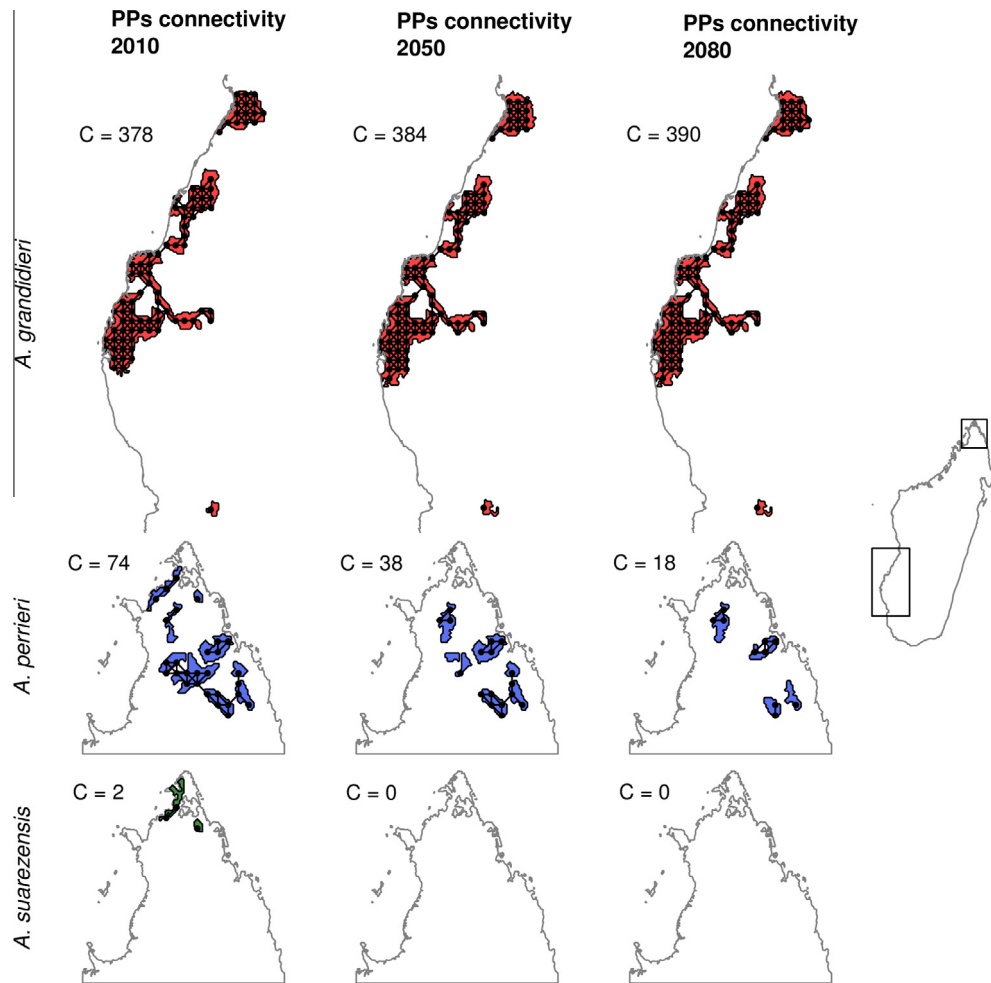
*A. perrieri* was classified as endangered species (EN) regarding criteria B1 and B2c (extent of occurrence estimated to be less than 5000 km<sup>2</sup>) and C2a (population estimated to number less than 2500 mature individuals) (IUCN, 2012a). We identified 99 individuals of *A. perrieri* in the field. Because trees cannot be seen easily (A.1), further locations are likely to exist but populations should be evidently very small. Moreover, the extent of occurrence of *A. perrieri* has a high probability to drop from 20,956 to 6539 km<sup>2</sup> (–69%) due to climate change. This might justify the classification of the species as critically endangered regarding criteria C1 (population estimated to number less than 250 mature individuals and declining) and maybe criteria A2c (reduction of at least 80% of the population within the next 10 years or three generations).

There is less interrogation regarding the necessity to actualise the conservation status of *A. suarezensis*. The species was classified as endangered (EN) regarding criteria B1 and B2c (IUCN, 2012a). When considering the vulnerability of the species to climate change (with a complete loss of the species habitat predicted

**Table 2**

Vulnerability of baobab species to climate change and effectiveness of the protected area network (IPCC emission scenario A2a). We computed the species distribution area (SDA), the surface of the protected patches (PPs) overlapping the SDA, the PPs surface relative to the SDA surface in 2010 in percentage and the connectivity between PPs (C).

Species	Date	SDA (km <sup>2</sup> )	PPs (km <sup>2</sup> )	PPs (%)	C
<i>A. grandidieri</i>	2010	26,232	6405	24.4	378
	2050	27,265	6731	25.7	384
	2080	27,148	6805	25.9	390
<i>A. perrieri</i>	2010	20,956	3077	14.7	74
	2050	10,085	1752	8.4	38
	2080	6539	953	4.5	18
<i>A. suarezensis</i>	2010	1200	307	25.6	2
	2050	17	0	0.0	0
	2080	0	0	0.0	0



**Fig. 4.** Evolution of the connectivity of the protected patches (PPs) in the context of climate change (IPCC emission scenario A2a). The PPs are obtained from intersecting the protected area network with the SDA for each species at each date (coloured polygons). To compute PPs connectivity (C), we used a regular grid of 5-min resolution cells covering the PPs. We defined a graph (see methods section) with nodes located at the centre of each grid cell (black dots) and arcs connecting neighbouring nodes (black segments). A direct measure of connectivity is the sum of the total number of arcs between nodes (Eq. (5)). PPs connectivity for *A. perrieri* and *A. suarezensis* is predicted to significantly decrease under climate change. A decrease in connectivity reflects a decrease of the total area of PPs and a loss of paths between PPs along which ecological flows can occur. This is not the case for *A. grandidieri* for which connectivity is predicted to slightly increase under climate change. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

before 2080), it should be preferable to shift the conservation status to critically endangered (CR) regarding criteria E (quantitative analysis showing the probability of extinction in the wild is at least 50% within 10 years or three generations).

#### 4.2. Uncertainty of the projections

In a previous study, Buisson et al. (2010) showed that, while using ensemble forecasting to project species distribution in the future, SDM contributed to the largest variation in projections, followed by GCM. Initial data-sets and emissions scenarios had little influence on the variability in projections. In our study, we were able to estimate the uncertainty (in percentage of the SDA surface) associated (i) to the SDM for determining the SDA in 2010 (Fig. 2), and (ii) to both the SDM and the GCM for SDA projections in 2050 and 2080 (Fig. 2). Although the uncertainty can be quite large (62% for the determination of *A. perrieri* SDA in 2010), trends regarding the evolution of the SDA for the three species were unequivocal (Fig. 2). Moreover, for the zero-colonisation hypothesis, we included the uncertainty relative to SDM (the buffer zone) for the definition of the initial SDA. We have thus been very conservative regarding the size of the projected SDA in 2050 and 2080. Regarding the climatic scenarios A2a and B2a, we observed the same

trend for the evolution of the SDA (see Fig. 2 in comparison to the figure in A.5). We thus confirm the results obtained by Buisson et al. (2010) regarding the small influence of emission scenarios A2a and B2a on the variability of future projections.

Other sources of uncertainty might be associated to our projections due to biological mechanisms that are not taken into account by models (Sinclair et al., 2010). On the one hand, SDMs might over-predict the SDA, because dispersal barriers and other biogeographic factors are not taken into account (Kremen et al., 2008). On the other hand, effects of climate change might be overestimated as we do not consider species adaptive mechanisms to climate change such as phenotypic plasticity (Geburek et al., 2008) and gene flow (introgression or hybridisation) (Currat et al., 2008; Mallet, 2005). As an example, recent results have demonstrated the ability for *A. perrieri* to introgress with *Adansonia za* Baill., leading to a potential adaptation to new climatic conditions (unpublished). Nevertheless, such adaptive mechanisms are still difficult to identify, quantify and include in predictive models.

#### 4.3. Conservation strategies in the Malagasy context

Several authors have already shown that existing PAN are likely to be less effective for biodiversity conservation in the future due





**Fig. A.1.** Pictures of *A. grandidieri*, *A. perrieri* and *A. suarezensis* in their natural habitat.

to potential shifts in the distribution of species in the context of climate change (Araujo et al., 2011; Coetzee et al., 2009; Hole et al., 2011). From existing knowledge, it was unclear if this would be the case in Madagascar. From IPCC report, global warming is expected to be greatest over land and at most high northern latitudes,

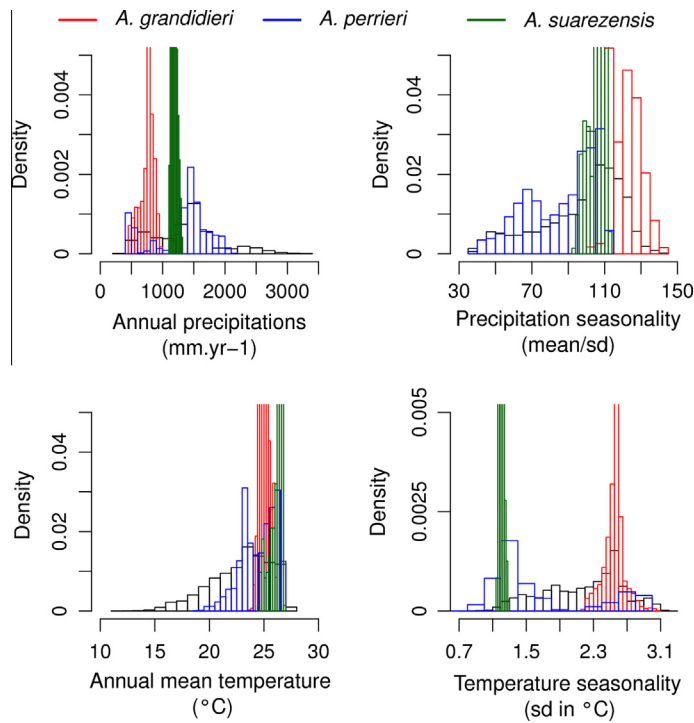
and least over the Southern Ocean (IPCC, 2007). But some studies have predicted dramatic climate changes (Tadross et al., 2008) resulting in high biome migration rates in Madagascar (Malcolm et al., 2006; Hannah et al., 2008). Nevertheless, these studies did not consider the existing PAN deployed in Madagascar which cover around 10% of the national territory (Kremen et al., 2008). Using the three most endangered baobab species as a case study, we confirm that the existing PAN in Madagascar is not likely to be effective for biodiversity conservation in the future. As Madagascar is considered as an international biodiversity hotspot (Brooks et al., 2006; Myers et al., 2000; Goodman and Benstead, 2005), there is a pressing need to account for climate change in designing an effective PAN. Biodiversity hotspots and protected areas in Madagascar are mostly located in residual tropical forests (Kremen et al., 2008; Harper et al., 2007). A large proportion of the original forest has disappeared due to harvesting of wood for construction or fuel, or through slash-and-burn for cattle grazing and agriculture, leaving place to ecologically degraded rural landscapes (Harper et al., 2007; Agarwal et al., 2005; Vieilledent et al., 2013). Consequently, spatially adapting the design of the PAN to potential future species distribution areas with regards to climate will probably not be sufficient for biodiversity conservation. Ecological restoration of degraded ecosystems outside the actual PAN should also be considered (Holloway, 2004; Pedrono et al., 2013). SDM and ensemble forecasting could be used to identify favourable sites for ecological restoration (Pearce and Lindenmayer, 1998). But as underlined by previous studies (Holl and Kappelle, 1999; Cuní Sanchez et al., 2011), it is only with an integration of ecological, social and economic studies, involving local communities and stakeholders, that we have a hope of restoring Malagasy ecosystems over the long term, which is a prerequisite to the development of an effective PAN in the future.

## Acknowledgements

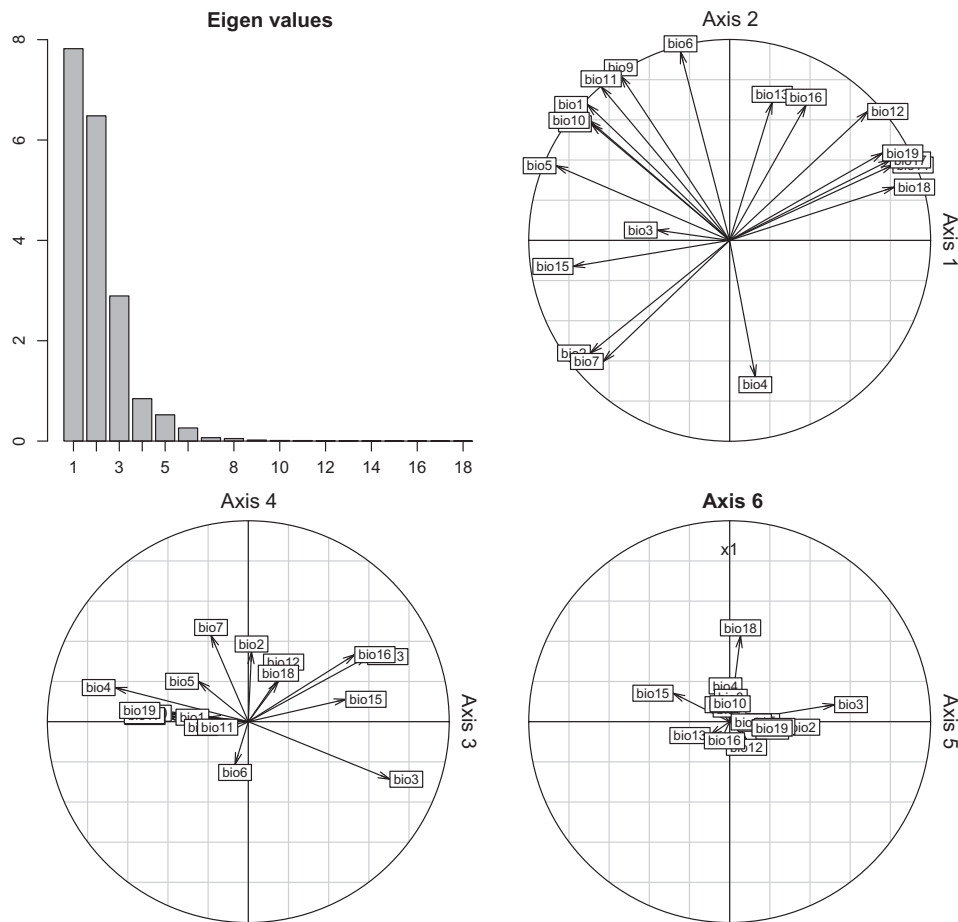
Authors warmly thank Wilfried Ramahafaly, Lucien Rasoanavison, Marcelo Saïdoune Maharitra, Emilson Rakotoarisoa, Sakda Bun and Morgan Alexaline (Cirad) for field assistance, Youna Hemery, Julien and Laura Mingui for fruitful discussions while prospecting for baobab trees around Diego-Suarez, Paulo van Breugel (World Agroforestry Center and University of Copenhagen) for making useful GRASS GIS scripts freely available (<http://pvanb.wordpress.com>), Wilfried Thuiller et al. (CNRS-LECA) for

Name	Description	Unit
bio1	Annual Mean Temperature	°C × 10
bio2	Mean Diurnal Range (Mean of monthly (max temp - min temp))	°C × 10
bio3	Isothermality ((bio2/bio7) × 100)	–
bio4	Temperature Seasonality (standard deviation × 100)	°C × 1000
bio5	Max Temperature of Warmest Month	°C × 10
bio6	Min Temperature of Coldest Month	°C × 10
bio7	Temperature Annual Range (bio5-bio6)	°C × 10
bio8	Mean Temperature of Wettest Quarter	°C × 10
bio9	Mean Temperature of Driest Quarter	°C × 10
bio10	Mean Temperature of Warmest Quarter	°C × 10
bio11	Mean Temperature of Coldest Quarter	°C × 10
bio12	Annual Precipitation	mm
bio13	Precipitation of Wettest Month	mm
bio14	Precipitation of Driest Month	mm
bio15	Precipitation Seasonality (Coefficient of Variation)	–
bio16	Precipitation of Wettest Quarter	mm
bio17	Precipitation of Driest Quarter	mm
bio18	Precipitation of Warmest Quarter	mm
bio19	Precipitation of Coldest Quarter	mm

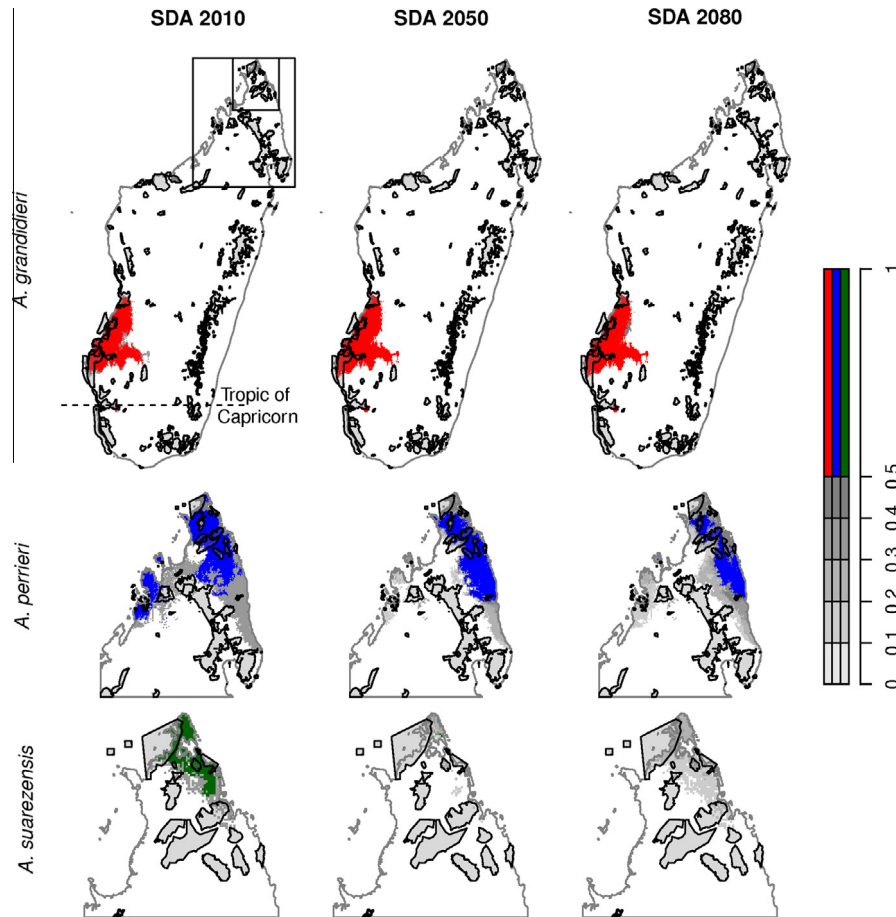
**Fig. A.2.** Bioclimatic variables computed from monthly precipitation, minimal and maximal temperatures. Raw climatic data at present, in 2050 and 2080 were downloaded from the WorldClim website (Hijmans et al., 2005) at a 30-s resolution.



**Fig. A.4.** Climatic niche of endangered baobab species in Madagascar. Based on the predicted species distribution area (SDA) in 2010, we represented the distribution of the grid cells defining the SDA regarding four main climatic variables: annual precipitation, mean annual temperature, precipitation seasonality and temperature seasonality.



**Fig. A.3.** Eigen values of the Principal Component Analysis (PCA) and correlation circles between the 19 bioclimatic variables and the 6 first axes of the PCA.



**Fig. A.5.** Evolution of the species distribution area (SDA) in the context of climate change (IPCC emission scenario B2a with zero-colonisation hypothesis) and effectiveness of the protected area network. Coloured grid cells, where the majority of the models predicted a presence, define the species distribution area. Grey grid cells, where a minority of the models predicted a presence, define an uncertainty zone regarding the species distribution area. Protected area network is represented with transparent grey areas delimited by plain black lines. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

providing the free open-source BIOMOD software, Steven J. Phillips et al. for providing the free MaxEnt software and Tantely Raminosoa (Missouri Botanical Garden) and people from the Rebioma web-portal for providing the geographical information on the protected area network in Madagascar. Financial support was provided by Cirad and the “Ministère français des Affaires Etrangères” (MAE) through the FSP Parrur Project.

## Appendix A

Figs. A.1, A.2, A.3, A.4, A.5.

## Appendix B. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2013.06.007>. These data include Google maps of the most important areas described in this article.

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