Potential, realised, future distribution and environmental suitability for *Pterocarpus angolensis DC* in southern Africa

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Abstract

The deciduous tree species *Pterocarpus angolensis* occurs in the dry woodlands of southern Africa and grows under a broad range of environmental conditions. It is threatened by overharvesting due to its valuable timber (Blood wood, Kiaat) and by land use changes. Information on the most suitable environmental conditions for the species is often old and anecdotal, while available data on its occurrence refer to range extent and not to distribution. Species distribution models (SDM) could provide more accurate information on distribution and environmental requirements and thereby assist sustainable management of this tree species.

Maxent models were developed to estimate the potential, realised and future distribution of *P. angolensis* and to identify detailed environmental requirements. Occurrences data of the species were sourced from herbaria and other published sources; environmental data from global GIS databases. Relevant environmental predictors were selected through a jack-knife test of the first model runs. The addition of information on competing species, fires and deforestation was tested to determine realised distribution. Model quality was evaluated with an independent

presence-absence dataset. The model was projected with two different climate change scenarios to study their effect on the distribution by 2080.

Results show that a potential distribution map can be obtained with good discrimination of the presence of the species (AUC 0.83) and fairly good calibration (correlation coefficient 0.61). Range extent and environmental requirements are more detailed than those described in literature. The distribution of the species is mainly influenced by the amount of summer rainfall, by the minimum temperature in winter and by temperature seasonality. Potential and realised distributions are very similar, with Madagascar as major exception where the species can grow but does not occur. Adding the fire history of the last 13 years or the distribution maps of potentially competing species as predictor variables did not improve the distribution model. It did illustrate that *P.angolensis* is mainly found in areas with annual fire frequency below 45% and that only a few of the tested species show signs of competition. Using a forest cover map improved the realised distribution slightly (Kappa coefficient 0.64). Climate change can decrease the species range considerably, especially in the west, threatening species existence in Namibia and Botswana. On the other hand, the species' occurrence is predicted to increase in Zambia.

1. Introduction

Pterocarpus angolensis DC. is a dry woodland tree species belonging to the family of the Fabaceae and can be found in most of tropical southern Africa, including the Miombo woodlands. The tree is intensively harvested for its attractive hardwood and is considered the most important timber tree over much of its range (Boaler, 1966a; Pedro et al., 1955).

Intensive exploitation goes back to the 1950s or earlier in the Democratic Republic of Congo, Tanzania, Zambia and Mozambique (Clarke, 1995; Hauman et al., 1954; Lees, 1962; Timberlake et al., 2010). A few decades later, Von Breitenbach (1973) mentioned that no other African species south of the equator had been exploited on such a large scale. Nowadays, unsustainable harvesting is reported for many areas in the region, although only a few reports are based on research into recruitment rate, growth rate and/or population size structure (Caro et al., 2005; Schwartz and Caro, 2003; Schwartz et al., 2002). The species has the status "Lower Risk/Near Threatened" on the IUCN Red List. As the natural regeneration of *P. angolensis* is reported to be limited in certain parts of the region (Caro et al., 2005; Chakanga, 2000; Dirninger, 2004; von Malitz and Rathogwa, 1999; van Daalen, 1991), it is a question if the species'conservation status can be maintained and if the species can remain an important timber resource without forest management interventions.

Accurate information about the distribution and environmental requirements of the species is needed to allow an assessment of the species' status and coordinate protection measures at a national and regional scale. Although a lot of information does exist on *P. angolensis*, it is mainly descriptive or general in nature (Vermeulen, 1990; Von Breitenbach, 1973) or focuses on one country (Banda et al., 2006; Shackleton, 2005; van Daalen, 1991; von Malitz and Rathogwa, 1999). The range extent or the distribution of the species is often summarised as a list of countries, herbaria sample locations or regions were the species can be found (Brummitt et al., 2007; Coates Palgrave et al., 1957; Gillett, 1971; Hauman et al., 1954; Palmer and Pitman, 1972). Existing maps refer to the species' range or extent of occurrence (EOO), not to the area of occupancy (AOO) (Boaler, 1966b; Coates Palgrave, 1983; Van Wyk and Van Wyk, 1997; Von Breitenbach, 1973). Very little information is given on how the maps were compiled; it can be assumed that they are based on collations of existing locality records at the margins of the range, as it is the case for many distribution or range maps in field guides and monographs (Gaston and Fuller, 2009). Therell et al. (2007) provide the most detailed range map but indicate that the northern limit of the range extent in the Democratic Republic of Congo is uncertain (figure 1).
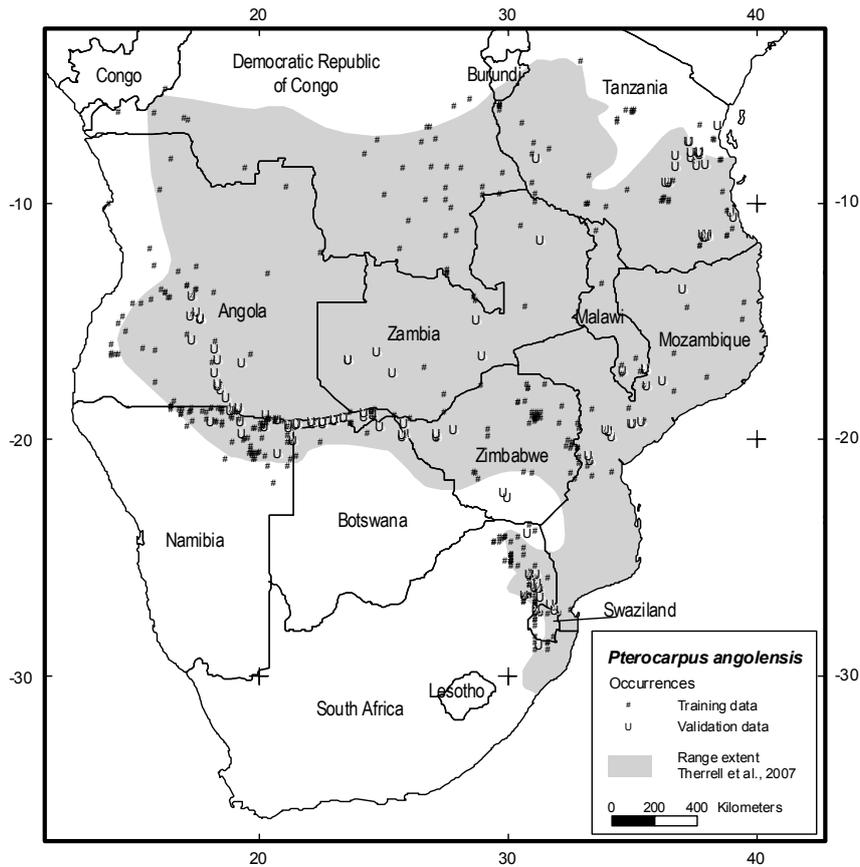
Figure 1 – Approximate range of *Pterocarpus angolensis* (Therell et al. (2007) based on Boaler (1966b), von Breitenbach (1973) and Palgrave (1983)) and locations of occurrence points used in this study. The northern limit of the current known range extent in the Democratic Republic of Congo is uncertain (Therrell et al., 2007).

Information on the environmental requirements of *P. angolensis* illustrates that the species tolerates a broad range of environmental conditions, as illustrated in section 2.1. However, the most suitable environmental conditions within these ranges are not clearly documented.

Species distribution models (SDM) can serve as a tool to produce more precise predictions of the environmental requirements and the geographical distribution than mere species observations, especially for large areas. The models correlate environmental data to species occurrences and sometimes species absences. They are also called ecological niche models (ENM) or species habitat models, although these terms place more emphasis on potential distribution modelling (Elith and Leathwick, 2009; Peterson et al., 2008). Only a minority of SDM or ENM studies focus on the African continent. Cayuela et al. (2009) illustrated that 8 %

of 123 SDM studies in the period 1995 – 2007 dealt with African species, and mainly plants from South Africa (4 %).

In the past, most SDM's were based on regression models. During the last decade, machine-learning methods have been used increasingly, and shown to outperform traditional regression techniques. This study estimates the potential and realised distribution as well as environmental requirements of *P. angolensis* in southern Africa with the machine-learning algorithm Maxent. Literature on the ecology of the species was reviewed in order to allow a proper interpretation of the results.

Africa is one of the most vulnerable continents to climate change (IPCC, 2007) and forest managers need to consider the potential effects on this important timber species in combination with all other short-term threats to southern Africa's woodlands. Therefore, the SDM for *P. angolensis* was also used to derive the future distribution of the species based on two global climate change scenarios.

2. Methods

2.1 Ecology of *P. angolensis*

P. angolensis is a deciduous tree that can be found in the mixed miombo or other deciduous woodlands and forests of southern Africa. It is about 10 - 20 m tall, sometimes reaching a height of 30 m (Gillett, 1971; Palgrave et al., 1957; Palmer and Pitman, 1972; Pedro et al., 1955). In certain parts of Angola, it is reported to belong to the shrub stratum with heights of 2 - 8 m (Groome et al., 1957; Monteiro, 1957). The diameter at breast height (DBH) of mature trees is 40 – 70 cm (Groome et al., 1957). The species can easily reach an age of 100 to 140 years (Therrell et al., 2007).

The tree is sometimes co-dominant or dominant in the canopy layer, with tree densities up to 75 trees/ha, but most often it is distributed scarcely with densities of 4 to 20 trees/ha (Backeus et al., 2006; Brummitt et al., 2007; Groome et al., 1957; Modest, 2006). There are no records of homogenous stands of this species (Pedro et al., 1955). Tree associates vary within the distribution area and include amongst others *Uapaca* species and *Oxystigma buchholzii* in Angola, *Burkea africana* in Namibia and South Africa, and *Julbernardia and Brachystegia* species in Mozambique and Tanzania (Groome et al., 1957; Pedro et al., 1955; Von Breitenbach, 1973).

The woodlands where *P. angolensis* occurs are characterised by disturbances, especially fire and shifting cultivation and the species is well adapted to this dynamic environment due to its fire tolerance and its light demands (Banda et al., 2006; Geldenhuys, C. J., 1977; Von Breitenbach, 1973). It has a long period of leaflessness, most often from May or June to September or October.

The first (up to 11) years of the tree are characterised by a suffrutex stage during which it dies back each dry season, a normal phenomenon in miombo woody species (Boaler, 1966b; Von Breitenbach, 1973). The species produces pods at a DHB from 11 to 19 cm onwards (Shackleton, 2002; De Cauwer, unpublished data). They can be dispersed several kilometres away from the mother tree by wind (Groome et al., 1957) and the warm updraught of fires.

The species is only commercially interesting when it reaches a DBH that is large enough to saw planks of the dark heartwood; the sapwood has no commercial value. In many countries this DBH is set at 35 to 45 cm, although illegal loggers and local users do harvest smaller sizes, mainly for construction of houses and fences. The wood is called Blood wood, Kiaat, Dolf or African Teak in Namibia and South-Africa.

The study species can be found in a wide range of localities where a dry season contrasts with a single wet season (Coates Palgrave, 1983; Von Breitenbach, 1973). It can be found from sea level up to 1650 – 1800 m altitude (Takawira-Nyenya et al., 2010; Von Breitenbach, 1973). Average rainfall in its range varies between 400 mm (Curtis and Mannheimer, 2005) and 1250 mm (Palmer, 1997; Von Breitenbach, 1973) and average temperature between 15 and 32 °C (Takawira-Nyenya et al., 2010). The species is sensitive to frost, especially young trees, (Groome et al., 1957; Vermeulen, 1990) and is limited to areas with a mean minimum temperature of at least 20 °C for the warmest month and 4 °C for the coldest month (Von Breitenbach, 1973). Extreme cold events can have an effect on the flowering of *P. angolensis*, which takes place between September and December, with the northern parts of the distribution area flowering earlier (Curtis and Mannheimer, 2005; Groome et al., 1957; Shackleton, 2002).

The species occurs on a wide range of soil types : from sandy to clayey, but is mainly found on deep sands with the biggest trees on well-drained soils with a sandy or loamy texture (Groome et al., 1957; Palmer and Pitman, 1972; Strohbach and Petersen, 2007; Vermeulen, 1990; World Agroforestry Centre (ICRAF), 2013). It is not adapted to black clays (Boaler, 1966b; World Agroforestry Centre (ICRAF), 2013) and can be found on plains, dunes and sometimes hill slopes (Curtis and Mannheimer, 2005; von Malitz and Rathogwa, 1999; World Agroforestry Centre (ICRAF), 2013).

2.2 Model algorithm

A presence-only (PO) species distribution model, Maxent (Phillips et al., 2006), was chosen because species data for *P. angolensis* have not been collected in a systematic matter at regional scale. Maxent is a general-purpose machine learning method, which uses a maximum-entropy approach. Its application in species distribution modelling is fairly recent and gives superior results compared to other methods (Elith et al., 2006; Kumar et al., 2009; Phillips et al., 2006, 2004; Poulos et al., 2012). The prediction of the model indicates the areas within the study region that satisfy the requirements of the species' ecological niche. It offers a natural probabilistic interpretation, giving a smooth gradation from marginally to most suitable conditions. The standard parameter set proposed by Maxent version 3.3.3k - with exception of the generation of the pseudo-absences or background points - was used as several test runs showed that altering them did not improve the results.

The model uses pseudo-absences to compensate for the lack of absence data; these are points that are randomly selected by the programme in the study area. Instead of letting the algorithm randomly select the 10,000 background points for each Maxent run, the random background dataset of one Maxent run was used for all models to allow a better comparison of validation results. Background points in Madagascar (606) were removed to reduce sample bias (Phillips, 2008a); the species does not occur in the country while large parts of it are potentially suitable according to all model runs.

2.3 Occurrences

A regional dataset of 570 observed presence locations was created for *P. angolensis* by consulting herbaria records, scientific articles and reports, data of tree atlas projects, e-floras, forest inventories and own or colleagues' field observations and data (annex A). The spatial accuracy was estimated and only data with a spatial accuracy less than 10 km and collected after 1940 were retained. A lot of the herbaria data originated from early colonial times but did not match the temporal range of the environmental data (1950-2000). Of the remaining 480 occurrences, 38 % are in Namibia and South Africa, while only 4 % of the range extent covers those countries (figure 1). This is explained by the fact that there is an easier access to data, rather than by a higher occurrence of the species in Namibia and South-Africa. Therefore, the dataset was randomly reduced for the two countries, resulting in a final dataset of 320 occurrences. This was split up in two independent datasets: the 220 points collected as incidental records or through unsystematic surveys, including herbaria and efloras, were used as

training data and for PO validation. The remaining 100 occurrences from systematic surveys and with accurate locations, were set aside for presence/absence (PA) validation (see 2.6).

The amount of training points (220) is high enough compared to other SDM studies performed on a regional scale (Anderson et al., 2003; Elith et al., 2006; Trabucco et al., 2010), although not yet the optimal sample size of at least 500 observations as advised by Hanberry et al. (2012).

The preliminary Maxent runs and the literature review on environmental requirements (2.1) indicated that the ecological requirements of *P. angolensis* may be different in the south-west compared to the rest of the study area. Therefore , the model was also run separately for two zones of the study area : the Kalahari basin and outside the basin. The Kalahari basin was determined based on a GIS dataset extracted from the South African Council of GeoSciences (Mendelsohn and el Obeid, 2004) (figure B.1 in annex B). Other divisions of the study area were tested – e.g. based on aridity and occurrence of frost – but yielded less good validation results.

2.4 Environmental data

The environmental data needed for a SDM must have the potential to ecologically explain the distribution of the species. After consideration of the environmental requirements of *P. angolensis* (see 2.1), the datasets listed in table 1 were collected.

Most datasets covered the period 1950/1960 to 1990/2000 while the CRUTS database database was reduced to represent the period 1941-2002. The Harmonised World Soil Database (HWSD) lists a range of soil attributes per soil unit. Only the dominant soil unit was linked to the map unit and when there were two dominant soil units, the soil attributes were averaged. Test runs showed that this method of establishing a one-to-one relation appeared to be the most suitable for the species.

All environmental datasets were converted to the ASCII raster file format necessary for Maxent, with a resolution of 30 arcsec (about 920 m at the equator). The data accuracy will be much lower because of the low density of climate stations in southern Africa (Hijmans et al., 2005). In total, 68 predictor variables were collated. However, there are several reason to reduce the number of variables in a model: to minimise computing time, to minimise the amount of correlated variables that can cause overfitting, to increase transferability, to increase signal to noise ratio and to better understand the causal relationships of the model (Mac Nally, 2000; Trabucco et al., 2010). After several test runs it was decided to select the twelve most relevant

Table 1 – Environmental predictor variables included in the first runs of the modelling with indication of the source database

Source	Variables
WorldClim (Hijmans et al., 2005)	Bioclimatic variables: Annual Mean Temperature, Mean Diurnal Range, Isothermality, Temperature Seasonality, Max Temperature Warmest Month, Min Temperature Coldest Month, Temperature Annual Range, Mean Temperature Wettest Quarter, Mean Temperature Driest Quarter, Mean Temperature Warmest Quarter, Mean Temperature Coldest Quarter, Annual Precipitation, Precipitation Wettest Month, Precipitation Driest Month, Precipitation Seasonality, Precipitation Wettest Quarter, Precipitation Driest Quarter, Precipitation Warmest Quarter, Precipitation Coldest Quarter
	Minimum temperatures of August, September and October
	Mean temperatures of July, August, September and October
	Average monthly precipitation of February, June, July, September, October, November & December, Rainmonths (months >= 20mm; derived in GIS)
	Altitude (SRTM), Slope (derived in GIS), Aspect (derived in GIS)
Harmonised World Soil Database (HWSD) and Digital Soil Map of the World (DSMW) (FAO/IIASA/ISRIC/ISSAS/JRC, 2009; Fischer et al., 2008)	Drainage class, Average Water Capacity (AWC) class, Ph Topsoil, Organic Carbon Topsoil, Base Saturation Topsoil, CEC Topsoil, $CaCO_3$ Topsoil, Sand/Clay/Gravel/Silt Fraction of Topsoil, Reference Soil Depth Derived soil qualities : Nutrient availability, Nutrient retention capacity, Rooting conditions
CGIAR-CSI (Consortium for Spatial Information) (Trabucco, 2010; Zomer et al., 2007)	Aridity Index, Potential Evapo-Transpiration (PET) of April, June, September, October and December, Soil water content (SWC) of January, April, July, September, October and December, Priestley-Taylor alpha coefficient
FAO-UN (FAO and IIASA, 2000)	Length of growing period (LGP)
Derived from Climatic Research Unit time-series datasets (CRUTS v.3.10.01) (Harris et al., 2013)	Frost days, Spring frost days (frost in September & October)

environmental variables to build the final model for the potential distribution of *P.angolensis*. Selection was based on the jack-knife tests and permutation importance calculated by Maxent for a model run with all environmental data. The jack-knife test gives a very good indication of how important the variable is in the model, by measuring the training gain obtained with and without any environmental variable, while permutation importance determines the contribution to the model of each variable (Phillips, 2008b).

2.5 Realised distribution

A minimum threshold of probability of occurrence was applied on the potential distribution model to represent the limits of species distribution. The 10% percentile training presence was chosen as threshold so that the 10 % lowest model probabilities fall outside the suitable zone for the species. This threshold accounts for the inaccurate location of some training points.

The distribution area predicted by a SDM will typically be larger than the species' realised distribution as few species occupy the entire area of the potential distribution(Phillips et al., 2006). The difference is caused by processes not controlled by the earlier mentioned environmental variables. Four factors with potential influence on the distribution of *P.angolensis* were considered: fire, competing species, geographic barriers and deforestation. Wood harvesting will have had a limited impact on the species' distribution as *P. angolensis* can reproduce long before it becomes commercially interesting to harvest. The species' distribution could also be influenced by browsers, but this was not considered in the study.

Burke (2006) already indicated that fire tolerance of the species may provide further understanding of its distribution. Fire is both a natural and anthropogenic disturbance in southern Africa, although most are currently ignited by humans (Archibald et al., 2009 ; own observations). The effect of fire on the distribution of *P. angolensis* was evaluated by adding it as explanatory variable to the model. A GIS layer was created that reflected the amount of years an area had burnt in the period 2000 – 2012. It was derived from MODIS fire observations extracted from NASA's archive (NASA, 2013). Only fire points with a confidence level over 50% were withheld.

No information in literature was found of tree species with a specific competing behaviour towards *P. angolensis*. Potentially competing tree species were selected that have a partially overlapping range extent with *P. angolensis*, that do occur in the upper tree canopy layers and for which at least 25 occurrence points from herbaria were available for the study area. It concerns (with indication of number of occurrence points) : *Brachystegia boehmii* (61), *Brachystegia microphylla* (28), *Brachystegia spiciformis* (33), *Brachystegia utilis* (44), *Burkea africana* (158), *Dalbergia melanoxylon* (172), *Faurea saligna* (166), *Julbernardia globiflora* (75), *Julbernardia paniculata* (25), *Pericopsis angolensis* (93) and *Schinziophyton rautanenii* (36).

The effect of competition of those tree species on the distribution of *P. angolensis* was evaluated by adding their distributions as explanatory variables to the model. The distribution maps of the competing species were created with Maxent using the same settings and predictor variables as

for *P. angolensis*. A number of studies (Hernandez et al., 2006; Phillips and Dudík, 2008; Stockwell and Peterson, 2002; Wisz et al., 2008) show that model performance increases with sample size of the occurrence data, but that results of satisfactory discriminatory power can be obtained when the sample size is larger than circa 25 to 30 points, especially with Maxent. AUC of the SDM's varied between 0.840 (*B. spiciformis*) and 0.967 (*B. microphylla*).

Areas where the species is known to be absent because of geographic barriers were removed. The only major geographic barrier in the study area is the ocean as there are no large mountain chains that could affect dispersal. Hence, only Madagascar was removed.

Clearing of woodlands for subsistence agriculture, cash crops or urbanisation plays an important role in the study area. Deforestation was taken into account by projecting the model on a woody vegetation map. The SAFARI2000 tree cover dataset of DeFries et al. (1999) was used for this purpose. It is based on 1992-1993 AVHRR data and has a resolution of ca. 1 km. Areas with shrubs or trees canopy coverage of at least 10% were considered as woody vegetation. The data of the Global Forest Resources Assessment 2000 (FRA2000) was also tested but gave less good results, especially for open shrub- and woodlands.

2.6 Model validation

Validation with PO data

Maxent allows to perform an automatic division of occurrence points and subsequent cross-validation in batch mode as explained by Elith et al. (2011). This method allows assessing how stable the performance of each algorithm is and can derive average performance measures. The Maxent models were tested with a 10-fold cross-validation procedure.

The AUC (area under the receiving operating characteristic (ROC) curve) was used as a validation tool. This test statistic was introduced by Fielding and Bell (1997) and is currently the most commonly used for testing SDM's outputs (Elith et al., 2006; Phillips et al., 2006, 2004). An advantage of AUC is its independence of a fixed threshold as it evaluates all presence threshold scenarios. For PO modelling, it represents the probability that a randomly chosen presence site is ranked better than a random pseudo-absence site: a value higher than 0.5 indicates performance better than random (Phillips et al., 2006). However, AUC increases with the proportion of the study area that falls outside the presence domain of a species (Lobo et al., 2008). AUC values obtained within this study can be compared as the same study area is used for all model runs; however they can not be compared with AUC values of other studies unless

they have a similar relative occurrence area. Furthermore, AUC only measures the model's capacity to discriminate between presence and absence. It does not consider the values of the predictions, thus how well the model is calibrated (Elith and Graham, 2009; Lobo et al., 2008; Phillips and Elith, 2010). An additional validation with independent PA data, was performed to assess model calibration.

Validation with PA data

An independent PA validation requires a dataset not used for the training. Next to the 100 occurrences set aside, 100 absences had to be collected. Obtaining absence data is less evident than presence data as their locations should reflect areas large enough compared to the model resolution (1 km^2). This is especially difficult to determine in areas with insufficient inventory data (Anderson, 2003). Most of the systematic surveys used for the occurrence data could not be used to derive absences as they covered a too small area, had a too small sample size or did not publish the complete inventory data.

Fifty absence points were added based on literature (Annex C), the tree atlases of Swaziland and Namibia (Curtis and Mannheimer, 2005; Loffler and Loffler, 2005) and the Seronga study area of The Future Okavango project. Another 50 absences were created by random generation in areas where *P. angolensis* is known to be absent (Coates Palgrave, 1983; Germishuizen et al., 2006; Kobisi, 2005; Setshogo and Venter, 2003) and that are within 500 km from the known range extent (Figure C.1).

The point bi-serial correlation coefficient (COR) and deviance were used as validation statistics. Both parameters measure discrimination and calibration of the model, with deviance more emphasising calibration (Elith and Graham, 2009; Phillips and Elith, 2010). COR is a measure for the correlation between the predicted probabilities and the actual absences (0) or presences (1). The better the correlation, the closer COR is to 1. Deviance is a measure of lack of fit between the model and the test data; the larger the deviance, the poorer the model. It is calculated as explained by Phillips and Dudík (2008) and averaged for all test points.

The realised distribution can be validated with the omission and commission error, as well as the Kappa coefficient (Cohen, 1960), as a threshold has been applied. Wrongly classified occurrence points are mapped to understand distribution of model errors and look for any residual geographic pattern (Elith and Leathwick, 2009; Guisan and Thuiller, 2005; Lobo et al., 2008).

2.7 Estimating future distribution

The effect of a changing global climate on the future distribution of *P. angolensis* was estimated in Maxent. Land use changes or the potential effect of climate change on fire occurrence were not taken into account. Projections of the 12 most relevant climate layers in the 2080's, based on the HADCM3 model with A2a and B1 SRES emission scenarios, were extracted from the WorldClim dataset. Global and regional climate change models vary a lot in their projections for the African continent (Hewitson, 2006) and by using these two scenarios – even if created with the same model - a worst- (A2a) and a best-case (B1) scenario are presented and their central tendency can be explored (Araújo et al., 2005). The A2a emission scenario predicts a global temperature rise of 2 to 5.4 °C by the end of the 21st century compared to the period 1980-1999, while the B1 scenario – with global population and carbon emissions projections that are much lower - predicts a temperature rise of 1.1 to 2.9 °C (IPCC, 2007). Future projections of the amount of frost days are not available and instead a Maxent model was used whereby the amount of frost days was replaced by the environmental variable with the next highest contribution to the model.

3. Results

3.1 Potential distribution

The AUC values of the Maxent model runs with different sets of environmental layers (table 2) all indicate a good discrimination, much better than random. The PA validation results for the potential distribution (models A, W and R) are not very different from those of the PO validation. The point bi-serial correlation coefficient (COR) gives a similar ranking of the models than AUC, while deviance indicates another model (A) as that with the lowest quality.

The model that uses all input data (A) shows a bias at the Namibian borders. This is caused by the soil dataset used, which is a compilation of existing regional and national soil databases thereby sometimes causing abrupt changes at country borders. A model without soil data (W) does not show this effect and has a better deviance. No soil data were therefore added to the model with the 12 most relevant environmental datalayers (R) (figure 2). This is also the potential distribution model that performs best; both for discrimination and calibration and will be used to derive the realised distribution.

Table 2 – Maxent model results with different sets of predictor layers (# layers). AUC gives the outcome of the presence-only validation, the point bi-serial correlation coefficient (COR) and deviance (DEV) are the measures of the presence-absence validation. The most relevant environmental data are listed in table 3.

Model	Predictor dataset	# layers	AUC	COR	DEV
A	All environmental data	68	0.810	0.576	1.206
W	All environmental data without soil	56	0.807	0.568	1.184
R	Most relevant environmental data	12	0.828	0.609	1.068
C	Most relevant environmental data + competing trees	23	0.844	0.540	1.215
F	Most relevant environmental data + fire history	13	0.834	0.573	1.128
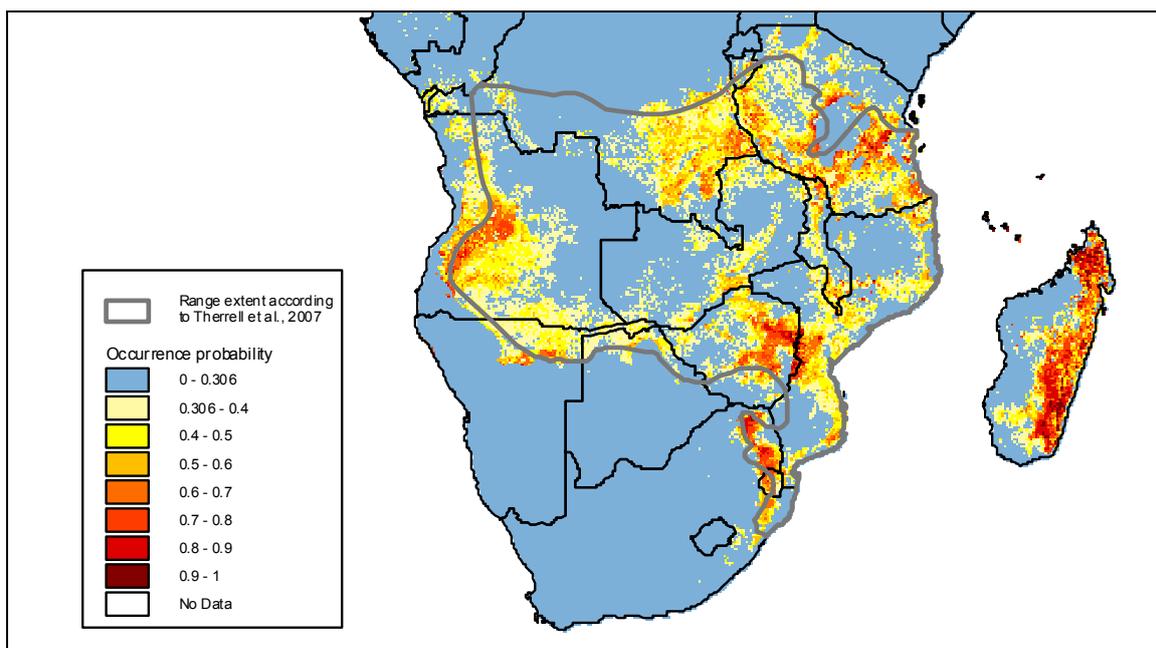
Figure 2 – Potential distribution for *Pterocarpus angolensis* with indication of the range extent from Therell et al. (2007). The model (R) was run in Maxent with the 12 most relevant datalayers (listed in table 3) ; output is the logistic format of Maxent. A threshold of 10% percentile training presence, equalling a logistic value of 0.306 was used to display the distribution.

The environmental layers used in model R are listed in table 3. The table indicates the contribution of each environmental variable to the model by listing the results of permutation importance and jack-knife test. The contributions are not a direct indicator of the ecological importance of each environmental variable on the distribution of *P. angolensis*, as they represent the best statistical solution for the whole region. If the study area is divided in two zones, the Kalahari basin and the area outside the basin (annex B), and models are created for each of these zones, the environmental factors get ranked very differently as indicated in table 3. Rainfall in October and February are more important predictors for the Kalahari model than for the non-Kalahari model.

Table 3 – Contribution of environmental variables to model R : for the total study area, the Kalahari basin and the area outside the Kalahari basin, ranked according to the training gain without the variable for the total area. Important variables have a high permutation importance and a low training gain obtained without the variable.

Variable	Training gain without variable	Permutation importance		
	ALL	ALL	Kalahari	non-Kalahari
Slope	0.834	4.2	0.5	4
Seasonality precipitation	0.846	24.7	15.4	3.1
Rainfall November	0.849	11.7	0	11.6
Rainfall February	0.852	12.3	20.3	7.9
Diurnal range	0.860	7.2	3.3	26.6
Min. temp. coldest month	0.877	6.8	0	2.7
Rainfall October	0.886	9.5	26.6	4.4
Rainfall driest month	0.888	7.9	19	7
Altitude	0.889	1.6	9.7	1.6
Frost days	0.896	6.3	3.8	9
Rainfall coldest quarter	0.899	1.5	1.4	5.2
Seasonality temperature	0.900	6.3	0	17

Response curves of each variable allow analysing the effect on the probability of occurrence for *P. angolensis* (figure 3). They indicate the optimal range for each of the variables, for example

the highest probability to find *P. angolensis* is when rainfall seasonality (coefficient of variation) is between 55 and 110 mm, rainfall in November is between 45 and 210 mm and the minimum temperature of the coldest month is between 4 and 18°C. The curves in figure 3 show the average for the total study area while the response curves for the two zones look very different (annex B).
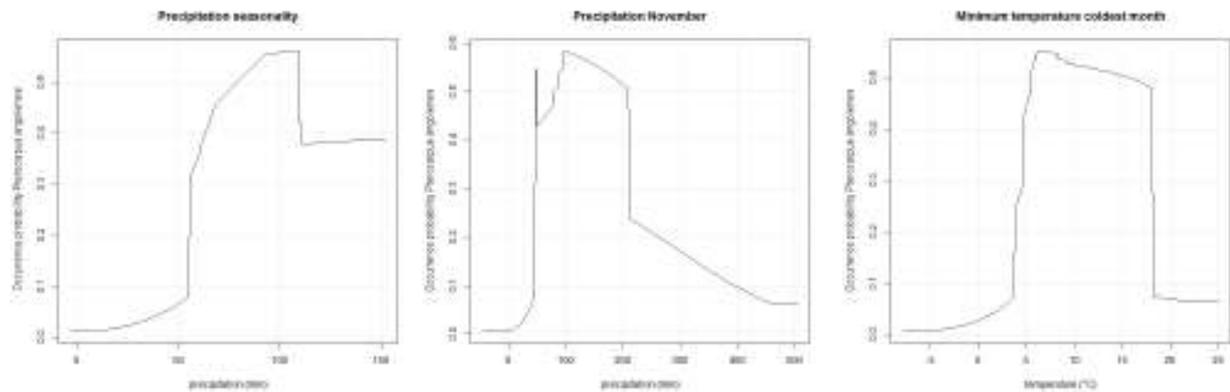

Figure 3 – Response curves of three environmental variables for model R. The effect of precipitation seasonality, rainfall in November and average minimum temperature of the coldest month on the probability of occurrence for *Pterocarpus angolensis* is shown by the calculation of univariate models containing only the variable.

3.2 Realised distribution

A threshold was applied to the best model (R) (figure 2) resulting in a potential distribution map of which the Kappa coefficient indicates fairly good agreement (table 4). Commission is much higher than omission and the errors occur almost all at the southern edges of the distribution. There is no obvious pattern in the location of the omission errors except that there are a relatively high number in Zambia (6 out of a total of 8 Zambian observed presence points).

Table 4 – Accuracies for two realised distribution maps : the potential distribution map on which a threshold was applied and the same map projected on a tree cover map of DeFries et al. (1999). Om reflects the omission error and Com the commission error.

	Om (%)	Com (%)	Kappa
Potential distribution with threshold	14	24	0.62
Realised distribution on SAFARI2000	18	18	0.64

Addition of recent fire history or potentially competing species as predictors to the SDM of *P. angolensis* did improve the PO but not the PA validation results (models F and C in table 2) and they were not added to the final model. However, similar to the environmental data, the response curves of fire and the potentially competing species do give useful information with regard to the occurrence of *P. angolensis*. There was a negative relation between fire occurrence and the species' occurrence probability for areas with 3 or more fires within the period 2000-2012. Grid cells with 6 or more fires during that period are considered as unsuitable.

The potential distributions of Manketti *(S. rautanenii),* Miombo *(B. boehmii)* and African Blackwood (*D. melanoxylon*), as well as precipitation in October, were the variables with the highest contributions to model C. The response curves indicate that with increasing occurrence probability of the two latter species, the probability of finding *P. angolensis* increases , (figure 4). The response is not following the line that would reflect perfect co-occurrence but it is fairly similar especially for occurrence probabilities over 50%. There is an average probability of 55% to find *P. angolensis* in areas where *S. rautanenii* or *J. paniculata* do not occur. Most of the remaining potentially competing species have a similar response curve as *B. boehmii* with exception of *B. africana*. The highest probability of finding *P. angolensis* is where the probability of occurrence for *B. africana* is lower than 70%.
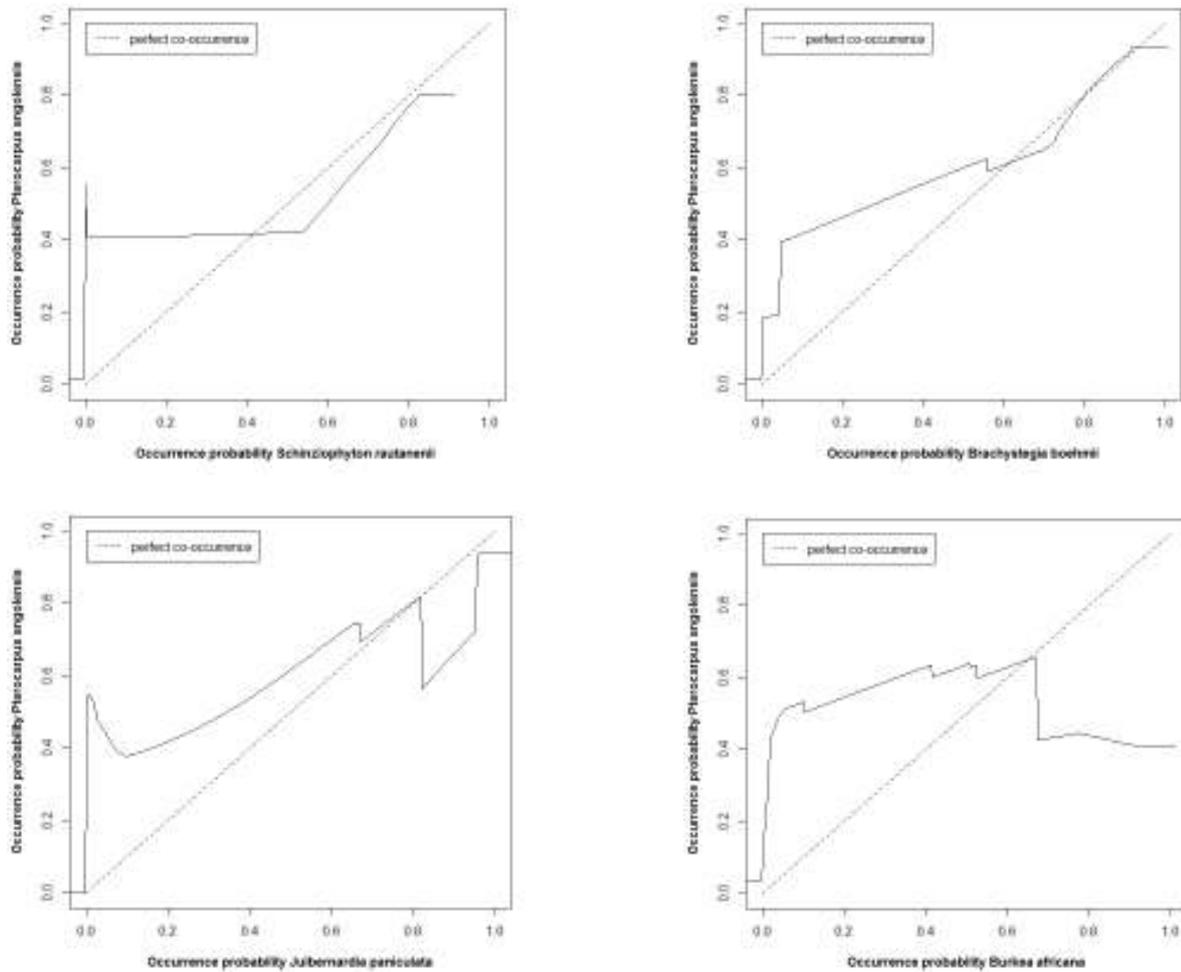
Figure 4 – Response curves of potentially competing tree species created by Maxent model C. The effect of potential distribution of those species on the model for *Pterocarpus angolensis* is shown by calculating univariate models containing only the considered species. The dashed lines represent perfect co-occurrence of species.

Projection on the SAFARI2000 data gave slightly better PA validation results than the potential distribution map and a better balance between omission and commission errors. Hence, the potential distribution map projected on the SAFARI2000 data and after removal of Madagascar was selected as realised distribution map (figure 5).

3.3 Future model

A Maxent model was used whereby the amount of frost days was replaced by the average rainfall in September, which contributed as 13th best to models A and W. This model gave similar validation results to that of model R with current climate data (AUC 0.825, COR 0.586).

The distribution area of *P. angolensis* decreases for both 2080 scenarios : 22 % for the B1 and 51 % for the A2a emission scenario (figure 5). The Maxent model predictions are not affected by environmental variables that are outside their training range; future values of the variables are still within the ranges of the current values for the study area.
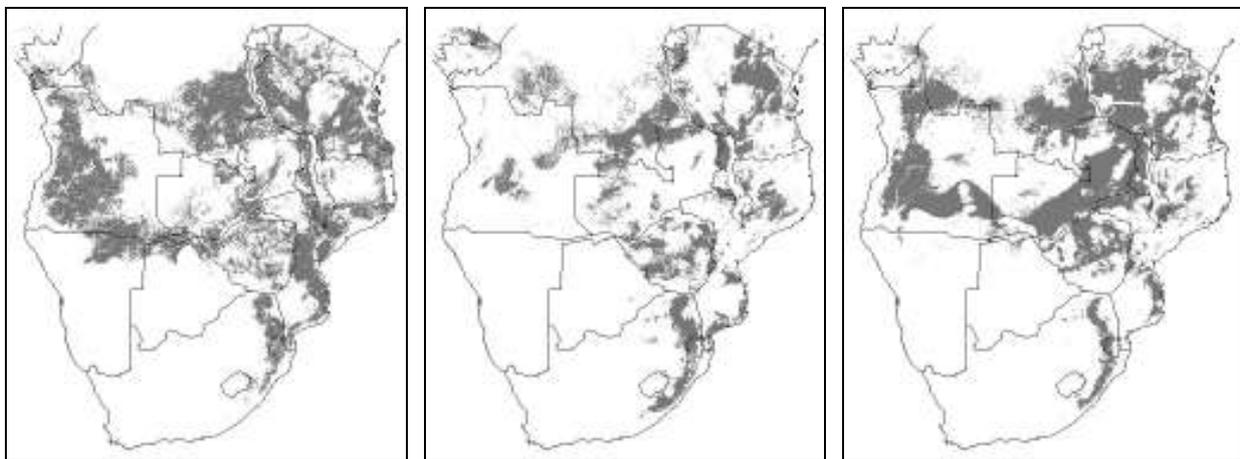

Figure 5 – Current and future (2080's) distribution scenarios for *Pterocarpus angolensis*. Left is the current distribution, the middle uses emission data from emission scenario A2a and the right from emission scenario B1. A minimum threshold of 10% percentile on occurrence probabilities was applied to delineate species distribution.

4. Discussion

Potential distribution of P. angolensis

Species distribution models allow creating detailed distribution maps for large regions with relatively little observations. This is especially useful for large areas with limited access such as southern Africa. Creating an accurate distribution map for *P. angolensis* with only field observations would need systematic and extensive collection of occurrences in countries lacking

good road infrastructure and/or on-going civil wars. The distribution models produced for *P. angolensis* show high AUC values, indicating a good discrimination of the species' presence. Deviance values are similar to slightly higher than those of Phillips and Dudik (2008), while correlation values are much higher indicating that there were several discrepancies between the model and PA dataset which are punished by a larger deviance. Correlation with actual absences and presences of held out data are good in comparison with other studies (Elith et al., 2011, 2006). It is however difficult to compare PA validation results of different studies without an objective way to characterise the absences dataset. Test runs showed that better validation results could easily be obtained by extending that part of the study area where absences were randomly selected. Currently not many SDM studies use independent PA datasets to validate their models and it may be advisable to document the location of absences in further studies.

The probability of occurrences (figure 2) shows that the most suitable areas for the species are in Zimbabwe, Tanzania, South Africa and to a lesser extent central Angola. Anecdotal references only confirm part of this. Vermeulen (1990) and Von Breitenbach (1973) indicate that maximum heights of the species are indeed achieved in Tanzania, but also in Zambia and Mozambique. The highest tree (27.4 m) was recorded in the Copper belt area of Zambia (Groome et al., 1957) while the probability of occurrences there is nowhere higher than 0.5.

Stahle et al. (1999) write that the natural woodlands supporting adequate stocks of *P. angolensis* for industrial extraction are confined to certain areas of north-western and north central Zimbabwe. However only central parts, together with the east of Zimbabwe, are shown as high probability areas in this study. It is possible that the majority of tall trees of the most suitable areas were already logged a few decades before previous mentioned studies. On the other hand, the input data may not represent the range of environmental conditions in the distribution area well enough – it is possible that there were not enough training points for Mozambique and Zambia which were represented by respectively 8% and 4% of the training datasetcompared to 17% and 16% of the range extent according to Therell et al. (2007).

The model does confirm reports that the species rarely attains large sizes on plateau soils (Groome et al., 1957). The most suitable sites as indicated by the model are situated on the foothills of the escarpment or on the slightly higher terrain that is surrounding the Kalahari basin. It does not concern a certain altitude range as the elevation of the basin's edges varies, but rather a relative altitude that is only obvious on a regional scale.

Realised distribution

The potential and realised distribution of *P. angolensis* are very similar, with exception of Madagascar where the environmental conditions are potentially suitable for the species but where it does not occur due to the Indian ocean acting as a geographic dispersal barrier. Another area where the species does not occur, unlike indicated in the potential distribution map, is north-east of the Etosha pan in Namibia which is a karst area (the Grootfontein-Tsumeb-Otavi triangle), as well as areas where forest and woodland have been removed, like for example in Burundi.

Fire history did not improve the model but this does not mean that it does not have an effect on the species' distribution. Rather, fire occurrence seems to be correlated to other predictors, especially rainfall, and thus the small contribution of fire history to the model. The finding that *P.angolensis* rarely occurs in areas with annual fire frequencies of over 45% could not be confirmed by literature although there are indications that a too high fire frequency prolongs the suffrutex stage and causes higher mortality in adult trees (Groome et al., 1957; Vermeulen, 1990). Several authors (Geldenhuys, 1992; Graz, 2004; Vermeulen, 1990) state that a certain amount of fire is needed to reduce competition in the sapling stage of *P. angolensis*, but this could not be derived from the model. It should be explored in more detail for smaller study areas and with a longer fire history.

Although the potentially competing trees did not improve the calibration of the model, their response curves provided interesting information about their interaction with the study species. Only a few of the species considered showed signs of competing behaviour with *P. angolensis :* *B. africana, S. rautanenii* and *J. paniculata.* The probability to find *P. angolensis* decreases in the most suitable areas for *B. africana*, a species that is at least as fire resistant as *P. angolensis* in the Namibian woodlands (Burke, 2006) and appears to have a competition advantage there. The distribution areas of *S. rautanenii* and *J. paniculata* do not overlap with the areas considered best for *P. angolensis* by the model, hence there is a good probability to find the study species in areas where those two do not occur.

The other species added as predictors to the model can be considered as co-occuring in most areas that have a higher probability (> 50%) to find *P. angolensis*, at least at a resolution of 1 km^2. Especially the occurrence of *B. boehmii* is an indication that there is a high probability (40 – 100%) that *P. angolensis* is in the same area. It would be interesting to test other potentially competing species, also those with ranges that hardly overlap such as *Colophospermum mopane*.

The final realised distribution model has a Kappa coefficient of 0.64, indicating fairly good accuracy (Fleiss, 1981). Better results may be obtained for the realised distribution map when a more recent forest cover map than that of DeFries et al. (1999) would be available. The final map shows that the species' distribution area is largest in Angola and Tanzania (about 550,000 km^2 in each country). It confirms the most northerly occurrence of *P. angolensis* in the vicinity of the southern shores of Lake Victoria, Tanzania (Boaler, 1966b), and not Lake Edward, DRC (Groome et al., 1957). The most southern part of the distribution appears to run about 300 km further south than the earlier reported Itala Game Reserve in South Africa (Vermeulen, 1990). It is possible that the species did occur here but was intensively harvested during previous centuries, considering the proximity to the seaport Durban. The range map of Therrell et al. (2007) indicated that the northern extent of the species in the DRC was not exactly known. Our model shows that it runs further south in the southwestern DRC than earlier published distribution maps suggested (figure 2). This border is mainly determined by the rainfall seasonality and rainfall in October, which get respectively too low and too high further north in the DRC.

The distribution map's area covers about 60% of the range extent published by Therrell et al. (2007). Large areas along the eastern border of Angola with the DRC and Zambia –included in the range extent by Therrell et al. (2007) – appear unsuitable for the species. This is an area with a lower altitude, a lower number of frost days and slightly higher precipitation than the areas to the east and west of it, but the limiting environmental factors for *P. angolensis* are not obvious. There is a possibility that the species occurs in the area but that there is no recent occurrence data available ; Monteiro (1957) mentions that the species occurs frequently in the Moxico province of Angola, which borders Zambia, as a shrub smaller than 3 m, while there is a species record of 1938 at Royal Botanic Gardens, Kew for Matonchi, which is near the border of Zambia and Angola, not too far from the DRC. However, climatic conditions may have been different then compared to the end of the 20th century.

Input data of SDM

The best results were obtained by reducing the amount of input data, especially the environmental variables or predictors. Currently, the choice of predictors remains a challenge (Ashcroft et al., 2011) and it is remarkable that a lot of studies do not use an objective selection method (Acevedo et al., 2012; Elith and Leathwick, 2009; Elith et al., 2006; Phillips et al., 2006; Thuiller et al., 2006; Zimmermann et al., 2009) considering that the choice of the predictors has

a significant effect on the final model (Araújo and Guisan, 2006), as was noticed during the test runs of this study. The analysis of training gain and permutation importance by Maxent provides an objective and quick tool to select predictors by evaluating their effect on the accuracy of the final model. The chosen predictors are not always obvious from existing knowledge of the species, such as for example the temperature seasonality or November rainfall for *P. angolensis*.

Early test runs of the models indicated that validation results also improved when both training and test points in Namibia and South Africa – that had a relative overrepresentation of occurrences and thus induced a bias in the data - were reduced. However, when only the training points were reduced, the model performed worse because of the bias in the test points. It is an indication of how easily results can be adapted by the choice of training and test points and confirms earlier studies that mention that biases and gaps in the input data may affect SDM results (Costa et al., 2009; Elith et al., 2011).

The soil data itself did not appear to contribute much to the final quality of the SDM, as in the study of Trabucco et al. (2010). Although this could be explained by the fact that the quality and resolution of the soil data is not good or not uniform enough for southern Africa or that soil is not an important contributor to the distribution of *P. angolensis*, it seems more likely that soil requirements are different for the species within certain zones of the distribution area. The results of the model run with training points of two subzones indicate that there are no clear soil preferences outside the Kalahari, unlike the Kalahari area where the species grows well on deep and sandy soil while it does not grow in the karst area of Namibia. Dividing the study area in relevant ecological zones in order to establish a SDM per zone is a challenge, and may be worth testing in further studies.

A lot of SDM studies focus on comparing algorithms but it is obvious that the quality of SDM's is at least as dependent on the quantity and quality of the input data, both occurrences and environmental predictors. Some authors do consider data quality as the most critical factor influencing model performance (Jiménez-Valverde et al., 2013; Lobo, 2008).

Environmental requirements for P. angolensis

The response curves created by Maxent can give a lot of detail on the environmental requirements of a species if the statistical response for the whole study area is similar to the ecological response of the species. They can form the basis of further ecological research into

the species and possible genetic varieties. The response curves in this study confirmed for example that the average minimum temperature in the coldest month has to be above 4°C for *P. angolensis*, as indicated in literature (Burke, 2006; Von Breitenbach, 1973). It is the variable that limits the distribution of the species in South Africa. Beyond that, the response curves provide information not available in literature, for example the species often occurs on slopes up to 30° and the probability to find it is highest on the steeper slopes outside the Kalahari basin and vice versa within. This may be caused by the fact that the species prefers well-drained soils (Von Breitenbach, 1973; World Agroforestry Centre (ICRAF), 2013), which are situated higher uphill in the areas of higher rainfall and permanent rivers outside the Kalahari basin. In the Kalahari basin, most soils further way from riverbeds are deep, sandy and well-drained.

The precipitation seasonality (coefficient of variation) indicates the extent of variability between dry and wet season and has to be higher than 55 mm in the distribution area. It is the main environmental variable that limits the species to occur further north, mentioned by Von Breitenbach (1973) as the border between the single-season rainfall and more northerly two-season rainfall regime. The diurnal range - mean of the difference between the monthly maximum and minimum temperature - should not exceed 18°C, especially outside the Kalahari basin, where the best chances to find the species are at much lower ranges. The optimal rainfall in the month of February is about 160 mm for the Kalahari basin, while *P. angolensis* can be found with a similar probability outside the basin for a February rainfall above 300 mm. Model A indicates that the probability to find the species increases sharply at an average annual rainfall of 430 mm/year (data not shown), confirming findings for the species in Namibia (Burke, 2006; Curtis and Mannheimer, 2005). The rain season has to be in full swing by November with at least 40 mm of rain that month. This is the most limiting factor for the distribution of the species towards the south in Namibia, part of Botswana and an area of lower altitude in central Tanzania.

There are less environmental variables that seem to influence the distribution of the species in the Kalahari Desert, and their response curves differ from those of the whole study area. For example, temperature range or seasonality (standard deviation of temperature) can be as high as 43°C in the Kalahari, while this is only 32°C for the rest of the study area. Higher values are limiting the distribution of the species towards the south in eastern Namibia and western Botswana. There should be no rainfall in the driest month in the Kalahari, while this can be up to 2.7 mm for the whole study area. *P. angolensis* has to handle much more extreme environmental conditions in the western part of its study area than in the wetter eastern part.

Adding a climate extreme like number of frost days did improve the model as also indicated by other studies (Bykova et al., 2012; Zimmermann et al., 2009). Our model shows that *P. angolensis* grows in areas with up to 19 frost days per year, especially in the Kalahari basin. Bykova et al. (2012) indicated that temperatures during the development of the flowers and seed maturation – indicated as spring frost in this study - may be an important factor to determine reproduction niche and thus species distribution, but it does not seem to be an important factor for *P. angolensis*.

Future distribution of P. angolensis

Both future models indicate that the distribution area of *P. angolensis* will decrease under global climate changes, with a clear northward shift for the western part. The main causes of the northward shift are rainfall in October and November that are projected to decrease, especially for scenario B1. HadCM3 is considered as one of the "drier" models (Midgley et al., 2005; Wolski, 2013), but the decreasing summer rainfall in the west of southern Africa is a consistent trend in other climate change studies (Hewitson, 2006). This makes a northward shift of the species' distribution a realistic scenario by the end of 21st century – although the rate maybe slower than indicated by both scenarios in figure 5 - especially considering that summer rainfall is a limiting factor in the area. Midgley et al. (2005) also predict a decrease in the tree cover and biomass in northern Namibia, southern Angola and eastern Botswana by 2080. However, biomass was shown to increase in the border area of Namibia, Zambia and Zimbabwe when they took the fertilisation effect of rising atmospheric CO_2 into account.

According to one of the worst-case scenarios (A2a) of global climate change, the species may even disappear in large areas of its western distribution, including Namibia and Botswana. The large reduction of the distribution area in Angola has its origin in the increase of the diurnal range. It should however be mentioned that there are few climate stations in the eastern and central parts of southern Africa for which temperature range data was available to establish the WorldClim layers (Hijmans et al., 2005). The interpolations between stations can cause inaccuracies that may have a large effect on a SDM.

Under emission scenario B1, the species' distribution area would actually increase in Zambia (+78%) and Malawi (+8%). Other studies (Midgley and Thuiller, 2011; Scheiter and Higgins, 2009) predict a gain of forest or woodland cover by 2100 in the same area. Rising minimum winter temperatures and decreasing rainfall in February may cause a slight southward

respectively eastward migration in South Africa. The increase in winter temperatures is another consistent trend in African climate change scenarios (Hewitson, 2006).

Currently, no evidence is available of a decrease of the species in the southwest of its distribution area or of an increase in Zambia. It will be difficult to collect considering the long lifespan of the species but could be supplied by long-term field research into mortality and regeneration rates, especially in Namibia, Botswana and in comparison with neighbouring areas. This would support policy makers and managers in the region who currently have few research based facts to support their decisions with regard to potential climate effects on dry woodlands (Midgley and Thuiller, 2011).

Finally, it should be taken into account that only one aspect of uncertainty associated with climate projections is presented here: the emission scenarios and not the modelling approach used for deriving the climate variables itself. The model may also be improved by adding atmospheric CO_2 as predictor or the effect of climate change on fire occurrence.

Conclusions

SDM allows establishing a distribution map for *P. angolensis* with fairly good accuracy (Kappa 0.64) that gives much more detail than the range extent and environmental requirements described in literature. More occurrence points for Zambia and Mozambique and a more recent forest map may improve the model, while more absence data along the distribution area's margins, especially in the north and Zambia, will increase the validity of the PA statistics. The distribution of the species is mainly influenced by the amount of rainfall in November and February, by the minimum temperature in winter, by temperature seasonality and by its preference for well-drained soils. Environmental requirements are slightly different for the species within the Kalahari basin compared to the area outside. The extensive plateau soils of southern Africa, that include the Kalahari basin, are less suitable for the species than some of the more hilly or sloping areas surrounding this relatively flat terrain.

Potential and realised distributions are very similar, with Madagascar as major exception where the species can grow but does not occur. Using fire occurrence and distribution maps of potentially competing species as predictor variables did not improve the final distribution maps of *P. angolensis*, however allowed to learn more about those factors with regard to the distribution of *P.angolensis* and provide interesting starting points for further ecological studies. Global climate changes can decrease the species' distribution area up to 50%, with Namibia and

Botswana most exposed. Unmitigated climate change clearly is another threat to the species, together with unsustainable logging, unmanaged fires and deforestation.

The distribution models can assist in assessing the conservation status of the species on a regional scale, especially by allowing to derive area of occupancy and range size for listing on the IUCN Red List of threatened species (Gaston and Fuller, 2009; Master et al., 2009). They can assist the identification of suitable areas for regeneration trials, controlled fire experiments or forest inventories and aid in assessments of historical logging operations. The future models can point out the regions where the species is most sensitive to climate change and thereby contribute to detect early signs of climate change in the field.

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Annex A – Sources of all occurrences found for *Pterocarpus angolensis*

Source	Number of occurrences
National Botanic Garden of Belgium (BR)	55
Tropicos, Missouri Botanical Garden (MO)	42
Jardim Botânico Tropical, Instituto de Investigação Científica Tropical, Lisboa (LISC)	35
Hyde et al., 2013 – Flora of Zimbabwe	26
SABIF - SANBI PRECIS, South Africa	22
Royal Botanic Gardens, Kew (K) - most through GBIF	20
Directorate of Forestry, Namibia, Forest Inventories	14
Dondeyne, University of Leuven – unpublished data	10
Tree Atlas Project Namibia	10
De Cauwer, 2006-2013, Polytechnic of Namibia - unpublished data	9
Revermann, 2011-2013, University of Hamburg – unpublished data	9
Burke and Strohbach, 2000	8
Therrell et al., 2007	7
Amri and Mamboya, 2012	6
Finckh, 2011, University of Hamburg – unpublished data	6
Hyde et al., 2013b – Flora of Mozambique	6
Shackleton, 2002	6
Svendsen and Hansen, 1995	6
Timberlake et al., 2009	4
Muller et al., 2012	3
Netherlands Centre for Biodiversity Naturalis, section National Herbarium of the Netherlands	3
van Daalen et al., 1992	3
Clarke, 1995	2
Frost, 2000	2
Mmolotsi et al., 2012	2
Real Jardín Botánico, Madrid (MA) - through GBIF	2
Timberlake and Mapaure, 2007	2
Abbot et al., 1997	1
Backeus et al., 2006	1
Bracebridge, 2006	1
Burgess et al., 1992	1
Campbell et al., 1996	1
Chidumayo, 1994	1
Coates Palgrave et al., 2007	1
Dowsett-Lemaire and Dowsett, 2009; Spottiswoode et al., 2008	1
Hogberg and Piearce, 1986	1
Holdo, 2006	1
Luoga et al., 2004	1
Lynam et al., 2003	1
Scholes et al., 2004	1
Schwartz et al., 2002	1
Shackleton and Scholes, 2011	1
Stromgaard, 1985	1
Syampungani, 2009	1
Timberlake et al., 2007	1
Vyamana et al., 2007	1
Xylarium, Royal Museum for Central Africa, Belgium	1

Annex B – Response curves of environmental variables for the Kalahari basin and outside the basin created during the potential distribution modelling of *Pterocarpus angolensis*

The study area was divided in two zones : the Kalahari basin and the area outside (figure B.1). The Kalahari basin was considered as a group of sediments of the same age (Mendelsohn and el Obeid, 2004). Maxent model R of this study was applied with the training points of each of the two zones. Response curves of the models are shown for variables with the largest contributions to each model (figure B.2).

Figure B.1 - Segmentation of the study area in two zones: the Kalahari basin in the southwest and the area outside the Kalahari basin. The position of the Kalahari Group deposits is based on data of Mendelsohn and el Obeid (2004)
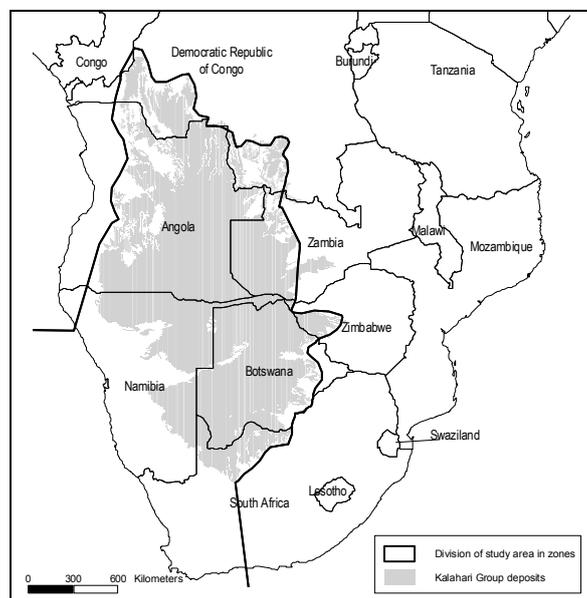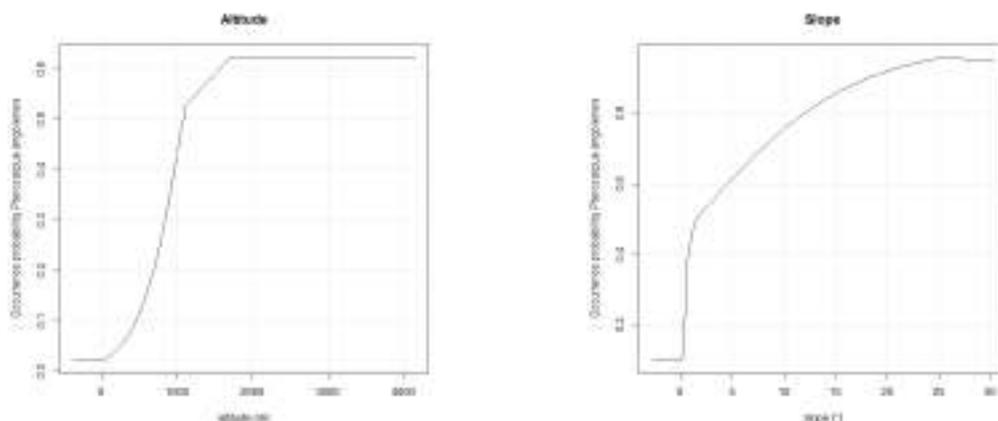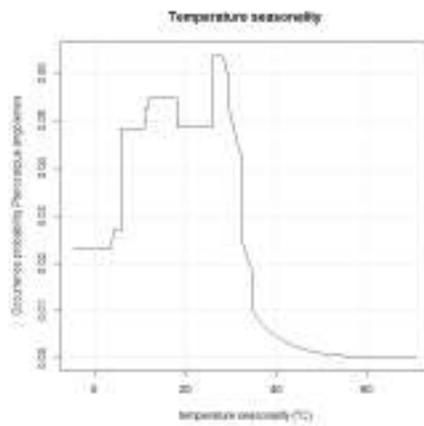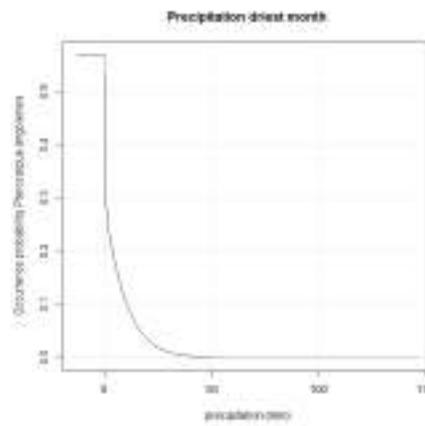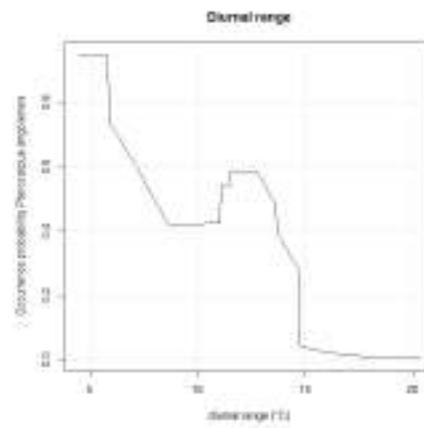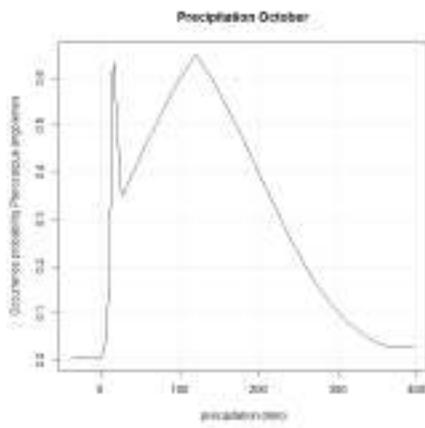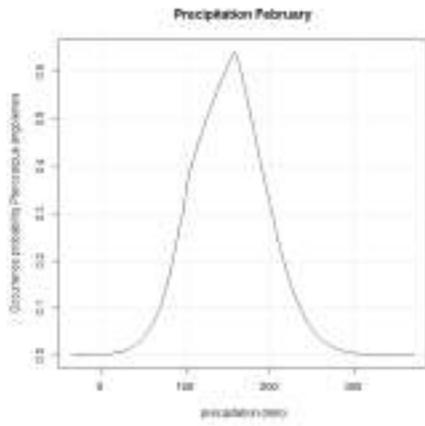

Figure B.2 – Response curves of model R for two zones: the Kalahari basin (left) and the area outside the Kalahari basin (right).

Precipitation February

Precipitation February

Precipitation October

Diurnal range

Precipitation driest month

Temperature seasonality

Annex C – Absences of *Pterocarpus angolensis* used in the presence-absence (PA) validation

Sources of the 20 absence points based on literature :

- Aarrestad et al., 2011
- Howell et al., 2012
- Lovett and Norton, 1989
- Lötter and Beck, 2004
- Malaisse et al., 1999
- Murray hudson et al., 2011
- Saad et al., 2012
- Steyn and Stalmans, 2001
- Timberlake and Childes, 2004
- Timberlake and Mapaure, 2007
- Timberlake et al., 2010

Figure C.1 – Location of all absence points used in the presence-absence validation