



Climate change threatens some miombo tree species of sub-Saharan Africa

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ABSTRACT

Climate change is affecting the distribution of species globally. Predicting the distribution of species under climate change is important for conservation of biodiversity. The aim of this research was to model the current distribution of miombo woodlands of sub-Saharan Africa using seventeen miombo tree species, and to project their distributions under different climate change scenarios. A maximum entropy method, Maxent, was used to model the distributions of the seventeen representative tree species, *Albizia antunesiana*, *Azelia quanzensis*, *Baikiaea plurijuga*, *Brachystegia bakeriana*, *Brachystegia boehmii*, *Brachystegia longifolia*, *Brachystegia microphylla*, *Brachystegia spiciformis*, *Brachystegia utilis*, *Cryptosepalum exfoliatum*, *Guibourtia coleosperma*, *Isoberlinia angolensis*, *Julbernadia globiflora*, *Julbernadia paniculata*, *Pericopsis angolensis*, *Pterocarpus angolensis*, and *Pterocarpus rotundifolius*. A total of 3 429 occurrence records, nineteen bioclimatic variables, monthly precipitation, minimum and maximum temperatures, soil characteristics and altitude were used in modeling. Distributions were hind-casted to the Mid-Holocene and forecasted to 2050 and 2070 under all four Representative Concentration Pathways (RCPs). Hindcasting showed that ranges for *A. antunesiana*, *B. bakeriana*, *B. boehmii*, *C. exfoliatum*, *G. coleosperma* and *Pterocarpus angolensis* were larger in the Mid-Holocene than they are currently, while the ranges of the other species were constricted during this period. When forecasted, range contraction was observed for nine species, *A. quanzensis*, *A. antunesiana*, *B. microphylla*, *B. spiciformis*, *B. utilis*, *C. exfoliatum*, *J. globiflora*, *Pericopsis angolensis* and *P. rotundifolius*. Range expansion was observed in the other eight species. Range contraction was acute in 2070 under RCP8.5 for *A. quanzensis* (-13%), *A. antunesiana* (-15%) and *B. microphylla* (-14%). Species whose forecasted ranges contracted should be prioritized for mitigation against climate change. All species should be protected from anthropogenic threats since most are unsustainably harvested.

1. Introduction

Species change their distributions in response to climate change (Walther et al., 2002). Evidence from palynology and fossil records have shown that, in the past, plants have responded to climate change through adaptation or tolerance, and migrating to track suitable habitat (Bush et al., 2004; Jump and Penuelas, 2005; Petit et al., 2008). Studies have also shown shifts in the distribution of plant species in response to current climate change (Kelly and Goulson, 2008; Parolo and Rossi, 2008; Chen et al., 2011; Crimmins et al., 2011; Feeley et al., 2012; Bitencourt et al., 2016). The recently measured atmospheric concentration of carbon dioxide of nearly 411 ppm (Earth System Research Laboratory, 2019) is unparalleled in history, and is likely to accelerate the rate of climate change with dire consequences for species survival. Surface temperature of the earth is projected to increase by between 1.0 °C to 3.7 °C by 2100, depending on the choice of greenhouse gas emission scenario or Representative Concentration Pathway (RCP;

IPCC, 2014). The relatively low speed of plant migration may render some species incapable of tracking suitable habitats because of the projected high rates of climate change. For those plants with low migration rates, climate change poses a critical threat.

Ecologists and conservation biologists may use forecasted species distributions to gain insights on the impacts of climate change. Forecasted distributions may help managers to mitigate against climate change in order to conserve biodiversity. Established methods to predict past and future distributions of species are the use of species distribution models (SDMs) or ecological niche models (ENMs; Guisan and Zimmermann, 2000; Crimmins et al., 2013). These models correlate environmental variables with species occurrence data using statistical or machine learning procedures. Despite their limitations (Thuiller et al., 2004; Roberts and Hamann, 2012) ENMs have been shown to be useful tools for species distribution modeling based on occurrence records and environmental variables (Soberon and Nakamura, 2009).

Among the commonly used ENMs is the maximum entropy method

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(Maxent; Phillips et al., 2006). The Maxent method uses presence-only records and correlates them to topographic, climatic, edaphic, biogeographic, or remotely sensed variables observed at the occurrence coordinates to predict species distributions. A niche-based model represents an approximation of a species' ecological niche in the examined environmental dimensions. A species' fundamental niche consists of the set of all conditions that allow for its long-term survival, whereas its realized niche is a subset of the fundamental niche that it actually occupies (Hutchinson, 1957). A general assumption of ENMs is that environmental conditions at the occurrence sites constitute samples from the realized niche (Phillips et al., 2006), particularly for non-vagile organisms. A niche-based model, therefore, represents an estimation of the realized niche in the study area and environmental variables under consideration. In that regard, the Maxent method has been shown to have high predictive power (Phillips et al., 2006; Pearson et al., 2007; Aguirre-Gutiérrez et al., 2013; Ramírez-Amezcu et al., 2016) compared to other models that use presence-only data. With its high predictive power, the Maxent method has been used for different purposes, including predicting impacts of climate change on the distribution of species and endemism patterns.

Modeling distributions of plant species in the developing world, regions likely to be highly impacted by climate change (Adger et al., 2003; Dasgupta et al., 2009), is critical for mitigating against impacts of climate change on plant communities. The miombo ecoregion of central and southern Africa, a swathe that maybe especially vulnerable to impacts of climate change, is the largest ecoregion of the continent (Jew et al., 2016). The ecoregion is characterized by distinct wet and dry seasons. The tree species of the ecoregion thrive in temperatures of 18.0–23.1 °C, and annual precipitation of 710–1365 mm (Frost, 1996). Most of the rain falls during the wet season, and trees shed their leaves during the dry season. Miombo woodlands are areas of high endemism and provide habitat for several locally and globally near-threatened, threatened, vulnerable and endangered plant and animal species, such as *Pterocarpus angolensis* (African teak), *Afzelia quanzensis* (Pod mahogany), *Diospyros crassiflora* (Ebony), *Diceros bicornis* (Black rhinoceros) and *Lycaon pictus* (African wild dog; IUCN, 2019).

Miombo woodlands are dominated by tree species in three genera, *Isobertinia*, *Julbernadia* and *Brachystegia*, which were formerly classified into subfamily Caesalpinoideae of Leguminosae (Frost, 1996). The three genera have now been reclassified into subfamily Detarioideae (The Legume Phylogeny Working Group (LPWG), 2017). The species provide a myriad of products, such as wood for woodcarving, furniture, charcoal, fencing and construction (Luoga et al., 2000; Syampungani et al., 2009; Dewees et al., 2010; Jinga and Ashley, 2018), and plant extracts that are used as traditional medicine (Germishuizen et al., 2005; Goncalves et al., 2017). The species form critical links of food chains in the woodlands. It has been estimated that over 100 million people depend on miombo woodlands for their livelihood (Syampungani et al., 2009). The effects of climate change on the distribution of miombo tree species need to be understood in order to better manage these woodlands. Distribution maps are important for locating, delineating and designing conservation areas and identifying suitable areas for reintroductions, establishment of corridors and botanical explorations. Gaps in the distribution of species maybe identified and possible causes suggested. The identification of environmental variables significantly affecting the distribution of species may help to manage unsuitable or degraded sites (Manel et al., 2001).

The aims of this study were to construct niche-based models of the distribution of seventeen representative miombo tree species, *Albizia antunesiana*, *Afzelia quanzensis*, *Baikiaea plurijuga*, *Brachystegia bakeriana*, *Brachystegia boehmii*, *Brachystegia longifolia*, *Brachystegia microphylla*, *Brachystegia spiciformis*, *Brachystegia utilis*, *Cryptosepalum exfoliatum*, *Guibourtia coleosperma*, *Isobertinia angolensis*, *Julbernadia globiflora*, *Julbernadia paniculata*, *Pericopsis angolensis*, *Pterocarpus angolensis*, and *Pterocarpus rotundifolius*, from occurrence records and to provide projections of past and future distribution ranges of the species

under different RCPs. We sought to answer the following questions: (i) What is the current distribution range of miombo woodlands and representative species? (ii) How have the ranges of the tree species changed since the Mid-Holocene? (iii) What are the projected ranges of tree species in 2050 and 2070 under different climate change scenarios? Answers to these questions are critically important for understanding the history of this important ecoregion and for evaluating threats posed by climate change.

2. Materials and methods

2.1. Study species

Seventeen tree species, *A. antunesiana*, *A. quanzensis*, *B. plurijuga*, *B. bakeriana*, *B. boehmii*, *B. longifolia*, *B. microphylla*, *B. spiciformis*, *B. utilis*, *C. exfoliatum*, *G. coleosperma*, *I. angolensis*, *J. globiflora*, *J. paniculata*, *Pericopsis angolensis*, *Pterocarpus angolensis*, and *P. rotundifolius*, were selected for modeling. The 17 species are dominant in miombo woodlands (Chidumayo and Frost, 1996; De Cauwer et al., 2014; Shirima et al., 2015; Syampungani et al., 2015; Goncalves et al., 2017) and their occurrence records could be recovered. The tree species belong to the legume family and some have been reclassified into new subfamilies (LPWG, 2017; Table 1). Available occurrence records (Appendix A) show that the species are endemic to miombo woodlands delineated by Campbell et al. (1996) and Byers (2001), and as such, they may be used to refine the distribution of miombo woodlands using ENMs. All species are deciduous and shed their leaves during the dry season, while new leaves are produced immediately before the onset of the wet season.

Seed dispersal in the genera *Brachystegia*, *Julbernadia* and *Isobertinia* is commonly by explosive dehiscence of pods while in *Albizia* and *Pterocarpus*, dispersal is by wind (Chidumayo and Frost, 1996). Dispersal distances of a few meters by explosive dehiscence (Ernst, 1988) and up to 100 m for wind dispersal (Chidumayo and Frost, 1996) have been reported. In *A. quanzensis*, dispersal is by monkeys and baboons (Gathua, 2000). Some tree species of miombo woodlands are unlikely to successfully track shifting favorable habitats under climate change due to short dispersal distances. Limited seed dispersal also entails that complete clearance of miombo woodlands by fire or any anthropogenic activity will likely result in an irreversible change in vegetation composition of the land. Apart from limited dispersal, seedling establishment of some dominant miombo tree species is hampered by post-

Table 1

Number of occurrence records used in modeling the distribution of miombo tree species, and mean Area Under the Receiver Operating Characteristic Curve (AUC) observed from replicate evaluation runs in Maxent (Phillips et al., 2006).

Species	Subfamily	Occurrence records	Mean AUC \pm σ
<i>Afzelia quanzensis</i>	Detarioideae	206	0.883 \pm 0.034
<i>Albizia antunesiana</i>	Caesalpinoideae	39	0.923 \pm 0.059
<i>Baikiaea plurijuga</i>	Detarioideae	270	0.976 \pm 0.007
<i>Brachystegia bakeriana</i>	Detarioideae	87	0.989 \pm 0.006
<i>Brachystegia boehmii</i>	Detarioideae	255	0.891 \pm 0.019
<i>Brachystegia longifolia</i>	Detarioideae	172	0.925 \pm 0.029
<i>Brachystegia microphylla</i>	Detarioideae	98	0.903 \pm 0.025
<i>Brachystegia spiciformis</i>	Detarioideae	556	0.881 \pm 0.017
<i>Brachystegia utilis</i>	Detarioideae	128	0.921 \pm 0.032
<i>Cryptosepalum exfoliatum</i>	Detarioideae	23	0.892 \pm 0.072
<i>Guibourtia coleosperma</i>	Detarioideae	198	0.972 \pm 0.007
<i>Isobertinia angolensis</i>	Detarioideae	112	0.914 \pm 0.025
<i>Julbernadia globiflora</i>	Detarioideae	362	0.897 \pm 0.020
<i>Julbernadia paniculata</i>	Detarioideae	215	0.951 \pm 0.013
<i>Pericopsis angolensis</i>	Papilionoideae	229	0.879 \pm 0.032
<i>Pterocarpus angolensis</i>	Papilionoideae	359	0.922 \pm 0.020
<i>Pterocarpus rotundifolius</i>	Papilionoideae	120	0.918 \pm 0.033

dispersal damage and predation. Seeds of *B. boehmii*, *J. globiflora* and *I. angolensis* have been observed to be damaged by beetle larvae after dispersal (Chidumayo, 1993).

2.2. Occurrence records and environmental variables

Occurrence records of the 17 study species were obtained from the Global Biodiversity Information Facility (GBIF; <http://www.gbif.org>) and Tropicos (<http://www.tropicos.org>) online data portals. Automatic filters on the GBIF portal were used to remove records with georeferencing errors. Records were also obtained from the Vegetation Database of the Okavango Basin (Revermann et al., 2016), the Makeni Savanna Research Project and published research papers. All records were checked in Microsoft Office Excel to remove duplicates.

To construct models, soil characteristics, climate variables and altitude were used as environmental variables. Soil characteristics were downloaded from the Harmonized World Soil Database version 1.2 (www.fao.org; Fischer et al., 2008). The soil characteristics include nutrient availability, workability, nutrient retention capacity, rooting conditions, oxygen availability and toxicity. Monthly precipitation, monthly maximum and minimum temperatures, 19 bioclimatic variables and altitude were obtained from the WorldClim dataset (www.worldclim.org) version 1.4 (Hijmans et al., 2005). Climate variables were downloaded from one Global Circulation Model (GCM), the Community Climate System Model version 4.0 (CCSM4.0; Lawrence et al., 2012). The bioclimatic variables are important abiotic factors of the distribution of plants and have been used widely in ENMs (Adeyemi et al., 2012; Ramírez-Villegas et al., 2014; Ramírez-Amezcu et al., 2016). All variables were interpolated to 30 s resolution.

2.3. Ecological niche modeling and model evaluation

A maximum entropy method, Maxent version 3.4.1 (Phillips et al., 2006), was used for ecological niche modeling and projections. We combined the records of all 17 species to model the distribution of miombo woodlands. We filtered out highly correlated environmental variables after performing a correlation analysis in R (R Development Core Team, 2019) using the package Caret (Kuhn, 2008). Variables are selected to minimize correlation that can cause overfitting of models and to reduce computation time (De Cauwer et al., 2014). We test-run models of the current distribution of all species while performing jackknife and permutation importance tests implemented in Maxent. The jackknife test determines how important a variable is in a model by measuring the training gain obtained with and without the variable, while a permutation importance test determines the contribution of each variable to the overall model (Phillips, 2008; Copot and Tanase, 2017). After the test-runs, we removed variables that had very low contribution to models in order to further reduce overfitting. A total of six variables were finally used in all models (Appendix B).

For model evaluation, we used an internal Area Under the Receiver Operating Characteristic Curve (AUC) statistic calculated by the Maxent method. The AUC is a measure of model performance in terms of sensitivity (correctly predicted presences) versus specificity (correctly predicted absences; Phillips et al., 2006). The value of the AUC varies from 0.5 to 1.0. An AUC value of 0.5 denotes random prediction, and the closer the value is to 1.0, the better the model performs (Phillips and Dudik, 2008; Wisz et al., 2008; Adeyemi et al., 2012). AUC estimates were obtained from 10 replicate model evaluation runs using the selected six environmental variables. For these runs, 75% of the total records were used to build the model and the remaining 25% were used for testing. The random seed option was enabled. The full sets of presence records were used to obtain the best estimate of the current distribution of miombo woodlands and the 17 species.

2.4. Past and future projections

We made past and future projections of the distribution of the 17 species. Projections were made under all four RCPs proposed by the IPCC to years 2050 and 2070. Projections were made under all RCPs to capture all likely impacts of climate change on the distribution of species. The RCPs predict climate variables, particularly temperature, under different greenhouse gas emission scenarios. Between 2046–2065, global mean surface temperatures are predicted to rise by 1.0 °C (RCP2.6), 1.4 °C (RCP4.5), 1.3 °C (RCP6.0) and 2.0 °C (RCP8.5). Between 2081–2100, the global mean surface temperatures are predicted to rise by 1.0 °C (RCP2.6), 1.8 °C (RCP4.5), 2.2 °C (RCP6.0), and 3.7 °C (RCP8.5; IPCC, 2013). For past distributions, the current species distribution models were hindcasted to the Mid-Holocene, approximately 6 000 years ago.

The species' range change was calculated as the percentage of niche gain or loss compared to the current modeled niche. Niche gain and loss calculations were performed on probability of occurrence above a threshold on the ROC curve that minimizes the distance to the 0, 1 corner of the sensitivity against 1-specificity curve, that is a point on the ROC curve that was closest to the upper-left corner. The point 0, 1 on the ROC curve represents a perfect test with 100% sensitivity and specificity (Cantor et al., 1999; Nenzen and Araujo, 2011). The threshold is recommended for presence-only data since areas below the threshold have been shown to represent true absences (Araujo et al., 2005; Diniz-Fihlo et al., 2009; Nenzen and Araujo, 2011). Niche gain and loss were calculated in ArcMap version 10.6 (ESRI, 2018) using the Conversion, Data Management and Spatial Analyst tools.

3. Results

3.1. Occurrence records and evaluation of models

After removing duplicates for each species, a total of 3 429 occurrence records were retrieved and used in distribution modeling (Appendix A). The number of occurrence records for each species ranged from 23 to 556 (Table 1). Evaluation models of the current distribution of miombo woodlands showed a high level of performance when compared to random sets. Mean test AUC value for miombo woodlands evaluation runs was 0.839 ± 0.002 . Similarly, evaluation models of the current distribution of the representative species showed high performances (Table 1). Visual inspection also showed that the evaluation models correctly predicted current distributions covering most of the test locations.

3.2. Current distribution of miombo woodlands

Models using current environmental variables showed miombo woodlands distributed in southern Africa, including parts of Malawi, Tanzania, Mozambique, Zimbabwe, Angola, Uganda, northern parts of Botswana and Namibia, north-eastern South Africa, and south-eastern DRC (Fig. 1). There are gaps, however, in the distribution of the woodlands, such as along the Zambezi Valley between Zimbabwe and Zambia, along the Limpopo Valley among Zimbabwe, South Africa and Mozambique, and along stretches of the Rift Valley. The woodlands are largely absent in the African equatorial region, the Namib desert of south-west Africa and the Mediterranean region of South Africa.

The environmental variable with highest gain when used in isolation is annual precipitation, suggesting that it has the most useful information by itself when modeling the current distribution of miombo woodlands. The environmental variable that decreases the gain the most when it is omitted is temperature seasonality, suggesting that it contributes most independent information (Appendix B). The current distributions show some representative species occurring mostly in west African miombo woodlands, such as *B. plurijuga*, *B. bakeriana* and *C. exfoliatum*. Some species are distributed across the entire range of

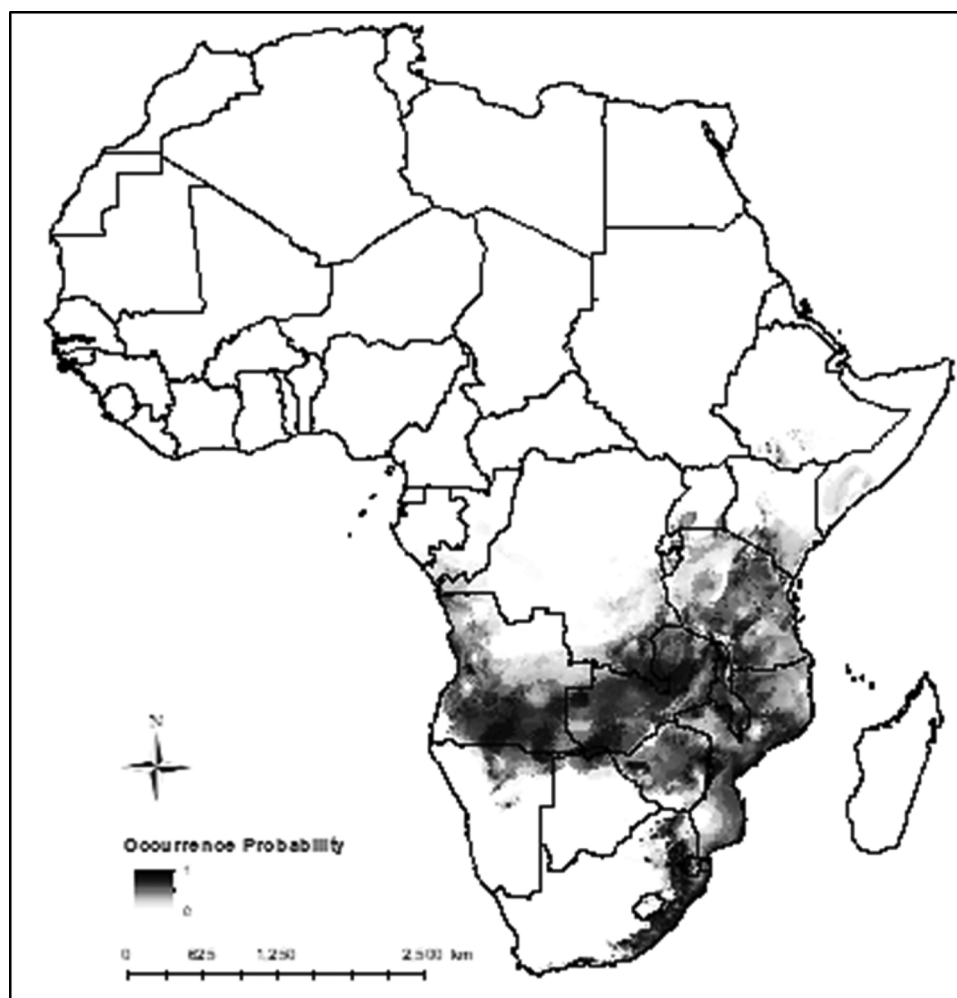


Fig. 1. Current distribution range of miombo woodlands modeled in Maxent (Phillips et al., 2006).

miombo woodlands, such as *A. quanzensis*, *B. boehmii* and *B. spiciformis*, while others are mostly distributed in east African miombo woodlands, such as *P. rotundifolius* (Appendix C).

3.3. Past and future projections

Hindcasting to the Mid-Holocene showed smaller ranges for eleven species while six species showed larger ranges (Fig. 2). The range of *B. bakeriana* has contracted the most (-98%) from the Mid-Holocene to the present, while the range of *B. plurijuga* has expanded the most (52%)

during this period.

When projected to 2050, the ranges of nine species contracted under almost all RCPs while those of eight species expanded (Fig. 3). *Afzelia quanzensis* (-8%, RCP6.0) and *B. microphylla* (-9%, RCP8.5) had highest contractions of their distributions. The highest expansion was observed for *B. bakeriana* (34%, RCP6.0).

Similarly, in 2070 there were range contractions for nine species while eight showed expansions (Fig. 4). *Albizia antunesiana* (-15%, RCP8.5), *A. quanzensis* (-13%, RCP8.5) and *B. microphylla* (-14%, RCP8.5) have distributions that were highly negatively impacted by

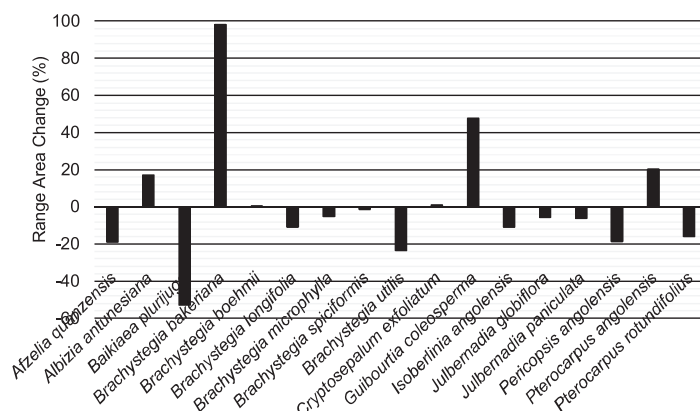


Fig. 2. Changes in range size when distributions of miombo tree species were hindcasted in Maxent (Phillips et al., 2006) to the Mid-Holocene.

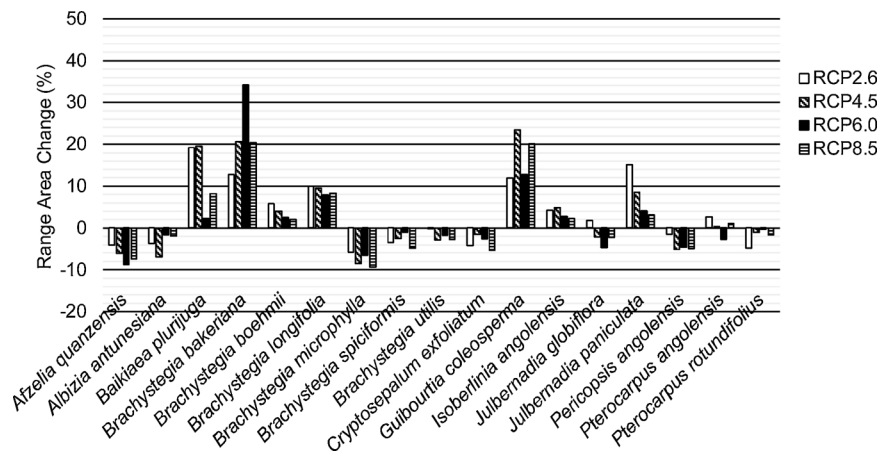


Fig. 3. Forecasted change in size of range of miombo tree species in 2050.

climate change. The distributions of two species, *B. boehmii* and *I. angolensis*, contracted under RCP8.5 while expanding under the other three RCPs in 2070. The distribution of *B. bakeriana* had the highest expansion in 2070 (44%, RCP4.5).

4. Discussion

In this study, we investigated the past, current and future distribution ranges of key species for an important ecoregion, the miombo woodlands of sub-Saharan Africa. Our study represents one of a few applications of ecological niche modeling to forecast range shifts in this region in the context of climate change. The miombo woodlands dominate in the southern sub-humid tropical zone of Africa, in areas receiving 710–1365 mm precipitation (Frost, 1996). Miombo woodlands have been delineated before (e.g. Campbell et al., 1996; Byers, 2001) implying a distribution range from Mozambique in the east to Angola in the west of Southern Africa. Our inferences, however, shows miombo woodlands stretching further south of the Limpopo River into northeastern South Africa, further north into Tanzania and southern Kenya and in eastern Angola than previously shown.

The Namib desert of Namibia is outside the range of miombo woodlands most likely because of extreme aridity. The desert is hot and dry almost all year round and has been classified as hyperarid (Henschel and Seely, 2008), thereby limiting growth of miombo tree species. The woodlands are also absent in south-west South Africa, in the Cape Floristic Province, which experiences a Mediterranean climate, that is cool wet winters and hot dry summers (Cowling et al., 2015). The hot dry summers are not conducive for the establishment

and growth of miombo tree species since their summer foliage development is synchronized with rainfall availability in their current range. The absence of miombo woodlands in some areas of the range, such as along the Limpopo and Zambezi valleys, maybe a result of low altitude and low precipitation since these valleys are low-lying and receive very little rainfall below 700 mm.

Hindcasting indicated that the miombo woodlands have been a dynamic system in the recent past, with individual species experiencing both range expansions and contractions. Of our modeled species, eleven had smaller ranges, while six species showed larger ranges compared to the present. Studies have shown a complex mosaic of drier and wetter conditions during the Mid-Holocene in central and southern Africa (Holmgren et al., 2003; Wanner et al., 2008; Burrough and Thomas, 2013) because of the impacts of tropical Atlantic and Indian Ocean moisture sources. Palynological records show the emergence of the Fabaceae (Nash et al., 2006) and the miombo woodlands (Scott et al., 2012) during the early Holocene in regions with seasonal rainfall patterns. There was a gradual displacement of drought-intolerant tropical seasonal forest by grassland and Zambezi woodlands in south-central Africa during the early Holocene (Ivory et al., 2012). The emergence of seasonality may have resulted in expansion of some miombo tree species from the Mid-Holocene to present.

Studies of distributions of plant species under future climate scenarios have commonly demonstrated range declines, migration towards the northern pole and to higher altitudes. Future range declines have been projected in Mexican alpine (Ramírez-Amezcu et al., 2016), Andean (Feeley and Silman, 2010; Tovar et al., 2013; Ramírez-Villegas et al., 2014) and rupestrian grassland biomes (Bitencourt et al., 2016)

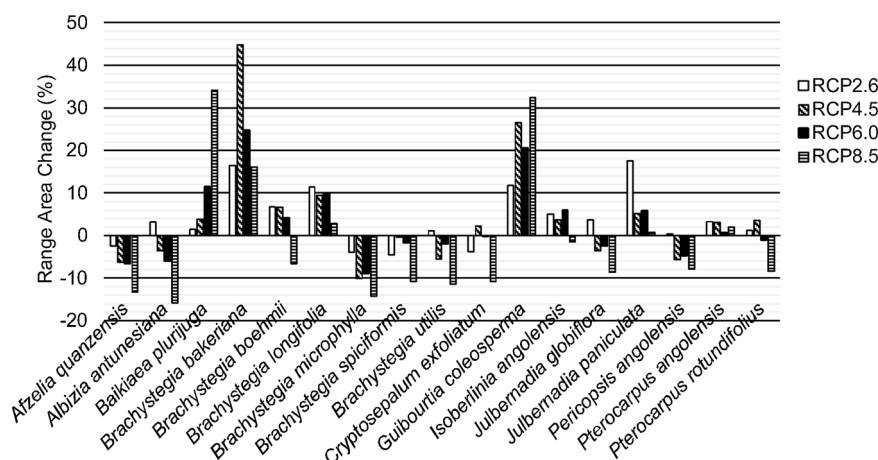


Fig. 4. Forecasted change in size of range of miombo tree species in 2070.

plant species. Range contraction of alpine vegetation in a progressively warming climate is largely expected since these plants are adapted to a low temperature habitat (3–6 °C mean annual temperature; Ramírez-Amezcu et al., 2016). Globally, 57% of plant species and 34% of animal species were predicted to lose at least 50% of their natural range by the 2080s, and even with mitigation, such range contractions are only expected to be reduced by 60% (Warren et al., 2013). A meta-analysis of studies of latitudinal and elevational distributions for several taxa showed that most species are migrating towards the northern pole and upwards in altitude (Chen et al., 2011).

In this study, the distribution of eight tree species expanded when forecasted while that of nine species contracted. Species of the same biome have been shown to respond differently to climate change (Thuiller et al., 2005; Hamann and Wang, 2006; Parolo and Rossi, 2008; Mathys et al., 2017). The assumption that species of the same biome respond similarly to environmental changes may not hold given differences in local adaptation, phenotypic plasticity and genetic structure (Linhart and Grant, 1996; Sultan and Spencer, 2002; Valladares et al., 2014). Thus, it is important to model species individually within an ecoregion for conservation purposes.

The miombo biome can be divided into wet and dry miombo woodlands. Dry miombo woodlands occur in areas receiving less than 1000 mm precipitation while wet miombo woodlands receive above 1000 mm (Frost, 1996). The marked expansion in the forecasted range of *B. bakeriana* in 2050 and 2070 in an increasingly warming environment suggests that the species thrives in hot and dry environments, characterizing it as a typical species of dry miombo woodlands. The future contractions in the range of nine species in a warming environment suggest that these species require more mesic and cooler conditions compared to *B. bakeriana*. The steep contraction in the forecasted range of *B. microphylla* characterizes it as a wet miombo woodlands species.

Climate change clearly already impacts ecosystems, and these impacts will intensify in the future. The decline in the future distribution of species found in miombo woodlands raises conservation concerns. The miombo woodlands have been collectively identified as a global wilderness area (Mittermeier et al., 2003) where conservation should be prioritized due to high endemism and the presence of threatened species (Seligmann et al., 2007). To maintain ecosystem integrity, the species whose ranges were predicted to contract should be protected from unsustainable harvesting and other anthropogenic threats such as the frequent occurrence of dry-season veld fires. Conservation activities may include germplasm preservation, reforestation and strengthening of local and national law enforcement to curb illegal logging and starting of veld fires.

Although climate change may not directly negatively affect the future distribution of some species, anthropogenic activities, particularly logging, pose a huge threat (Neke et al., 2006; Gerhardt and Todd, 2009). Some miombo species are logged for several uses, including for woodcarving. Woodcarvings derived from *A. quanzensis* dominate at market stalls (Braedt and Standa-Gunda, 2000; Braedt and Schroeder, 2003), and such dominance increases pressure on the resource in the wild. In the Limpopo Province of South Africa, community dwellers target *P. rotundifolius* for fuelwood and other uses (Neke et al., 2006). The failure of formal and informal institutions to regulate harvesting of natural resources in sub-Saharan Africa has rendered them freely available (Braedt and Schroeder, 2003), often resulting in unsustainable use. Dry season veld fires have also been identified as a factor that hinders establishment of miombo tree species (Chidumayo et al., 1996). The damaging effect of fires takes place in the early stages of establishment. Although fire should not be completely excluded because of the cultural and ecological roles it plays in some communities, increased fire frequency needs to be curbed. Anthropogenic impact on all miombo tree species should be mitigated since they pose a threat to the long-term persistence of the woodlands regardless of future climate trends.

Niche models tacitly assumes that species can disperse to projected ranges, an assumption that may not hold given the heterogeneity of landscapes. Barriers to seed dispersal in the form of urban areas, mountain ranges, large water bodies and farmlands may restrict dispersion (Funk et al., 2005; Antolin et al., 2006; Riley et al., 2006; Storfer et al., 2007). In addition, climate change may have indirect impacts on species distributions, for example, through the action of pests and diseases. Such biotic interactions are important for species survival but are not taken into consideration when using ENMs. The relatively long generation times of long-lived tree species may decrease establishment in suitable habitats within a short period of time (Ramírez-Villegas et al., 2014). Taken collectively, these factors may restrict the projected future range expansion of some species.

5. Conclusions

Climate change is a strong potential threat to the persistence of some miombo tree species. The forecasted distributions of nine miombo tree species showed range contractions among almost all climate change scenarios. Range expansion was forecasted for eight tree species. The nine tree species showing range contraction in a warming and drying environment should be prioritized for mitigation against climate change. The tree species whose forecasted range expanded may thrive in dry and hot environments and climate change may not be a direct threat. However, other indirect impacts of climate change remain uncertain. With these uncertainties, conservation of all miombo tree species should be a priority since most of them are unsustainably harvested in unprotected forests in sub-Saharan Africa.

Data statement

Species coordinates locations, a list of environmental variables used in modeling and maps showing the current distribution of 17 representative miombo tree species are available as supplementary information.

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