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Dry and wet miombo woodlands of south-central Africa respond differently to climate change

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Abstract It is important to understand how species distributions will shift under climate change. While much focus has been on species tracking temperature changes in the northern hemisphere, changing precipitation patterns in tropical regions have received less attention. The aim of the study was to estimate the current distribution of wet and dry miombo woodlands of sub-Saharan Africa and to predict their distributions under different climate change scenarios. A maximum entropy method (Maxent) was used to estimate the distributions and for projections. Occurrence records of dominant tree species in each woodland were used for modeling, together with altitude, soil characteristics, and climate variables as the environmental variables. Modeling was done under all four representative concentration pathways (RCPs) and three general circulation models. Three dominant tree species were used in models of dry miombo while seven were used for wet miombo. Models estimated dry miombo to cover almost the entire known distribution of miombo woodlands while wet miombo were estimated to predominate in parts of Angola, southern Democratic Republic of Congo, Malawi, Tanzania, Zambia, and Zimbabwe. Future climate scenarios predict a drier climate in sub-Saharan Africa, and as a result, the range of dry miombo will expand. Dry miombo were predicted to expand by up to 17.3% in 2050 and 22.7% in 2070. In contrast, wet miombo were predicted to contract by up to − 28.6% in 2050 and − 41.6% in 2070. A warming climate is conducive for the proliferation of dry miombo tree species but unfavorable for wet miombo tree species.

Keywords Climate change · Ecological niche model · Maxent · Miombo woodlands · Representative concentration pathway · Species distribution

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Introduction

Miombo woodlands are the largest forest type in sub-Saharan Africa, covering an area approximately 2.4–3.6 million km^2 (Byers 2001; Dewees et al. 2010; Giliba et al. 2011; Jew et al. 2016). The woodlands are distributed in countries of south-central Africa, including in Angola, Malawi, Mozambique, Tanzania, Zambia, and Zimbabwe, in areas receiving more than 700 mm of rainfall per year (Campbell et al. 2007; Dewees et al. 2010). Miombo woodlands are identified and differentiated from other woodlands by the presence of particular woody species, especially those in Leguminosae and the genera *Brachystegia*, *Julbernadia*, and *Isoberlinia* (Campbell et al. 2007; Moura et al. 2018). The three genera are hardly found outside miombo woodlands.

Most of the tree species are deciduous, with a flush of new leaves immediately before the onset of the wet season and leaf fall in the dry season.

Miombo woodlands were classified into wet and dry miombo by White (1983), separated by a 1000-mm annual precipitation isohyet. In dry miombo woodlands, the dominant tree species are *Brachystegia spiciformis*, *B. boehmii*, and *Julbernardia globiflora* (Frost 1996; Kapinga et al. 2018; Moura et al. 2018). The canopy height of dry miombo woodlands is less than 15 m and the vegetation is floristically poor. Wet miombo woodlands occur in areas receiving more than 1000 mm rainfall per year and have a canopy height of greater than 15 m, reflecting the mesic conditions that support plant growth (Frost 1996). The vegetation of wet miombo woodlands is floristically more diverse and includes nearly all characteristic miombo tree species, such as *B. floribunda*, *B. glaberrima*, *B. longifolia*, *B. wangermeeana*, *J. paniculata*, *Isoberlinia angolensis*, and *Marquesia macroura* (Frost 1996; Munishi et al. 2011; Kapinga et al. 2018). The distributions of the woodlands have often been described at country level where the dominant tree species have been identified. Determining the fine distribution of wet and dry miombo woodlands is vital for their ecological and economic management.

It has been estimated that miombo woodlands support the livelihood of 100 million people (Syampungani et al. 2009). To local communities, miombo tree species provide medicinal extracts, fuelwood, charcoal, and wood for construction and woodcarving (Dewees et al. 2010; Kutsch et al. 2011; Jew et al. 2017; Jinga and Ashley 2018; Moura et al. 2018). Globally, miombo woodlands are important for carbon sequestration and as centers of endemism (Lupala et al. 2015; Jew et al. 2017). The human population in sub-Saharan Africa is predicted to double by 2050 (Eastwood and Lipton 2011), thereby increasing pressure on the woodlands (Goncalves et al. 2017). The increased demand for fuelwood and charcoal due to increase in cost and infrequent supply of electricity, land clearing for agriculture and urban areas expansion, and the increase in the occurrence of veld fires have all led to deforestation of the woodlands (Chidumayo 1988, 1993; Campbell et al. 2007; Dewees et al. 2010; Jew et al. 2019). There is growing concern that these human activities may cause an irreversible change in miombo woodlands, resulting in loss of goods and services derived from the woodlands.

Apart from anthropogenic threats, climate change is also impacting the distribution and occurrence of tree species. Distributions of several tree species have been shown to be affected by climate change (Bitencourt et al. 2016; Dyderski et al. 2018; Lamsal et al. 2018; Hoffmann et al. 2019; Niskanen et al. 2019). The continuously increasing atmospheric CO_2 concentration, currently at nearly 411 ppm (Earth System Research Laboratory 2019), indicates that climate may continue to significantly change going forward. Surface temperatures are predicted to increase by up to 3.7 °C in 2100, depending on the choice of greenhouse gas emission scenario or representative concentration pathway (RCP) (IPCC 2013). These predictions may be conservative given the slow implementation of mitigation measures of greenhouse gas emission (USGCRP 2018). Climate change will thus profoundly impact plant distributions.

Species distributions can be estimated by ecological niche models (ENMs). To generate distribution maps, ENMs correlate occurrence records to environmental variables known to affect the occurrence of the target species (Guisan and Zimmermann 2000; Elith and Leathwick 2009; Crimmins et al. 2013). Some areas, especially in the tropics, are botanically unexplored due to inaccessibility (Pearson et al. 2007), and occurrence records for rare species and those that are difficult to detect are often limited to small samples in museum collections (van Proosdij et al. 2016). ENMs can overcome these shortcomings by predicting the suitability of even botanically unexplored and inaccessible habitats and determining the distribution of species with few occurrence records. ENMs can also be used to hindcast and forecast the distribution of species in response to climate change (Phillips et al. 2006; Phillips and Dudik 2008). Among the commonly used ENMs is the maximum entropy method (Maxent) (Phillips et al. 2006). Maxent is popular because of its use of presence-only records, high predictive power with small samples, and the user-friendly graphical user interphase. As a result, Maxent has been used in a variety studies, such as determining the impact of climate change on the distribution of species (Dyderski et al. 2018; Zwiener et al. 2018; Jinga and Ashley 2019), predicting the occurrence of underground minerals (Liu et al. 2018) and determining the routes of invasive species (Lamsal et al. 2018).

The aims of this study were to estimate the current distribution of dry and wet miombo woodlands and to investigate the impact of climate change on the woodlands. Current distribution maps help in guiding botanical explorations into previously unknown potential habitats. Forecasting distributions under different RCPs identifies woodlands that will be negatively or positively impacted in the future, thereby helping in planning management programs. Our research questions were (i) What is the current range of dry and wet miombo woodlands? (ii) How is the distribution of dry and wet miombo woodlands impacted in 2050 and 2070 under different climate change scenarios? (iii) Which areas will gain or lose miombo woodlands? Answers to these questions are important for management of the woodlands that sustain livelihoods in sub-Saharan Africa.

Materials and methods

Representative tree species of dry and wet miombo woodlands

Tree species were selected and categorized into dry and wet miombo following Chidumayo (1987), Frost (1996), Munishi et al. (2011), Kapinga et al. (2018), and Moura et al. (2018). Tree species with ambiguous categorization were excluded. Dominant and widely distributed tree species in dry miombo woodlands are *Brachystegia spiciformis*, *B. boehmii*, and *Julbernadia globiflora*, while those in wet miombo are *B. floribunda*, *B. glaberrima*, *B. longifolia*, *B. wangermeeana*, *J. paniculata*, *Isoberlinia angolensis*, and *Marquesia macroura*. The genera *Brachystegia*, *Isoberlinia*, and *Julbernadia* were formerly classified into subfamily Ceasalpinioideae of the family Leguminosae. The three genera have been reclassified into subfamily Detarioideae (LPWG 2017). *Marquesia macroura* is classified into family Dipterocarpaceae, subfamily Monotoideae. Although *M. macroura* does not belong to family Leguminosae, whose woody species commonly define miombo woodlands, it is also naturally distributed and dominant in the woodlands.

Occurrence records and environmental variables

Occurrence records of representative tree species were obtained from the Global Biodiversity Information Facility (GBIF 2019) (www.gbif.org) and Tropicos (www.tropicos.org) online data portals. The advantage of including GBIF data is that areas not usually covered by forest inventories and those that are too large for reliable sampling by researchers are represented since some data in GBIF are also collected by citizen science tools (Dyderski et al. 2018). Some occurrence records were also obtained from the Vegetation Database of the Okavango Basin (Revermann et al. 2016) and the Makeni Savanna Research Project, Zambia. All occurrence records were populated in Microsoft Office Excel where duplicates were identified and removed.

The predictive accuracy of ENMs is affected by geographically biased occurrence records. Modeling with spatially biased data causes environmental variables in areas of high intensity sampling to be overrepresented, resulting in inaccurate predictions (Fourcade et al. 2014). To correct spatially biased data, occurrence records were resampled until an even distribution was obtained across the sampling area. Occurrence records were resampled in R (R Development Core Team 2019) (www.r-project.org/) using the package spThin (Aiello-Lammens et al. 2015). The resampling process implemented in spThin takes a set of occurrence records and generates several new subsets that meet a specified minimum nearest neighbor distance (NND) constraint (Aiello-Lammens et al. 2015). One of the newly generated subsets with the largest number of occurrence records is then selected for modeling. Several NND constraints were tested until data sets with uniform distribution of occurrence records were obtained. We resampled occurrence records of both dry and wet miombo woodlands.

Climate variables, soil variables, and altitude were used as the environmental variables in generating models. Climate variables and altitude were obtained from the WorldClim version 1.4 (www.worldclim.org) online data portal (Hijmans et al. 2005). Climate variables were monthly precipitation, minimum, and maximum monthly temperatures, and 19 bioclimatic variables derived from precipitation and temperature. The bioclimatic variables have been shown to affect the distribution of plant species and have been widely used in Maxent (Peterson et al. 2007; Carnaval and Moritz 2008; Kumar 2012; Rebelo et al. 2012; Copot and Tanase 2017). Soil variables were obtained from the Harmonized World Soil Database version 1.2 (www.fao.org) (Fischer et al. 2008). The soil variables were soil toxicity, nutrient retention capacity, nutrient availability, oxygen availability, and soil workability. All variables were at 30 arc seconds resolution, approximately 0.86 km^2 at the equator.

Apart from spatially biased occurrence records, models are also affected by highly correlated environmental variables. Correlated variables increase computation time and overfitting while reducing signal to noise ratio and transferability (De Cauwer et al. 2014). Correlation analysis of environmental variables was performed separately for wet and dry miombo woodlands in R using the package Caret (Kuhn 2008). Variables with a correlation coefficient of > 0.75 were treated as proxies of each other and one of them was selected. Environmental variables were further screened by trial runs in Maxent with permutation importance and jackknife tests. The jackknife test provides a good estimation of how important a variable is by measuring the training gain obtained when the target variable is both included and excluded, while a permutation importance test estimates the contribution of each variable to a model (Phillips 2008; De Cauwer et al. 2014). Environmental variables showing very low contribution were removed in final models.

Ecological niche modeling and model evaluation

Maxent software was used for modeling the current distribution of dry and wet miombo woodlands and for all projections. Maxent determines the habitat suitability for a species from a set of environmental variables and sample locations in the form of latitude and longitude coordinates (Phillips et al. 2006). The method then expresses the suitability of each grid cell as a function of the environmental variables in that grid cell. The computed Maxent model is a probability distribution over all the grid cells of a landscape. Pixels of the demarcated study area make up the space on which the Maxent probability distribution is defined, pixels with known species occurrence records constitute the sample points, and features are the environmental variables (Phillips et al. 2006; Kumar 2012). We used default settings in Maxent since these have been validated over many taxa, environmental variables, sample sizes, and biases (Elith et al. 2011). Maxent has been shown to make more accurate estimations of species distributions when compared to other ENMs (Elith et al. 2006; Phillips et al. 2006; Pearson et al. 2007; Elith et al. 2011).

To evaluate models of the current distribution of dry and wet miombo woodlands, we split occurrence records into training (75%) and testing (25%) and performed 10 replicate runs for each woodland. Model performance was measured by an area under the receiver operating characteristic curve (AUC) statistic calculated internally in Maxent. The AUC statistic measures the model's power to discriminate in terms of sensitivity (correctly predicted presences) against specificity (correctly predicted absences) (Phillips et al. 2006). The value of the statistic ranges from 0.5 to 1.0. A value of 0.5 denotes random prediction while a value closer to 1.0 indicates high discrimination power (Phillips and Dudik 2008; Wisz et al. 2008). After evaluation of the models, all occurrence records were used to model the current distribution of the woodlands.

Projections

Projections of distributions of dry and wet miombo woodlands were made to 2050 and 2070 under all four RCPs proposed by the Intergovernmental Panel on Climate Change (IPCC). Representative concentration pathways are a scenario set containing emission and concentration of greenhouse gases as well as the resultant sea level and temperature trajectories (van Vuuren et al. 2011). They are identified by their approximate total radiative forcing in year 2100 relative to 1750. The RCPs include one mitigation scenario leading to a very low forcing level (RCP2.6), two stabilization scenarios (RCP4.5 and RCP6.0), and one scenario with unmitigated greenhouse gas emission (RCP8.5). Temperatures are predicted to increase by between 1.0 and 2.0 °C in the years 2046 to 2065 and between 1.0 and 3.7 °C in the years 2081 to 2100 (IPCC 2013). All RCPs were used in projections in order to capture the full range, from the optimistic to the pessimistic, of the potential impacts of climate change on dry and wet miombo woodlands.

Projections were made on variables from three general circulation models or global climate models (GCMs), which were the Community Climate System Model version 4.0 (CCSM4.0) (Lawrence et al. 2012b), the Institut Pierre Simon Laplace Coupled Model version 5A Low Resolution (IPSL-CM5A-LR) (Marti et al. 2010), and the Model for Interdisciplinary Research on Climate, Earth System Model (MIROC-ESM) (Watanabe et al. 2011). Multiple GCMs were used since there is variability among them (Goberville et al. 2015). The GCMs that were chosen have complete data at high resolution under all four RCPs and projection periods.

Table 1 Contribution of environmental variables to a Maxent model (Phillips et al. 2006) of the current distribution of dry miombo woodlands in south-central Africa

Variable	Percent contribution	Permutation importance (%)
Precipitation of the seventh month	29.5	39.0
Precipitation of the third month	24.5	1.5
Precipitation of the wettest quarter	20.8	33.6
Precipitation seasonality	12.0	4.5
Precipitation of the eleventh month	7.2	8.4
Mean diurnal temperature range	2.8	4.2
Isothermality	1.7	4.6
Altitude	1.1	1.8
Maximum temperature of the tenth month	0.4	2.4

The variables of the three GCMs were obtained from the WorldClim data portal at 30 arc seconds resolution.

We measured the change in size of predicted ranges as an indication of the impact of climate change on the woodlands. The size of each forecasted range was calculated above a threshold probability of occurrence used to convert distributions into a binary presence and absence. The threshold was determined using the receiver operating characteristic curve (ROC) (Araujo et al. 2005). The ROC threshold has been used widely for presence-only data since areas above the threshold have been observed to show true presences (Araujo et al. 2005; Nenzen and Araujo 2011). All calculations of change in size of ranges were performed in ArcMap version 10.6.1 (ESRI, Redlands, CA).

Table 2 Contribution of environmental variables to a Maxent model (Phillips et al. 2006) of the current distribution of wet miombo woodlands in south-central Africa

Variable	Percent contribution	Permutation importance (%)
Precipitation of the second month	51.9	41.2
Precipitation of the seventh month	13.6	8.8
Precipitation of the third month	11.4	20.0
Altitude	7.6	6.9
Maximum temperature of the fourth month	6.9	4.1
Precipitation of the eleventh month	5.7	13.2
Precipitation of the coldest quarter	2.9	5.8

Results

Occurrence records and environmental variables

A total of 1 173 occurrence records were obtained for dry miombo woodlands (*B. boehmii* (255), *B. spiciformis* (556), and *J. globiflora* (362)). Dry miombo occurrence records showed high intensity sampling in parts of Mozambique, Zambia, and Malawi (Online Resource 1). After resampling, 165 occurrence records showing uniform distribution across the sampling landscape were used in building a model of the current distribution of dry miombo woodlands (Online Resource 1).

For wet miombo woodlands, a total of 653 occurrence records were recovered (*B. floribunda* (77), *B. glaberrima* (23), *B. longifolia* (172), *B. wangermeeana* (43), *J. paniculata* (215), *I. angolensis* (112), and *M. macroura* (11)). The data set of wet miombo woodlands also showed spatial bias with heavy sampling in parts of southern DRC, Zambia, Angola, and Tanzania (Online Resource 2). To build a model of the current distribution of wet miombo woodlands, we finally used 128 occurrence records showing uniform distribution after resampling (Online Resource 2).

After correlation analyses and jackknife tests, nine and seven environmental variables were used to construct models of the distribution of dry and wet miombo woodlands, respectively. The variables that contributed significantly to a model of the current distribution of dry miombo woodlands were precipitation of the seventh month (29.5%), precipitation of the third month (24.5%), precipitation of the wettest quarter (20.8%), and precipitation seasonality (12%) (Table 1).

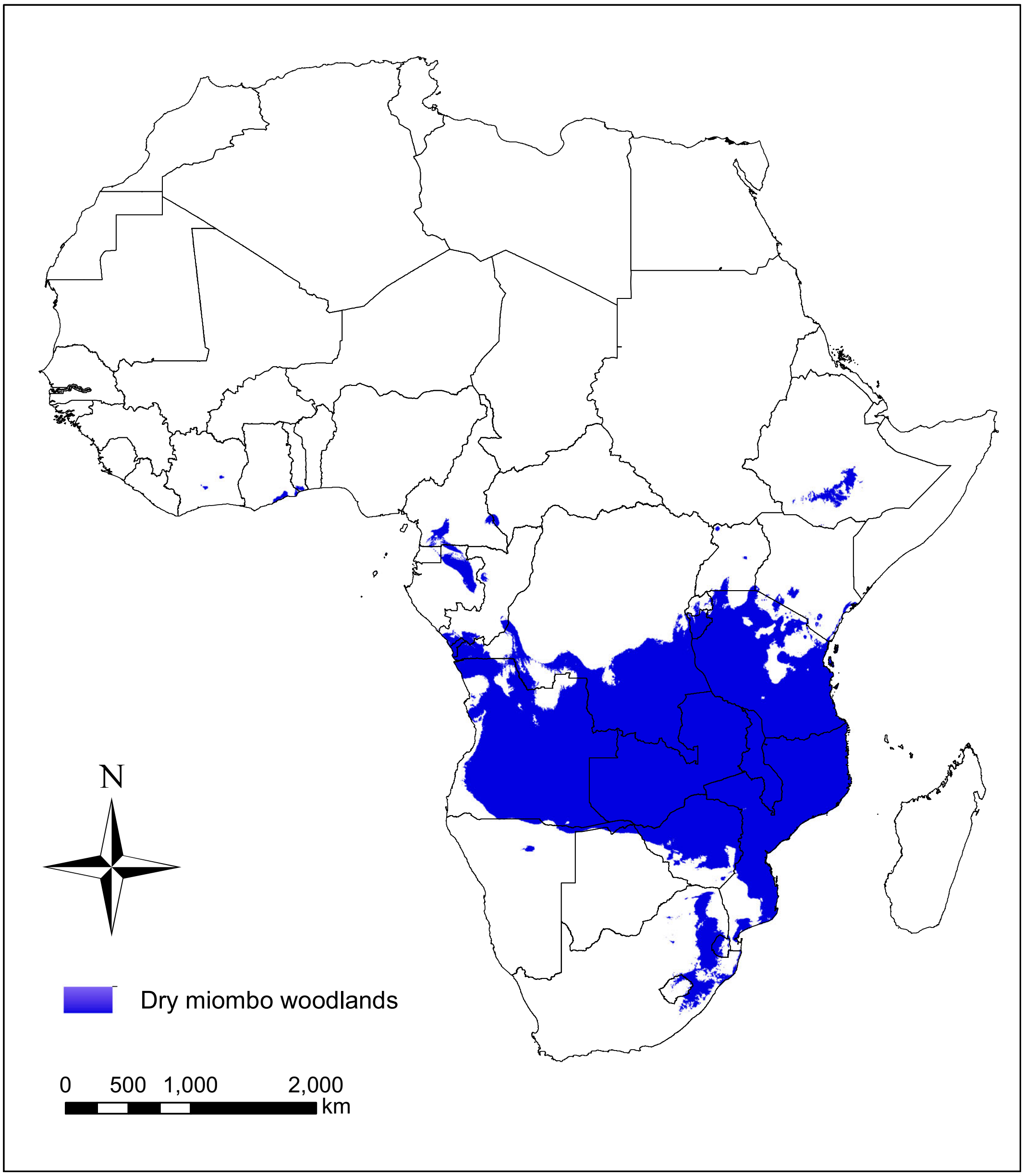

Fig. 1 Current range of dry miombo woodlands in south-central Africa estimated in Maxent (Phillips et al. 2006) using occurrence records of three dominant tree species

Results of the jackknife test of variable importance on dry miombo show that the environmental variable with the highest gain when used in isolation is precipitation of the third month while precipitation of the wettest quarter decreases the gain the most when it is excluded (Online Resource 3). The jackknife test results imply that precipitation of the third month has the most useful information by itself while precipitation of the wettest quarter has most information that is absent in the other variables.

Variables that contributed markedly to a model of wet miombo woodlands were precipitation of the second month (51.9%), precipitation of the seventh month (13.6%), precipitation of the third month (11.4%), and altitude (7.6%) (Table 2). Results of the jackknife test of wet miombo woodlands showed that precipitation of the second month has the most useful information by itself which is also absent in other variables (Online Resource 4).

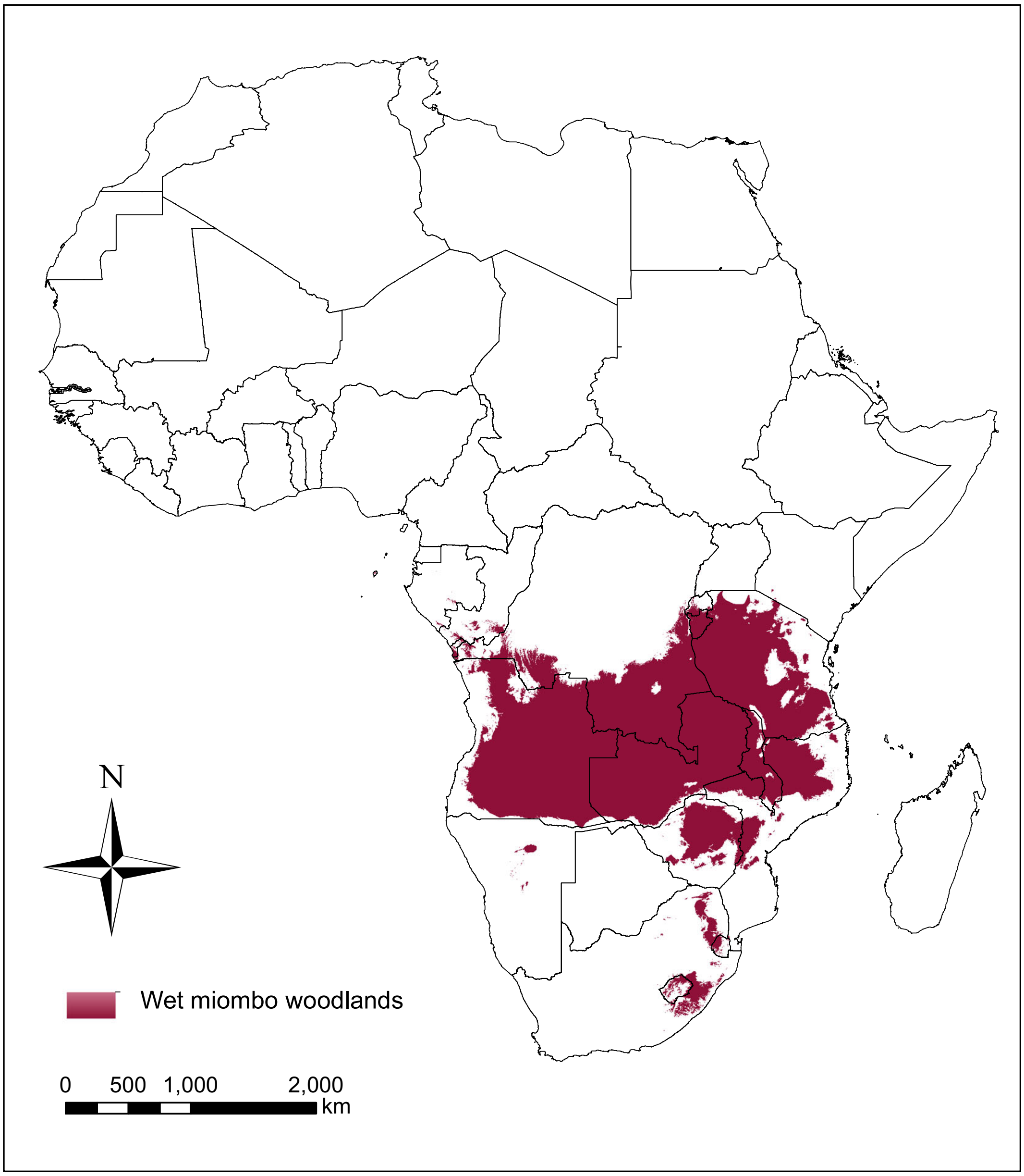

Fig. 2 Current range of wet miombo woodlands in south-central Africa estimated in Maxent (Phillips et al. 2006) using occurrence records of seven dominant tree species

Model evaluations and current distributions

Evaluation of models showed better than random predictions, with mean AUC for dry miombo models of 0.931 ± 0.007 and for wet miombo models of 0.945 ± 0.005. Visual inspection of Maxent output pictures of the results of replicate evaluation models showed most test locations covered by current distributions.

Dry miombo woodlands occur in almost the entire known distribution of miombo woodlands, in parts of Angola, southern DRC, Malawi, Mozambique, north-eastern South Africa, Tanzania, Zambia, and Zimbabwe (Fig. 1). Dry miombo woodlands are especially widely distributed in Malawi and Zambia. In South Africa, dry miombo woodlands are restricted to the north-eastern provinces while in Zimbabwe, they are largely absent in the extremely dry southern lowveld. On the northern

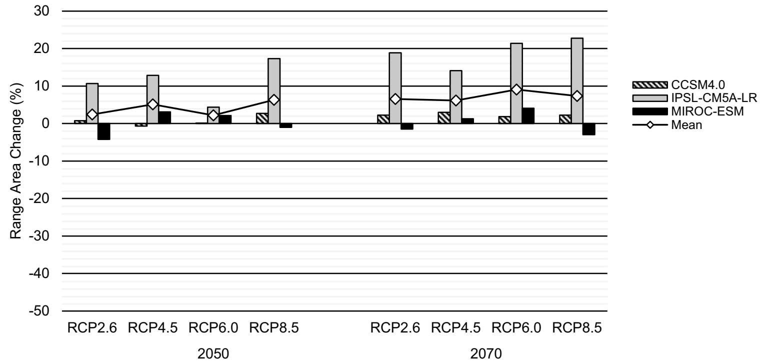

Fig. 3 Change in size of range of dry miombo woodlands in 2050 and 2070 forecasted in Maxent (Phillips et al. 2006) under four representative concentration pathways and three general circulation models

edge, the mesic conditions of the Guineo-Congolian rainforest are not conducive for growth of dry miombo tree species. Dry miombo woodlands are ubiquitous in south-central Africa, distributed in low-lying areas, such as the coastal areas of Mozambique, as well as high-altitude areas, such as the central highveld watershed of Zimbabwe.

Wet miombo woodlands are widely distributed in Angola, southern DRC, Malawi, Tanzania, and Zambia (Fig. 2). They are not as widespread as dry miombo woodlands. Wet miombo woodlands occur in the central highveld watershed of Zimbabwe and in some parts of northern Mozambique. They also occur in scattered patches of north-eastern South Africa. However, they are absent in low-lying areas, such as the Zambezi valley between Zimbabwe and Zambia, the Save-Limpopo valley between Zimbabwe and South Africa and the coastal areas of Mozambique and Angola.

Projections

The distribution of dry miombo woodlands, on average, expanded under all RCPs (Fig. 3). When projected to 2050, the highest expansion of the range of dry miombo was observed under RCP8.5 (6.3%), while in 2070, the highest expansion was under RCP6.0 (9.1%). In contrast, the range of wet miombo woodlands, on average, contracted under all RCPs (Fig. 4). Wet miombo woodlands were heavily impacted by unmitigated climate change, contracting by − 17.0% in 2050 and − 30.1% in 2070 under RCP8.5.

Forecasting to 2050 showed the range of dry miombo woodlands expanding especially in northern Angola and Tanzania (Fig. 5). In 2070, dry miombo woodlands expanded further north and in north-eastern South Africa, particularly under IPSL-CM5A-LR (Fig. 6). Wet miombo woodlands contracted on both the southern and northern edges of the current distribution in 2050 (Fig. 7) and 2070 (Fig. 8). In 2070, the range of wet miombo woodlands heavily contracted in Angola, DRC, Mozambique, Tanzania, Zambia, and Zimbabwe, especially under RCP8.5. In Zimbabwe, wet miombo were almost completely wiped out from their central highveld distribution, especially under IPSL-CM5A-LR and MIROC-ESM. Similarly, the distribution of wet miombo significantly contracted in northern Mozambique (Fig. 8).

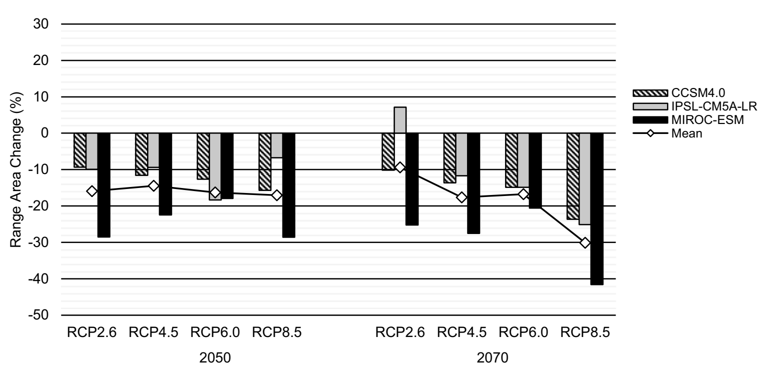

Fig. 4 Change in size of range of wet miombo woodlands in 2050 and 2070 forecasted in Maxent (Phillips et al. 2006) under four representative concentration pathways and three general circulation models

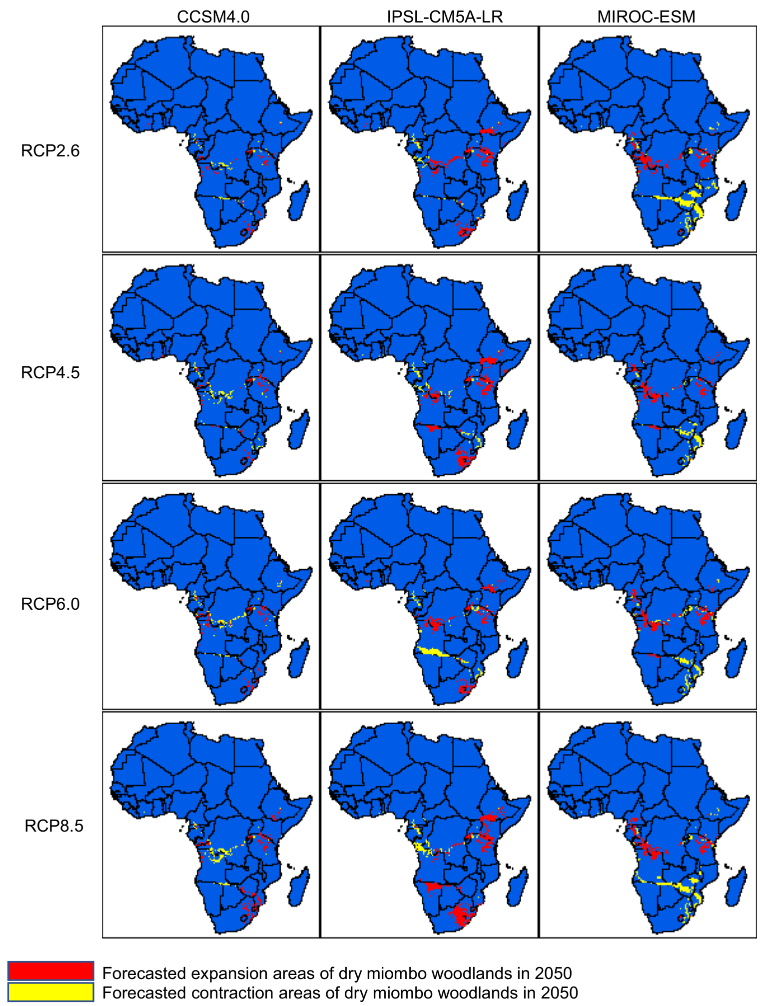

Fig. 5 Areas of niche gain and loss of dry miombo woodlands in 2050 forecasted in Maxent (Phillips et al. 2006) under three general circulation models and four representative concentration pathways

Discussion

The distribution of miombo woodlands, combining both dry and wet, has been described (White 1983; Campbell et al. 1996; Byers 2001; Jinga and Ashley 2019); however, this study is the first to use ENM to estimate the different distributions of the two distinct types of miombo woodlands. Dry miombo woodlands are widely distributed and occur even in drier parts of south-central Africa, covering almost the entire miombo ecoregion (Fig. 1). The range of dry miombo woodlands suggests that the tree species thrive in both mesic and drier conditions. Studies have indicated a wide distribution of dry miombo tree species, including in Tanzania (Lupala et al. 2015), Malawi (Jackson 1968), Mozambique (Moura et al. 2018), Zimbabwe (Frost 1996), Zambia (Fanshawe 1971), and Angola (Chiteculo and Surovy 2018). Some dry miombo woodlands tree species, such as *B. spiciformis*, resist shoot die-back due to water stress (Chidumayo 1992), while others, such as *J. globiflora*, rapidly resprout from suckers (Grundy et al. 1994). These physiological traits allow the species to occur in areas of low precipitation.

Wet miombo woodlands are distributed in areas that receive relatively high rainfall, immediately south of the Guineo-Congolian rainforest as well as the central watershed of Zimbabwe (Fig. 2). The range of wet miombo woodlands can be described as a transition from the mesic Guineo-Congolian rainforest in the north to the more arid Zambezian woodlands in the south. Wet miombo trees species, such as *B. floribunda*, *B. longifolia*, *J. paniculata*, and *M. macroura*, have typically been identified in areas of high rainfall within the miombo ecoregion (Jackson 1968; Lawton 1978;

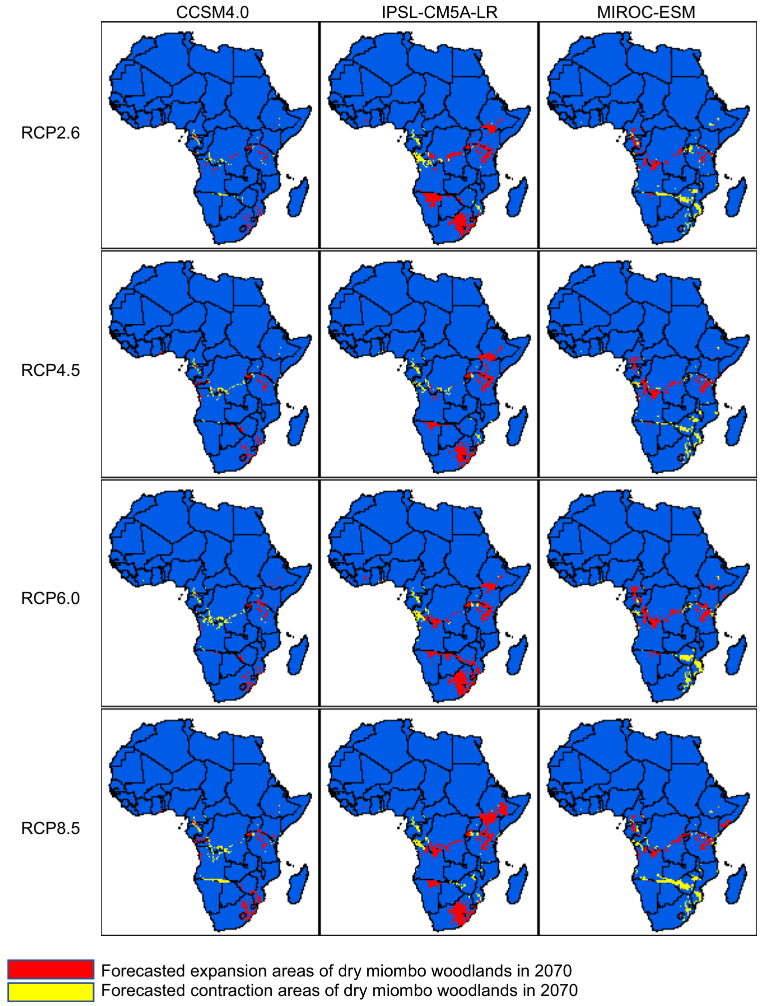

Fig. 6 Areas of niche gain and loss of dry miombo woodlands in 2070 forecasted in Maxent (Phillips et al. 2006) under three general circulation models and four representative concentration pathways

Chidumayo 1989; Malaisse 1993). *Marquesia macroura* is an evergreen canopy tree species (Lawton 1978), indicating its requirement of mesic conditions in seasonally dry forests.

Although dry miombo tree species thrive under drier conditions, they are not completely xeric, they require at least 700 mm precipitation per year. Wet miombo occur in areas receiving a minimum of 1000 mm. However, apart from precipitation, wet miombo woodlands are restricted by elevation. The mean elevation of dry miombo woodlands occurrence locations was 956 m while that for wet miombo woodlands was 1281 m. High elevation is associated with low temperatures which reduce transpiration and increase water availability to plants. Huge variability in microclimate is observed at small elevation changes (Okea and Thompson 2015) and affects the distribution of mesic tree species (Adhikari et al. 2012). Wet miombo are not widely distributed in low-lying areas of south-central Africa since these are very hot and dry. In contrast, elevation does not significantly affect the distribution of dry miombo; hence, they occur in low-lying and elevated areas across the entire miombo ecoregion.

Projections to 2050 and 2070 show the range of wet miombo woodlands contracting while that of dry miombo woodlands expanding. Globally, studies have shown that tree species respond differently to climate change due to differences in life history traits and physiological plasticity. In Europe, late successional tree species, such as *Abies alba*, *Fagus sylvatica*, and *Fraxinus excelsior*, expanded their ranges when projected, while pioneer species, such as *Betula pendula*, *Larix decidua*, and *Picea abies*, showed contracted ranges (Dyderski et al. 2018). The ranges of late successional tree species

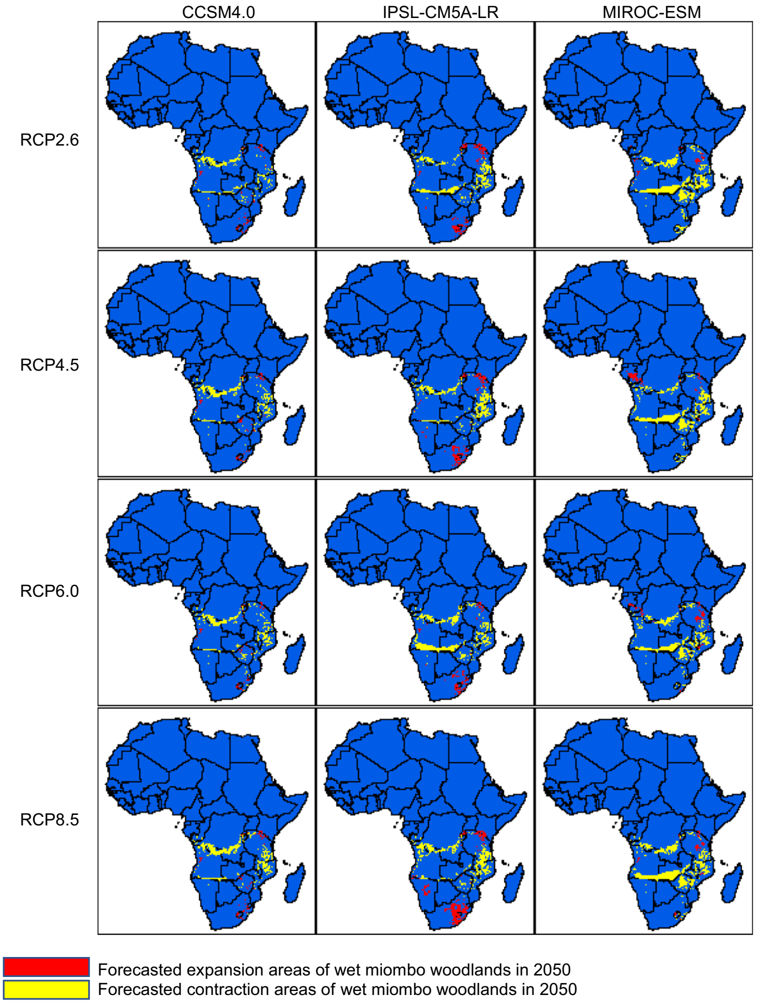

Fig. 7 Areas of niche gain and loss of wet miombo woodlands in 2050 forecasted in Maxent (Phillips et al. 2006) under three general circulation models and four representative concentration pathways

expand in a warming climate because of their tolerance to drought (Nogues-Bravo et al. 2014). Pioneer species are threatened by climate change because they run out of colonizable area since they already have a far northern distribution (Dyderski et al. 2018). Species with a high latitude distribution generally have poor drought tolerance (Nogues-Bravo et al. 2014). Similarly, 71–92% of high-altitude arctic plant species were projected to lose more than half of their present range by year 2100 (Niskanen et al. 2019). In southern Africa, the range of an important miombo woodland timber species, *Pterocarpus angolensis*, was predicted to decrease in Namibia and Botswana (De Cauwer et al. 2014). In east Africa, different climate change scenarios decrease the range of *Prunus africana*, a mesic tree species of economic importance (Mbatudde et al. 2012; Vinceti et al. 2013).

The contraction of wet miombo woodlands was highest under RCP8.5, a scenario of no mitigation of greenhouse gas emission. This scenario predicts a dramatic loss of wet miombo woodlands of up to − 41.6%. Contraction of wet miombo is also predicted even under mitigation and stabilization scenarios, so future reductions in greenhouse gas emission may be inadequate to stem the tide. Our results suggest that wet miombo tree species lack the evolutionary characteristics and plasticity to thrive in drying conditions. Contraction of the range of wet miombo woodlands results in species composition changes and ultimately ecosystem changes. Such ecosystem changes may trigger undesirable effects especially in coevolved systems (Fussmann et al. 2007; Lawrence et al. 2012a).

In addition to climate change, wet miombo woodlands may be negatively impacted by limited seed

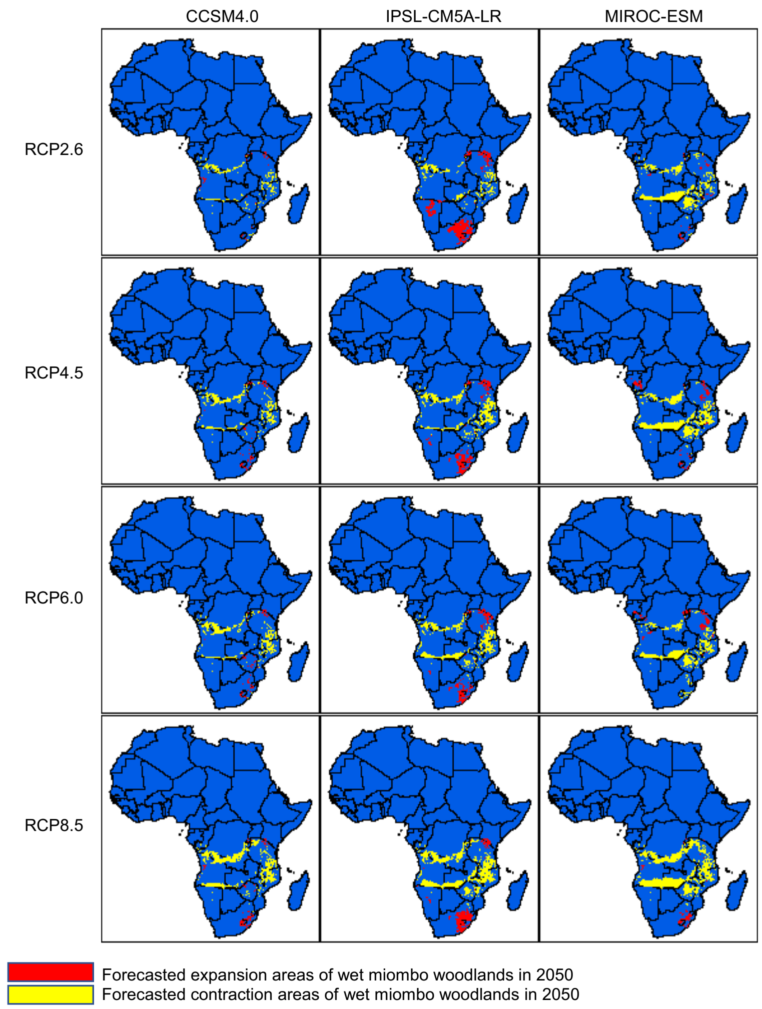

Fig. 8 Areas of niche gain and loss of wet miombo woodlands in 2070 forecasted in Maxent (Phillips et al. 2006) under three general circulation models (GCMs) and four representative concentration pathways

dispersal. Seeds in the genera *Brachystegia*, *Isoberlinia*, and *Julbernadia* are commonly dispersed by explosion of pods (Chidumayo and Frost 1996). Dispersal distance after explosive dehiscence is limited compared to other mechanisms, such as animal and wind dispersal. Maximum dispersal distances of 22.0 m and 5.6 m have been reported in *J. globiflora* (Strang 1969) and *B. spiciformis* (Ernst 1988), respectively. *Marquesia macroura* fruits are ovoid-conical, surrounded by wings derived from sepals (Flora Zambesiaca 2019). Winged fruits in *M. macroura* may allow long-distance dispersal through wind, unlike explosive dehiscence in the genera *Brachystegia*, *Isoberlinia*, and *Julbernadia*. Tree species with limited dispersal may be impacted more by climate change since they are unable to rapidly track conducive habitats. Trees with short-tailed dispersal kernels may have poor seedling recruitment because of competition with the mother tree for light, space, water, and nutrients (Nathan 2006; Sullivan et al. 2018). Limited dispersion, in conjunction with long generation times, may result in long-lasting vegetation composition changes in miombo woodlands.

The forecasted range of dry miombo woodlands expanded under a warming environment because of the associated decline in precipitation. The range of drought tolerant plant species has been predicted to increase under a warming climate in other African ecosystems. The range of *Vachellia karroo*, a dominant tree species in arid savannas of southern Africa, increased by up to 69% when forecasted to 2070 (Shekede et al. 2018). *Vachellia karroo* has an extensive and deep root system that allows the tree species to withdraw water from larger depths. Similarly, the range of *Dracaena surculosa*, a west African tree species whose growth is limited by low temperature and high precipitation, increased when forecasted to 2050 (Bogawski et al. 2019). Dry miombo tree species have adaptations to thrive in relatively drier conditions, such as the presence of small leaves, resprouting and resistance to shoot die-back. These adaptations allow dry miombo tree species to expand their range in an increasingly drying environment.

Although climate change does not directly threaten dry miombo woodlands, other threats exist. Suitable habitat for dry miombo woodlands increases under climate change but range expansion may be unsuccessful due to seed dispersal barriers. Plant dispersal may be limited by farmlands, urban areas, and lakes (Storfer et al. 2007). In addition, the transnational distribution of the woodlands can make transnational conservation programs difficult to implement (Rosaleen 2006). The rapidly increasing human population in sub-Saharan Africa means anthropogenic activities will continue to pose a substantial threat to the occurrence of miombo woodlands.

Conclusions

Our models show that dry miombo woodlands are currently distributed in the entire miombo ecoregion. Dry miombo woodlands occupy areas of variable precipitation, in semi-arid and mesic conditions. Elevation does not strongly affect the distribution of dry miombo woodlands since they occur at low and high elevation. Wet miombo woodlands may be regarded as a transition from the Guineo-Congolian rainforest to the seasonally dry southern Africa vegetation. Elevation strongly affects the distribution of wet miombo woodlands since they are restricted to high elevation areas. The distribution of dry miombo woodlands was forecasted to expand under all climate change scenarios. The expansions were highest under the pessimistic climate change scenario, implying that climate change may not directly imperil dry miombo woodlands. Forecasting showed the distribution of wet miombo woodlands contracting under all climate change scenarios. Wet miombo require mesic conditions to persist hence the contraction in a warming and drying environment. Wet miombo should be a priority for conservation since they are directly threatened by climate change.

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Availability of data and material Some tree species occurrence records are available from the Global Biodiversity Information Facility (www.gbif.org) and Tropicos (www.tropicos.org) online data portals. Environmental variables are available from the WorldClim (www.worldclim.org) and the Harmonized World Soil Database (www.fao.org) online data portals.

Authors' contributions Percy Jinga was responsible for conception and design of the research and acquisition, analysis, and interpretation of data. Percy Jinga also drafted the article while Jason Palagi critically revised it for intellectual content.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethics approval This article does not contain any studies with human participants or animals performed by any of the authors.

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