Tropical Ecology
https://doi.org/10.1007/s42965-023-00294-w

International Society
for Tropical Ecology

RESEARCH ARTICLE

Climate change and the potential distribution of the invasive shrub, *Leucaena leucocephala* (Lam.) De Wit in Africa

Maxwell C. Obiakara[1] · **Oluseun S. Olubode**[2] · **Kanayo S. Chukwuka**[1]

Received: 26 October 2021 / Revised: 24 December 2022 / Accepted: 27 March 2023

Abstract

Leucaena leucocephala, previously known as 'miracle tree' because of its numerous agroforestry uses has become a serious invasive species in tropical regions. Despite the risks associated with the spread of *L. leucocephala*, changes in its distribution with respect to climate are poorly understood, particularly in Africa where it has been widely introduced in more than 30 countries. To provide first-line information for the management of *L. leucocephala*, we examined its potential distribution in Africa using ecological niche modelling. We identified bioclimatic variables that determine the global distribution of *L. leucocephala*, and calibrated niche models using MaxEnt and species occurrences recorded between 1973 and 2013. The potential distribution of this species was estimated from model projections in Africa based on current and future climatic conditions. We tested the hypothesis of niche conservatism for *L. leucocephala* by comparing its climatic niche in Africa to that of its native range. Under current conditions, *L. leucocephala* is constrained between 30° S and 20° N in Africa, with the broadest distribution in East Africa. High rainfall areas in Central Africa with no known records of this species hitherto, were found to be highly suitable for its establishment. We predicted a significant decrement in the extent of areas at risk of invasion by *L. Leucocephala* under changing climates in Africa. Our results revealed that the study species occupies a similar but non-identical climatic niche in Africa in relation to its native niche. Climate change is likely to impede the spread of *L. leucocephala* in Africa.

Keywords Biological invasions · Climatic suitability · Leguminous tree · Maximum entropy · Niche dynamics · Sub-Saharan Africa

Introduction

The rapid development and increasing efficiency of intercontinental transportation and exchange systems were predicted as the main drivers of biological invasions six decades ago (Elton 1958). Currently, the spread of alien invasive species poses one of the most important threats to human wellbeing. One-sixth of global terrestrial biomes are susceptible to biological invasions (Early et al. 2016), and about 4% of global vascular plants (excluding the flora of temperate regions of Asia) have been established in new ranges worldwide due to human agency (Van Kleunen et al. 2015). Worryingly, the world's most diverse ecosystems, mainly located within resource-limited regions are more likely to face extirpations as a result of alien species invasions (Nuñez and Pauchard 2010; Early et al. 2016). In addition, the uncertainties surrounding alien species invasions in developing countries would be heightened by changing climatic conditions as humans continue to erode biogeographic barriers and augment species' dispersal potentials.

Woody plants constitute an emerging group of invasive species (Richardson and Rejmánek 2011; Rejmánek 2014). More than 700 trees and shrubs belonging to 90 families have become alien invasive species globally (Rejmánek and Richardson 2013). In Africa, leguminous trees, with 119 species out of the 289 introduced worldwide stand as the most important invaders (Richardson and Rejmánek 2011; Rejmánek and Richardson 2013). The proliferation of these plants in Africa has been mainly driven by their capacity to provide a wide range of ecosystem services

✉ Maxwell C. Obiakara
mc.obiakara@gmail.com

[1] Plant Ecology Unit, Department of Botany, University of Ibadan, Ibadan, Nigeria

[2] Department of Crop Protection and Environmental Biology, University of Ibadan, Ibadan, Nigeria

including timber, fuel wood, and erosion control (Nair et al. 1985; Schroth et al. 1996; Okogun et al. 2000; Chakeredza et al. 2007). However, these so-called multipurpose trees, also known as conflict species, often cause more harm than good in their new habitats (Dickie et al. 2014). Amidst the heightened risks posed by invasive plants globally, some guidelines have been recently published with hopes to preventing and mitigating the deleterious impacts of alien trees (Brundu et al. 2020).

Leucaena leucocephala is a small, fast-growing leguminous tree, usually 3–15 m tall, and one of the world's worst invasive species. It originates from Central America, specifically, Mexico (Hughes 2012). This shrub was widely introduced into tropical Africa in the 19th century mainly as an agroforestry species (Heuzé and Tran 2015). The widespread introduction of *L. leucocephala* is mainly due to its numerous uses; its leaves are highly nutritious and serve as an important dietary supplement for ruminants in Sub-Saharan Africa (Mtenga and Shoo 1990; Garcia et al. 1996; Akingbade et al. 2001; Chakeredza et al. 2007; Pamo et al. 2007). Although this species is an important source of domestic biofuel (Fuwape and Akindele 1997; Ishengoma et al. 1997) and green manure (Kang et al. 1994; Dzowela et al. 1998), its high invasive potential appears to be underrated in Africa. Among the traits that promote the spread of *L. leucocephala* in introduced habitats, its capacity for self- and cross-fertilization is noteworthy (Hughes 2012). This shrub is also remarkable for its fecundity and seed longevity, with up to 30,000 viable seeds (per plant) that can persist in soil for at least 10 years after dispersal (Raghu et al. 2005).

Apart from the important role of reproductive traits in the invasiveness of *L. leucocephala*, this species efficiently utilises atmospheric nitrogen through symbiosis with rhizobia-type bacteria. The potential of *Leucaena leucocephala* for biological nitrogen fixation greatly surpasses that of other nitrogen-fixing invasive trees such as *Gliricidia sepium* (Jacq.) Walp., *Albizia lebbeck* (L.) Benth. and *Casuarina equisetifolia* L. Danso et al. (1992) and Liya et al. (1990) estimated the nitrogen fixation rate of *L. leucocephala* at 304 kg ha^{-1} annually. However, higher rates between 448 and 548 kg ha^{-1} year^{-1} suggest a potential for dramatic shifts in soil nitrogen (Sanginga et al. 1985). Moreover, the poor establishment of *L. leucocephala* in previously non-invaded soils as reported by Sanginga et al. (1985) indicates that a low abundance of rhizobia in the soil is a major constraint to the invasive success of this species. Although invasion-induced shifts in soil nitrogen have not been explicitly linked with *L. leucocephala*, this species, like most nitrogen-fixing alien invaders is more likely to profoundly alter soil microbial communities and nitrogen cycling in invaded habitats (Castro-Díez et al. 2014).

The spread of *L. leucocephala* currently poses serious problems in 32 African countries (Roskov et al. 2006). In East Africa, this species aggressively colonizes humid habitats in coastal lowland and riparian areas (Witt et al. 2018). It has been classified as a potential transformer in South Africa given its capacity to irreversibly alter species diversity in invaded habitats (Henderson 2001). Severe ecological impacts have been attributed to the persistence of *L. leucocephala* in Kenya where it displaces native species and creates suitable conditions for further expansion (Witt et al. 2018). Despite this, the ecological impacts of this species are poorly documented in many regions of Africa. So far, the extent of habitats that might be susceptible to invasion by *L. leucocephala* in Africa has not been assessed, and it is not clear whether the spread of this species is driven by a niche shift, a phenomenon whereby it would be able to thrive well outside its native range, even under dissimilar ecological conditions (Pearman et al. 2008; Soberón and Nakamura 2009; Guisan et al. 2014). Indeed, the prevalence of climatic niche shifts is higher than previously estimated among alien invasive plant species (Atwater 2021), and this has raised concerns about the validity of geographic projections of species niches across space and time (Pili et al. 2020).

Estimations of species' ecological in geographic space are commonly known as species distribution models or bioclimatic niche models (Franklin and Miller 2010; Peterson et al. 2012). They have found a wide range of applications in ecology and biogeography, and have been driven by the increasing availability of extensive, open-source online repositories housing climatic, edaphic and species occurrence data (Sofaer et al. 2019). In this study, we used bioclimatic niche models to identify potentially suitable geographic areas at risk of invasion by *L. leucocephala* under current and future climate scenarios in Africa, and determined whether the climatic niche of this species has changed after its introduction. Specifically, our objectives were to (1) identify the combination of climate variables that influence the distribution of *L. leucocephala* in Africa, (2) estimate its potential current and future distributions and (3) test the hypothesis of niche conservatism for this species in Africa.

Methods

Species occurrence data

Since *L. leucocephala* has spread beyond tropical areas, we considered its occurrences from all continents, except Antarctica (Fig. 1). We downloaded georeferenced occurrence data for this species from the Global Biodiversity Facility

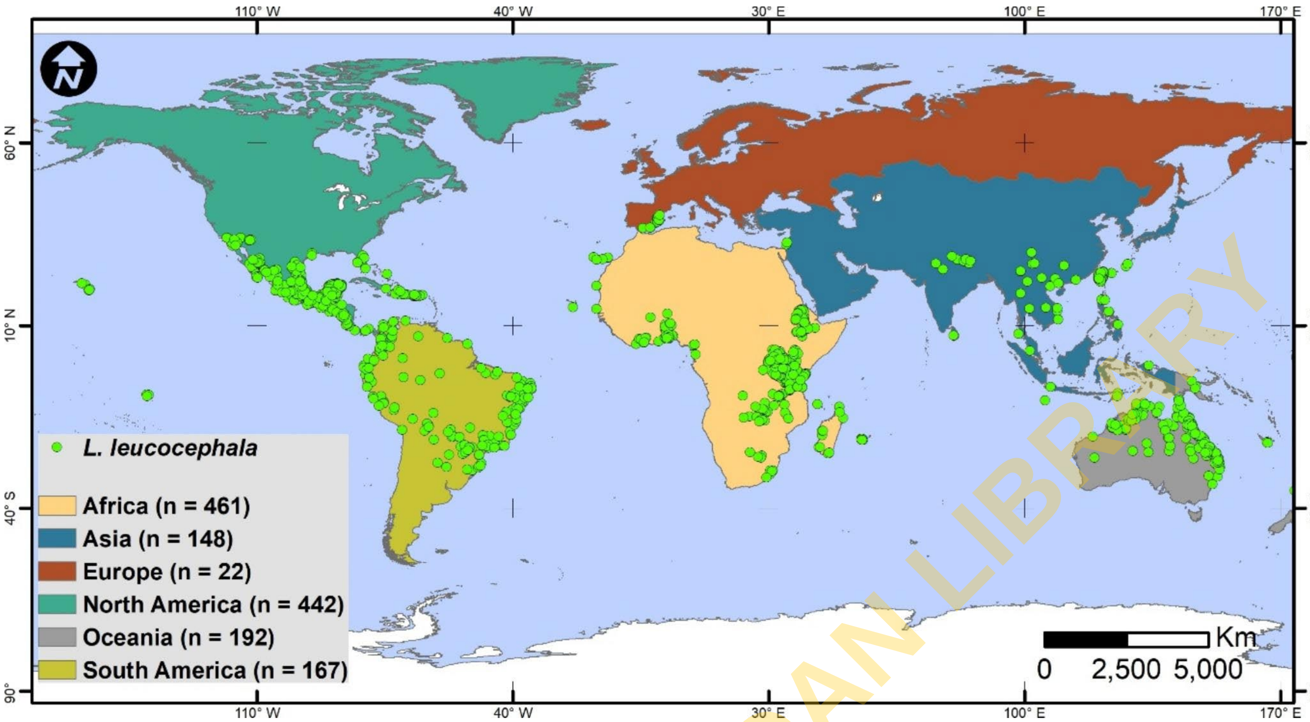


Fig. 1 Global distribution of *Leucaena leucocephala*. Map based on current GBIF records between 1973 and 2013

(https://www.gbif.org/). To match the timeframe of the climate dataset used in this study (Sect. 2.2), our GBIF query was restricted to all native and introduced occurrences of *L. leucocephala* recorded between 1973 and 2013. We cleaned these data by first focusing on locations for which positional accuracy was unknown, and retained those published by research institutions, including nongovernmental organisations. Data in these categories were further filtered to include only records from human observations and herbarium/preserved specimens, while those without a known basis of record were excluded. Occurrence records for which no institution of origin was available were restricted to reliable human observations, often supported with evidence of the study species growing in the wild. Finally, we removed geographically inaccurate records, that is, those with coordinate uncertainty > 10 km—the resolution at which our analyses were performed.

To further improve the quality of our dataset, the last cleaning steps consisted in the removal of wrongly georeferenced records, including those that mapped in oceans, outliers on small and remote islands, and managed specimens in non-naturalized ranges. We used the functionalities of the *CoordinateCleaner* package (Zizka et al. 2019) to exclude occurrences that are likely to be cultivated or wrongly documented based on proximity to research institutions such as universities, botanical gardens or herbaria. Outlying occurrences, which we defined as geographically isolated points that occurred mainly on small islands, in oceans and at zero degrees of longitude and latitude were also excluded. Finally, we applied a spatial filtering algorithm based on a minimal distance of 10 km between occurrences using the *spThin* package (Aiello-Lammens et al. 2015). In the end, the data cleaning procedure resulted in 1,432 unique occurrences of *L. leucocephala* distributed across Africa (461), Asia (148), Europe (22), North America (442), Oceania (192) and South America (167) (Fig. 1).

Bioclimatic variable selection

The bioclimatic data used as predictors in this study are derived from basic climatic variables. These variables represent relevant seasonal trends and physiological limits of species (Pearson and Dawson 2003; O’donnell and Ignizio 2012). Current bioclimatic variables (Table 1) were downloaded from the climatologies at high resolution for the earth’s land surface areas database, CHELSA (Karger et al. 2017). We chose the CHELSA dataset because of its more recent temporal coverage for the current climate (1973–2013), and improved performance for predicting species distributions (Karger et al. 2017). For future climates, data from AFRICLIM were considered as they effectively capture fine-scale climatic variations, especially over coastal and high-elevation areas in Africa (Platts et al. 2015). We selected the means of AFRICLIM-ENSEMBLES 3.0, which are derived from a wide range of general circulation models under the intermediate Representative Concentration

Table 1 List of bioclimatic variables used in this study

Variable	Code	Unit
Annual Mean Temperature	**Bio 1**	**°C/10**
Mean Diurnal Range	Bio 2	°C
Isothermality (Bio 2/Bio 7) (× 100)	Bio 3	None
Temperature Seasonality (standard deviation ×100)	Bio 4	°C
Max Temperature of Warmest Month	**Bio 5**	**°C/10**
Min Temperature of Coldest Month	**Bio 6**	**°C/10**
Temperature Annual Range (Bio 5 - Bio 6)	Bio 7	°C/10
Mean Temperature of Wettest Quarter	Bio 8	°C/10
Mean Temperature of Driest Quarter	Bio 9	°C/10
Mean Temperature of Warmest Quarter	**Bio 10**	**°C/10**
Mean Temperature of Coldest Quarter	**Bio 11**	**°C/10**
Annual Precipitation	**Bio 12**	**mm/year**
Precipitation of Wettest Month	**Bio 13**	**mm/month**
Precipitation of Driest Month	**Bio 14**	**mm/month**
Precipitation Seasonality (Coefficient of Variation)	Bio 15	None
Precipitation of Wettest Quarter	**Bio 16**	**mm/quarter**
Precipitation of Driest Quarter	**Bio 17**	**mm/quarter**
Precipitation of Warmest Quarter	Bio 18	mm/quarter
Precipitation of Coldest Quarter	Bio 19	mm/quarter

Variables in bold which represent temperature and rainfall extremes were selected

Pathway (RCP 4.5) and its worst-case equivalent (RCP 8.5) for which average global temperature is predicted to increase by 1.8° C and 3.7° C, respectively, at the end of this century (Stocker 2013). CHELSA bioclimatic layers were cropped to all continents where *L. leucocephala* occurs (excluding Antarctica) and aggregated to match the 5' resolution of AFRICLIM data using SDM Toolbox 2.4 (Brown 2014).

As a species that essentially occurs in tropical regions where the climate is characterised by alternating dry and wet seasons, the temperature and rainfall requirements of *L. leucocephala* range between 25 and 30 °C and 650–3000 mm, respectively (Shelton and Brewbaker 1994). Thus, out of the initial dataset comprising 19 bioclimatic variables, we selected 10 that better reflect annual, quarterly and monthly trends in temperature and precipitation in the study area, and excluded derived variables such as Isothermality, Temperature Seasonality, Temperature Annual Range and Precipitation Seasonality (Table 1). We also excluded variables that present a combination of temperature and rainfall data because of spatial inconsistencies associated with them (Escobar et al. 2014). The 10 selected bioclimatic variables were combined into 20 simple candidate predictor sets, each containing four to six variables as follows: (1) annual averages of temperature (Bio 1) and rainfall (Bio 12), (2) variables capturing monthly (Bio 5 and Bio 6) and quarterly (Bio 10 and Bio 11) temperatures extremes, and (3) those representing monthly (Bio 13 and Bio 14) and quarterly (Bio 16 and Bio 17) rainfall extremes as illustrated in Fig. 2.

The final step in the selection of optimal bioclimatic variables (described below) was based on the performance of models created with each set of candidate predictors. The relative importance of bioclimatic variables in the best predictor sets was also determined as described in the last paragraph of the next section.

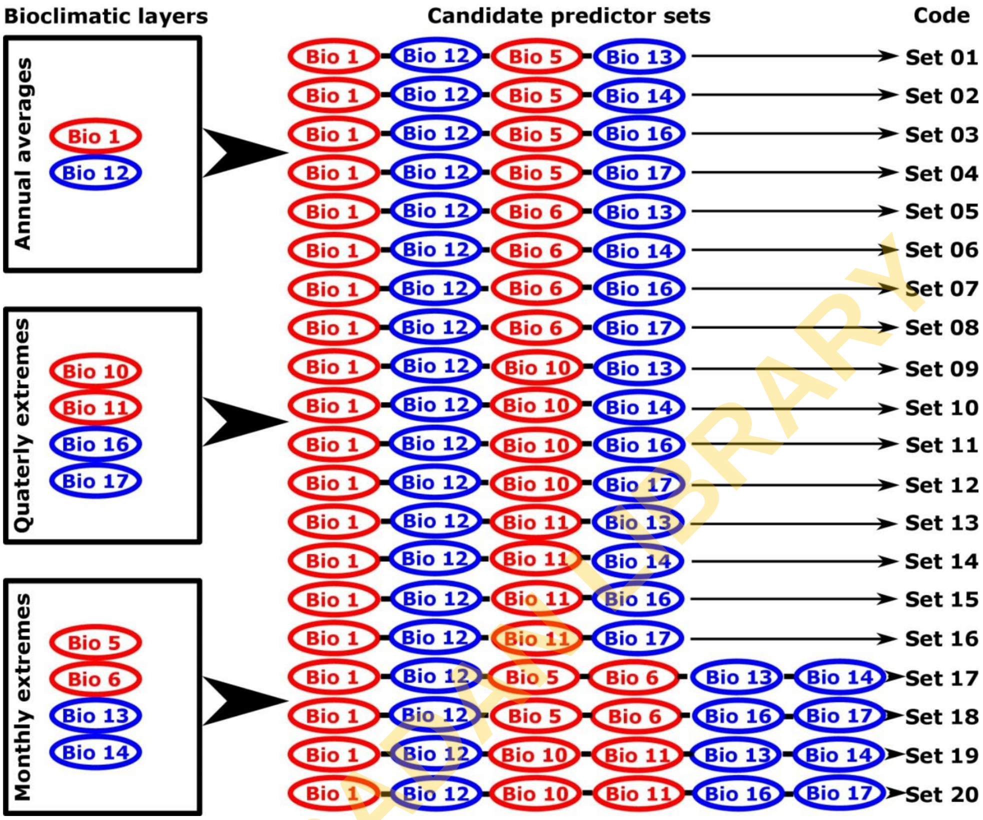
Ecological niche modelling

Models were generated across the global distributional range of *L. leucocephala* using the maximum entropy modelling algorithm (Phillips et al. 2006) implemented in MaxEnt 3.4.0. Although numerous approaches have been developed and used to model species' niches, our preference for MaxEnt is based on its solid performance among algorithms requiring only presence data (Kaky et al. 2020; Lissovsky and Dudov 2021) and its efficiency in handling collinearity among in predictor variables (De Marco and Nóbrega 2018; Feng et al. 2019). We exploited the functionalities of *kuenm*, an R package for building detailed ecological niche models with MaxEnt (Cobos et al. 2019b). The *kuenm* package is particularly handy for fine-tuning MaxEnt models by assessing the effect of predictor variables on model performance across multiple parameters and facilitating important post-modelling analyses. The workflow used in this section is represented in Fig. 3.

To determine the best climate predictor set for *L. leucocephala* and its potential distribution, we calibrated 100 models for each predictor set, using 20 regularization multipliers (0.10 – 1.0 at 0.1 interval, then, 2.0, 2.5, 3.0, 3.5, 4.0, 5.0, 6.0, 7.0, 8.0 and 10.0) and five basic feature classes (linear = l, linear-quadratic = lq, linear-quadratic-product = lqp, linear-quadratic-product-threshold = lqpt and linear-quadratic-product-threshold-hinge = lqpth) (Cobos et al. 2019b). Feature classes are mathematical transformations, which when applied to predictor variables can provide an assessment of their biological tenability in a model. Regularisation multipliers reduce model over-fitting to training data by penalising models wherein the presence of additional parameters fails to increase predictive power.

To ensure better model transferability across geographic space (Roberts et al. 2017), spatial autocorrelation in training and testing data was minimized by partitioning occurrences using the *ENMeval* package (Muscarella et al. 2014). We assigned occurrence records into four equal spatial blocks and created three datasets with randomly selected

Fig. 2 Climate variable selection scheme. Twenty candidate predictor built from 10 bioclimatic variables



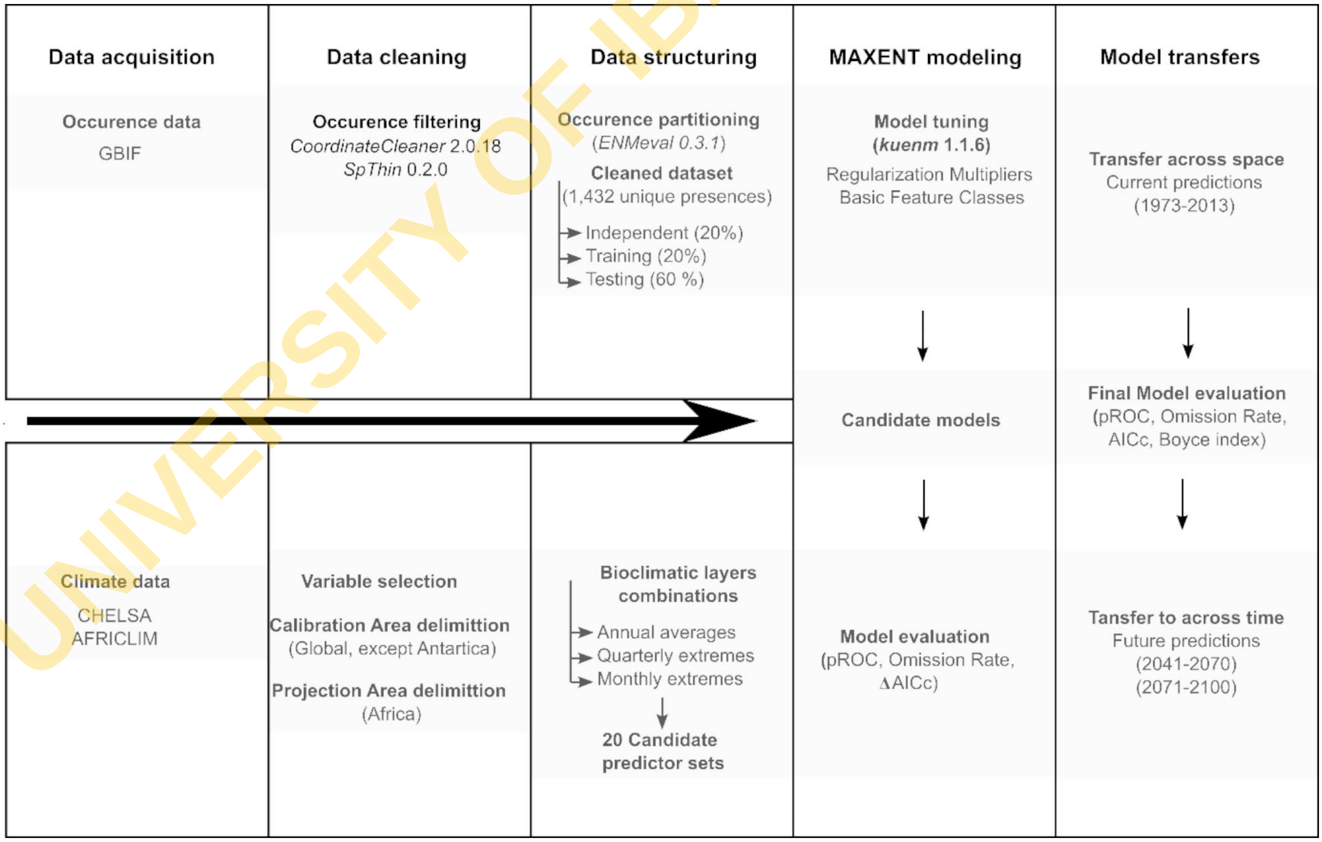


Fig. 3 Workflow of ecological niche modelling. These steps are described in Sect. 2.3

occurrences within each block for model calibration, internal validation and final/out-of-sample validation. Data were pooled across blocks so that calibration and internal validation were performed with 60% and 20% of the occurrences, respectively. The remaining 20% of *L. leucocephala* records, amounting to 287 were held out for final model evaluation. Finally, we selected 10,000 random points across the study area as background locations for model fitting.

MaxEnt models built using *kuenm* are evaluated through three criteria. First, statistical significance is assessed using the partial area under the Receiver Operating Characteristic approach, pROC (Peterson et al. 2008). Then, models are screened based on predictive power and complexity through the omission rate, OR (Anderson et al. 2003) and Akaike Information Criterion corrected for small sample sizes ΔAICc (Warren and Seifert 2011), respectively. Here, the previously identified, best set of predictor variables was used to calibrate 30 candidate models with simpler feature classes (l, q, p, lq, lp, and qp) and five regularisation multipliers (0.08–0.12 at 0.01 interval). We considered statistically significant models ($\text{pROC} \leq 0.05$) and selected the one with the lowest ΔAICc and an $\text{OR} \leq 5\%$ as the best and final model. While evaluating this model, we created 100 replicates and set the percentage of training data omission error at 5%. Further evaluation was also performed with the Continuous Boyce Index (Hirzel et al. 2006) using the *ecospat* package (Di Cola et al. 2017). The final model was transferred to Africa and projections were created by extrapolation and clamping. The risk of extrapolation in current climatic conditions in Africa was assessed using the mobility-oriented parity metric, MOP (Owens et al. 2013).

Future projections were also made for 2041–2070 and 2085–2100 to assess potential changes in the distribution of the species. The probability of occurrence of *L. leucocephala*, p was estimated using the complementary log-log (*cloglog*) transformed output of Maxent (Phillips et al. 2017). Climatic suitability was categorised by reclassifying model outputs as follows: very low suitability ($0 \leq p \leq 0.25$), low suitability ($0.25 < p \leq 0.50$), high suitability ($0.50 < p \leq 0.75$) and very high suitability ($0.75 < p \leq 1.00$). MaxEnt offers numerous thresholding options for converting continuous predictions into binary outputs. We used the 10th percentile training presence threshold which allows for the selection of 9/10th of the training locations that the model predicted correctly and assumes that the remaining training sites were erroneously predicted as suitable for the study species.

The variables that mostly influence the distribution of *L. leucocephala* were assessed based on metrics of contribution percentage, permutation importance and a jackknife analysis. In this procedure, model accuracy was compared with predictions from a set of models calibrated by leaving out one of the six bioclimatic variables each time, and another set of models built using each variable separately.

Niche change quantification

The climatic niche of *L. leucocephala* was quantified using the PCA-environment approach proposed by Broennimann et al. (2012). This method has been widely used to investigate niche dynamics in invasive plant species (Petitpierre et al. 2012; Goncalves et al. 2014; Atwater et al. 2018; Datta et al. 2019). We performed a principal component analysis between climate data for Mexico, which was considered as the native range of *L. leucocephala* (Hughes 2012) and Africa using the best set of bioclimatic variables identified in Sect. 2.3. Occurrence records for this species were weighted to ensure that ranges were represented in the same proportion (Broennimann et al. 2012). We considered the two scenarios of occurrence density correction to assess possible changes in niche overlap results. The resulting two-dimensional climatic space was then divided into a grid of 100 × 100 cells. Occurrences and available climates within each cell were smoothed using a Gaussian kernel density function (Broennimann et al. 2012). Then, to quantify the degree of niche overlap between the native and exotic ranges of *L. leucocephala*, we used Schoener's index (D) (Schoener 1968), defined as 0 (no overlap) $\leq D \leq$ 1 (perfect overlap). Low values of D suggest niche divergence. This metric was computed across a range of percentiles (5%, 10%, 15%, 20% and 25%) used to exclude areas with low climatic density values and assess the influence of rare climatic conditions on niche dynamics (Guisan et al. 2014).

We statistically evaluated the observed overlap (D_{obs}) between the two niches using the niche equivalency and similarity tests developed by Warren et al. (2008). In the first test, niche overlap (D_{sim}) was recalculated using simulated niches created by combining and randomly reassigning occurrences of *L. leucocephala* between the native and exotic ranges. We compared these values and rejected the hypothesis of niche equivalency when D_{obs} was significantly lower ($p < 0.05$) than D_{sim}. This test is conservative as it only takes into account climatic conditions at the exact geographical locations of the species of interest and does not consider those in background environments (Warren et al. 2008). In the complementary similarity test, a new overlap D'_{sim} was computed between niches built using environmental conditions, randomly selected at background locations within the study ranges. The niches of *L. leucocephala* were considered more similar than expected by chance if $D_{obs} > D'_{sim}$. These tests were based on 1,000 random replicates for increased statistical power (Broennimann et al. 2012).

Table 2 Model parameters and performance

P.set	RM	FC	pROC	OR_b	OR_a	AICc	ΔAICc	wAICc	N
Set 17	0.08	LQ	0.00	0.045	0.038	29761.23	0.00	0.60	12
Set 17	0.09	LQ	0.00	0.045	0.042	29762.01	0.78	0.40	12

P.set: Predictor set; RM: Regularization multiplier; pROC: partial ROC; OR_b, OR_a: Omission rate before and after final model evaluation respectively; AICc, ΔAICc, wAICc: Akaike Information criterion, delta AICc, weighted AICc respectively; N: number of model parameters

Finally, niche dynamics was assessed using the *Unfilling*, *Expansion* and *Stability* metrics of the COUE framework proposed by Guisan et al. (2014). *Expansion* (*E*) represents occupied areas in the exotic niche space that do not exist in the species' native range. Conversely, *Unfilling* (*U*) is the proportion of the native niche occurring solely in the indigenous range. *Stability* (*S*) is a measure of niche conservatism, and depicts the conditions common to both niches (Guisan et al. 2014). These metrics range between 0 and 1. Thus, a species' niche is considered perfectly conserved when S = 1. We calculated these metrics using all available climates in both ranges and at the intersection of both niche spaces. To assess the effect of marginal climates on these metrics, we compared the results obtained with 95%, 85% and 75% of shared climatic conditions between native and exotic ranges (Guisan et al. 2014). These analyses were implemented using the *ecospat* package (Di Cola et al. 2017).

Results and discussion

Optimal climate variables for *L. leucocephala*

Only two out of the 2,030 candidate models calibrated in this study were statistically significant and met the omission rate and ΔAICc criteria (Table 2). Although both models were similar in many aspects, including feature class combination, predictor set and the number of parameters, the best model was chosen after final evaluation, i.e., using occurrences withheld from model calibration (omission rate < 0.04, ΔAICc = 0). Further model performance assessment showed an exponential increase in the predicted-to-expected ratio as a function of climatic suitability (Appendix 1) and a Boyce index of 0.99. Thus, the current and future predictions of *L. leucocephala* were based on this model.

Environmental variable selection is a crucial step in correlative species distribution modelling, and several methods have been used in this process (Fan et al. 2018). Here, we relied on a recent approach that identifies the most suitable variable combinations and optimal model settings for increased predictive power (Cobos et al. 2019a). In our approach to determining relevant predictors for the distribution of *L. leucocephala*, we found that only one of the 20 candidate datasets best reflected the climatic requirements of this species. The identified set of predictors comprised Annual Mean Temperature (Bio 1), Maximum Temperature of Warmest Month (Bio 5), Minimum Temperature of Coldest Month (Bio 6), Annual Precipitation (Bio 12), Precipitation of Wettest Month (Bio 13) and Precipitation of Driest Month (Bio 14).

Table 3 Importance metrics of bioclimatic variables for predicting the potential distribution of *L. leucocephala*

Variable	Variable contribution (%)	Permutation importance (%)	TG_a	TG_b
Bio 1	2.85	13.40	0.76	1.16
Bio 5	8.02	16.34	0.54	1.11
Bio 6	78.30	42.92	0.89	1.12
Bio 12	4.63	10.14	0.41	1.10
Bio 13	1.82	12.47	0.48	1.11
Bio 14	4.39	4.73	0.05	1.12

TG_a: Training gain with variable; TG_b = Training gain without variable

Jackknife results shown in Table 3 revealed that the three most important bioclimatic predictors were Minimum Temperature of the Coldest Month (Bio 6), Annual Temperature (Bio 1) and Maximum Temperature of the Warmest (Bio 5). When considered separately, Bio 6 provided the most significant amount of information not present in other variables, and explained 78% of the potential distribution of *L. leucocephala.* All other variables had a marginal contribution, below 10%. The higher contribution and permutation importance of Bio 6, Bio 5 and Bio 1 suggest that temperature rather than rainfall is a crucial factor that determines the geographic range of the study species. This finding is consistent with the results of Wan et al. (2018). Similarly, Chiou et al. (2013) showed that, even at local scales, mean annual temperature is a key variable for *L. leucocephala*, with a contribution of 22% in relation to thirteen other predictors comprising landscape and anthropogenic factors. Among the three rainfall-derived variables in our study, variable contribution was highest for Annual Precipitation (Bio 12) as previously reported (Wan et al. 2018).

There are indications that *L. leucocephala* is constrained by variables other than climate, especially elevation and soil pH (Shelton and Brewbaker 1994). However, such factors play a more defining role at local scales as evidenced by the findings of Chiou et al. (Chiou et al. 2013) in Taiwan, wherein altitude was the second most important contributor after annual precipitation. A similar trend can be expected for edaphic variables, considering the negligible contribution of soil pH, sand and clay content in the global niche model of *L. leucocephala* developed by Wan et al. (2018). These findings support the notion that the environmental factors that define the distribution of *L. leucocephala* are scale-dependent (Pearson and Dawson 2003).

Current potential distribution of *L. leucocephala* in Africa

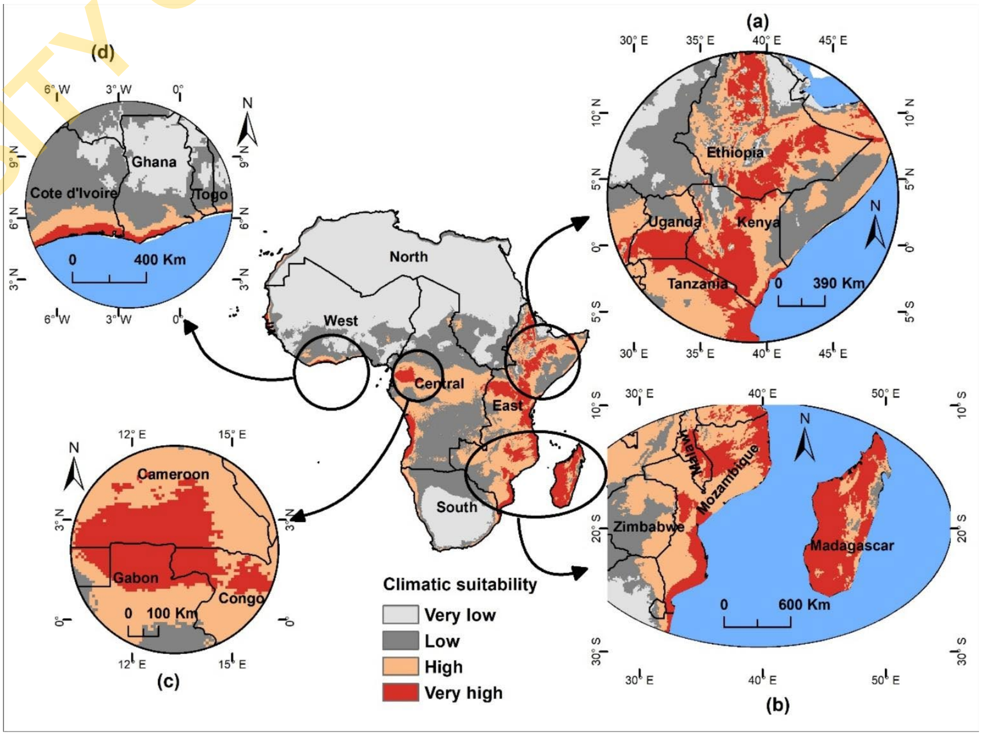
Using presence records of *L. leucocephala* from across its native range and the rest of the world, we found that a substantial extent of the climatic space in Africa, defined by the six selected bioclimatic variables was suitable for this species. Climatic suitability based on the minimum training presence threshold indicated that the study species is essentially limited to Sub-Sahara Africa, and has little or no chance of establishing in arid regions (Fig. 4). This prediction closely matches the observed spatial distribution of *L. leucocephala* in Africa, and ties well with the results of Wan et al. (2018). However, the reliability of these predictions cannot be ascertained for North Africa due to high extrapolation. The results of the MOP analysis suggest that climatic conditions in this region were different from the prevalent ones in the calibration area (Appendix 2).

Although Southern Africa has the highest number of invasive leguminous trees and shrubs (Rejmánek 2014), our models predicted that the current climate in this region was largely unfavourable for *L. leucocephala* (Fig. 4). This is a confirmation of the previously reported reduced invasive potential of the study species, particularly in South Africa due to suboptimal climatic conditions (Olckers 2011). Extensive herbivory has also been associated with the low occurrence of *L. leucocephala* in this country (Neser and Klein 1998). However, the presence of suitable climatic conditions in coastal areas in two South African provinces, namely Mpumalanga and KwaZulu-Natal suggests that this region can support the establishment of the study species. These predictions are largely reliable as annual rainfall in these provinces exceed the minimum rainfall requirements of this species (Olckers 2011).

In line with the predictions of Wan et al. (2018), climate across Eastern Africa was highly suitable for *L. leucocephala*. Areas with the highest predicted suitability were mainly concentrated between 30° S and 20° N in this region, across Ethiopia, Kenya, Madagascar, south of Uganda, and throughout the coast of Mozambique. Climatic suitability for *L. leucocephala* decreased from East to West Africa (Fig. 4). Despite the absence of occurrence records of the study species in Central Africa, areas with favourable climates were identified in this region, mainly along the borders between Gabon and Congo. The risk of establishment of the study species was lowest in West Africa as highly suitable areas were restricted along the Atlantic coast, from Benin to Côte d'Ivoire. It is worth noting that current model projections highlight the affinity of *L. leucocephala* for coastal climates throughout Africa.

Areas where climatic suitability for *L. leucocephala* was low included south-eastern Nigeria, south-western Cameroon, Liberia, Guinea, Gambia and Sierra Leone. The risk

Fig. 4 Current distribution of *L. leucocephala* in Africa. Continuous predictions in all regions (a-b) are based on potentially suitable climates for this species using data global presence records



map obtained in the present study is comparable to that of Wan et al. (2018) though we recorded different suitability levels, especially in eastern Ethiopia and the Democratic Republic of Congo. The discrepancies reported here can be attributed to the choice of predictor variables. Though the inclusion of edaphic variables may have enhanced model performance (Velazco et al. 2017; Zuquim et al. 2020), their study comprised several species, and therefore, could not have been specifically optimized for *L. leucocephala*. Model predictions for Central Africa would be of great interest given the absence of the study species in the biologically diverse Central African region.

Invasion risk of *L. leucocephala* in Africa under climate change

Our models predicted an important loss in the future potential range of *L. leucocephala* in Africa (Fig. 5). For example, 17.44% of the study area predicted as suitable ($0.50 < p \leq 0.75$) in the current climate would reduce to 10.03% and 8.67% from 2041 to 2070 under RCP 4.5 and RCP 8.5, respectively (Fig. 5a & b). A further decrease was recorded for the second period (2071–2100), with only about 5% of the study area for RCP 8.5 (Fig. 5d). For the highest suitability class ($p > 0.75$), the predicted area across the selected future climate change scenarios was below 2%. Thus, these results support the notion that climate change will not promote the expansion of *L. leucocephala.* Although there is evidence for range contractions for some invasive plants species as a result of climate change (Taylor et al. 2012), the converse is often associated with anticipated future changes in temperature and rainfall patterns (Thuiller et al. 2007; Early et al. 2016). In line with previous results (Bellard et al. 2013), *L.leucocephala* is one of the world's worst terrestrial invasive plants for which range contraction is predicted as a result of climate change by the end of this century.

Niche dynamics of *L. leucocephala* in African regions

The first two principal components generated using the PCA-env approach captured 84.34% of the climatic data in the study space (Fig. 6a). Among the selected variables, Annual Mean Temperature (Bio 1), Maximum Temperature of Warmest Month (Bio 5) and Annual Precipitation (Bio 12) had the highest contribution (Appendix 3). Regardless of the threshold used to exclude rare climatic conditions, niche overlap between Mexico and Africa, computed after correcting occurrence densities of *L. leucocephala* as recommended by Broennimann et al. (2012) was low (Schoener's $D = 0.19$). A higher overlap ($D = 0.59$) was obtained when occurrence densities in each range were not corrected. Although density correction is meant to reduce bias in niche space, especially when the species in question occurs in geographically isolated regions (Broennimann et al. 2012), this procedure underestimated niche overlap in our study. Indeed, this approach has been shown to alter the original pattern in presence data, and might not be useful, especially in high-elevation areas (Datta et al. 2019).

The estimated niche overlap in the climatic space occupied by *L. leucocephala* between its native range and Africa was approximately 0.6, which is considered moderate (Rödder and Engler 2011). This overlap fell well below the simulated overlap values (*p-value* < 0.05; Fig. 6b), thereby suggesting non-equivalency of niches. However, the niche similarity test, which examined whether the observed niche overlap is affected by background environmental space, revealed that the climatic niche occupied by the study species in Africa was more similar to that of its native range than would be expected by chance (Fig. 6c). Niche dynamics indices computed at the intersection of both ranges showed very limited expansion in the exotic range ($E = 0.01$) and a high degree of stability ($S = 0.99$). These values were similar regardless of the percentage used to exclude marginal climates.

Our results revealed that the study species occupies a similar but non-identical climatic niche in Africa in relation to its native range. This implies that *L. leucocephala* has conserved its climatic niche in Africa. There is no consensus on alien invasive species niche dynamics as previous works have reported niche conservatism (Petitpierre et al. 2012; Early and Sax 2014; Liu et al. 2020), while others support large niche shifts, especially in perennial species (Atwater et al. 2018). Our findings support the hypothesis of niche conservatism in *L. leucocephala* and provide a robust basis for the use of ecological niche modelling for predicting its distribution in Africa. Niche conservatism in *L. leucocephala* can be explained by its relatively short residency time since its introduction in Africa (Peterson 2011).

Conclusion

In this study, we assessed the potential distribution of the invasive *L. leucocephala* under present and future climatic conditions in Africa and analysed its climatic niche dynamics. Our results highlighted several suitable areas, especially in eastern Africa where more detailed risk assessments would be necessary. The results of this study are based on the application of the most recent approaches for building more meaningful ecological niche models, including extensive parameterization across distinct candidate sets of predictor variables sets and a stepwise use of multiple

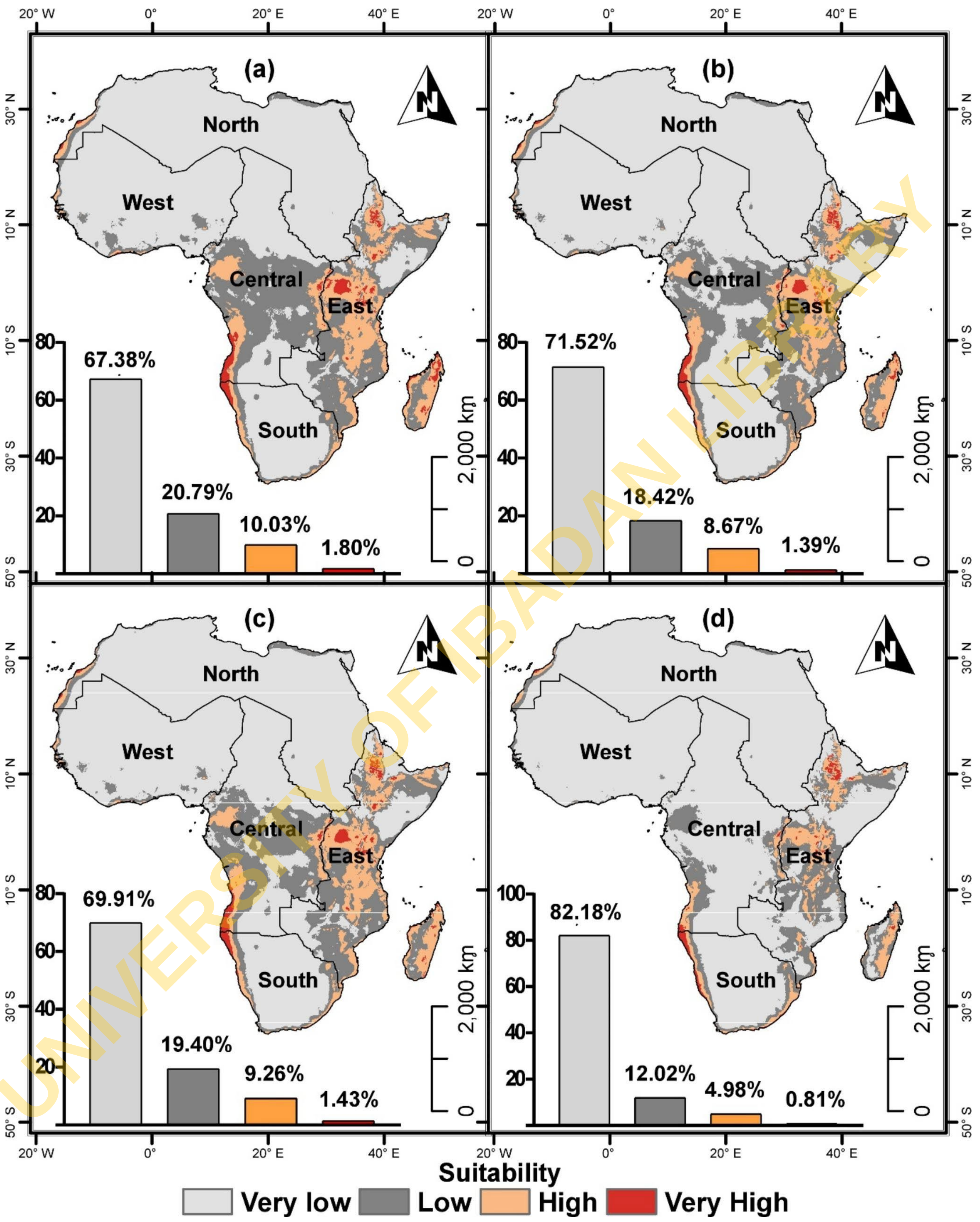


Fig. 5 Potential distribution of *L. leucocephala* in Africa under climate change. Climate change scenarios are RCP 4.5 (a & c) and RCP 8.5 (b & d) for 2041–2071 (top row) and 2071–2100 (bottom row). Bar plots show the proportions of each climate suitability class derived from the maps

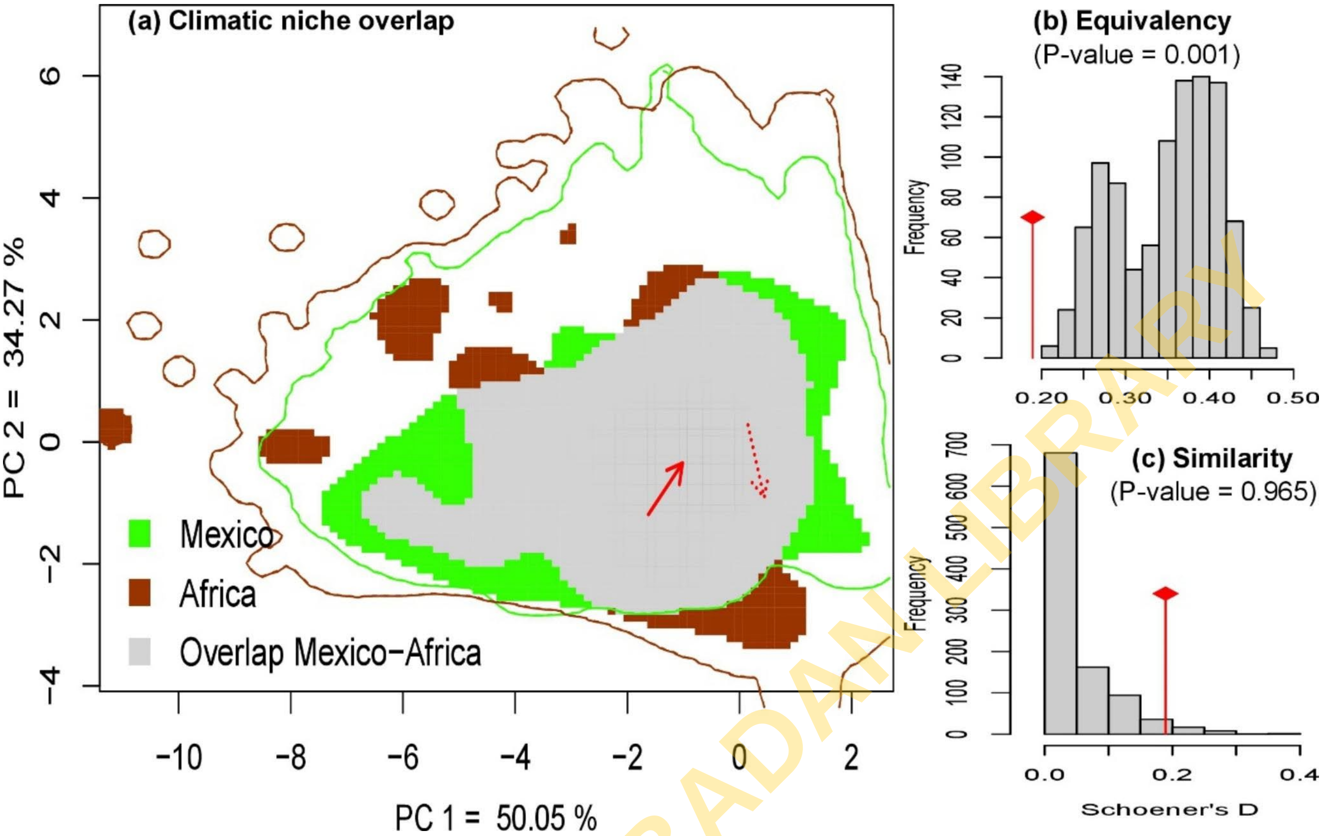


Fig. 6 Climatic niche dynamics of *L. leucocephala*. Green and brown depict climatic areas occupied by the study species in its native and invaded ranges, respectively; grey indicates climates occupied in both ranges (a). The left arrow (continuous line) represents the centroid shift from the native to invaded niche, while the right one (dashed line) shows the shift between native and invaded range. Niche equivalency (b) and similarity (c) were performed with 1000 replications. The red diamond represents the observed overlap between the two niches

evaluation metrics. However, the main limitation here was our inability to clearly define the extent of areas accessible to this species given its near cosmopolitan distribution. The projections produced in this study would provide first-line information in control programmes for *L. leucocephala* in tropical Africa. While predictions made in this study can provide useful insights into the regional risk of invasion for *L. leucocephala* in tropical Africa, local investigations, especially those including variables other than the climate in model development are still needed.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s42965-023-00294-w.

Author Contribution MCO: Conceptualization, Methodology, Formal Analysis, Visualisation, Writing - Original draft.
OOO: Writing - Review and Editing.
KSC: Writing - Review and Editing, Supervision.

Funding This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

Data Availability Occurrences of *L. leucocephala* from the Global Biodiversity Facility can be found at the GBIFData download link: DOI: https://doi.org/10.15468/dl.ztncpu. The R code used in Sect. 2.1 and 2.2 is given in Appendix 4.

Declarations

Conflict of interest The authors have no conflict of interest.

References

Aiello-Lammens ME, Boria RA, Radosavljevic A, Vilela B, Anderson RP (2015) spThin: an R package for spatial thinning of species occurrence records for use in ecological niche models. Ecography 38:541–545

Akingbade AA, Nsahlai IV, Bonsi MLK, Morris CD, Du Toit LP (2001) Reproductive performance of south african indigenous goats inoculated with DHP-degrading rumen bacteria and maintained on *Leucaena leucocephala*/grass mixture and natural pasture. Small Rumin Res 39:73–85

Anderson RP, Lew D, Peterson AT (2003) Evaluating predictive models of species' distributions: Criteria for selecting optimal models. Ecol Modell 162:211–232

Atwater DZ, Ervine C, Barney JN (2018) Climatic niche shifts are common in introduced plants. Nat Ecol Evol 2:34–43

Bellard C, Thuiller W, Leroy B, Genovesi P, Bakkenes M, Courchamp F (2013) Will climate change promote future invasions? Glob Chang Biol 19:3740–3748

Broennimann O, Fitzpatrick MC, Pearman PB, Petitpierre B, Pellissier L, Yoccoz NG, Thuiller W, Fortin MJ, Randin C, Zimmermann NE, Graham CH, Guisan A (2012) Measuring ecological niche overlap from occurrence and spatial environmental data. Glob Ecol Biogeogr 21:481–497

Brown JL (2014) SDMtoolbox: a python-based GIS toolkit for landscape genetic, biogeographic and species distribution model analyses. Methods Ecol Evol 5:694–700

Brundu G et al (2020) Global guidelines for the sustainable use of non-native trees to prevent tree invasions and mitigate their negative impacts. NeoBiota 61:65–116

Castro-Díez P, Godoy O, Alonso A, Gallardo A, Saldaña A (2014) What explains variation in the impacts of exotic plant invasions on the nitrogen cycle? A meta-analysis. Ecol Lett 17:1–12

Chakeredza S, Hove L, Akinnifesi FK, Franzel S, Ajayi OC, Sileshi G (2007) Managing fodder trees as a solution to human-livestock food conflicts and their contribution to income generation for smallholder farmers in southern Africa. Nat Resour Forum 31:286–296

Chiou C-R, Wang H-H, Chen Y-J, Grant WE, Lu M-L (2013) Modeling potential range expansion of the Invasive Shrub *Leucaena leucocephala* in the Hengchun Peninsula, Taiwan. Invasive Plant Sci Manag 6:492–501

Cobos ME, Peterson AT, Osorio-Olvera L, Jiménez-García D (2019a) An exhaustive analysis of heuristic methods for variable selection in ecological niche modeling and species distribution modeling. Ecol Inf 53:100983

Cobos ME, Townsend Peterson A, Barve N, Osorio-Olvera L (2019b) *kuenm*: an R package for detailed development of ecological niche models using Maxent. PeerJ 7:e6281

Danso SKA, Bowen GD, Sanginga N (1992) Biological nitrogen fixation in trees in agro-ecosystems. Plant Soil 141:177–196

Datta A, Schweiger O, Kühn I (2019) Niche expansion of the invasive plant species Ageratina adenophora despite evolutionary constraints. J Biogeogr 46:1306–1315

De Marco P, Nóbrega CC (2018) Evaluating collinearity effects on species distribution models: an approach based on virtual species simulation. PLoS ONE 13:e0202403

Di Cola V, Broennimann O, Petitpierre B, Breiner FT, D'Amen M, Randin C, Engler R, Pottier J, Pio D, Dubuis A, Pellissier L, Mateo RG, Hordijk W, Salamin N, Guisan A (2017) ecospat: an R package to support spatial analyses and modeling of species niches and distributions. Ecography 40:774–787

Dickie IA, Bennett BM, Burrows LE, Nuñez MA, Peltzer DA, Porté A, Richardson DM, Rejmánek M, Rundel PW, van Wilgen BW (2014) Conflicting values: ecosystem services and invasive tree management. Biol Invasions 16:705–719

Dzowela BH, Wandera PF, Were J, Mohammed-Saleem MA (1998) Leucaena in smallholder farming systems in Africa: challenges for development. In: ACIAR Proceedings Series, Hanoi, pp 311–318

Early R, Sax DF (2014) Climatic niche shifts between species' native and naturalized ranges raise concern for ecological forecasts during invasions and climate change. Glob Ecol Biogeogr 23:1356–1365

Early R, Bradley BA, Dukes JS, Lawler JJ, Olden JD, Blumenthal DM, Gonzalez P, Grosholz ED, Ibañez I, Miller LP, Sorte CJB, Tatem AJ (2016) Global threats from invasive alien species in the twenty-first century and national response capacities. Nat Commun 7:12485

Elton CS (1958) The Ecology of Invasions by animals and plants. University of Chicago Press, Chicago

Escobar LE, Lira-Noriega A, Medina-Vogel G, Townsend Peterson A (2014) Potential for spread of the white-nose fungus (pseudogymnoascus destructans) in the Americas: Use of Maxent and NicheA to assure strict model transference. Geospat Health 9:221–229

Fan JY, Zhao NX, Li M, Gao WF, Wang ML, Zhu GP (2018) What are the best predictors for invasive potential of weeds? Transferability evaluations of model predictions based on diverse environmental data sets for Flaveria bidentis. Weed Res 58:141–149

Feng X, Park DS, Liang Y, Pandey R, Papeş M (2019) Collinearity in ecological niche modeling: confusions and challenges. Ecol Evol 9:10365–10376

Franklin J, Miller JA (2010) Mapping species distributions: spatial inference and prediction. Cambridge University Press, Cambridge

Fuwape JA, Akindele SO (1997) Biomass yield and energy value of some fast-growing multipurpose trees in Nigeria. Biomass Bioenergy 12:101–106

Garcia GW, Ferguson TU, Neckles FA, Archibald KAE (1996) The nutritive value and forage productivity of *Leucaena leucocephala*. Anim Feed Sci Technol 60:21–41

Goncalves E, Herrera I, Duarte M, Bustamante RO, Lampo M, Velásquez G, Sharma GP, García-Rangel S (2014) Global Invasion of Lantana camara: has the climatic niche been conserved across continents? PLoS ONE 9:e111468

Guisan A, Petitpierre B, Broennimann O, Daehler C, Kueffer C (2014) Unifying niche shift studies: insights from biological invasions. Trends Ecol Evol 29:260–269

Henderson L (2001) Alien weeds and invasive plants: a complete guide to declared weeds and invaders in South Africa, including another 36 species invasive in that region. Plant Protection Research Institute (South Africa)

Heuzé V, Tran D (2015) Leucaena (*Leucaena leucocephala*). Feed a pogramme by INRAE, CIRAD, AFZ FAO. https://www.feedipedia.org/node/282

Hirzel AH, Le Lay G, Helfer V, Randin C, Guisan A (2006) Evaluating the ability of habitat suitability models to predict species presences. Ecol Modell 199:142–152

Hughes C (2012) Global Invasive Species Database. http://www.iucngisd.org/gisd/speciesname/Leucaena+leucocephala

Ishengoma RC, Gillah PR, Majaliw AS, Rao RV (1997) The quality of charcoal produced from *Leucaena leucocephala* in earth kilns from Tanzania. Indian J For 20:265–268

Kaky E, Nolan V, Alatawi A, Gilbert F (2020) A comparison between Ensemble and MaxEnt species distribution modelling approaches for conservation: a case study with egyptian medicinal plants. Ecol Inf 60:101150

Kang BT, Akinnifesi FK, Ladipo DO (1994) Performance of selected woody agroforestry species grown on an Alfisol and an Ultisol in the humid lowland of West Africa, and their effects on soil properties. J Trop For Sci 7:303–312

Karger DN, Conrad O, Böhner J, Kawohl T, Kreft H, Soria-Auza RW, Zimmermann NE, Linder HP, Kessler M (2017) Climatologies at high resolution for the earth's land surface areas. Sci Data 4:170122

Lissovsky AA, Dudov SV (2021) Species-distribution modeling: Advantages and Limitations of its application. 2. MaxEnt. Biol Bull Rev 11:265–275

Liu C, Wolter C, Xian W, Jeschke JM (2020) Most invasive species largely conserve their climatic niche. Proc Natl Acad Sci U S A 117:23643–23651

Liya SM, Odu CTI, Agboola AA, Mulongoy K (1990) Estimation of N2 fixation by nitrogen fixing trees in the subhumid tropics using 15-N dilution and difference methods In: Paper Presented at Fourth African Association for Biological Nitrogen Fixation, IITA, Ibadan, pp 23–28

Mtenga LA, Shoo RA (1990) Growth rate, feed intake and feed utilization of small east african goats supplemented with *Leucaena leucocephala*. Small Rumin Res 3:9–18

Muscarella R, Galante PJ, Soley-Guardia M, Boria RA, Kass JM, Uriarte M, Anderson RP (2014) ENMeval: an R package for conducting spatially independent evaluations and estimating optimal model complexity for Maxent ecological niche models. Methods Ecol Evol 5:1198–1205

Nair PKR, Fernandes ECM, Wambugu PN (1985) Multipurpose leguminous trees and shrubs for agroforestry. Agrofor Syst 2:145–163

Neser S, Klein H (1998) Assessment of the environmental impact of releasing Acanthoscelides macrophthalmus (Bruchidae) for the biological control of excessive seed production in *Leucaena leucocephala*. Unpublished report of the ARC-Plant Protection Research Institute, Pretoria, South Africa

Nuñez MA, Pauchard A (2010) Biological invasions in developing and developed countries: does one model fit all? Biol Invasions 12:707–714

O'donnell MS, Ignizio DA (2012) Bioclimatic Predictors for Supporting Ecological Applications in the Conterminous United States, U.S. Geological Survey Data Series 691:4–9

Okogun JA, Sanginga N, Mulongoy K (2000) Nitrogen contribution of five leguminous trees and shrubs to alley cropped maize in Ibadan, Nigeria. Agrofor Syst 50:130–136

Olckers T (2011) Biological control of *Leucaena leucocephala* (Lam.) De Wit (Fabaceae) in South Africa: a tale of opportunism, seed feeders and unanswered questions. Afr Entomol 19:356–365

Owens HL, Campbell LP, Dornak LL, Saupe EE, Barve N, Soberón J, Ingenloff K, Lira-Noriega A, Hensz CM, Myers CE, Peterson AT (2013) Constraints on interpretation of ecological niche models by limited environmental ranges on calibration areas. Ecol Modell 263:10–18

Pamo ET, Boukila B, Fonteh FA, Tendonkeng F, Kana JR, Nanda AS (2007) Nutritive value of some grasses and leguminous tree leaves of the Central region of Africa. Anim Feed Sci Technol 135:273–282

Pearman PB, Guisan A, Broennimann O, Randin CF (2008) Niche dynamics in space and time. Trends Ecol Evol 23:149–158

Pearson RG, Dawson TP (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Glob Ecol Biogeogr 12:361–371

Peterson AT (2011) Ecological niche conservatism: a time-structured review of evidence. J Biogeogr 38:817–827

Peterson AT, Papeş M, Soberón J (2008) Rethinking receiver operating characteristic analysis applications in ecological niche modeling. Ecol Modell 213:63–72

Peterson AT, Soberón J, Pearson RG, Anderson RP, Martínez-Meyer E, Nakamura M, Araújo MB (2012) Ecological niches and geographic distributions. Princeton University Press

Petitpierre B, Kueffer C, Broennimann O, Randin C, Daehler C, Guisan A (2012) Climatic niche shifts are rare among terrestrial plant invaders. Science 335:1344–1348

Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. Ecol Modell 190:231–259

Phillips SJ, Anderson RP, Dudík M, Schapire RE, Blair ME (2017) Opening the black box: an open-source release of Maxent. Ecography 7:887–893

Pili AN, Tingley R, Sy EY, Diesmos MLL, Diesmos AC (2020) Niche shifts and environmental non-equilibrium undermine the usefulness of ecological niche models for invasion risk assessments. Sci Rep 10:1–18

Platts PJ, Omeny PA, Marchant R (2015) AFRICLIM: high-resolution climate projections for ecological applications in Africa. Afr J Ecol 53:103–108

Raghu S, Wiltshire C, Dhileepan K (2005) Intensity of pre-dispersal seed predation in the invasive legume *Leucaena leucocephala* is limited by the duration of pod retention. Austral Ecol 30:310–318

Rejmánek M (2014) Invasive trees and shrubs: where do they come from and what we should expect in the future? Biol Invasions 16:483–498

Rejmánek M, Richardson DM (2013) Trees and shrubs as invasive alien species – 2013 update of the global database. Divers Distrib 19:1093–1094

Richardson DM, Rejmánek M (2011) Trees and shrubs as invasive alien species - a global review. Divers Distrib 17:788–809

Roberts DR, Bahn V, Ciuti S, Boyce MS, Elith J, Guillera-Arroita G, Hauenstein S, Lahoz-Monfort JJ, Schröder B, Thuiller W, Warton DI, Wintle BA, Hartig F, Dormann CF (2017) Cross-validation strategies for data with temporal, spatial, hierarchical, or phylogenetic structure. Ecography 40:913–929

Rödder D, Engler JO (2011) Quantitative metrics of overlaps in Grinnellian niches: advances and possible drawbacks. Glob Ecol Biogeogr 20:915–927

Roskov YR, Bisby FA, Zarucchi JL, Schrire BD, White RJ (2006) International legume database & information service: ILDIS world database of legumes : draft checklist, version 10. https://www.ildis.org/

Sanginga N, Mulongoy K, Ayanaba A (1985) Effect of inoculation and mineral nutrients on nodulation and growth of *Leucaena leucocephala* In: Proceedings of the First Conference of the African Association for Biological Nitrogen Fixation (AABNF). Nairobi

Schoener TW (1968) The Anolis Lizards of Bimini: resource partitioning in a Complex Fauna. Ecology 49:704–726

Schroth G, Kolbe D, Pity B, Zech W (1996) Root system characteristics with agroforestry relevance of nine leguminous tree species and a spontaneous fallow in a semi-deciduous rainforest area of West Africa. For Ecol Manage 84:199–208

Shelton HM, Brewbaker JL (1994) *Leucaena leucocephala* - the Most Widely Used Forage Tree Legume. In: Gutteridge and HM Shelton (eds) Forage tree legumes in tropical agriculture. CAB International, Wallingford, UK

Soberón J, Nakamura M (2009) Niches and distributional areas: concepts, methods, and assumptions. Proc Natl Acad Sci U S A 106:19644–19650

Sofaer HR, Jarnevich CS, Pearse IS, Smyth RL, Auer S, Cook GL, Edwards TC, Guala GF, Howard TG, Morisette JT, Hamilton H (2019) Development and delivery of species distribution models to inform decision-making. Bioscience 69:544–557

Stocker T (2013) IPCC Summary for Policymakers in Climate Change 2013: the physical science basis: Working Group I contribution to the Fifth assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge

Taylor S, Kumar L, Reid N, Kriticos DJ (2012) Climate change and the potential distribution of an invasive shrub, *Lantana camara* L. PLoS ONE 7:e35565

Thuiller W, Richardson DM, Midgley GF (2007) Will Climate change promote alien plant invasions? In: Biological Invasions. Springer, Berlin, Heidelberg, pp 197–211

Van Kleunen M et al (2015) Global exchange and accumulation of non-native plants. Nature 525:100–103

Velazco SJE, Galvão F, Villalobos F, De Marco P (2017) Using worldwide edaphic data to model plant species niches: an assessment at a continental extent. PLoS ONE 12:e0186025

Wan JZ, Zhang ZX, Wang CJ (2018) Identifying potential distributions of 10 invasive alien trees: implications for conservation management of protected areas. Environ Monit Assess 190:1–15

Warren DL, Seifert SN (2011) Ecological niche modeling in Maxent: the importance of model complexity and the performance of model selection criteria. Ecol Appl 21:335–342

Warren DL, Glor RE, Turelli M (2008) Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. Evolution 62:2868–2883

Witt A, Beale T, van Wilgen BW (2018) An assessment of the distribution and potential ecological impacts of invasive alien plant species in eastern Africa. Trans R Soc South Africa 73:217–236

Zizka A, Silvestro D, Andermann T, Azevedo J, Duarte Ritter C, Edler D, Farooq H, Herdean A, Ariza M, Scharn R, Svantesson S, Wengström N, Zizka V, Antonelli A (2019) *CoordinateCleaner*: standardized cleaning of occurrence records from biological collection databases. Methods Ecol Evol 10:744–751

Zuquim G, Costa FRC, Tuomisto H, Moulatlet GM, Figueiredo FOG (2020) The importance of soils in predicting the future of plant habitat suitability in a tropical forest. Plant Soil 450:151–170