



Potential distribution of selected invasive alien plants under current and future climate change scenarios in South Africa

Achamyeleh G. Mengistu^{a,*}, Weldemichael A. Tesfahuney^a, Yali E. Woyessa^b, Abraham S. Steyn^a

^a University of the Free State, Department of Soil, Crop and Climate Sciences, 205 Nelson Mandela Drive, Park West, Bloemfontein 9300, Bloemfontein, South Africa

^b Central University of Technology, Free State, Department of Civil Engineering, 20 President Brand Street, Bloemfontein 9300, South Africa

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ABSTRACT

Invasive alien plants are one of the main causes for the decline of native biodiversity worldwide. Hence, it is crucial to understand the dynamics of invasive plants in the context of a changing climate. The main aim of this study was to evaluate the potential distribution of two major invasive alien plants, *Prosopis* spp and *Acacia mearnsii*, under current and future climate change scenarios across South Africa. The maximum entropy (MaxEnt) model was used with species occurrence data and bioclimatic variables. The Species occurrence data was obtained from the Global Biodiversity Information Facility (GBIF), while the bioclimatic variables were downloaded from the WorldClim database. The model evaluation metrics for training and test samples were the area under curve (AUC) of 0.76 and 0.77 for *Prosopis* spp, and 0.91 and 0.89 for *A. mearnsii*, respectively. It showed that MaxEnt performed well in mapping the distribution of both species. Model results indicated that the near-current potential distribution of *Prosopis* spp and *A. mearnsii* in South Africa is significant (93.8% and 9.7% of the total land area, respectively). With the projected climate, *Prosopis* spp showed an inconsistent result across the General Circulation Models (GCMs), projection times and climate change scenarios. However, with respect to the current potential distribution, the geographical ranges of *A. mearnsii* will significantly contract (by about 75%) due to climate change. Therefore, it is imperative that policy makers, environmental managers and other stakeholders implement integrated management and control strategies to restrict the distribution of *Prosopis* spp.

1. Introduction

Climate change is a major global threat that affects almost all aspects of life on earth. As the southern African region (including South Africa) is identified as one of the hotspots for climate change [1–4], it is essential to understand the impact of climate change and its associated consequences on invasive plants in the region. The most widely used and fast-growing method for this type of analysis is the use of species distribution models (SDMs). SDMs work based on the relationship between the species distribution (other biotic response variable) and the physical (abiotic) environment [5,6]. The maximum entropy (MaxEnt) method is currently one of the widely used SDMs that uses presence-only data [7–9].

* Corresponding author.

E-mail address: acha.mengistu@gmail.com (A.G. Mengistu).

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The impact of climate change on invasive alien plants is highly complex [10–13]. Various elements of global change, including global warming, elevated atmospheric CO₂, N-deposition and habitat fragmentation, showed an interacting influence to exacerbate or retard alien plant invasion [14]. Indeed, all ecosystems are not equally vulnerable to global changes such as climate change. Climate change and variability do not harm or benefit all invasive alien plants in the same way [12,13], hence the response should be species-specific. For instance, climate change may trigger the geographical ranges of species, decrease them, or, in some cases, not affect them significantly. Also, with a changing climate, a species that is currently not invasive may be invasive in the future [13,15]. For instance, the prediction of suitable niche range for *Lantana camara* will increase with climate change in South Africa and China, whereas its range contracts in other countries in Central and Latin America [16,17]. This suggests that the impact of climate change may vary from place to place even on similar species. The niche range of invasive plants, such as *Cirsium arvense*, will increase with an increasing atmospheric CO₂ concentration due to its significant influence on the efficiency of photosynthesis and changing leaf defence for potential herbivores [18]. Moreover, the climate of the plant's native place and biogeography also plays an important role in the invasion process in the event of climate change [1,13].

The impact of climate change on invasive alien plants are rarely studied in South Africa. Besides, most of the available studies focus on the impact of invasive plants on the environment, such as water resources, soil properties (physical, chemical and biological), etc. Based on a thorough literature review conducted as part of this study, only two articles were identified to deal with this issue within the South African context [19,20]. The first study [19] was conducted on 162 non-native trees and found that over half of these trees would show a geographic range contraction, even though they did not specify which of them would actually show range expansion or contraction. The other study [20] indicated that there would be a geographic range contraction in the growth of *A. mearnsii* in the future climate scenario. Studies from other countries, [such as 21–23], showed a general geographical range expansion for *Prosopis glandulosa* and *Prosopis velutina*, which are the most dominant tree species of the genus *Prosopis*.

In general, the response of invasive alien plants to a changing climate is still an active area of research in South Africa. This is evident by the very few published works, given that alien plant invasion is a global threat to biodiversity. Besides, questions such as whether invasive alien plant invasion in South Africa is exacerbated, retarded or remains neutral during climate change require answers based on specific research on many interacting factors. A specific species should be studied within a specific location for specific environmental factors. Hence, this study was carried out to evaluate the potential distribution of two invasive alien plants, *Prosopis* spp and *A. mearnsii*, under current and future climate change scenarios across South Africa. It is important to note that *Prosopis* spp refers mainly *Prosopis glandulosa* and *Prosopis velutina* in this study. The reason to analyse *Prosopis* at genus level is explained in Section 2.2 of the current study. Furthermore, this study only assessed the possible niche range conditions by considering merely the important

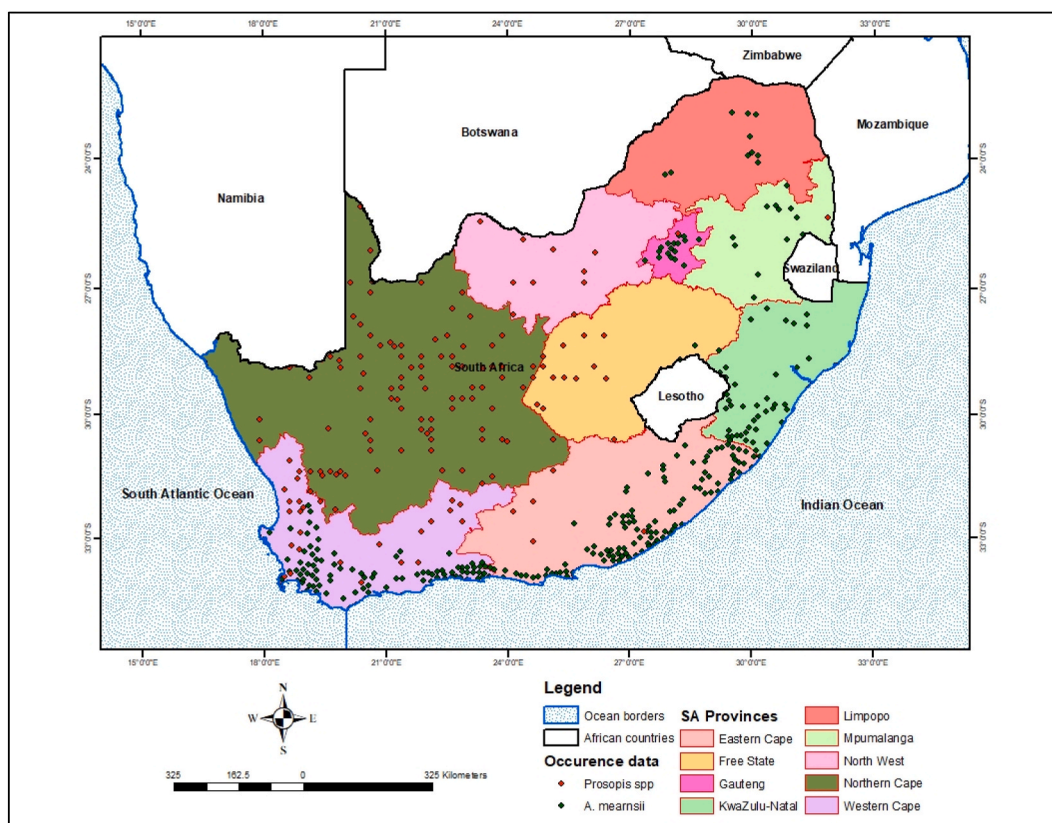


Fig. 1. Location of the study area (South Africa).

climatic variables described in the methodology. Other environmental factors (e.g. soil properties, land use competition with other plants and water resources) were assumed to remain constant.

2. Materials and methods

2.1. The study area

The study was conducted on the South African mainland, excluding the surrounding islands. South Africa is at the southern tip of Africa, bordering with Namibia in the north-west, the South Atlantic Ocean in the west and south-west, the Indian Ocean in the south, south-east and east, Swaziland and Mozambique in the north-east, and Zimbabwe and Botswana in the north (Fig. 1). Lesotho is a sovereign country surrounded by South African territory in the south-eastern part of the country. The country is divided into nine administrative provinces.

The long-term (1991–2020) mean annual temperature and precipitation are 18.3 °C and 456 mm, respectively [24]. The provincial distribution of long-term mean precipitation and temperature is shown in Table 1. The precipitation distribution increases from the western and south-western to the eastern and north-eastern provinces (Fig. 1 and Table 1). Hence, the eastern and north-eastern provinces like KwaZulu-Natal, Mpumalanga, the Eastern Cape and Gauteng have higher rainfall distributions than the western provinces (e.g. the Northern Cape). The distribution of the annual temperature has an opposite pattern to the precipitation in that the temperature increases from the eastern and south-eastern to northern and north-western directions. As a result, Limpopo, North West and the Northern Cape have higher temperatures. Generally, South Africa is dominated by arid and semi-arid climates [25].

2.2. Description of the tree species

Prosopis spp (commonly known as mesquite in South Africa) are all trees or shrubs of varying sizes, categorized under the Fabaceae family, that grow in arid to semi-arid environments [27,28]. These plants are declared as one of the most aggressive plants that affect ecosystems, and particularly known to invade open woodlands, grasslands, shrub lands and floodplains. According to previous research, its impact on water resources is also significant in South Africa. The most prominent invasive species from this taxon are *P. glandulosa* (honey mesquite), *P. velutina* (velvet mesquite) as well as their hybrids [29,30]. It is evident that these species have similar environmental requirements. For instance, both can tolerate extreme high and low temperatures and can grow in arid and semi-arid areas [31,32]. As a result, their analysis was conducted at genus level (*Prosopis* spp). Images of *P. glandulosa* and *P. velutina* is shown in Fig. 2, panels A1-2 and B1-2.

A. mearnsii (black wattle), on the other hand, is a large shrub/small tree of the genus *Acacia* and Fabaceae family that is native to Australia [34,35]. This plant is also declared as invasive, as it invades grazing area and riverine forests, however, it is also used in commercial forestry in South Africa. Images of *A. mearnsii* is shown in Fig. 2, panels C1-2.

2.3. The MaxEnt model

2.3.1. Model background

The MaxEnt model is one of the most widely used SDMs in ecological studies. MaxEnt uses the presence-only data (species occurrence locations) and other environmental data, such as climate, soil and topography, to estimate the probability of presence of a given species [7,8]. The estimation of the probability of distribution is dependent only on the relationship between the occurrence points and the gridded environmental data. The algorithms in MaxEnt generate a model to develop predictive maps of suitability for the entire study area. In other words, this prediction is usually done without background information knowledge of the species in terms of its environmental requirement for optimum growth. The model assumes that each corner of the study area has the same chance of being sampled (random sampling), which would otherwise complicate it in reality [8,36]. However, the model has many advantages as well [7,8], such as its requirement for presence-only data, the use of both continuous and categorical data, and a regularization protocol to protect against overfitting. Generally, the model shows good predictive performance.

Table 1

Long-term (1991–2020) average climate of South African provinces (Adapted from Ref. [26]).

No.	Province	Mean annual precipitation (mm)	Annual temperature (°C)		
			Mean	Max	Min
1	Mpumalanga	736	17.1	23.1	10.2
2	KwaZulu-Natal	845	18.1	22.7	2.2
3	Eastern Cape	552	16.1	20	5.4
4	Gauteng	668	16.5	19.3	15
5	Free State	532	15.8	17.9	3.9
6	Limpopo	527	20	23.8	14.1
7	North West	481	18.3	21.1	15.6
8	Western Cape	348	16.5	20.3	9.2
9	Northern Cape	202	17.4	22.5	10.4

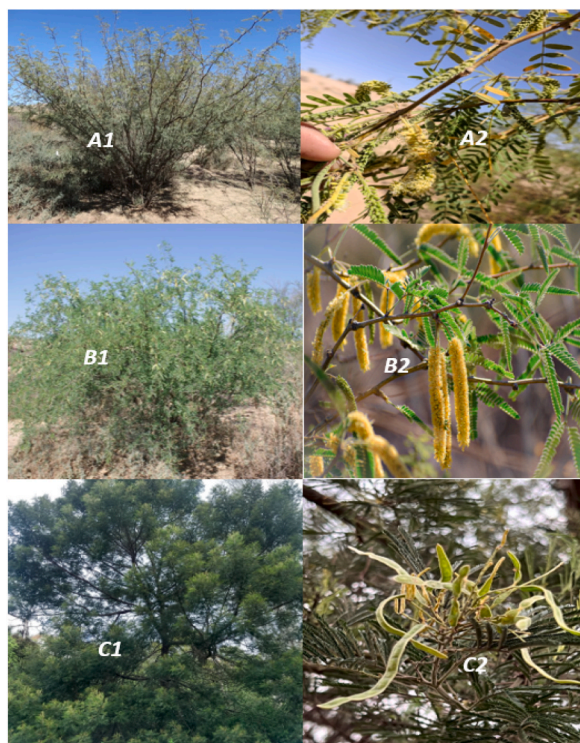


Fig. 2. Tree species studied: A1) *P. glandulosa* tree stand, A2) *P. glandulosa* pods, B1) *P. velutina* tree stand, A2) *P. velutina* pods, C1) *Acacia mearnsii* tree stands and C2) *Acacia mearnsii* pods. The pictures are taken from iNaturalist website [33].

2.3.2. Model inputs

Two major data types are crucial for the MaxEnt model, namely the current occurrence data and the gridded environmental data. The occurrence data is downloaded from the Global Biodiversity Information Facility (GBIF) website (www.gbif.org). The data downloaded from the GBIF website for this study could not be used directly due to the presence of higher spatial autocorrelation. Hence, only part of it was used for the training and testing of the model (Table 2). The gridded environmental data (19 bioclimatic variables) were also downloaded from the WorldClim dataset (www.worldclim.org). The latest dataset, called the Coupled Model Intercomparison Project Phase 6 (CMIP6), with a resolution of 2.5' by 2.5" (around 4.34 km × 4.34 km), was downloaded, including the near-current climate data (1970–2000). Three GCMs were selected, namely, BCC-CSM2-MR, CNRM-ESM2-1 and MICROC6. The near-current climate was assumed to represent the current climate, whereas, for future predictions, two projection times (mid and late century) and two climate change scenarios (SSP2-4.5 and SSP5-8.5) were used. The projected WorldClim data (CMIP6) was bias-corrected and averaged for every 20 years, and the projection times were averaged accordingly. For instance, the 2041 to 2060 data was averaged as the 2050s (also referred to as the mid-century projections) and the 2081 to 2100 data were averaged as the 2090s (also referred to as the late-century projections). Hence, in this study, the 2050s and mid-century scenario refer to the same thing. Similarly, the 2090s and late-century projections have the same meaning.

The framework of the new climate change scenario in the CMIP6 dataset consists of two major components (Fig. 3), namely the level of radiative forcing of the climate and the alternative trajectories of future socio-economic circumstances [37–39]. The level of radiative forcing is represented by the former representative concentration pathways (RCPs) of the CMIP5 dataset, while the future socio-economic trajectory is represented by the shared socio-economic pathways (SSPs). The detailed explanation of RCPs appears in the IPCC climate change report [40]. SSPs consist of two key elements, namely a narrative storyline and a set of quantified measures of development [38,41]. Based on the storylines and sets of development trajectories, five SSPs (SSP1 to SSP5) were formulated, where SSP1, SSP2, SSP3, SSP4 and SSP5 represent sustainability, middle-of-the-road, regional rivalry, inequality and fossil-fuelled development, respectively (Fig. 3). Finally, the matrix diagram shown in Fig. 3, which is the level of radiative forcing on the y-axis (RCPs) in conjunction with the SSPs on the x-axis, is formed. Therefore, the new climate change scenarios form the matrix of SSPs and RCPs.

Table 2

Occurrence data used for model training and testing.

No.	Common name	Scientific name	Available occurrence data	Used occurrence data
1	Mesquite	<i>Prosopis</i> spp	37,252	6064
2	Black wattle	<i>A. mearnsii</i>	23,630	2779

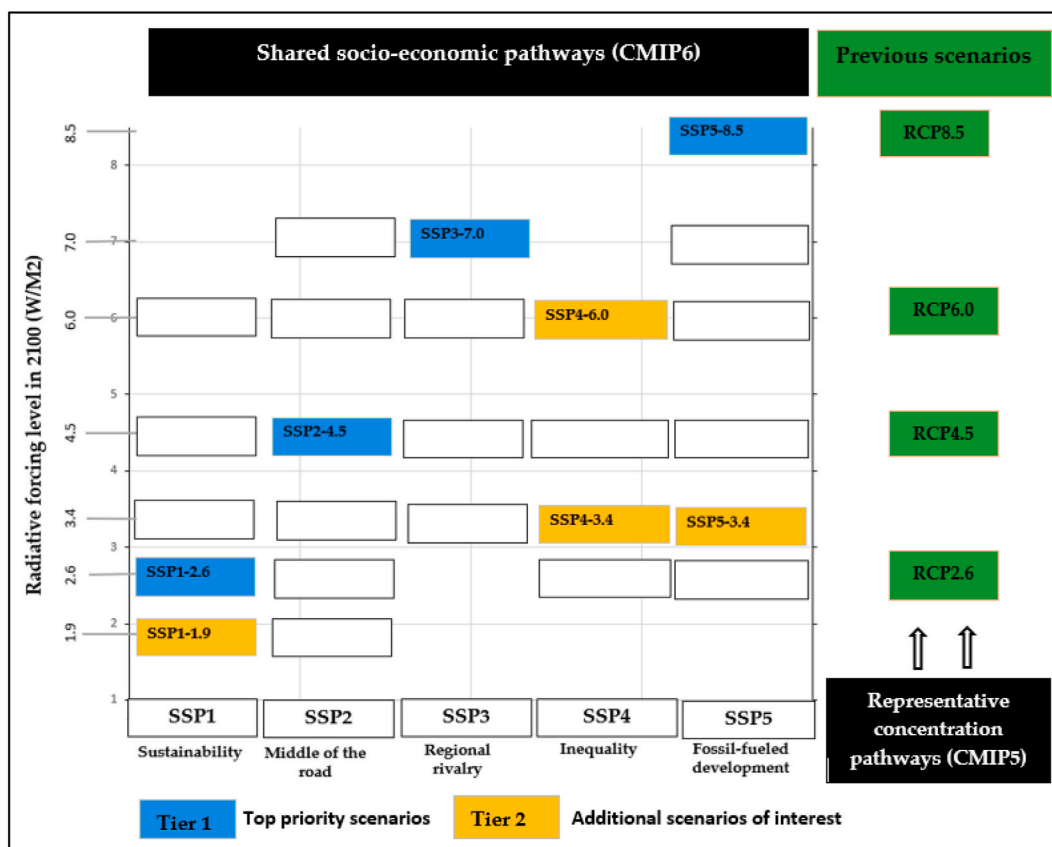


Fig. 3. The shared socio-economic pathways vs representative concentration pathways (SSP-RCP) scenario matrix (Adapted from 39).

Currently, the CMIP6 dataset for SSP1-2.6, SSP2-4.5, SSP3-7.0 and SSP5-8.5 scenarios are readily available for climate change studies. A detailed explanation can be obtained from Refs. [37–39].

2.3.3. Model setup and configuration

In this study, MaxEnt model ver. 3.4.4 [9] was used. The model was setup to simulate global extents, however, the model outputs were clipped for the study area (South Africa) for further analysis. Most of the data management activities (e.g. clipping, adjusting data projection, minimizing spatial autocorrelation of occurrence data and data formatting) were conducted using SDMToolbox ver. 2.5 [42,43]. SDMToolbox is a python-based ArcGIS tool that is currently used by researchers in the fields of ecology, evolution and genetics [43]. The “Spatially rarefy tool” (within the SDMToolbox) was used to reduce spatial autocorrelation in the occurrence data. This tool removes the autocorrelated occurrence points by reducing multiple occurrence records to a single record within a specified distance to decrease sampling bias and enhance model performance. Hence, a 10 km threshold (default value) was used, and the number of records were reduced from 37,252 to 23,630 to 6064 and 2779 for *Prosopeis* spp and *A. mearnsii*, respectively (Table 2).

The SDMToolbox was also important to identify correlated environmental data. The “Remove highly correlated variables” tool checks the correlation coefficient matrices among the 19 bioclim data variables and suggests the highly correlated data to be excluded from the model. Variables that had higher correlation coefficients ($\geq \pm 0.8$) were excluded from the model. Hence, only 12 bioclim data variables were used in the model (Table 4). Moreover, the “Basic tools” under the SDMToolbox were essential for the preparation of occurrence and bioclim data before the main modelling task in the MaxEnt model was performed.

The model was set to use 75% of the occurrence data for model training and the remaining 25% for testing the model performance. Besides, MaxEnt was also adjusted to run 5000 iterations for each species. The maximum training sensitivity plus the specificity threshold value was applied. The rest of the model setup and configuration tasks were left for default settings.

2.4. Analysis of the model outputs

The two most important qualities of SDMs are the low over-fitting and high discriminatory ability [43,44]. The presence of low over-fitting of the model was evaluated by the performance of the omission rate during model training and testing. The area under curve (AUC) under the receiver operating characteristic (ROC) curve was also used to evaluate the model’s performance to successfully demarcate suitable and unsuitable areas.

The two species (*Prosopis* spp and *A. mearnsii*) were modelled separately. MaxEnt automatically selects the best model based on the given criteria and prints the results of this model. The potential distribution maps were clipped for the study area (South Africa) using ArcGIS ver. 10.7.1. Suitability maps were produced with four classes, each of which has its own range derived from the probability of presence/absence of the given species (Table 3). The area of each suitability class was calculated, and the result compared with respect to the present suitability maps to assess the presence of climatic range expansion or contraction. The resulting negative values indicate the reduction of climatically suitable areas, whereas positive values indicate the expansion of climatically suitable areas due to climate change.

3. Results

3.1. MaxEnt model performance evaluation

The model performance indicators for both *Prosopis* spp and *A. mearnsii* are shown in Fig. 4. The omission rate and the predicted area as a function of the cumulative threshold is given in plate a and c, while the ROC curve is depicted in plate b and d of Fig. 4. The omission rate is closer to the predicted omission and the difference in omission rate between the training and test samples is minimum. This indicates that the model has a low over-fitting during model training and testing. The AUC in the ROC curve is 0.76 and 0.77 for *Prosopis* spp for training and testing samples, respectively. Similarly, the AUC in the ROC curve was 0.91 and 0.89 for *A. mearnsii* for training and testing samples, respectively. This also shows that the model performed well in predicting the probability of presence of the two species.

3.2. Variable response and contribution

The contribution of the main environmental (climatic) variables in the distribution of both *Prosopis* spp and *A. mearnsii* is shown in Table 4. The main climatic variables that affect the distribution of *Prosopis* spp were temperature seasonality (Bio4) at 48.4%, annual precipitation (Bio12) at 19.4%, and mean temperature of wettest quarter (Bio8) at 9.6%. Whereas, for *A. mearnsii*, the main climatic variables were Bio4 at 33.4%, min temperature of coldest month (Bio6) at 26.4%, and Bio8 at 22.3%. The jackknife test (Fig. 5, plate a and b) also shows more or less a similar result. The curves in Fig. 6 show the major variables' response curves during MaxEnt prediction. The curves show how the predicted probability of presence changes with changing environmental variables, keeping all other variables at their average sample value.

3.3. Current potential distribution

The current potential distribution of *Prosopis* spp (Fig. 7, plate a) shows that, generally, South Africa is climatically a highly suitable country for the expansion of *Prosopis* spp, except for the narrow strip of land mass stretching from the Northern Cape towards the Western Cape provinces and other scattered patches of land in the north-eastern and eastern parts of South Africa. Whereas, for *A. mearnsii* (Fig. 7, plate b), only a small portion of the country is suitable for expansion. The spatial pattern of the highly suitable class is confined to the southern and eastern tips (bordering the Indian Ocean) and scattered patches of land to the north-eastern regions.

The percentage share of the climatic suitability of the two species (*Prosopis* spp and *A. mearnsii*) are given in Table 5. About 114,693,612.2 ha (93.8%) is highly suitable and the rest 7,617,795.2 ha (6.2%) is moderately suitable for the distribution of *Prosopis* spp. Whereas for *A. mearnsii*, 11,815,346.7 ha (9.7%) of land is highly suitable and 29,742,631.9 ha (24.3%) is unsuitable. The rest 39,634,735.9 ha (32.4%) and 41,125,520.9 ha (33.6%) of land is moderately and marginally suitable for *A. mearnsii*, respectively. Generally, the climatic suitability of *Prosopis* spp is much greater than that of *A. mearnsii* in the current climatic conditions in South Africa. However, this does not mean that the current real distribution of *Prosopis* spp is greater than *A. mearnsii*.

3.4. Future climatic suitability

The future potential distributions of *Prosopis* spp and *A. mearnsii* are depicted in Fig. 8, plate a and b, respectively. Although there is a significant variation between the total areas allocated to each suitability class, the spatial distribution patterns are the same as the current potential distribution for both species, irrespective of the GCMs. However, there is a significant difference among the model outputs in relation to the type of GCMs (BCC-CSM2-MR, CNRM-ESM2-1 and MIROC6), projection times (mid vs late century) and the SSPs (SSP2-4.5 vs SSP5-8.5). Table 6 shows the details of such potential distribution variations between specific environmental

Table 3

The suitability classes derived from the outcomes of MaxEnt's probability of presence (Adapted from Ref. [45]).

No.	Habitat suitability class	Suitability ranges
1	Unsuitable	<0.1
2	Marginally suitable	0.1–0.3
3	Moderately suitable	0.3–0.6
4	Highly suitable	>0.6

Table 4
 Percentage contribution of each parameter to the modelling of *Prosopis* spp and *A. mearnsii*.

Variable code	Description	Percent contribution	
		<i>Prosopis</i> spp	<i>A. mearnsii</i>
Bio4	Temperature seasonality	48.4	33.4
Bio12	Annual precipitation	19.4	0.4
Bio8	Mean temperature of wettest quarter	9.6	22.3
Bio9	Mean temperature of driest quarter	6.3	0
Bio10	Mean temperature of warmest quarter	5.4	0.3
Bio15	Precipitation seasonality	3.4	14
Bio6	Min temperature of coldest month	2.7	26.4
Bio19	Precipitation of coldest quarter	2.4	0
Bio1	Annual mean temperature	1.7	1.1
Bio2	Mean diurnal range	0.7	0.7
Bio3	Isothermality	0.1	0
Bio14	Precipitation of driest month	0	1.4

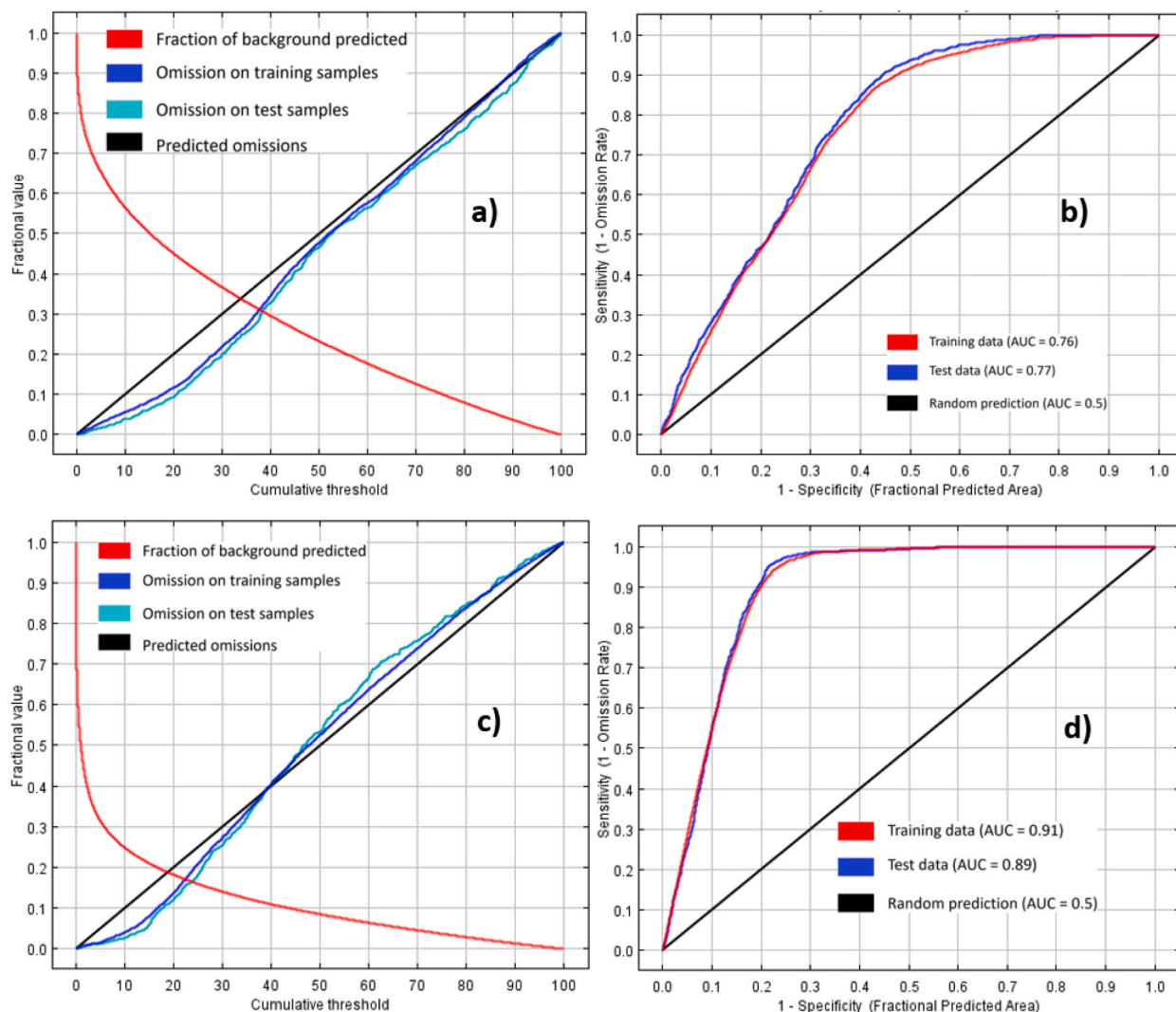


Fig. 4. Model performance evaluation: a) omission and predicted area for *Prosopis* spp; b) receiver operating characteristic (ROC) curve for *Prosopis* spp; c) omission and predicted area for *A. mearnsii*; and d) receiver operating characteristic (ROC) curve for *A. mearnsii*.

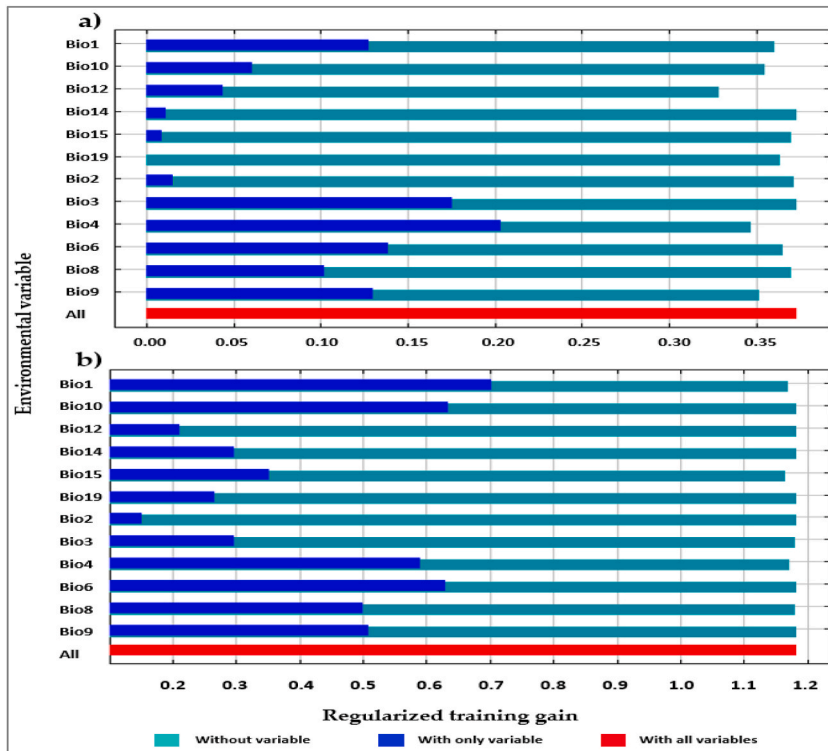


Fig. 5. Jackknife of regularized training gain for: a) *Prosopis* spp and b) *A. mearnsii*.

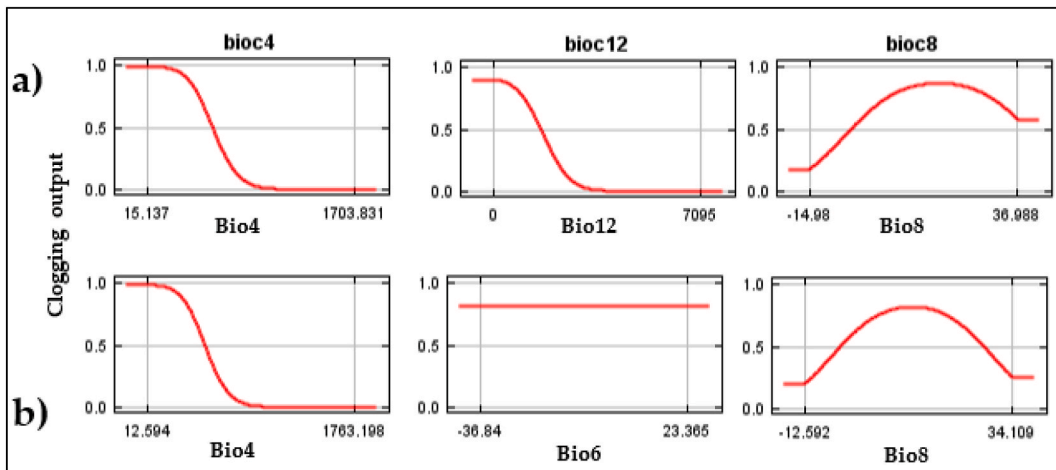


Fig. 6. Major parameters response curve for the model: a) for *Prosopis* spp, b) *A. mearnsii*.

conditions.

The *Prosopis* spp model showed inconsistent results among GCMs and the scenario levels. However, two major results were clearly seen for all GCMs, including the model average. On the one hand, the combination of mid-century projection with SSP2-45 scenario level resulted in a slight increase in the potential distribution of *Prosopis* spp in South Africa. On the other hand, the late-century projection with SSP5-85 resulted in a significant decrease of the expansion of *Prosopis* spp as compared to the current potential distribution. Other scenario levels did not show consistent results (Fig. 8 and Table 6). The case of *A. mearnsii* is straightforward in that the suitable area diminishes in the coming decades until the end of the current century. This is true for all GCMs and scenario levels. Comparing the GCMs, the prediction by MaxEnt with the use of CNRM-ESM2-1 data showed larger decrease in the expansion of *Prosopis* spp. For instance, the use of CNRM-ESM2-1 in the late projection time with SSP5-8.5 diminished the climatic suitability by 35.5% as compared to the current potential distribution. Whereas, for *A. mearnsii*, similar environmental conditions (the use of CNRM-

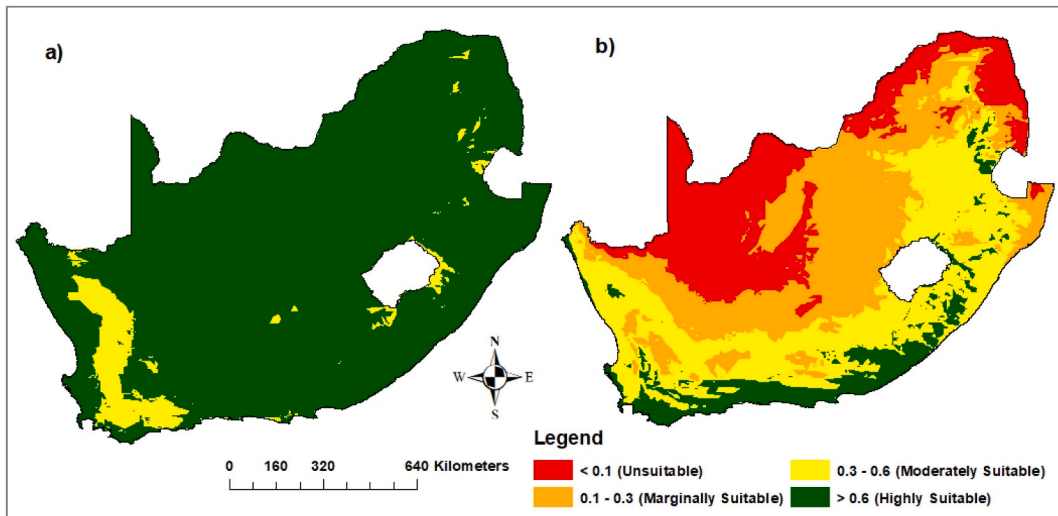


Fig. 7. Current potential distribution of the Maxent model for: a) *Prosopis* spp, b) *A. mearnsii*.

Table 5
Current potential distribution of *Prosopis* spp and *A. mearnsii* in South Africa.

No.	Suitability class	Current potential suitability			
		<i>Prosopis</i> spp		<i>A. mearnsii</i>	
		Area (ha)	% Cover	Area (ha)	% Cover
1	S1 (Unsuitable)	0.0	0.0	29,742,631.9	24.3
2	S2 (Marginally suitable)	6828.0	0.0	41,125,520.9	33.6
3	S3 (Moderately suitable)	7,617,795.2	6.2	39,634,735.9	32.4
4	S4 (Highly suitable)	114,693,612.2	93.8	11,815,346.7	9.7
	Total	122,318,235.5	100.0	122,318,235.5	100.0

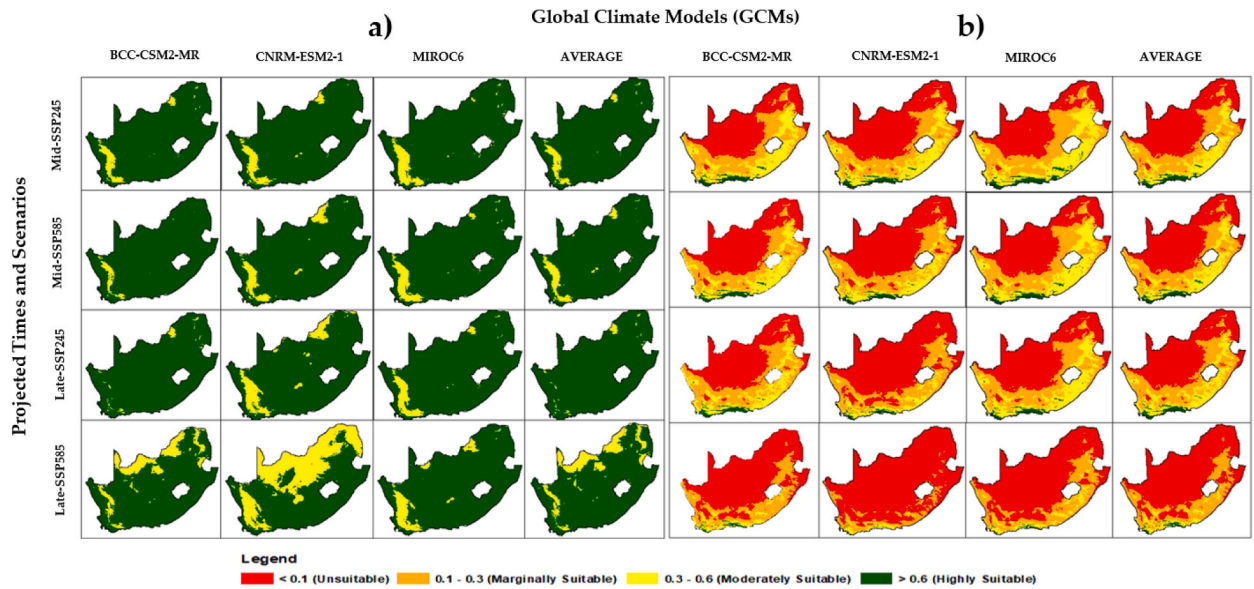


Fig. 8. Future climatic suitability for: a) *Prosopis* spp and b) *A. mearnsii*.

Table 6
Summary of the climatic range expansion/contraction of *Prosopis* and *A. mearnsii* in South Africa.

GCM	Projection time	SSP type	Climatic suitability							
			<i>Prosopis</i> spp				<i>A. mearnsii</i>			
			S1	S2	S3	S4	S1	S2	S3	S4
BCC-CSM2-MR	Mid	SSP2-4.5	NA	-100	-16.1	1.1	83.7	-12.2	-31.1	-63.7
		SSP5-8.5	NA	-100	-53.6	3.6	106.2	-16.5	-41.9	-69.0
	Late	SSP2-4.5	NA	-100	-72.6	4.8	102.0	-9.2	-46.0	-70.6
		SSP5-8.5	NA	-52.2	153.7	-10.2	178.0	-27.4	-78.9	-88.2
CNRM-ESM2-1	Mid	SSP2-4.5	NA	-100	-9.6	0.6	103.8	-15.7	-41.5	-67.3
		SSP5-8.5	NA	-100	11.2	-0.7	129.3	-18.4	-55.3	-75.6
	Late	SSP2-4.5	NA	113.5	63.4	-4.2	162.6	-24.2	-71.5	-85.2
		SSP5-8.5	NA	123.4	534.0	-35.5	253.0	-66.5	-91.4	-98.6
MIROC6	Mid	SSP2-4.5	NA	-45.0	4.2	-0.3	62.1	-6.8	-22.9	-55.8
		SSP5-8.5	NA	-100	-0.8	0.1	85.5	-12.0	-31.6	-67.2
	Late	SSP2-4.5	NA	-100	-6.1	0.4	98.9	-12.4	-39.4	-73.5
		SSP5-8.5	NA	-100	26.5	-1.8	181.9	-29.5	-77.9	-93.6
Model Average	Mid	SSP2-4.5	NA	-100	-24.8	1.7	97.1	-11.2	-41.6	-65.5
		SSP5-8.5	NA	-100	-3.8	0.3	98.2	-15.5	-43.9	-72.0
	Late	SSP2-4.5	NA	-100	-52.6	4.9	107.0	-11.2	-49.0	-74.6
		SSP5-8.5	NA	-59.2	163.9	-13.2	198.0	-37.4	-88.9	-83.2

Note the following: S1 refers to the climatic unsuitable class; S2 refers to the marginally suitable class; S3 refers to the moderately suitable class; and S4 refers to the highly suitable class; NA means 'not applicable'.

ESM2-1 in the late projection time with SSP5-8.5) decreased the climatic suitability by 98.6%. This comparison is obtained by considering only the classes of S4 (highly suitable). Further comparison between the other suitability classes can be obtained from Table 6.

4. Discussion

This study was conducted to model the potential distribution of the two most important invasive alien plants in South Africa (i.e. *Prosopis* spp and *A. mearnsii*) under current and future climate change scenarios, using the MaxEnt model. The model prediction indicates that the current climate of almost the whole South Africa is suitable for the expansion of *Prosopis* spp, except a narrower strip of land in the south and south-western and smaller scattered patches of land in the eastern and north-eastern parts of the country (Fig. 6, plate a). Unless there are other prohibiting factors, almost the whole country (about 94%) could be invaded by *Prosopis* spp based on the current climate, which is a very serious threat to South African biodiversity. On the other hand, the climatic suitability for *A. mearnsii* is diminishing significantly. Only smaller parts of the country (about 10%) is suitable currently. The prediction also indicates that *A. mearnsii* is more strongly influenced by temperature-driven bioclimatic variables than *Prosopis* spp. Temperature seasonality (Bio4), minimum temperature of the coldest month (Bio6) and minimum temperature of the wettest quarter (Bio8) are the top three variables influencing the distribution of *A. mearnsii*. However, besides the above climate variables, *Prosopis* spp is also affected by precipitation-driven variables like the annual precipitation (Bio12). This finding is consistent with other results [e.g., 46–49].

Furthermore, future projections (Fig. 8 and Table 6) reveals that there is a significant climatic range contraction for *A. mearnsii*, irrespective of GCMs, projection times and climate change scenarios. However, in the case of *Prosopis* spp, inconsistent results are shown across GCMs, projection times and climate change scenarios. Mid-century projections with low level emission scenarios resulted in a further increase in expansion, while late-century projections with high level emission scenarios resulted in a significant decrease of expansion in *Prosopis* spp. With regard to the average of GCMs, projection times and scenarios compared to the current potential distribution, there will be a 3.5% decrease of potential suitability of *Prosopis* spp (considering the highly suitable class only). On the other hand, *A. mearnsii* will further diminish significantly by about 75% (average of the GCMs, considering the highly suitable class only). These results are in line with other observations [19,20]. This may indicate that South Africa may probably not be suitable for the growth of *A. mearnsii* in the long-term climate change projections. This may have another impact on the economy as these tree species are used as important commercial forest plantations [50,51].

The native geographical range for the distribution of *Prosopis* spp stretches from 37° N to 48° S [27], as shown in Fig. 9, indicating a wider geographical range. This area includes the whole of Africa, Australia, southern Asia, southern USA and almost the whole of South America. The range shift is defined as the distribution of a species outside its previous known latitudinal or altitudinal range [52,53]. As *Prosopis* spp has a wider geographical range (Fig. 9), and since the whole South Africa is inside the geographic ranges of distribution for *Prosopis* spp, reference to range shift may not be applicable. However, Fig. 9 and other global studies [48,54,55] show that there is a considerable range shift when considering its global distribution. Currently, its expansion towards some southern European countries, the Middle East and northern USA is particularly evident. However, the geographical ranges of *A. mearnsii* is relatively small as compared to *Prosopis* spp. The latitudinal ranges for the distribution of *A. mearnsii* in its native place (Australia) is between 33 to 43° S [34], which is also shown in Fig. 9. This geographical area in South Africa includes the southern parts of Eastern Cape and Western Cape provinces. Therefore, *A. mearnsii* shows a greater range shift in South Africa. Even though previous studies on this topic are very

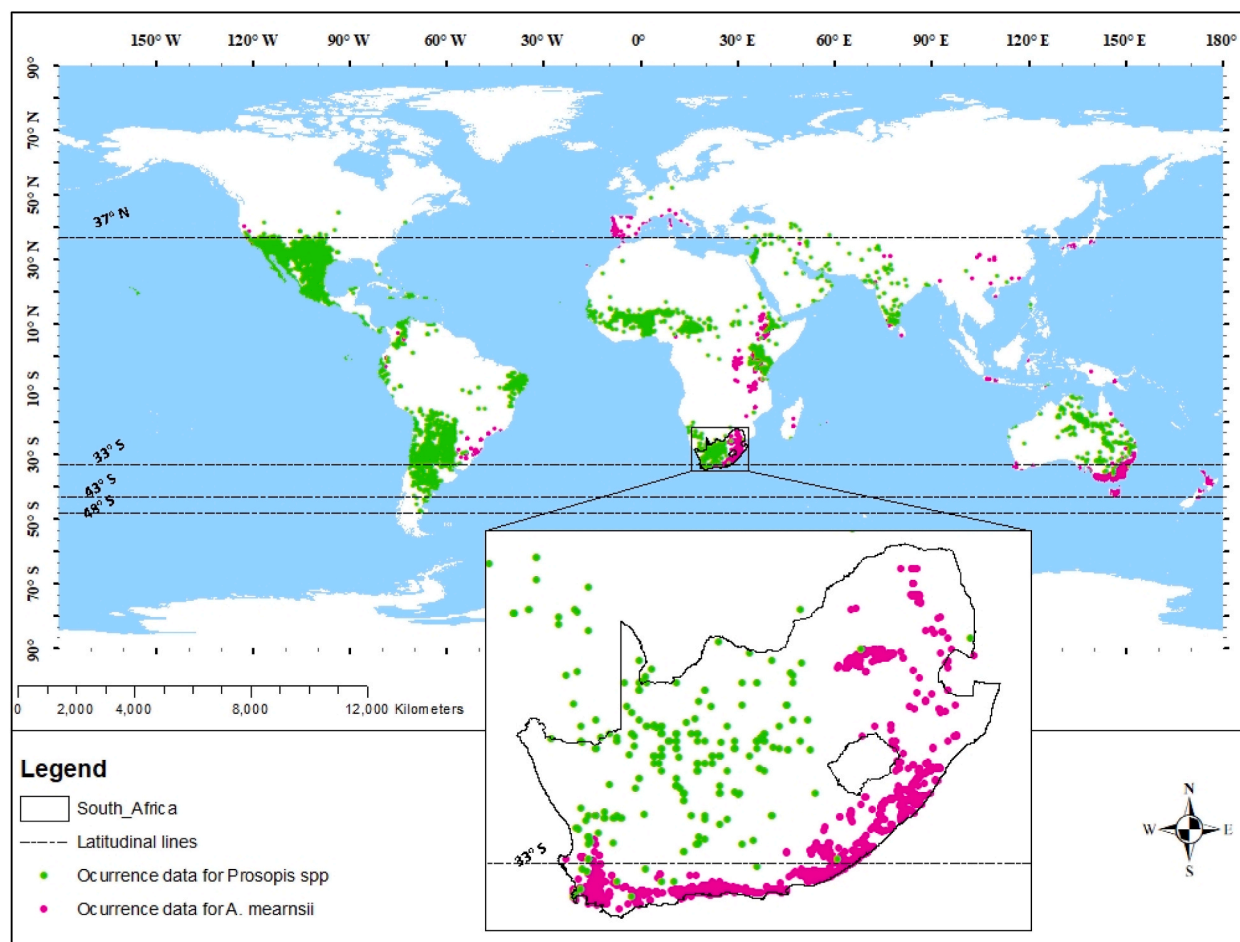


Fig. 9. Global distribution of presence points for *Prosopis* spp (green colour) and *A. mearnsii* (pink colour) to show the geographic (latitudinal) ranges and current biological invasion by the two plant species.

scarce, the current global distribution indicates that *A. mearnsii* is growing in many countries, i.e. outside of its native range. These results are in line with the observations of other research reports [e.g., 56,57].

According to the IPCC report [4], southern Africa is a climate change hotspot and there will be unprecedented climate impact changes, including extreme weather conditions. This will affect the ecology of plants significantly in this region that includes South Africa [2,58]. However, invasive plants have a better ability to adapt and escape such harsh climatic conditions than native plants [47, 59–63]. Previous research [27,47,60] indicate that *Prosopis* spp is known to ameliorate the soil condition (including macro- and micro-nutrients) in such a way that the soil becomes suitable for its own optimum growth through time. Moreover, the leaves of *Prosopis* spp are found to contain various chemicals that affect the germination of seeds and growth of other trees [27,47]. The root of this plant is also long enough to extract groundwater in the presence of drought, particularly in riverbeds. Furthermore, this plant forms intermingled and interwoven branches that extends its competition for sunlight [47]. The seeds can also be transported over long distances by animals and floods. All these adaptation mechanisms may help *Prosopis* spp to expand further, although our results indicate that expansion may decrease as the climate becomes warm and harsh. However, the real case of *Prosopis* spp to decrease in its expansion in higher emission levels needs further investigation. There are some reports that *A. mearnsii* may proliferate in changing climate scenarios due to its peculiar traits to adapt to climate change [22,62,64,65]. Most of these traits are related to the breaking of seed dormancy from soil seed banks [22,65,66], increase in water-use efficiency [64] and nutrient (nitrogen) recycling [62]. Others [51] indicate that extreme temperature and lower relative humidity may disrupt its reproduction process. Also, extreme precipitation and high rainfall may not enhance the invasive potential of *A. mearnsii* [65]. However, all these studies are based on small scale experiments that are not supported by a detailed species distribution study. Hence, further research is required to identify the fundamental causes of the significant shrinking of *A. mearnsii* across the country.

5. Conclusion

The potential distribution of two important invasive alien plants in South Africa, *Prosopis* spp and *A. mearnsii*, was predicted using

the MaxEnt model. The evaluation metrics showed that SDMs for both *Prosopis* spp and *A. mearnsii* were constructed successfully and could predict reasonable outputs.

Unlike *A. mearnsii*, nearly the whole of South Africa was found to be climatically suitable for the distribution of *Prosopis* spp in the current climate. The distribution of *A. mearnsii* will, however, diminish with the expected climate change. In the model prediction, precipitation-derived bioclimatic variables were relatively higher for *Prosopis* spp than for *A. mearnsii*.

It is evident that the geographical ranges of *Prosopis* spp continue to expand significantly throughout the country in the current climate, although there is no consistent evidence of change under future climate conditions. Hence, government bodies in South Africa, including policy makers, environmental managers and other stakeholders, should focus on and give priority to the management and control of *Prosopis* spp, rather than that of *A. mearnsii*. Further study is also required to better understand the decline of the potential distribution of *both* plants in this era of climate change in South Africa.

Author contribution statement

Achamyeleh G. Mengistu: Conceived and designed the experiments; Performed the experiments; Analyzed and interpreted the data; Contributed reagents, materials, analysis tools or data; Wrote the paper.

Weldemichael A. Tesfahuney: Conceived and designed the experiments; Performed the experiments; Analyzed and interpreted the data.

Yali E. Woyessa and Stephan A. Steyn: Conceived and designed the experiments; Performed the experiments.

Data availability statement

Data will be made available on request.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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List of Abbreviations

AUC	the area under the curve
CMIP6	the Coupled Model Intercomparison Project Phase 6
GBIF	Global Biodiversity Information Facility
GCMs	General Circulation Models
IPCC	Inter-governmental Panel for Climate Change
MaxEnt	the maximum entropy model
mm	millimetre
°C	Degree Celsius
RCPs	representative concentration pathways
ROC	receiver operating characteristic curve
SA	South Africa
SDMs	species distribution models
Spp	species
SSP	shared socioeconomic pathways
Tmax	maximum temperature
Tmin	minimum temperature

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