Tropical Ecology
https://doi.org/10.1007/s42965-020-00101-w

International Society
for Tropical Ecology

RESEARCH ARTICLE

Regional dynamics in distribution of *Prosopis juliflora* under predicted climate change in Africa

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Received: 22 May 2020 / Revised: 16 August 2020 / Accepted: 18 August 2020

Abstract
Climate change is considered to be one of a principle reason for spread of invasive alien species. Thus, it is essential to examine potential invasion dynamics of *Prosopis juliflora* at continental scale under climate change scenario to better guide management of the invasive species. A consensus model derived from five models were used to examine the current and future (2050 and 2070) climatic suitability for *P. juliflora* under two climate scenarios (RCP4.5 and RCP8.5) in Africa. The mean area under the receiver operating characteristic curve (AUC) and the threshold-dependent true skill statistic (TSS) value of the models were 0.85 and 0.94, respectively, this put the models in the "very good" category. Results showed that temperature related variables were the main determinant factor accounting for 65.7% of the distribution of *P. juliflora*. Under current climatic scenario, 75.6% of the continent was unsuitable for *P. juliflora* establishment and invasion while 5.6% was highly suitable. The total suitable areas for *P. juliflora* under RCP4.5 and RCP8.5 would increase by 2050 and 2070 compared to the current conditions. Meanwhile, a decrease in total unsuitable areas would be expected by 2050 and 2070 under both RCP4.5 and RCP8.5. This study has revealed that; the rates of *P. juliflora* invasion will expand further inland across Africa as climatic conditions become favourable. Negative environmental and economic impacts caused by *P. juliflora* will be high if management measures are not earnestly taken. We recommend for a cross-border continental wide effort towards combating *P. juliflora* expansion to new areas, especially in countries predicted as frontiers of potential expansion.

Keywords Climate suitability · Conservation planning · Management of invasive species · *Prosopis juliflora* · SDM

Introduction

Invasive species are one of the most important ecological and societal threats globally (Tadros et al. 2020). In the twentieth century, about 60% of species extinction has been caused by factors associated with invasive species (Bellard et al. 2018). They also seriously affect ecosystem services and economic growth (Simberloff et al. 2013). Problems associated with loss of biodiversity caused by biological invasions are expected to increase in the future due to climate change (Hulme 2009; Beaury et al. 2020; Sintayehu et al. 2020). Climate changes can facilitate the introduction, establishment and spread of invasive plant species (Diez et al. 2012; Wakie et al. 2014; Qin et al. 2016; Shiferaw et al. 2019a), and subsequently have a major negative impact on the environment and people's livelihoods. For instance, as the climate warms some invasive plant species are changing their geographic distribution towards higher elevation (Bradley et al. 2010; Shrestha et al. 2018). Moreover, climate variability stresses native species and ecosystems (Bradley et al.

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s42965-020-00101-w) contains supplementary material, which is available to authorized users.

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Published online: 29 August 2020

2010; Corlett and Westcott 2013) and increases ecosystem disturbances through extreme climate events such as draught (Diez et al. 2012), potentially provide new opportunities for the spread of invasive plant species and cases biodiversity and ecosystem services loss by the displacement of native plants (Edrisi et al. 2020; Eshete et al. 2020). Therefore, it is vital to assess the relationship between the invasion of invasive plant species and climate change to design appropriate management strategies that accounts for climate change.

Several Invasive Plant Species (IPS) were introduced in Africa from different regions of the world for different purposes (Abebe 2018; Witt et al. 2018). For instance, *Lantana camara* was introduced in Africa as an ornamental plant because of its attractive aromatic flowers (Shackleton et al. 2017). Similarly, *Prosopis juliflora* (Sw.) DC. was first introduced in Sudan in 1917 with the aim to support combating desertification and provision of fuel-wood (Hoshino et al. 2012). In the 1980s, this species was brought to Lake Baringo of Kenya to similarly help address the issue of fuel wood shortage (Mbaabu et al. 2019). It found its way into Ethiopia in the 1970s and 1980s, under the soil and water conservation management programmes (Shiferaw et al. 2019a, b, c). Other several Prosopis have been introduced in Africa, for instance *P. chilensis*, *P. glandulosa* and *P. velutina* are very common in South Africa. *P. juliflora* are also occur in South Africa but not common (Shackleton et al. 2015). Now, *P. juliflora* is listed among the world's ten worst invasive weeds (Shrestha et al. 2018) and emerged as a significant threat to Africa's ecological landscapes (Wakie et al. 2014). It has invaded millions of hectares of natural and cultivated lands, causing great ecological and economic damage (Eshete et al. 2020). Despite its negative impact on the ecology and socio-economy, actions taken to reduce expansion of the species in Africa were not successful.

Climate change is one of the major driver for spread of IPS (Beaury et al. 2020). When climate change happens, many native plant species will be under severe pressure and lag behind to colonize newly suited habitat or new ecological niches and could face difficulties to acclimate to the new environment (Corlett and Westcott 2013). This could provide *P. juliflora* a window of opportunity especially when the actions of limiting the invasion hardly have any effect of curbing the spread of the species or rehabilitating invaded areas. Global mean temperature has been increased in the last century and projected to increase significantly in the foreseeable future (IPCC 2001, 2014). Africa is a highly threatened due to climate change (Sintayehu 2018). IPCC (2014) report showed that Africa has warmed 0.7 °C over the twentieth century. The temperature of the continent is predicted to increase between 0.2 °C (under low scenario) to 0.5 °C (under high scenario) per decade (IPCC 2014). Precipitation is also uneven in Africa; however, records from 1951 to 2010 showed that there has been an increase in eastern, central and parts of southern Africa and a decrease in western Africa and parts of southern Africa, particularly Zimbabwe and Zambia (Girvetz and Zganjar 2014). In the high emission scenario (RCP8.5), annual mean precipitation is expected to increase in many parts of eastern Africa by 5 to 75%, while it is predicted to decrease across parts of southern Africa by 15–45% and western Africa up to 15% by 2100 (Sillmann et al. 2013). Thus, knowing the associations between invasion of invasive plant species and climate variability is crucial in managing the species.

Although invasion of *P. juliflora* has noticeably negative impacts on environment and socio-economic of the communities, attempts to manage the species are inadequate. Recent studies repotted the importance of assessment of invasive species range expansion in order to develop better management strategies (Kettunen et al. 2009). *Prosopis juliflora* is highly susceptible in early establishment phases when efforts to manage the species are more effective and cost-efficient. Similarly, Heshmati et al. (2019)found that prediction and early detection was most important for managing invasion of alien invasive species. Species distribution models (SDMs) are a statistical approach used to evaluate the current and future geographical distributions of invasive species and examining the responses of the species to environmental change. Although previous studies have examined the impact of climate change on *P. juliflora* distribution, most of studies have focused on either global scale (Heshmati et al. 2019), sub-regional scale (Eckert et al. 2020) or have been limited to a smaller geographical area of Africa (Ng et al. 2018; Sintayehu et al. 2020). Other studies in Africa in particular in Eastern Africa have focused on its impacts on land use, land cover and livelihoods (Mbaabu et al. 2019), total and spatial coverage (Shiferaw et al. 2019a), biodiversity and associated ecosystem services loss (Edmund et al. 2019; Eshete et al. 2020), alternative uses of the plant and possible control strategies (Ilukor et al. 2016). In spite of the fact that this invasive plant species is rapidly expanding and threatening the environment and the economy of the continent (Wakie et al. 2014; Witt et al. 2018; Shiferaw et al. 2019a), our understanding on future invasion under the changing climate at continental level is limited. Understanding climatic suitability for *P. juliflora* at continental scale is critical for early detection and successful control and management of the species. Thus, we examined the current and predict future (2050 and 2070) continental suitability for *P. juliflora* invasion under the changing climate.

Materials and methods

Description of the species

Prosopis juliflora is an extremely invasive plant species, infesting over four million hectares of lands in arid and semi-arid part of Africa (Ng et al. 2018; Heshmati et al. 2019; Shiferaw et al. 2019a; Eckert et al. 2020). *Prosopis juliflora* is a fast-growing tree—reaching 5–10 m in height—native to frost-free tropical regions of Peru, Central America, and the Caribbean. The species has characterized by deep rooting systems that enables water absorption at low depth and fix nitrogen (Ng et al. 2018).

Occurrence data collection

Regional occurrence records of *P. juliflora* were collected from the Global Biodiversity Information Facility (GBIF; www.gbif.org/) and previous studies (Wakie et al. 2014; Mbaabu et al. 2019; Shiferaw et al. 2019a, b, c). For visual assessment and check spatial accuracy, all points were mapped using ArcGIS 10.8. Duplicate occurrence points were removed. Finally, a total of 791 documented regional presence records were used to build the models (Figure SI-1.doc). Again, we generated 1000 pseudo-absence points by means of random sampling (Fournier et al. 2017). To reduce the influence of false absences, we removed points that were closer than 10 km to species presence point following the method of Eckert et al. (2020).

Predictor variables

Nineteen bioclimatic variables at 10-arc-sec resolution were obtained from WorldClim version 2 (https://worldclim.org/version2). To avoid running models using highly correlated variables, we separated the 19 acquired environmental variables into two uncorrelated groups; the temperature variables and the precipitation variables group. Variance inflation factor (VIF) was used to detect collinearity effects between the variables and minimize redundancy among the initial variable set. Using a step wise procedure, we excluded variables with VIF values greater than three. Accordingly, four precipitation-related variables and four temperature-related variables, totaling eight bioclimatic variables were used to build the final model in R statistical software (Hijmans and Elith 2017; Table 1; Figure SI-1.doc).

The improved fifth version of the atmosphere–ocean General Circulation Model (GCM) was used for projection of the continental future climate. Currently, it is not clear which future climate change scenario provides the best predictions for invasive species (Hayes and Piaggio 2018; Sintayehu et al. 2020), thus we used two Representative Concentration Pathways-RCP4.5 and RCP8.5 for the greenhouse gas concentration trajectories of 2050 and 2070.

Species distribution modeling (SDM)

Numerous algorithms for SDM are available and their performances vary significantly (Elith et al. 2006). A single modelling algorithm does not provide the best predictive accuracy in SDM, therefore an ensemble of multiple algorithms is considered to produce better accuracy (Araújo and New 2007). Our modelling framework was thus based on five modelling algorithms analyzed under the sdm package in R statistical software: (i) generalized linear models using logistic regression and maximum likelihood estimation (GLM), (ii) support vector machine (SVM), (iii) a random forest algorithm (RF), (iv) boosted regression trees (BRT), and (v) multivariate adaptive regression splines (MARS) (Sintayehu et al. 2020). We combined five prediction models into an "ensemble" by averaging the models with a true skill statistic (TSS) greater than 0.7 to obtain a "consensus model" and to avoid the integration of weak models (Allouche et al. 2006). The presence and pseudo-absence data were divided into two sets: 70% of the data were used for training the models while 30% were used for evaluating the model accuracy (Araújo and New 2007).

Evaluating model performance

Model performance was assessed based on the threshold-independent area under the receiver operating characteristic curve (AUC) (Liu et al. 2005) and the threshold-dependent true skill statistic (TSS) (Allouche et al. 2006). Model performance was considered as 'good' only if both measures (AUC and TSS) were fulfilled (Phillipsa et al. 2006). All

Table 1 Predictor variables used for modelling the potential distribution of *Prosopis juliflora* in Africa

Label	Variable	Units
bio1	Annual Mean Temperature	Degree Celsius
bio2	Diurnal Range (Mean of monthly (max temp—min temp))	Degree Celsius
bio3	Isothermality (bio2/bio7)	Dimensionless
bio8	Mean Temperature of Wettest Quarter	Degree Celsius
bio12	Annual Precipitation	Millimeter
bio15	Precipitation Seasonality (Coefficient of Variation)	Percentage
bio16	Precipitation of Wettest Quarter	Millimeter
bio17	Precipitation of Driest Quarter	Millimeter

analyses were carried out using the sdm package for R statistical software v.3.6.3 (R Core Team 2017).

Area change analysis

Climate suitability was calculated and change in suitability was analyzed for the year 2050 and year 2070 for RCPs: 4.5 and 8.5. The final map was classified into four suitability categories according to Hamid et al. (2019): not suitable (0.0–0.25), low suitable (0.25–0.50), moderately suitable (0.50–0.75) and highly suitable (0.75–1.00) using ArcGIS 10.8. Percentage area change (lost or gain areas) by the 2050 and 2070 (AC) compared to the current scenario were calculated as (Sintayehu et al. 2020):

$$AC = \frac{Af - Ac}{Ac} \times 100\%$$

where Af is the predicted area suitability area for *P. juliflora* in the future; and Ac is the predicted area of non suitable area under current conditions.

Results

Model performance and relative importance of variables

AUC and TSS statistics for each of the five SDM models (GLM, SVM, MARS, BRT and RF) are shown in Table 2. The mean AUC values ranged from 0.84 (lowest) to 0.96 (highest) with an overall average of 0.91. The RF has shown the highest AUC score (0.96), and SVM receiving the lowest (0.84) AUC score. The average TSS values ranged from 0.91 (lowest) to 0.95 (highest) with an average of 0.93. The RF received the highest sensitivity (0.95), and GLM received the lowest sensitivity (0.91) among the five SDM models. Based on the quantitative assessments of model performance criteria, i.e. AUC and TSS statistics our result revealed the performance of the model were considered as very high.

The relative contribution of each predictor variables to individual models were analyzed (Supplementary material S1-Fig. 1). Of all the predictors' variables, Isothermality (bio3) was found to be the most contributing variable affecting the distribution of *P. juliflora*, followed by annual precipitation (bio12) and annual mean temperature (bio1) by explaining 33.6%, 21.7%, and 13.0% of the variation in the model, respectively, and 68.3% collectively.

Table 2 Accuracy assessment of five applied models predicting current and future (2050 and 2070) habitat suitability for *Prosopis juliflora* in Africa under RCP4.5 and RCP8.5 climate change scenario

Performance indicator	GLM	SVM	MARS	BRT	RF
AUC	0.89	0.84	0.92	0.93	0.96
TSS	0.91	0.94	0.94	0.92	0.95

Distribution *Prosopis juliflora* under the current climatic condition

Our results revealed that 5.6% of the African continent is showing high suitability for *P. juliflora* under the current climatic conditions while 75.6% is unsuitable under similar climatic conditions. We find that additional 7.4% of the area has a moderate suitability. Compared to the current distribution, by 2050, the total highly suitable area for *P. juliflora* under RCP4.5 and RCP8.5 will gradually increase to 8.9% and 25%, respectively. Unsuitable habitats will decrease by 10.8% and 16.5% under RCP4.5 and RCP8.5, respectively (Table 3). Under similar scenario RCP4.5 and RCP8.5 in 2050s will see areas with moderate suitability increase by 63.5% and 86.5%. By 2070, unsuitable habitat for the species is projected to decrease to 14.5% and 23.4% under RCP4.5 and RCP8.5 scenario, respectively. In the same period, the total area of highly suitable area for *P. juliflora* under RCP4.5 and RCP8.5 scenario will increase by 17.8% and 28.6%, respectively. Overall, by 2070 areas considered with low suitability in the continent will increase to 25.4% and 65.8% under RCP4.5 and RCP8.5 scenarios, respectively. However, for that period the RCP4.5 and RCP8.5 scenarios show that moderately suitable habitats will increase by 85.1% and 106.8%, respectively.

According to the current climatic scenario (Fig. 1), high and moderately suitable areas for *P. juliflora* are predicted to occur in the eastern Africa region, areas bordering the Red Sea and extending into West Africa with some suitability across the Sahel. High to moderate occurrence are predicted for Sudan, Eritrea, Ethiopia, South Sudan, Kenya, Somalia, Uganda and Tanzania extending westwards along the central parts of the continent mainly to Mauritania and Mali in the west. Parts of southern Madagascar, small areas in Southern Africa and Mozambique were also found to be suitable habitats for this invasive plant species. Lower suitable areas for the invasion of *P. juliflora* were predicted in northern and southern Africa (Fig. 1).

Distribution of *Prosopis juliflora* under future climatic conditions

The predicted climatically suitable areas for *P. juliflora* under RCP4.5 and RCP8.5 climate change scenario would expand across Africa in the year 2050 (Fig. 2a, b; Table 3) and further expansion will be anticipated by 2070 (Fig. 2c,

Table 3 Percentage of climatically suitable class for *Prosopis juliflora* at present and in the future (2050 and 2070) in Africa under RCP4.5 and RCP8.5 climate change scenarios

Decades	Scenarios	Total suitability (%)				Change (%) Compared to the current suitability			
		Not suitable	Low	Moderate	High	Not suitable	Low	Moderate	High
Current	–	75.6	11.4	7.4	5.6				
2050	RCP4.5	68.2	13.6	12.1	6.1	– 10.8	19.3	63.5	8.9
	RCP8.5	63.9	15.3	13.8	7	– 16.5	34.2	86.5	25
2070	RCP4.5	65.4	14.3	13.7	6.6	– 14.5	25.4	85.1	17.8
	RCP8.5	58.6	18.9	15.3	7.2	– 23.4	65.8	106.8	28.6

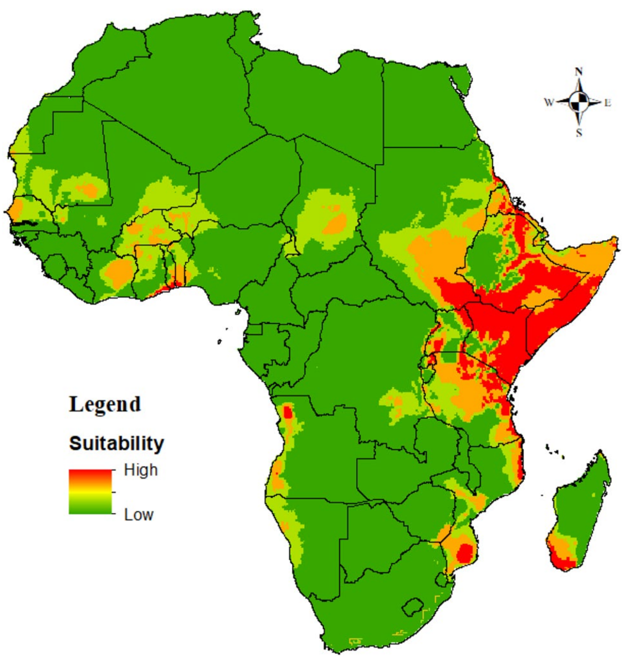

Fig. 1 Maps showing current climatic suitability for *Prosopis juliflora* in Africa. Green to red colors shows the gradient of suitability from low to high (color figure online)

d; Table 3). In both climate change scenarios (RCP 4.5 and RCP 8.5) during the periods 2050 and 2070, the high and moderate suitable area for *P. juliflora* presence were predicted to be increased (gained) in the eastern, central and western Africa. Concurrently, the potential area for species presence will expand in parts of Chad, Niger, Burkina Faso, Ghana, Nigeria, Senegal and Côte d'Ivoire (Fig. 2).

Discussion

The results of our study showed that climate change would determine the distribution of *P. juliflora* in Africa. The model indicates that there would be a gain in both the highly and moderately suitable areas particularly in eastern, central and western Africa by 2050 and 2070 under both climate change scenarios. Our model is similar with previous studies that have showed expansion for *P. juliflora* invasion at different scale (Wakie et al. 2014; Ng et al. 2018; Heshmati et al. 2019; Eckert et al. 2020). In particular, areas closer to the present distribution *P. juliflora* are those that are under high risk of invasion. Thus, it calls for all concerned bodies including scientific community, policy makers, land resource managers and others to refrain from the usual piecemeal approach and work together to develop efficient management strategies in order to prevent the expansion and also manage invasion of *P. juliflora* in the continent.

Current scientific findings showed that climate variability significantly influence species distributions by causing species range expansions, shifts, or reductions (Thomas et al. 2004; Corlett and Westcott 2013; Sintayehu 2018). Similarly, our research findings have demonstrated that the area of high and moderate suitability for *P. juliflora* due to climate change will increase in future with reference to the current area at the expense of non and low suitable habitats. This is because climate change often favors invasive species as environmental conditions worsen for indigenous species undermining their competitive power against invaders in ecosystem resources (Hellmann et al. 2008). Invasive species like *P. juliflora* have the inherent ability to tolerate wider environmental ranges or adapt to new environmental conditions (Vilà et al. 2011; Qin et al. 2016; Kariyawasam and Kumar 2019). This means that In the long run the inherent characteristic attributed by the species and lack of their native competitors may provide opportunity for niche shift in new regions. This means that invasive species may experience a process of niche shift in new regions due to their inherent plasticity.

Moreover, changes in the frequency and intensity of extreme climatic events, due to climate change, can disturb ecosystems, making them vulnerable to invasions, thus providing exceptional opportunities for dispersal and growth of invasive species. A plausible explanation to such characteristics could underlined by the fact thermophilic species tend to expand their ranges with increasing temperature under climate change (Ju et al. 2015). The dynamics of expansion

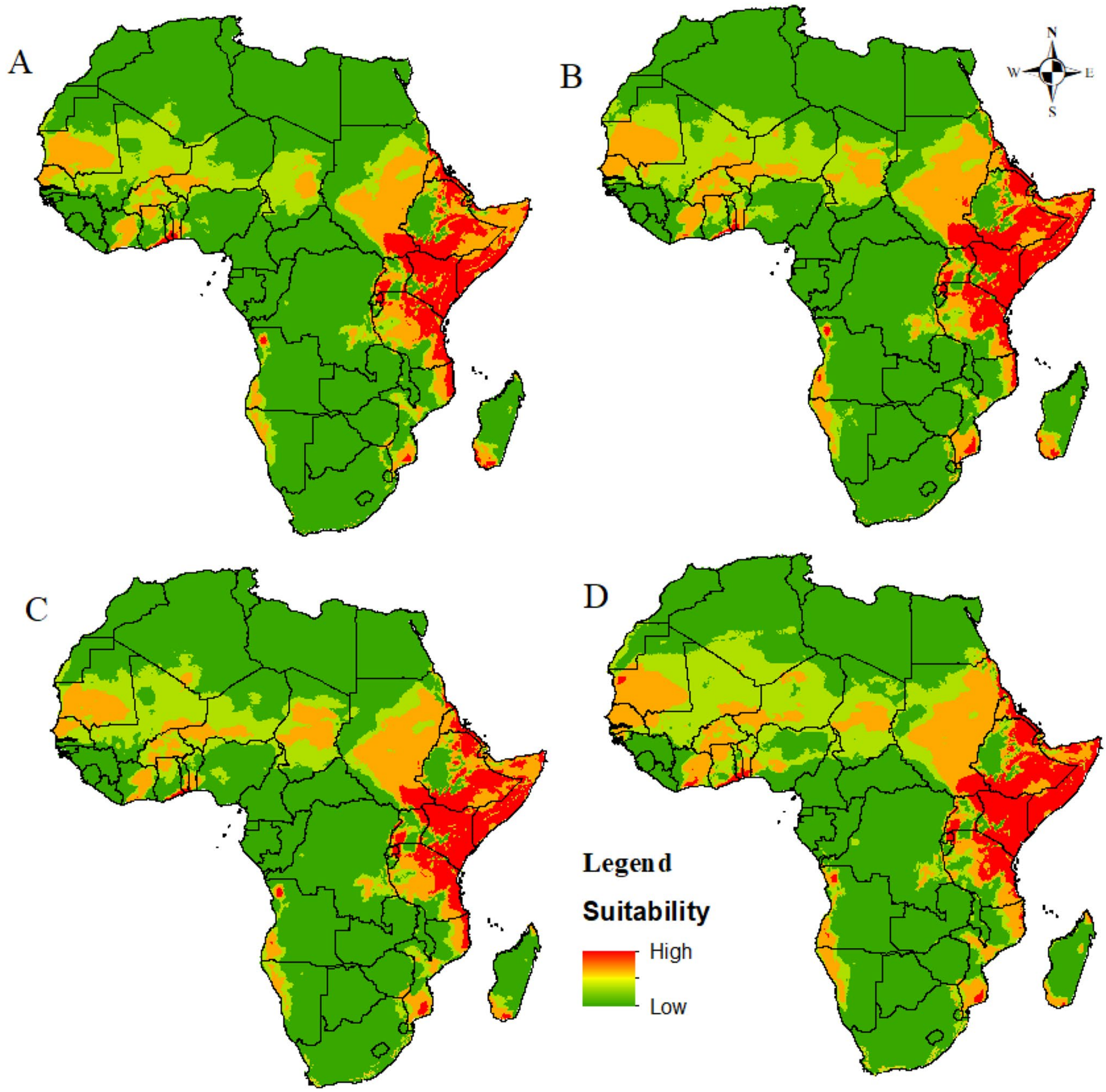

Fig. 2 Projected continental change in *Prosopis juliflora* habitat suitability by 2050 under RCP4.5 (**a**) and RCP 8.5 (**b**) and by 2070 under RCP4.5 (**c**) and RCP 8.5 (**d**). Green to red colors shows the gradient of suitability from low to high (color figure online)

predicted for *P. juliflora* can be best explained with the expected changes in patterns of precipitation and increasing temperature under climate change. The areas predicted as unsuitable under current climate scenario but suitable in the future may have advantaged from temperature and/or precipitations increases, both are expected to have a positive trend. Change in climate in the future will facilitate the rate of invasion of *P. juliflora* in the new areas. Accordingly, preemptive management strategies need to be put in place to control its spread in such High-Risk areas. It becomes urgent for scientific community, land resource managers, policy makers and other stakeholders in these High-Risk regions to develop efficient and collaborative management strategies in order to prevent introductions and control of this invasive species.

Climate change induces habitat expansion of invasive species (Petitpierre et al. 2016). Our study showed that low elevation was high and moderate suitable under the current climate condition. Further, we also predicted future range expansion of *P. juliflora* in Ethiopia, Sudan, Kenya, Chad, Niger and Mali towards high elevation by removing current climatic barriers and shifting habitats to higher elevations. Range loss prediction also showed that there will be a loss of the current range distribution for low elevation, for instance in Madagascar, as high altitude zones begin to post ambient growth conditions for the invasive species. Similar other studies predicted the range expansion of invasive plants species towards higher elevations in response to climate change (Hellmann et al. 2008; Shrestha et al. 2018; Mbaabu et al. 2019).

Invasive plant species native to tropical countries, like *P. juliflora,* have much higher critical thermal maxima than do native species, indicating that they can thrive in higher temperatures and could be suppress native species under future and predicted climate change conditions. Additionally, invasive species have some important characteristics, such as short reproduction cycles, high fecundity, strong dispersal ability, and high environmental tolerance that help them establish well in new environments (Bradley et al. 2010). Along with climate change, several non-climatic components, including anthropogenic activities such as rapid land use and land cover change, road construction, urban development, foreign trade, agriculture, and tourism promote invasion (Martin et al. 2013). Although this study provided critical information about potential plant invasions in Africa under current and future climatic conditions, our models were based only on bioclimatic variables, disregarding land use and land cover change, dispersal capacities, biotic interaction (e.g. facilitation and competition), and vectors driving species invasions as described by Martin et al. (2013) and Pysek and Richardson (2010). Thus, the results of this study have to be described with these limitations in mind.

The model predictions are in consonance with the current continental *P. juliflora* distribution records (Eckert et al. 2020) and global prediction of *P. juliflora* invasion (Heshmati et al. 2019). The suitable habitat predicted by our ensemble model is wider than findings derived from country level studies (Ng et al. 2018; Sintayehu et al. 2020). Discrepancies in model prediction between Sintayehu et al. (2020) country level study and the present study at continental level may be largely due to differences of environmental data sets employed and its resolution. Three factors are known to govern the distribution of species namely: abiotic factors, biotic factors and human activities (Shiferaw et al. 2019a; Eckert et al. 2020). However, such data on the biotic factors (e.g. dispersal abilities, species interactions and propagule pressure) are not available and their inclusion increases the complexity in modelling technique. Moreover, change temperature and precipitation is considered as the major determinate factor determining species distributions at the continental scales as is true for the present study. Nevertheless, at the local scale or country level, factors like substrate and biotic interactions typically become more important.

Therefore, future research has to incorporate the biotic (i.e. competition, propagule pressure and dispersal ability) and other (i.e. land use and land cover changes) factors in the distribution models in order to have a more refined understanding of the species distributions under changing climate at local scale.

Conclusion

We predicted the current and future climate suitability for *P. juliflora* for which additional suitable areas are likely to be created for predicted climate change models. The continuous increase in the climatically suitable habitats for the species has already caused adverse impacts on biodiversity, ecosystem services, food security, and livelihood in the continent as majority of Africa depends on biodiversity and associated ecosystem services for their survival. The results of this provide a precautionary note to ecosystem managers across Africa and to policy leaders in the high-risk countries to consider the transboundary character of *P. juliflora* and develop cross-border invasive species management strategies. The results of this study will also support early detection and rapid response (EDRR) of invasive plant species in their potentially suitable areas. Based on our study, we urge that it is necessary to perform early identification and eradication actions no national level, especially focusing on the west, central and eastern part of the continent.

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