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Adapting distribution patterns of desert locusts, *Schistocerca gregaria* in response to global climate change

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Abstract

The desert locust (*Schistocerca gregaria*) is a destructive migratory pest, posing great threat to over 60 countries globally. In the backdrop of climate change, the habitat suitability of desert locusts is poised to undergo alterations. Hence, investigating the shifting dynamics of desert locust habitats holds profound significance in ensuring global agricultural resilience and food security. In this study, we combined the maximum entropy modelling and geographic information system technology to conduct a comprehensive analysis of the impact of climate change on the distribution patterns and habitat adaptability of desert locusts. The results indicate that the suitable areas for desert locusts (0.2976×10^8 km^2) are concentrated in northern Africa and southwestern Asia, accounting for 19.97% of the total global land area. Key environmental variables affecting the desert locust distribution include temperature annual range, mean temperature of the coldest quarter, average temperature of February, and precipitation of the driest month. Under the SSP1–2.6 and SSP5–8.5 climate scenarios, potential suitable areas for desert locusts are estimated to increase from 2030 (2021–2040) to 2090 (2081–2100). By 2090, highly suitable areas for SSP1–2.6 and SSP5–8.5 are projected to be 0.0606×10^8 and 0.0891×10^8 km^2, respectively, reflecting an expansion of 1.84 and 2.77% compared to existing ones. These research findings provide a theoretical basis for adopting prevention and control strategies for desert locusts.

Introduction

The desert locust, *Schistocerca gregaria* is known to be the oldest migratory insect (Song *et al*., 2017), capable of covering distances of 150–200 km daily with the airflow (Yuga and Wani, 2022). They feed on over 400 types of plants, including wheat, corn, rice, potatoes, and various other crops and each locust can consume fresh green leaves equivalent to its body weight daily (FAO, 2020; Yuga and Wani, 2022). Thriving in semi-arid and arid environments, desert locusts find suitable breeding sites in bare lands (Latchininsky and Sivanpillai, 2010) and are widely distributed in African and the Middle Eastern deserts. They pose a threat to food security and significantly impact local agricultural production (Brader *et al*., 2006; Kimathi *et al*., 2020). Desert locusts affect at least 1/10th of the world's population directly or indirectly (Latchininsky *et al*., 2016).

With the advancement of civilisation, the excessive use of fossil fuels has led to a tremendous emission of greenhouse gases, including carbon dioxide, significantly contributing to global warming (Aminu *et al*., 2017). Studies indicate that global warming may expand pest geographical distribution, increase overwintering survival rates, boost reproductive rates, and alter plant–pest interactions (Skendžić *et al*., 2021). Simultaneously, it provides an opportunity for pests to move from one region to another in search of food and colonise new areas (FAO, 2020). Research has indicated a close correlation between the occurrence and migration of desert locusts with climate factors. Climate change, such as rainfall, can cause seasonal disasters of desert locusts (Uvarov, 1966). In 2020, a desert locust plague in East Africa was attributed to a cyclonic storm in the Arabian Peninsula in 2018. The abnormal climate brought additional rainfall to the Arabian Desert, increasing the hatching rate of desert locust eggs. Abundant rainfall also promoted vegetation growth, providing ample food supply for desert locusts. The combination of warm weather and abundant rainfall triggered an 8000-fold increase in locusts in the Arabian Desert (Stone, 2020). However, 2019 saw a decrease in rainfall in the Arabian Peninsula. As a result, the vegetation failed to meet the needs of high-density desert locusts, leading to the eastward migration of desert locusts and causing locust infestations in bordering areas, such as the India–Pakistan border in 2020 (Salih *et al*., 2020). There is a close correlation between the occurrences of desert locusts and the environment. Nevertheless, their rapid escalation into outbreaks in the short term and the uncertainty surrounding outbreak area make prediction efforts particularly crucial. Since the 1900s, efforts have been made to forecast desert locusts, mainly through remote-sensing technology (Klein *et al*., 2021). This involves on-site investigations to record the growth conditions and population dynamics of desert locusts, combined with historical ecological data to predict the distribution of desert locusts in the near future (Cressman, 2013).

Maximum entropy (MaxEnt) modelling, a programme that models species distributions from occurrence records of 'presence-only' species (Phillips *et al*., 2004), analyses the relationship between the species record locations and environmental characteristics. Locations with similar environmental characteristics are predicted as potential distribution areas for the species (Elith *et al*., 2011; Sillero, 2011; Ahmed *et al*., 2015; Li *et al*., 2020; Muyobela *et al*., 2023). MaxEnt model demonstrates a notable advantage, requiring a relatively low number of species sampling points (≥5 points) for accurate predictions, making it a user-friendly and computationally efficient approach with high accuracy (Phillips and Dudík, 2008). Wen *et al*. (2023) analysed the habitat suitability of *Oedaleus asiaticus* on the Mongolian Plateau; the results showed that the suitable area of *O. asiaticus* was increasing. Accumulated precipitation and surface temperature are identified as the main driving factors for the changes in the distribution of *O. asiaticus*. Abou-Shaara *et al*. (2022) analysed the potential habitable areas of the pest *Plecia nearctica* offering insights that can provide information for making control measures. Until now, MaxEnt has been widely used in predicting suitable areas for insects. In this study, we used MaxEnt model and employed environmental data from known distribution points to identify critical factors influencing their distribution. After factor optimisation, we analysed the potential geographical distribution of desert locusts under the present and future climate parameters, aiming to make accurate predictions in advance and guide efforts for the prevention and control of desert locusts.

Materials and methods

Species occurrence data

The occurrence data of desert locusts were sourced from the Locust Hub (https://locust-hub-hqfao.hub.arcgis.com/) of the Food and Agriculture Organization of the United Nations (FAO). To mitigate spatial autocorrelation between occurrence locations (Verbruggen *et al*., 2013) and address sampling bias induced by clustering effects, the collected occurrence data were loaded into ArcGIS. This process involved removing non-natural points eliminating duplicate coordinates in latitude and longitude. To avoid the bias caused by unbalanced data points, we checked and confirmed that each grid cell had only a single distribution point based on climatic precision. Ultimately, 1915 occurrence data points of desert locusts were used for modelling (table S1, fig. 1).

Environmental data

The environmental data were sourced from the global climate database, WorldClim (https://worldclim.org/), with a spatial resolution of 2.5 arc-minutes and encompassing 43 environmental factors, comprising 19 bioclimatic variables and 24 climate variables. The current climate data were composed of historical climate data from 1970 to 2000. The BCC-CSM2-MR model was selected for future climate data (Wu *et al*., 2019). The study also chose the climate change scenario data for the years 2030 (average for 2021–2040), 2050 (average for 2041–2060), 2070 (average for 2061–2080), and 2090 (average for 2081–2100) under the sustainable development pathway (SSP1–2.6), and the

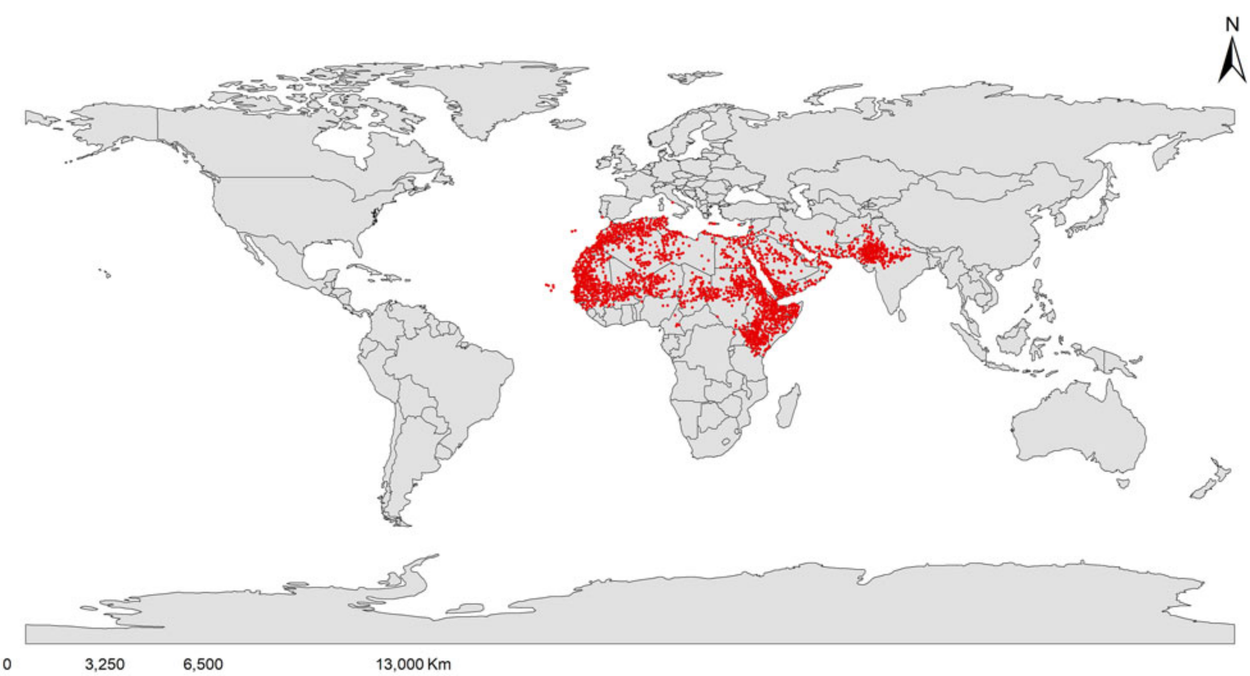

Figure 1. Global occurrence records of locusts. Each red point refers to an occurrence record.

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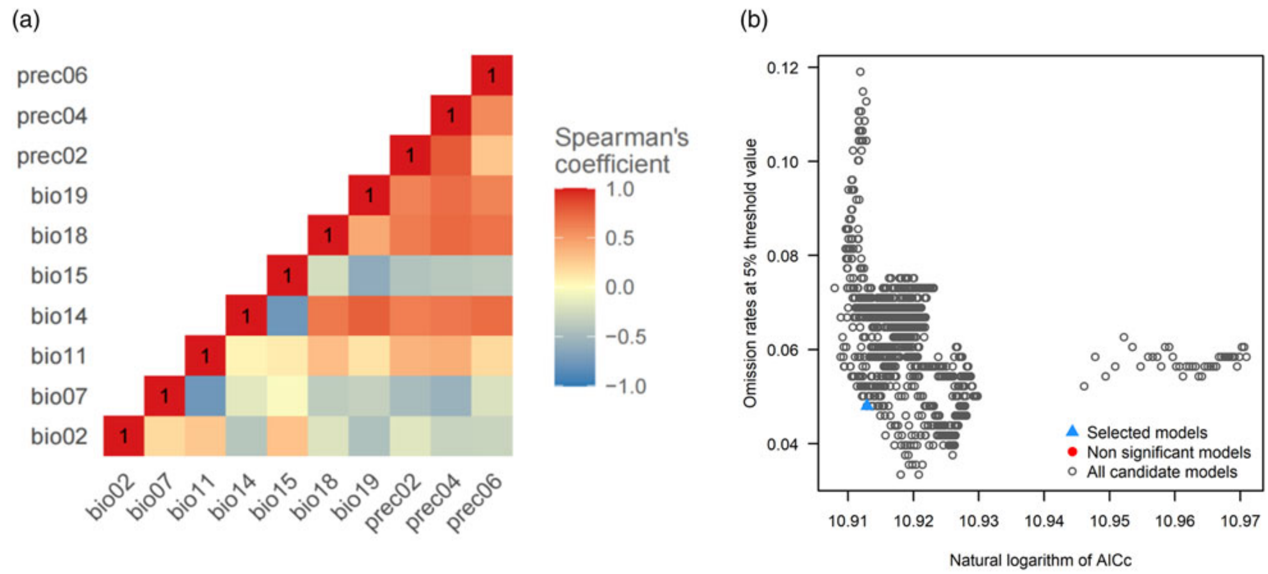

Figure 2. Model optimisation. (A) Heat map showing the correlation coefficient matrix of ten selected environmental variables. (B) Optimal model selection for predicting potential suitable areas of desert locusts.

fossil fuel-intensive development pathway (SSP5–8.5) (Popp *et al.*, 2017; Meinshausen *et al.*, 2020).

To address multicollinearity among environmental variables and improve the simulation accuracy of the MaxEnt model (Feng *et al.*, 2019), the 'SDMtune' package was used for appropriate variable selection (Vignali *et al.*, 2020). The dataset was divided into 25% testing data and 75% training data to train the MaxEnt model. Environmental variables with a correlation coefficient greater than 0.8 were removed based on their contribution percentages (fig. 2A). Finally, ten biologically meaningful climate variables were selected for modelling, including mean diurnal temperature range (bio02), temperature annual range (bio07), mean temperature of the coldest quarter (bio11), precipitation of the driest month (bio14), precipitation seasonality (bio15), precipitation of the warmest quarter (bio18), precipitation of the coldest quarter (bio19), precipitation of February (prec02), precipitation of April (prec04), and precipitation of June (prec06).

Optimisation of model parameter

The calibration, creation, and evaluation of the model were conducted using the 'Kuenm' package in R (Cobos *et al.*, 2019), in which the two most critical parameters are feature combination (FC) and regularisation multiplier (RM) (Merow *et al.*, 2013). Here, FC covers five main features: linear features, quadratic features, product features, threshold features, and hinge features, with a total of 29 other parameter combinations. Similarly, RM parameters were set with intervals of 0.1, ranging from 0.1 to 4, resulting in a total of 40 RM values. This yielded 1160 (29 FC × 40 RM) parameter combinations. Model performance was assessed based on the omission rate (E), model complexity, and the Akaike information criterion (AICc) (Sugiura, 1978; Akaike, 1998). A smaller omission rate (E) should be less than 5%, while a lower AICc value indicates a better fit between the model and the data. For delta_AICc, a lower value indicates more accurate predictions, and the model is deemed optimal when delta_AICc = 0. Ultimately, the model exhibited the highest performance when RM = 0.3 and FC = QP (Quadratic features, Product features), with $E = 0.048$ (table S2, fig. 2B).

Based on MaxEnt 3.4.4, the potential suitable areas of desert locusts were predicted. This study randomly selected 25% of the desert locust data as the testing set, while the remaining 75% were used as the training set. After ten runs, the output prediction results were averaged, with the area under curve (AUC) as the evaluation metric for model accuracy. Higher AUC values correlate with greater accuracy (Phillips *et al.*, 2006). AUC values between 0.5 and 0.7 indicate low prediction accuracy, between 0.7 and 0.8 indicate moderate accuracy, and above 0.8 indicate high accuracy. The jackknife method was employed to test the importance of each environmental factor in the suitable area distribution of desert locusts (Guan *et al.*, 2021). A larger regularisation training gain value in the jackknife method indicates a greater influence of that factor. Finally, the ASC (ASCII File) result files were imported into ArcGIS to delineate the suitable areas of desert locusts.

Suitable area division and spatial pattern changes

The minimum training presence logistic threshold was chosen as the classification threshold for non-suitable and suitable areas (Escalante *et al.*, 2013). The output values from MaxEnt software range from 0 to 1, where values closer to 1 indicate a higher likelihood of species presence. Given that the value of the minimum training presence logistic threshold was 0.0649 (table S3), the suitable area range was divided into four levels: non-suitability area (0–0.0649), low-suitability area (0.0649–0.35), moderate-suitability area (0.35–0.55), and high-suitability area (0.55–1.0).

The output from MaxEnt software was loaded into ArcGIS, and the reclassify tool in spatial analysis was used for visual representation of the predicted results. Finally, the proportions of different suitability levels were calculated.

Results

Modelling result evaluation

The prediction model of suitable areas for desert locusts exhibited an average AUC value of 0.900 over ten runs (fig. 3A), indicating

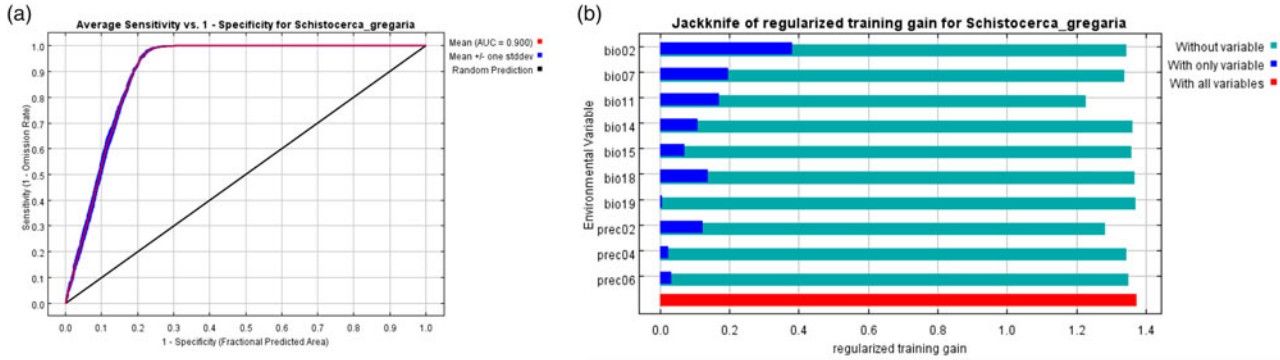

Figure 3. (A) Model suitability test on the basis of AUC value in predicting desert locusts' suitable areas. (B) Importance of ten selected environmental variables evaluated by jackknife testing.

higher prediction accuracy of the MaxEnt model and its suitability for predicting the suitability of areas for desert locusts.

Factors influencing spatial distribution pattern of desert locusts

According to the contribution results of environmental variables (table S4), temperature annual range (bio07), mean temperature of coldest quarter (bio11), precipitation of February (prec02), and precipitation of driest month (bio14) were the major factors affecting the model prediction results. These factors displayed respective contributions of 43.6, 33.5, 8.3, and 4.5%, with a cumulative contribution of 89.9%. Temperature annual range (bio07) and mean temperature of coldest quarter (bio11), as shown in the results of the jackknife test (fig. 3B), exhibited the greatest gain in prediction effect, indicating their greatest influence on the model prediction results.

Analysis of the curves of the most important contributing environmental variables in the MaxEnt model of desert locusts (fig. 4A) shows that within a 1°C range of annual temperature variations, the occurrence probability of desert locusts is as high as 68.5% and decreases with an increase in the value of annual temperature variations. As the average temperature in the coldest season rises (fig. 4B), the occurrence probability of desert locusts declines and levels off at around 29°C, with an occurrence probability of about 40.0%. Desert locusts tend to avoid areas with excessive precipitation. When the precipitation in February (fig. 4C) is 1 mm, the probability of occurrence is the highest. As precipitation

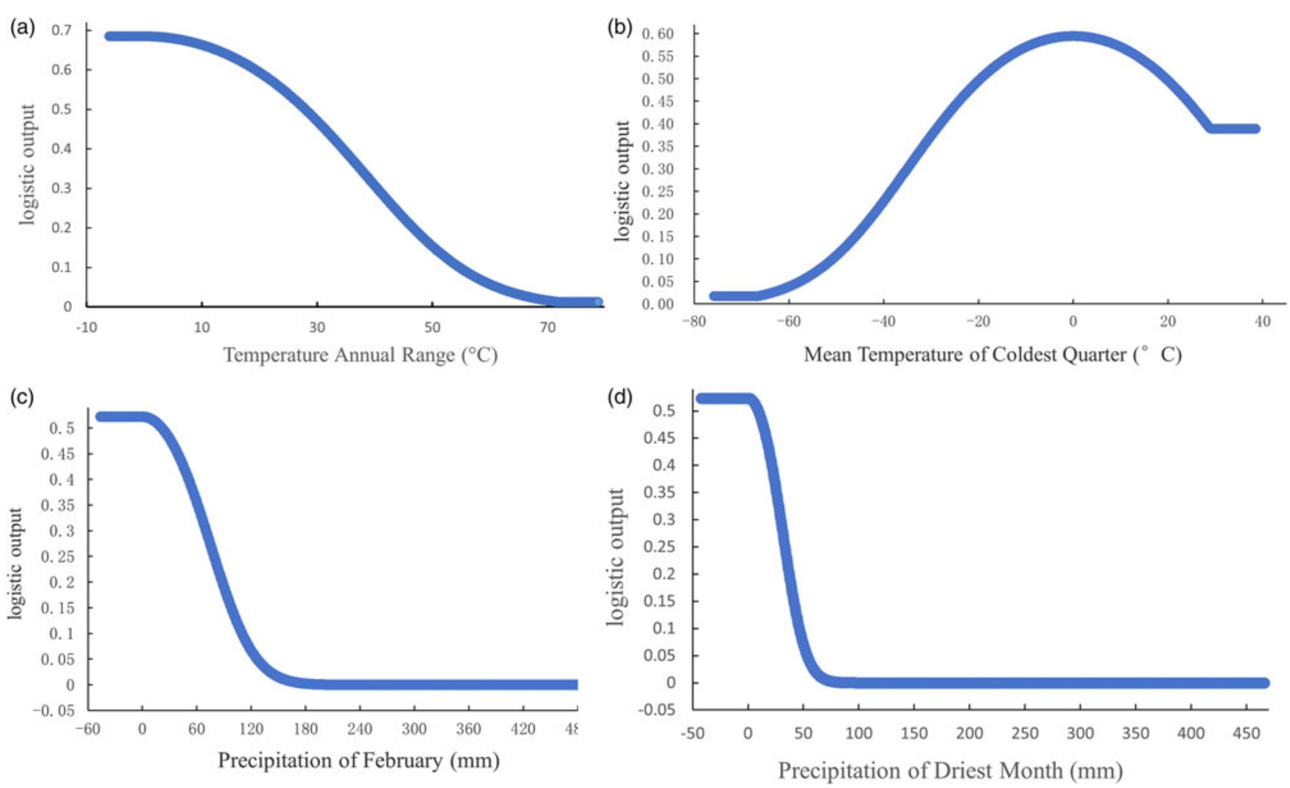

Figure 4. Response curves of the important contributing environmental variables in the MaxEnt model: (A) temperature annual range; (B) mean temperature of coldest quarter; (C) precipitation of February; (D) precipitation of driest month.

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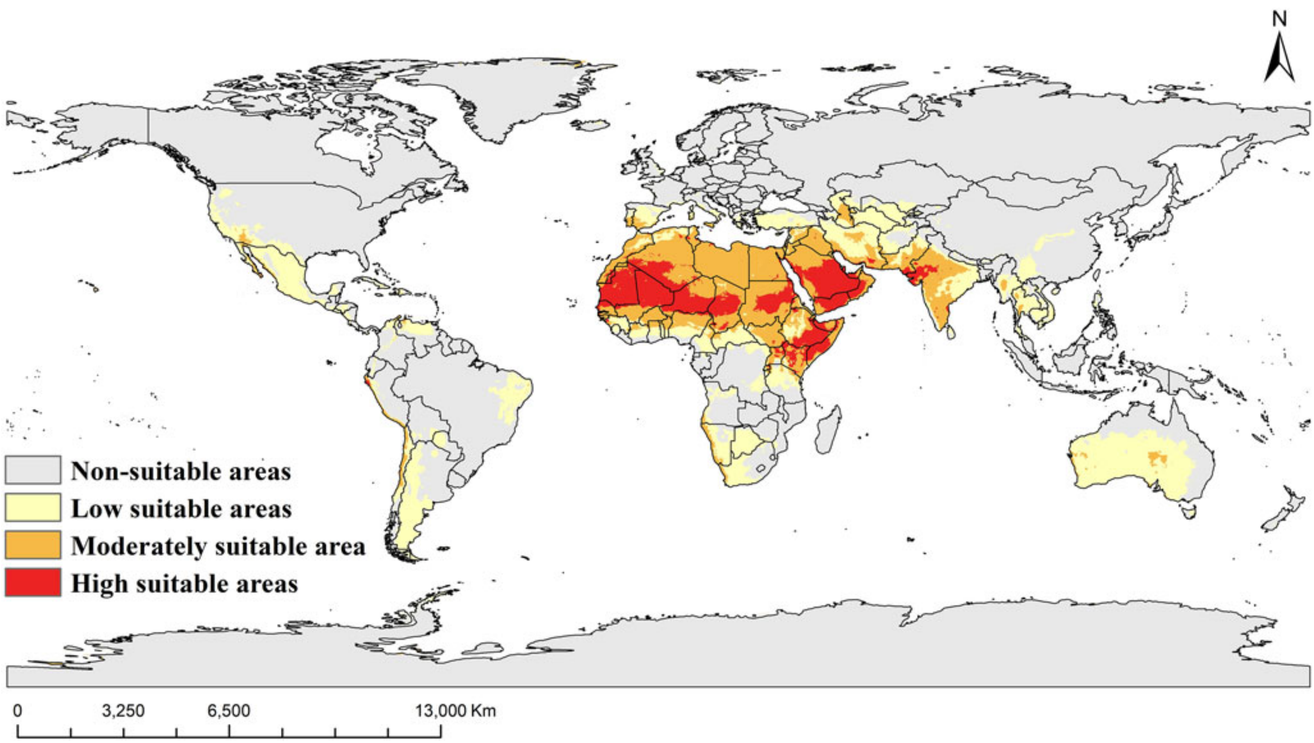

Figure 5. Potential suitable areas for desert locusts under current climate conditions.

increases, the probability of occurrence decreases and tends to stabilise at 160 mm; higher rainfall in the driest month (fig. 4D) corresponds to a lower occurrence probability of desert locusts, with the occurrence probability close to 0 when it reaches 80 mm.

Distribution of potential suitable areas for desert locusts under current climate

Under the current climate, the major suitable areas for desert locusts are located in northern Africa and southwestern Asia, near the Horn of Africa (fig. 5). These areas include Morocco, Algeria, Libya, Egypt, Western Sahara, Mauritania, Mali, Niger, Chad, Sudan, Eritrea, Djibouti, Ethiopia, Central Africa, Cameroon, Nigeria, Benin, Togo, Ghana, Guinea, Bissau, Senegal, Uganda, Kenya, Syria, Jordan, Iraq, Saudi Arabia, Yemen, Oman, Iran, Afghanistan, Pakistan, India, and other regions. In the coastal areas of the Americas, there are low suitable areas, such as Mexico, Venezuela, Peru, Chile, etc. In Oceania, only Australia has low suitable areas. Europe also has low suitable areas distributed in very few areas near Africa, Portugal, Spain, Italy, Greece, and other regions. High-suitability areas are mainly distributed in Mauritania, Mali, Niger, Chad, Sudan, Ethiopia, Kenya, Somalia, Saudi Arabia, Yemen, Oman, India, and other regions.

Statistically, the suitable areas for desert locusts cover an area of about 0.2976×10^8 km^2, around 19.97% of the global land. High-suitability areas, mainly distributed in Mauritania, Mali, Nigeria, Chad, Sudan, Ethiopia, Kenya, Saudi Arabia, Yemen, Pakistan, India, etc., cover 0.0479×10^8 km^2, 3.21% of the global land. Moderate-suitability areas cover 0.1005×10^8 km^2, 6.75% of the global land, while low-suitability areas, mainly distributed in the Americas, Oceania, and western Asia, cover 0.1492×10^8 km^2, 10.01% of the global land.

Changes in suitable areas of desert locusts under future climate conditions

Under the SSP1–2.6 scenario (fig. 6A, C), the total suitable areas for desert locusts exhibit a decreasing trend and become relatively stable after 2050. Similarly, the low- and moderate-suitability areas show a decreasing trend, with these areas being transformed into high-suitability areas, which exhibit an increasing trend until 2070. Under the SSP5–8.5 scenario (fig. 6B, D), the total suitable areas undergo a decrease followed by an increase. However, the high-suitability areas show expansion throughout the period.

In 2030, the high-suitability areas under the SSP1–2.6 scenario cover 0.0567×10^8 km^2 (0.6%) more than the current area. Similarly, under the SSP5–8.5 scenario, the high-suitability areas cover 0.0606×10^8 km^2 (1.85%) more than the current area. By 2090, the high-suitability areas under the SSP1–2.6 and SSP5–8.5 scenarios will respectively cover 0.0603×10^8 and 0.0891×10^8 km^2, with expansions of 1.84 and 2.77% compared to the current area. In comparison with the current high-suitability areas, the future high-suitability areas will mainly expand in North African regions such as Algeria, Libya, Chad, Egypt; and India, Iran, Saudi Arabia, and Iraq.

A comparative analysis has been conducted between the potential high-suitability areas under different climates in 2090 and the current ones. The results showed that under the SSP1–2.6 scenario (fig. 7A), the stable areas of desert locusts cover an area of 0.0788×10^8 km^2, with an increase of 0.0231×10^8 km^2 in the high-suitability areas, mainly concentrated in Algeria, Chad, Sudan, Saudi Arabia, Nigeria, and other regions. Under the SSP5–8.5 scenario (fig. 7B), the stable areas of desert locusts cover an area of 0.0717×10^8 km^2, with an increase of 0.0759×10^8 km^2 in the high-suitability areas, mainly concentrated in Algeria, Niger, Libya, Chad, Egypt, Sudan, Saudi Arabia, Iran, Pakistan, and other regions. The high-suitability areas exhibit

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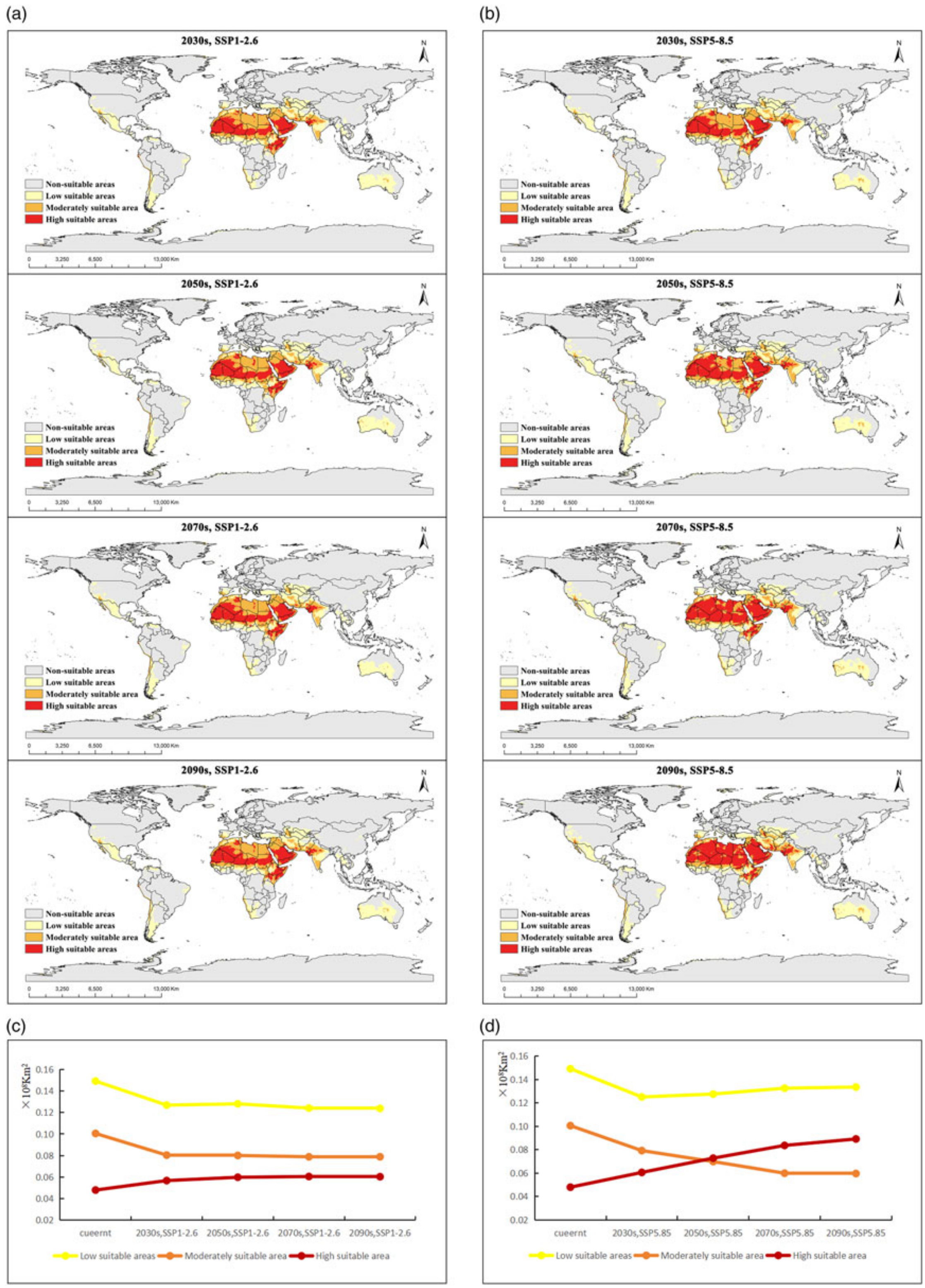

Figure 6. Potential suitable areas for desert locusts under the future climate scenario: (A) under the SSP1–2.6 scenario and (B) under the SSP5–8.5 scenario. Changes in each suitable area of desert locusts from current to 2090: (C) under the SSP1–2.6 scenario and (D) under the SSP5–8.5 scenario.

northward expansion in this scenario compared with SSP1–2.6. The regions of the stable areas are almost the same in both scenarios, but the increase in high-suitability areas under SSP5–8.5 is larger than that under SSP1–2.6 by 0.0528×10^8 km^2.

Discussion

In this study, we collected 1915 representative occurrence data points and used an optimised model to predict the distribution area changes during climate change. Actually, the default

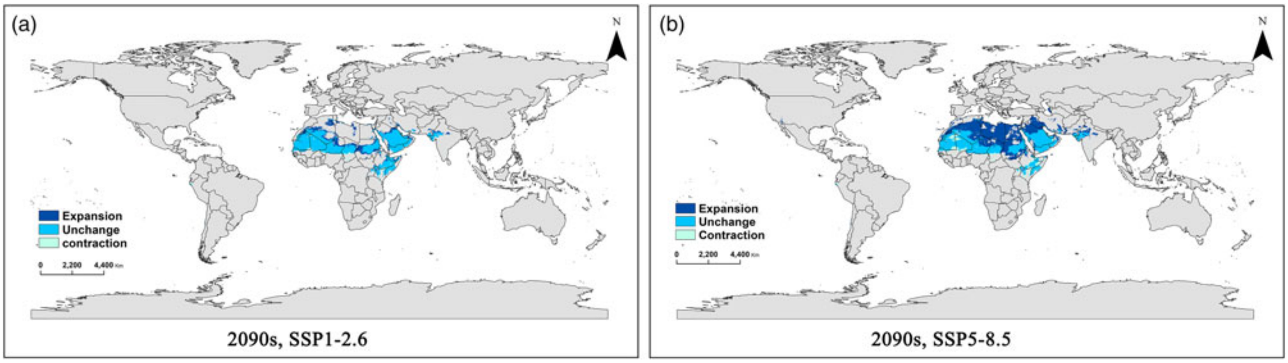

Figure 7. Changes in high suitable areas of desert locusts in 2090: (A) under the SSP1–2.6 scenario and (B) under the SSP5–8.5 scenario.

parameters of the MaxEnt model were initially designed to simulate the actual spatial distribution of 266 species in six different regions. However, for the prediction of the spatial distribution areas of species, the model may face issues such as overfitting, higher complexity, and lower accuracy, which require further optimisation (Warren and Seifert, 2011; Radosavljevic and Anderson, 2014). It has been shown that adjustments to the model parameters made by delta_AICc can constrain the model complexity (Akaike, 1998). Larger values of delta_AICc indicate higher model complexity, and vice versa (Sugiura, 1978). In our study, 'Kuenm' package in R was employed to optimise the MaxEnt model, with the parameter of $E < 2$ and the smallest delta_AICc value selected to avoid overfitting and improve prediction accuracy. Additionally, the selection of environmental variables is crucial for predicting the distribution of suitable areas. For the selection of environmental variables, the 'SDMtune' data package (Vignali *et al.*, 2020) was applied for correlation analysis of 43 variables to eliminate environmental variables with strong correlations. The optimised model exhibits an AUC value of 0.900, indicating a better fit between the model prediction and the actual spatial distribution, allowing for accurate prediction of the potential geographic distribution of desert locusts.

The study found that the distribution probability of desert locusts decreased with the increase in the average temperature in the coldest season, levelling off at 29°C. This suggests that despite the preference of desert locusts for high temperatures, overly high temperatures can also affect their survival, possibly because higher temperatures induce a decrease in the hatching rate or survival rate of their eggs. The egg-hatching rate of desert locusts was proportional to the temperature rise from 15 to 35°C, but too high temperature will reduce the hatching rate (Hunter-Jones, 1970). The 2020 desert locust outbreak was caused by abundant precipitation (Ceccato *et al.*, 2007; Wang *et al.*, 2021; Zhao *et al.*, 2023). However, this study found that desert locusts avoid areas with excessive precipitation, and their distribution probability remains almost zero when precipitation reaches 80 mm in the driest month. Additionally, overly wet soil fails to meet their reproduction requirements. Previous studies have found that desert locusts will not lay eggs until precipitation exceeds 25 mm since sufficient moisture ensures egg hatching and larvae growth (Roffey and Popov, 1968). However, extreme rainfall could overwhelm locust eggs and result in death (Ackonor, 1989; Dinku *et al.*, 2010). Only suitable temperature and humidity can provide the necessary conditions for desert locusts' survival.

The spread and diffusion of organisms is a process influenced by various environmental factors, with outbreaks being the result of the combined effects of climate, vegetation, soil, and other factors. Previous studies showed extreme climate events can enhance the process of biological invasion (Bellard *et al.*, 2013), and a series of chain reactions caused by global climate change have made invasive species adaptable to new habitats (Hoffmann and Sgrò, 2011), which raises threats to local production and economies. Given the influence by abnormal climatic conditions, in 2018, the Arabian Peninsula and the Indian Peninsula's desert areas witnessed an increase in rainfall, leading to the formation of seasonal lakes in the desert that provided favourable conditions for plant growth and also for the breeding and growth of desert locusts. The population of desert locusts considerably rose in a short period, resulting in the widespread locust plague in early 2020 (Salih *et al.*, 2020; Stone, 2020). Additionally, as a migratory invasive insect, desert locusts can also spread through air currents (Wang *et al.*, 2021), with their main dispersal routes influenced by the monsoon. In the summer, desert locusts move towards Central Asia and the Arabian Peninsula in the northeast direction with the help of the southwest monsoon, then continue to disperse eastwards to India and Pakistan, and northwards up to the surroundings of the Caspian Sea (Rainey, 1951), severely threatening agriculture and pastoral production. With great cautious, these newly emerged suitable areas should pay additional attention to monitor the migration and prevent the establishment of desert locusts.

Conclusion

We used optimised MaxEnt model and parameters to predict potential geographical distribution of desert locusts. The main climatic factors affecting the distribution of desert locusts are: temperature annual range, mean temperature of coldest quarter, precipitation of February, and precipitation of driest month. The results showed an increase of high risk area in the future climate conditions, especially in North Africa. The newly emerged suitable areas included Brazil, Argentina, Chile, Venezuela, America, Mexico, Spain, Turkey, and Australia. Our study provided important evidence for desert locusts' monitoring and management.

Supplementary material. The supplementary material for this article can be found at https://doi.org/10.1017/S0007485324000440.

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Competing interests. None.

References

Abou-Shaara HF, Amiri E and Parys KA (2022) Tracking the effects of climate change on the distribution of *Plecia nearctica* (Diptera, Bibionidae) in the USA using MaxEnt and GIS. *Diversity* **14**, 690.

Ackonor JB (1989) Laboratory studies on the effects of flood on egg development, survival and hatchling weight in *Locusta migratoria migratorioides* (Reiche and Fairmaire). *International Journal of Tropical Insect Science* **10**, 485–490.

Ahmed SE, Mcinerny G, O'Hara K, Harper R, Salido L, Emmott S and Joppa LN (2015) Scientists and software – surveying the species distribution modeling community. *Diversity and Distributions* **21**, 258–267.

Akaike H (1998) Information theory and an extension of the maximum likelihood principle. In Petrov BN and Csaki F (eds), *Second International Symposium on Information Theory*. Budapest: Akademiai Kiado, pp. 199–213.

Aminu DM, Nabavi AS, Rochelle AC and Manovic V (2017) A review of developments in carbon dioxide storage. *Applied Energy* **208**, 1389–1419.

Bellard C, Thuiller W, Leroy B, Genovesi P, Bakkenes M and Courchamp F (2013) Will climate change promote future invasions? *Global Change Biology* **19**, 3740–3748.

Brader L, Djibo H, Faye FG, Ghaout S, Lazar M, Luzietoso PN and Babah MO (2006) Towards a more effective response to desert locusts and their impacts on food security, livelihoods and poverty. In *Multilateral Evaluation of the 2003–05 Desert Locust Campaign*. Rome: Food and Agriculture Organisation, pp. 1–92.

Ceccato P, Cressman K, Giannini A and Trzaska S (2007) The desert locust upsurge in West Africa (2003–2005): information on the desert locust early warning system and the prospects for seasonal climate forecasting. *International Journal of Pest Management* **53**, 7–13.

Cobos ME, Peterson AT, Barve N and Osorio-Olvera L (2019) Kuenm: an R package for detailed development of ecological niche models using MaxEnt. *PeerJ* **7**, e6281.

Cressman K (2013) Role of remote sensing in desert locust early warning. *Journal of Applied Remote Sensing* **7**, 075098–075098.

Dinku T, Ceccato P, Cressman K and Connor SJ (2010) Evaluating detection skills of satellite rainfall estimates over desert locust recession regions. *Journal of Applied Meteorology and Climatology* **49**, 1322–1332.

Elith J, Phillips SJ, Hastie T, Dudík M, Chee YE and Yates CJ (2011) A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions* **17**, 43–57.

Escalante T, Rodríguez-Tapia G, Linaje M, Illoldi-Rangel P and González-López R (2013) Identification of areas of endemism from species distribution models: threshold selection and Nearctic mammals. *TIP Revista Especializada en Ciencias Químico-Biológicas* **16**, 5–17.

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

Food and Agriculture Organization (2020) Desert locust crisis: Appeal for rapid response and anticipatory action in the greater Horn of Africa. ReliefWeb. Accessed 29 January 2020.

Guan J, Li M, Ju X, Lin J, Wu J and Zheng J (2021) The potential habitat of desert locusts is contracting: predictions under climate change scenarios. *PeerJ* **9**, e12311.

Hoffmann A and Sgrò C (2011) Climate change and evolutionary adaptation. *Nature* **470**, 479–485.

Hunter-Jones P (1970) The effect of constant temperature on egg development in the desert locust *Schistocerca gregaria* (Forsk.). *Bulletin of Entomological Research* **59**, 707–718.

Kimathi E, Tonnang HE, Subramanian S, Cressman K, Abdel-Rahman EM, Tesfayohannes M, Niassy S, Torto B, Dubois T, Tanga CM and Kassie M (2020) Prediction of breeding regions for the desert locust *Schistocerca gregaria* in East Africa. *Scientific Reports* **10**, 11937.

Klein I, Oppelt N and Kuenzer C (2021) Application of remote sensing data for locust research and management – a review. *Insects* **12**, 233.

Latchininsky AV and Sivanpillai R (2010) Locust habitat monitoring and risk assessment using remote sensing and GIS technologies. In Ciancio A and Mukerji K (eds), *Integrated Management of Arthropod Pests and Insect Borne Diseases*, vol. **5**, Dordrecht: Springer. pp. 163–188.

Latchininsky A, Piou C, Franc A and Soti V (2016) Applications of remote sensing to locust management. In Baghdadi N and Zribi M (eds) *Land Surface Remote Sensing*, London, Oxford: Elsevier and ISTE Press. pp. 263–293.

Li Y, Li M, Li C and Liu Z (2020) Optimized MaxEnt model predictions of climate change impacts on the suitable distribution of *Cunninghamia lanceolata* in China. *Forests* **11**, 302.

Meinshausen M, Nicholls ZR, Lewis J, Gidden MJ, Vogel E, Freund M, Beyerle U, Gessner C, Nauels A, Bauer N and Canadell JG (2020) The shared socio-economic pathway (SSP) greenhouse gas concentrations and their extensions to 2500. *Geoscientific Model Development* **13**, 3571–3605.

Merow C, Smith MJ and Silander JA (2013) A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. *Ecography* **36**, 1058–1069.

Muyobela J, Pirk CW, Yusuf AA and Sole CL (2023) Spatial distribution of *Glossina morsitans* (Diptera: Glossinidae) in Zambia: a vehicle-mounted sticky trap survey and MaxEnt species distribution model. *PLoS Neglected Tropical Diseases* **17**, e0011512.

Phillips SJ and Dudík M (2008) Modeling of species distributions with MaxEnt: new extensions and a comprehensive evaluation. *Ecography* **31**, 161–175.

Phillips SJ, Dudík M and Schapire RE (2004) A maximum entropy approach to species distribution modeling. In Proceedings of the twenty-first international conference on Machine learning (p. 83).

Phillips SJ, Anderson RP and Schapire RE (2006) Maximum entropy modeling of species geographic distributions. *Ecological Modelling* **190**, 231–259.

Popp A, Calvin K, Fujimori S, Havlik P, Humpenöder F, Stehfest E, Bodirsky BL, Dietrich JP, Doelmann JC, Gusti M, Hasegawa T, Kyle P, Obersteiner M, Tabeau A, Takahashi K, Valin H, Waldhoff S, Weindl I, Wise M, Kriegler E and van Vuuren DP (2017) Land-use futures in the shared socio-economic pathways. *Global Environmental Change* **42**, 331–345.

Radosavljevic A and Anderson RP (2014) Making better MaxEnt models of species distributions: complexity, overfitting and evaluation. *Journal of Biogeography* **41**, 629–643.

Rainey RC (1951) Weather and the movements of locust swarms: a new hypothesis. *Nature (London)* **168**, 1057–1060.

Roffey J and Popov G (1968) Environmental and behavioural processes in a desert locust outbreak. *Nature* **219**, 446–450.

Salih AA, Baraibar M, Mwangi KK and Artan G (2020) Climate change and locust outbreak in East Africa. *Nature Climate Change* **10**, 584–585.

Sillero N (2011) What does ecological modelling model? A proposed classification of ecological niche models based on their underlying methods. *Ecological Modelling* **222**, 1343–1346.

Skendžić S, Zovko M, Živković IP, Lešić V and Lemić D (2021) The impact of climate change on agricultural insect pests. *Insects* **12**, 440.

Song H, Foquet B, Mariño-Pérez R and Woller DA (2017) Phylogeny of locusts and grasshoppers reveals complex evolution of density-dependent phenotypic plasticity. *Scientific Reports* **7**, 6606.

Stone MA (2020) A plague of locusts has descended on East Africa. Climate change may be to blame. National Geographic. 15 February 2020.

Sugiura N (1978) Further analysis of the data by Akaike's information criterion and the finite corrections. *Communications in Statistics – Theory and Methods* **7**, 13–26.

Uvarov BP (1966) *Grasshoppers and Locusts. A Handbook of General Acridology. Volume I. Anatomy, Physiology, Development, Phase Polymorphism, Introduction to Taxonomy*. Cambridge: Cambridge University Press.

Verbruggen H, Tyberghein L, Belton GS, Mineur F, Jueterbock A, Hoarau G, Gurgel CFD and Clerck OD (2013) Improving transferability of introduced species' distribution models: new tools to forecast the spread of a highly invasive seaweed. *PLoS ONE* **8**, e68337.

Vignali S, Barras AG, Arlettaz R and Braunisch V (2020) SDMtune: an R package to tune and evaluate species distribution models. *Ecology and Evolution* **10**, 11488–11506.

Wang L, Zhuo W, Pei Z, Tong X, Han W and Fang S (2021) Using long-term earth observation data to reveal the factors contributing to the early 2020 desert locust upsurge and the resulting vegetation loss. *Remote Sensing* **13**, 680.

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

Wen F, Lu L, Nie C, Sun Z, Liu R, Huang W and Ye H (2023) Analysis of spatiotemporal variation in habitat suitability for *Oedaleus decorus asiaticus* Bei-Bienko on the Mongolian Plateau using MaxEnt and multi-source remote sensing data. *Insects* **14**, 492.

Wu T, Lu Y, Fang Y, Xin X, Li L, Li W, Jie W, Zhang J, Liu Y, Zhang L and Zhang F (2019) The Beijing Climate Center climate system model (BCC-CSM): the main progress from CMIP5 to CMIP6. *Geoscientific Model Development* **12**, 1573–1600.

Yuga ME and Wani P (2022) Assessing the impact of desert locust infestation on crops, pasture and livestock health in Eastern Equatoria State, South Sudan. *European Journal of Applied Sciences* **10**.

Zhao L, Li H, Huang W, Dong Y, Geng Y, Ma H and Chen J (2023) Outbreak mechanism of locust plagues under dynamic drought and flood environments based on time series remote sensing data: implication for identifying potential high-risk locust areas. *Remote Sensing* **15**, 5206.