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Xanthium strumarium L., an invasive species in the subtropics: prediction of potential distribution areas and climate adaptability in Pakistan

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Abstract

Invasive species such as *Xanthium strumarium* L., can disrupt ecosystems, reduce crop yields, and degrade pastures, leading to economic losses and jeopardizing food security and biodiversity. To address the challenges posed by invasive species such as *X. strumarium*, this study uses species distribution modeling (SDM) to map its potential distribution in Pakistan and assess how it might respond to climate change. This addresses the urgent need for proactive conservation and management strategies amidst escalating ecological threats. SDM forecasts a species' potential dispersion across various geographies in both space and time by correlating known species occurrences to environmental variables. SDMs have the potential to help address the challenges posed by invasive species by predicting the future habitat suitability of species distributions and identifying the environmental factors influencing these distributions. Our study shows that seasonal temperature dependence, mean temperature of wettest quarter and total nitrogen content of soil are important climatic factors influencing habitat suitability of *X. strumarium*. The potential habitat of this invasive species is likely to expand beyond the areas it currently colonizes, with a notable presence in the Punjab and Khyber Pakhtunkhwa regions. These areas are particularly vulnerable due to threats to agriculture and biodiversity. Under current conditions, an estimated 21% of Pakistan's land area is infested by *X. strumarium*, mainly in upper Punjab, central Punjab and Khyber Pakhtunkhwa. The range is expected to expand in most regions except Sindh. The central and northeastern parts of the country are proving to be particularly suitable habitats for *X. strumarium*. Effective strategies are crucial to contain the spread of *X. strumarium*. The MaxEnt modeling approach generates invasion risk maps by identifying potential risk zones based on a species' climate adaptability. These maps can aid in early detection, allowing authorities to prioritize surveillance and management strategies for controlling the spread of invasive species in suitable habitats. However, further research is recommended to understand the adaptability of species to unexplored environments.

Keywords Invasive plant, Species distribution model, Climate change, Subtropical region, MaxEnt model

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Introduction

The increasing globalization of trade, travel and anthropogenic activities has led to an unprecedented rate of transboundary species displacement [1]. While many non-native species coexist harmoniously with their new environment, some exhibit invasive traits that can disrupt the balance of ecosystems and threaten native biodiversity [2–4]. Subtropical regions, with their transitional climates and diverse habitats, are particularly susceptible to the growth and spread of invasive plants due to the combination of favorable conditions and human activities [5]. The invasion of exotic plant species into new ecosystems has become a pervasive and complex issue in the field of ecology and conservation biology [6]. The introduction of invasive plants can disrupt the delicate balance of native habitats and adversely affect biodiversity, ecological functions and human activities [7]. Understanding the ecological niche of these invasive plants and predicting their future invasion risk is crucial for effective management and conservation measures [8, 9]. Subtropical regions, which occupy a significant portion of the world's landmass, have a rich diversity of ecosystems, from tropical rainforests to dry grasslands [10]. These regions are known for their distinct climatic patterns with moderate to high temperatures and fluctuating rainfall throughout the year [11]. These conditions create a unique ecological environment in which invasive plants can thrive [12]. The vulnerability of subtropical regions to plant invasions is exacerbated by human activities such as urbanization, agriculture and trade, which facilitate the introduction and spread of alien species [13].

Species distribution model (SDM) plays a crucial role in understanding and controlling the spread of invasive plant species [14]. By integrating environmental variables and species occurrence data, SDM enables the prediction of potential invasion areas, contributing to early detection, efficient resource allocation and informed management strategies [15]. SDM supports conservation planning by identifying threatened habitats, adapting to climate change impacts, assessing risks, optimizing resource use, guiding research efforts, and providing data-driven insights for proactive management of invasive species to ensure conservation of native ecosystems and mitigate ecological and economic impacts [16, 17]. The creation of SDM to determine the range of a species requires data that includes the species' occurrence and influential environmental factors such as land use, climate variables and topography [18]. When creating an SDM, the relationship between the occurrence data and the predictive variables is analyzed using statistical algorithms and machine learning techniques. This model is then used to estimate the potential occurrence of the species in larger geographic areas [19]. Once an SDM is developed, it can be used to predict the occurrence of species in regions without occurrence data. In addition, SDMs can identify areas with a high probability of species occurrence based on prevailing environmental conditions. By examining ecological parameters that influence the distribution of a particular species, SDMs can identify regions where environmental conditions are favorable for the species to thrive [3, 9, 20]. Such findings are used to prioritize invasive areas and guide habitat restoration studies [21].

Invasive alien species are widely recognized as a major cause of global biodiversity loss [17]. *Xanthium strumarium*, commonly known as common cocklebur, considered as one of the worst weeds in the world, has become a serious problem in Pakistan, significantly affecting the biodiversity of agricultural lands, roadsides, pastures, riverbanks, embankments, parks, lakes and even urban areas [22–24]. The spread of this plant has considerable ecological and economic consequences [25]. It poses a serious threat to various agricultural crops such as maize, soybean, sunflower, peanut and cotton in many regions of the world, including Pakistan [26]. *X. strumarium* is an annual plant that was originally native to North and South America, is widely naturalized (between 53° N latitude and 33° S longitude) and occurs mainly in the temperate zone, but also in subtropical and Mediterranean climates. The seeds of *X. strumarium* are easily dispersed as the thorny fruits can adhere to animal bodies, facilitating their transfer to new habitats. The plants can quickly become the dominant plant in an area due to their prolific seed production and high germination and survival rates [27]. The plant was introduced to Pakistan in the early 1980s, coinciding with the Afghan war [22]. The large-scale migration of Afghan nomads and their livestock led to the spread of this highly invasive weed from small to large areas [28]. *Xanthium strumarium* is widely distributed in several countries, including regions such as Pakistan, Australia, India, South Africa, the United States, and Turkey, where it is known as a serious weed [29]. Its occurrence and invasiveness in Pakistan has been documented in several regions including Islamabad, northwest Pakistan, Khyber Pakhtunkhwa and the upper Indus plains in Punjab [22–24, 28–30]. Currently, it is considered one of the most problematic and widespread weeds in Pakistan.

In our study, we used MaxEnt and ArcGIS to delineate suitable habitats for *X. strumarium* in Pakistan, considering various factors such as soil properties, bioclimatic conditions, terrain features, and human activities. The integration of global climate models allowed us to predict potential climate changes and their impact on the species' distribution. This approach provides valuable insights for planning and managing invasive species and supports conservation efforts by identifying areas suitable for eradication and considering the effects of climate change. The study had two main objectives: (1) assessment of current and projected future distribution patterns of *X. strumarium* while evaluating the comparative importance of different environmental parameters in the context of climate change scenarios and (2) to analyze the associated habitat changes related to the projected future suitability of *X. strumarium* in the subtropical region of Pakistan. We hypothesized that there is a significant relationship between environmental factors and the spread of *X. strumarium* in subtropical regions, suggesting that factors such as climatic conditions and soil characteristics influence the spread and that future climate change will increase the risk of invasion of this invasive species.

Materials and methods

Presence data

The subtropical region of Pakistan, characterized by its diverse topography and climatic conditions, is of great ecological and agricultural importance. Situated between the arid plains of the Indus Valley and the temperate zones of the Himalayas, this region encompasses a variety of habitats ranging from dense forests to fertile plains and plateaus. It is an important hotspot for biodiversity and is home to numerous endemic animal and plant species. In addition, the subtropical climate of this region with its distinct rainy and dry seasons offers ideal conditions for agriculture and enables the cultivation of various crops such as cotton, wheat, rice, and sugar cane. However, the region is also prone to environmental problems such as soil erosion, deforestation and the invasion of alien plant species such as *X. strumarium*, which pose a particular threat to the region's ecosystems and agricultural productivity. These invasive plants can compete with native species for resources, disrupt ecosystem dynamics, and cause economic losses to farmers. Given the ecological importance and agricultural productivity of the subtropical region, it is important to study and address the challenges posed by invasive species such as *X. strumarium*. First, we conducted a comprehensive field survey to systematically map the areas infested by *X. strumarium* in the subtropical region (Fig. 1). The species, *X. strumarium*, was identified by Muhammad Waheed. A voucher specimen, labeled bearing the designation OKW23, was safely deposited at the Herbarium of the University of Okara. We used the quadrat method, a widely recognized technique in ecological research, to record the occurrence of different plant species. Our surveys were conducted in regions where X. strumarium had previously been reported as an invasive species and in surrounding areas to understand distribution patterns comprehensively.

From January 2020 to December 2022, we collected data on *X. strumarium* in different land use categories, including forests, farmland, roadsides, river basins and parklands. Our survey method involved the establishment of 10×10 m^2 field plots in the surveyed regions. These plots were strategically placed at random to ensure a representative sample of the landscape. Within these plots, we accurately recorded the extent of *X. strumarium* stands. Only plots with 100% *X. strumarium* cover were considered for modeling and analysis. This strict selection criterion ensured that our modeling efforts were focused on areas where *X. strumarium* was present and dominant in significant quantity, allowing for more accurate insights into its distribution patterns and potential impacts. Over the course of three years, we conducted field surveys in Punjab, Pakistan, to collect information on the current occurrence of *X. strumarium.* In the first survey, all occurrences of this species in their natural habitats were documented and geo-referenced. A total of 53 records in Punjab were carefully documented to produce a comprehensive distribution map for *X. strumarium* in the region (Fig. 2) (Supplementary data; Table 1). In addition, 29 records were collected by the Global Biodiversity Information Facility (GBIF.org (August 26, 2022) GBIF Occurrence download epub https://doi.org/10.15468/dl.mj5kqd). We checked and excluded sites that were less than 10 km from locations (or habitats) where the species was observed (Fig. 2). This step was taken to avoid errors that could occur if we incorrectly assume that the species doesn't occur, when in fact it does [3]. Most species occurrence prediction methods assume that species occurrence data are distributed across different locations [11]. When creating and evaluating predictive models, it's important that many sites aren't grouped too closely together. If there are many such grouped sites, the models may focus too much on these and not provide good results for other sites. This can give a false impression of the accuracy of the model [17].

Data collection and selection of environmental variables

As part of our study, we compiled a comprehensive dataset of 19 bioclimatic variables with a spatial resolution of 2.5 arc minutes and elevation data with a higher resolution of 30 arc seconds from WorldClim (version 2.1) (www.worldclim.org, accessed June 15, 2022). In addition, we integrated 10 edaphic variables from https://soilgrids.org/ (accessed June 15, 2022) (Supplementary data; Table 2). To enhance our spatial data, we used ArcGIS 10.5 software to select and extract topographic information such as elevation, slope, and aspect. These layers were subjected to spatial analysis procedures to create a digital elevation model (DEM). For our future simulations, we obtained two sets of common socio-economic paths (SSPs), namely SSPs 245 and SSPs 585, from the Coupled Model Intercomparison Project, Phase 6 (CMIP6). The shared socio-economic pathways (SSPs) comprise a range of potential future pathways, with

Fig. 1 **a**) *Xanthium strumarium* plant; **b**) Invasion on agricultural land; **c**) Invasion on railway track; **d**) Flower of *X. strumarium*. (The photographs were captured by the first author during the field survey conducted in 2020)

SSP2-4.5 representing a moderate greenhouse gas emissions scenario and SSP5-8.5 representing a high emissions pathway with significant climate impacts, each providing insights into the potential impacts of different socio-economic pathways on future climate change. These pathways were used for two different time periods: the 2050s (2041–2060) and the 2070s (2061–2080). The global climate model BCC-CSM2-MR, which is known for its resolution of 2.5 arc minutes, was used for these simulations. A detailed flowchart of the methodology used in this study is shown in Fig. 3.

Initial processing of the variables

To determine the key variables, a two-stage procedure was used in this study to ensure data independence and eliminate spatially related data. First, a preliminary model with default settings was run to assess the contribution of each variable. Variables that did not meet the criterion of contributing more than 1% were then filtered out. Second, the remaining variables that exceeded the contribution threshold were subjected to pairwise analysis using the Pearson correlation coefficient (r) to identify and eliminate potential spatial associations. Further reduction of variables was achieved by applying a threshold ($r \geq = 0.8$). In cases where two variables had an r value above this threshold, the one with the lower contribution was excluded from the analysis [31, 32].

Key variables selections

After applying Pearson contribution thresholds and the correlation coefficient, we identified six notable bioclimatic and edaphic variables. These variables include seasonal temperature (bio04), mean temperature of the wettest quarter (bio08), seasonal precipitation (bio15), precipitation of the warmest quarter (bio18), total nitrogen and cation exchange capacity (cec) [33]. In addition, the pairwise correlations between these selected variables were recorded (Fig. 4).

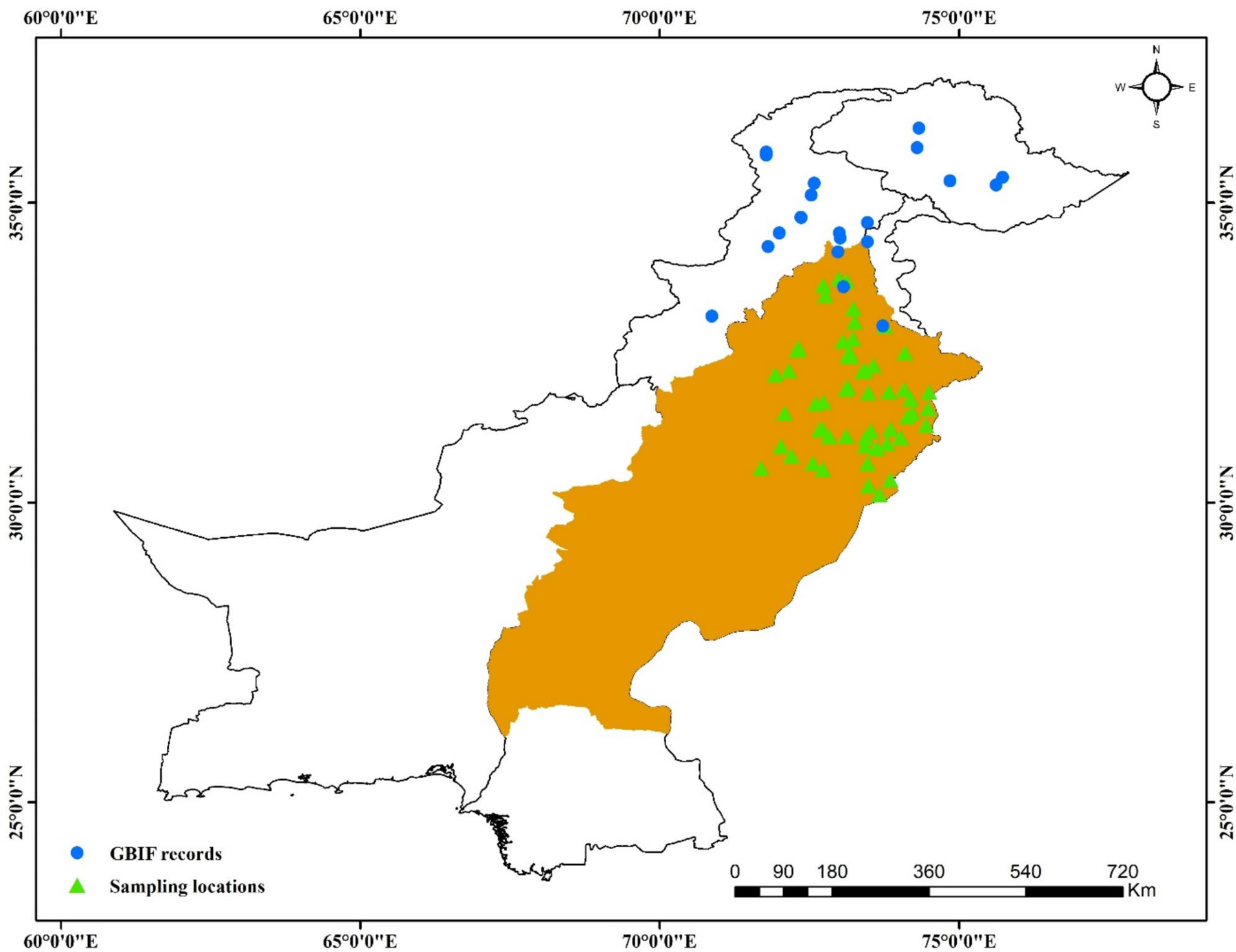

Fig. 2 A map of the study area showing the subtropical regions of Pakistan and distribution points of *X. strumarium*. (The map was created using ArcGIS software, version 10.3.)

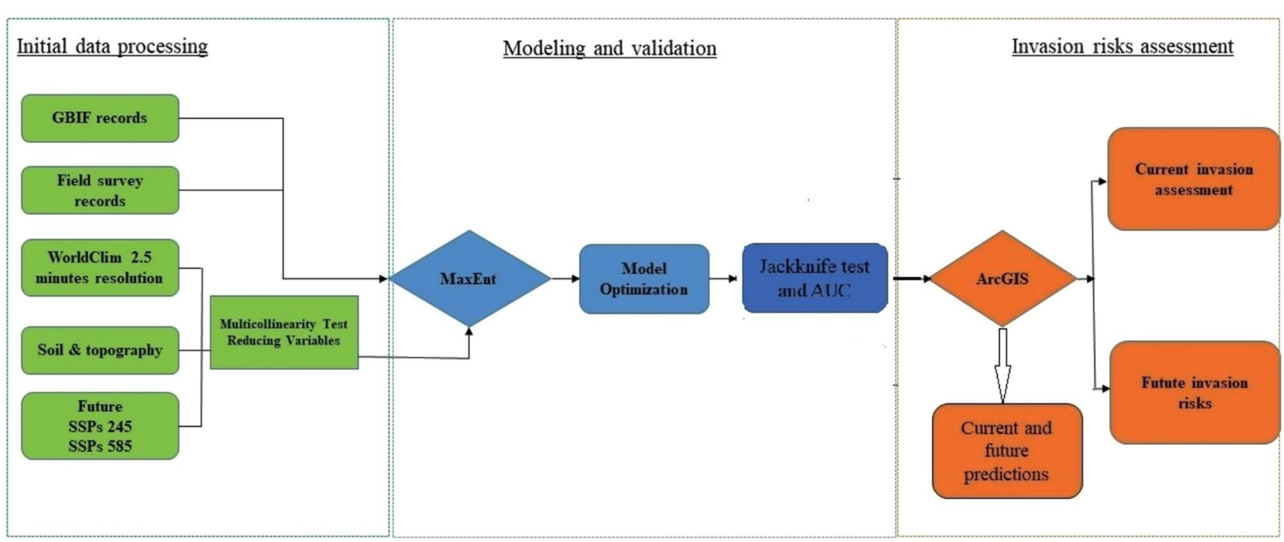

Fig. 3 Flowchart of the methodology used in the MaxEnt modelling of *X. strumarium*. (The flowchart diagram was crafted using Microsoft PowerPoint 2016)

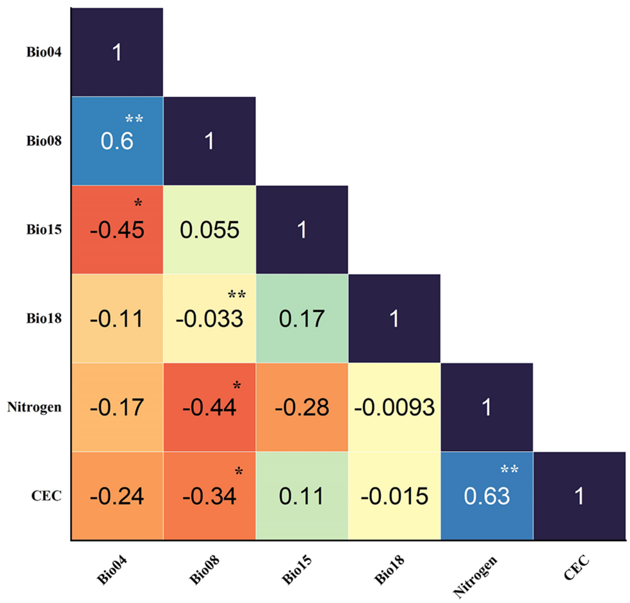

Fig. 4 Pearson correlation analysis was used to create a heat map showing the pairwise correlations between the climatic and soil variables used in modeling the distribution of *X. strumarium*, with a correlation threshold of ±0.8. **p* < 0.05; ***p* < 0.01; and ****p* < 0.001

Calibration and fine-tuning of the model

In the field of species distribution model (SDM), the critical process of fine-tuning MaxEnt predictive models plays a crucial role in selecting the most effective model. This involves optimizing the model by adjusting various parameters, such as the values of the regularization multiplier (RM) and the feature classes (FC), with the aim of improving the reliability of the prediction and avoiding overfitting. To determine the optimal settings of the MaxEnt model, we used threshold-dependent evaluation metrics, including the omission rate, to ensure the practicability of the model. In our study, we explored a variety of combinations of eight RM values (from 0.5 to 4 with intervals of 0.5) and six FCs (L, LQ, H, LQH, LQHP, and LQHPT, where L=linear, Q=quadratic, H=hinge, P=product, T=threshold) [34, 35] to find the optimal configuration. To facilitate the model implementation, the bias file was formulated using the R package ENMEval, which contains both occurrence and environmental data [16].

MaxEnt 3.4.4, which is based on ecological niche theory [36], was used to analyze and predict the optimal habitats of *X. strumarium* in the study area. MaxEnt is known for its precision and uses presence data to predict the distribution of species in a given area [37]. As an outstanding technique in species distribution model (SDM), MaxEnt is characterized by its efficiency [38, 39] and outperforms other methods in accuracy [40–42]. Our main goal was to uncover the relationships between climatic variables and species occurrence. To ensure the highest level of accuracy and performance in our analyses, we used a number of different MaxEnt configurations. These configurations included several key elements, including setting the presence probability threshold to the 10th percentile, implementing 10-fold cross-validation, using a complementary log-log (clog-log) output format, including a dataset of 10,000 background points, performing 10 replicates of the analysis, performing 500 iterations, generating response curves, and assessing the importance of variables using jackknife analysis in all of our final optimized species distribution models (SDMs). With this comprehensive approach, we aimed to achieve robust and reliable results in our study on climate variables and species distribution.

Transforming the predictions and evaluating the model

We evaluated the optimized species distribution models (SDMs) using the area under the curve (AUC) measurements of the receiver operator characteristic (ROC) curve. A high AUC-ROC value indicates improved predictive accuracy of the model, with values of 0.9 or higher indicating good performance [42, 43]. The AUC value reflects the ability of the model to faithfully represent the test data and its ability to discriminate variations in species distribution under potential future climate scenarios [36]. An AUC value of 0.5 corresponds to chance-level performance, while a value of 1.0 indicates above-average performance [42]. To predict potential invasion risks associated with *X. strumarium*, we used the averaged MaxEnt prediction results, which range from 0 to 1. The results of the model were divided into four categories of invasion risk: No Risk Zones (NRZ) for values between 0 and 0.4, Low-Risk Zones (LRZ) for values between 0.41 and 0.6, Medium Risk Zones (MRZ) for values between 0.61 and 0.8, and High-Risk Zones (HRZ) for values between 0.81 and 1 [17, 44]. The cumulative extent of Low-Risk Zones (LRZ), Medium Risk Zones (MRZ), and High-Risk Zones (HRZ) is combined to form the Total Risk-Zone (TRZ). The spatial extent of each of the classified categories was then determined using Map Algebra in ArcGIS version 10.3 in a two-step process.

Results

We ran 10 repetitions of MaxEnt and averaged the results to increase the stability of the model. The results of the model calibration showed that the highest AUC value of 0.964 was attained with an RM value of 2.5 and the LQHPT feature class, indicating the best prediction performance for *X. strumarium*. Lower RM values of 0.5, 1, and 1.5 and simpler feature classes (L and LQ) yielded AUC values of 0.792, 0.823, and 0.847. RM 2.0 with the H feature class had an AUC of 0.869, improving model performance. At RM 3.0 and 3.5, combined with LQHP and LQHPT, AUC values reached 0.912 and 0.925.

Performance dropped at RM 4.0 with an AUC of 0.917. The area under the curve (AUC) is a common tool for assessing model performance, with the best candidate model achieving an AUC value of 0.964 (Fig. 5). Using MaxEnt, we determined values for habitat suitability (0 to 0.99) of *X. strumarium* in the subtropical region of Pakistan. The AUC values, ranging from 0.5 (random) to 1.0 (perfect discrimination), indicate the prediction accuracy, with the average AUC value of our model being 0.964, which is significantly higher than the random prediction AUC value of 0.5. This proves the high predictive power of the model and the agreement with the actual species distribution.

Environmental variables responsible for spread

In the context of understanding the habitat suitability of *X. strumarium*, several influencing factors have been identified that contribute significantly to its ecological preferences. These factors play a critical role in shaping the distribution patterns of *X. strumarium* and provide valuable insights into its habitat requirements. Among these critical factors, seasonal temperature dependence, referred to as bio04, emerges as an important factor. This indicator provides information on the extent of temperature variation throughout the year and captures the sensitivity of the plant to seasonal temperature fluctuations. In addition, the mean temperature during the wettest quarter, represented by bio08, has a significant influence. It provides valuable information about the plant's preference for certain temperature conditions during the wettest period of the year and gives insight into its ecological niche. In addition, the role of the total nitrogen content in the soil should not be underestimated. This nutrient parameter is an important factor for the habitat suitability of *X. strumarium*. It reflects the dependence of the plant on the nitrogen content of the soil for its growth and development and provides important insights into its adaptability to different soil types. Conversely, certain factors were found to have minimal effects on the species distribution models (SDMs) of *X. strumarium*. For example, cation exchange capacity (CEC), a measure of the soil's ability to bind and exchange cations, was found to be of little importance in shaping the plant's distribution patterns. Seasonal precipitation (bio15), which characterizes the seasonal variation of precipitation, and precipitation in the warmest quarter also proved to be factors with little influence. These results, presented in Table 1, illustrate the nuanced interplay of environmental variables in determining habitat suitability for *X. strumarium*. By identifying these influencing factors and their relative importance, this study improves our understanding of the ecological preferences of this invasive plant species

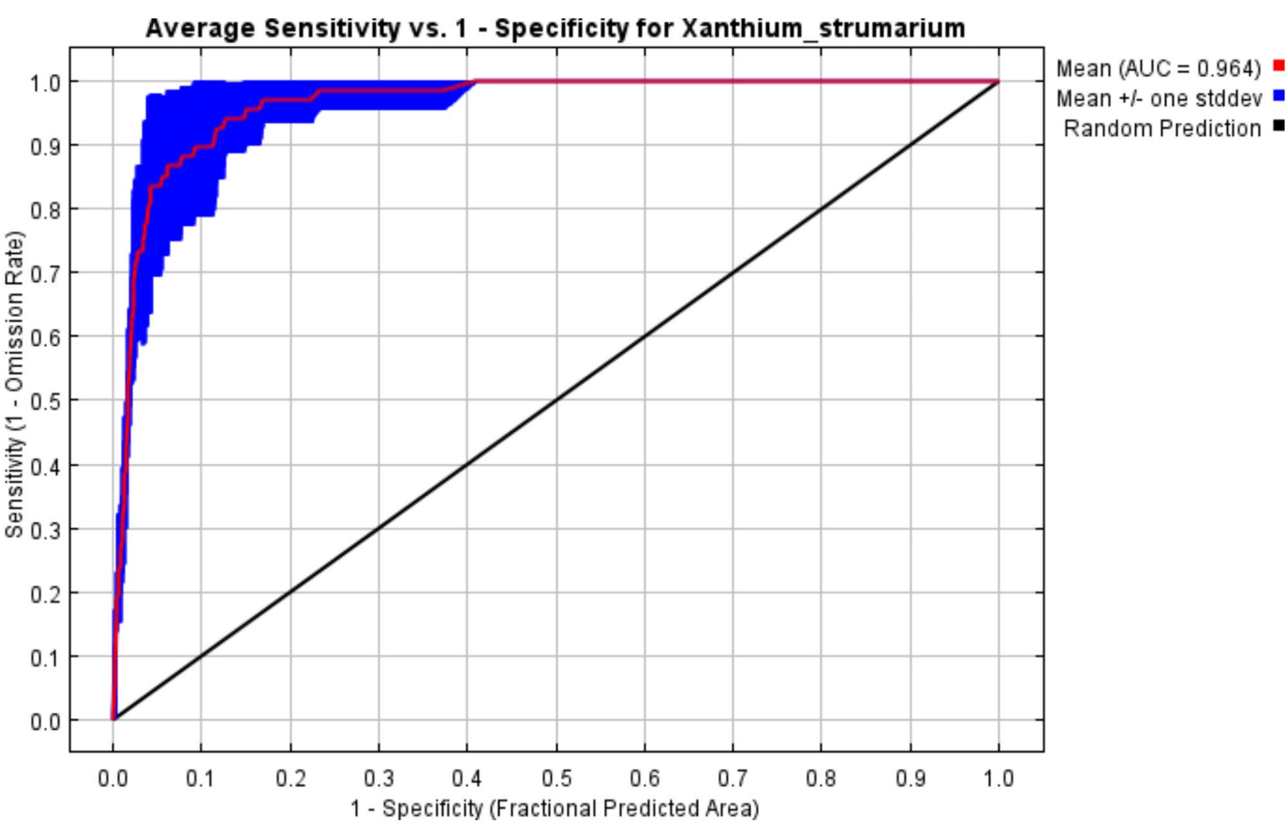

Fig. 5 The MaxEnt model was used for the ROC prediction and an accuracy of 0.964

Table 1 Selected environmental factors and their respective percent contributions

Description	Code	Percent contribution
Temperature Seasonality (sd ×100)	bio04	28
Mean Temperature of Wettest Quarter	bio08	27.2
Total Nitrogen	nitrogen	25.8
Cations Exchange Capacity (pH: 7)	cec	8.1
Precipitation Seasonality (CV)	bio15	5.7
Precipitation of Warmest Quarter	bio18	5.2

and provides a basis for informed conservation and management strategies.

The results of the jackknife test underlined the importance of various environmental factors for the spread of *X. strumarium* (Fig. 6). In particular, temperature-seasonality (bio04), mean temperature of the wettest quarter (bio08) and total nitrogen were identified as the most important influencing factors, accounting for 28.3%, 27.2% and 25.8% of the explanatory power of the MaxEnt model, respectively. A targeted analysis revealed that the increasing contribution of bio04 initially increased the probability of *X. strumarium* occurrence before stabilizing (Fig. 6). Figure 6 illustrates the assessment of the contribution of environmental variables through a jackknife analysis of the regulated training gain in MaxEnt models for *X. strumarium.*

Similarly, an increase in average temperature in the wettest quarter led to an initial increase, followed by a decrease and subsequent increase in the probability of presence. In addition, total nitrogen showed a positive correlation with the probability of presence of a species, peaking at 20 cg/kg. This complicated interaction between temperature and nitrogen highlights the need for further research to fully understand the relationship between these two factors and species occurrence. In particular, the seasonal temperature dependence above 600 °C indicates particularly suitable sites with a probability of over 0.6, peaking above 700 °C. The range for particularly suitable habitats ranged in temperature dependence from 600 to 800 °C (Fig. 7).

Current invasion risks

The MaxEnt results were reformatted and classified using ArcGIS, which led to the identification of high risk areas for *X. strumarium* invasion in Pakistan, covering 255,957 km² or 21% of the total area of the country. The high risk areas were mainly concentrated in central, upper and southern Punjab with 104,362 km² or 11.8% of suitable habitats. High-risk areas in upper Punjab included Rawalpindi, Gujrat, Mianwali, Jhelum and Chakwal, while in central Punjab, areas such as Kasur, Sahiwal, Hafizabad, Nankana Sahib, Sheikhpora and Okara were considered suitable. The high-risk regions in southern Punjab included Layyah, Dera Ghazi Khan, Muzaffargarh, Khanewal, Lodhran and Vehari (Fig. 8). In Balochistan and Khyber Pakhtunkhwa, particularly suitable areas were found in Nowshera, Peshawar, Laki Marwat, Bannu, Kohat, Quetta, Karak, Mastung, Sibi and Kech. Moderate risk areas were observed from northeastern Punjab to central Khyber Pakhtunkhwa and Balochistan. The lowest risk zones were observed in northern Sindh, eastern Balochistan, western Khyber Pakhtunkhwa and mid-hill regions of Balochistan provinces.

Projected habitat suitability in a future climate change scenario

After a thorough investigation of the possible effects of future climate change, it is clear that the current optimal habitat of *X. strumarium* is gradually expanding. This expansion is expected to result in a shift of the plant's habitat to the eastern region of Khyber Pakhtunkhwa, as indicated by the projections for the 2050s and 2070s in all four SSP scenarios. Consequently, we expect the

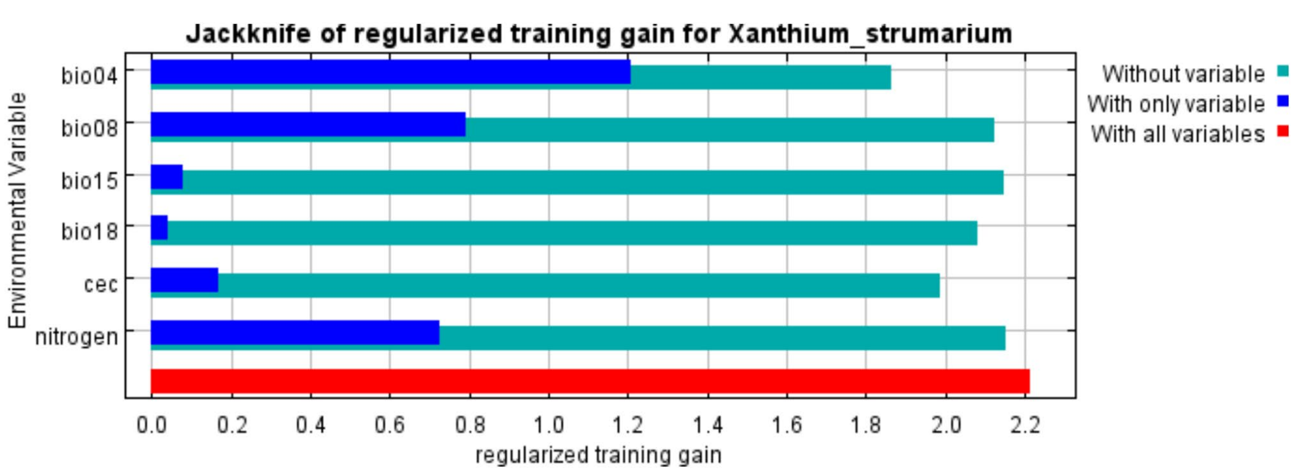

Fig. 6 Assessment of the predictive capability of environmental variables in MaxEnt models for *X. strumarium*

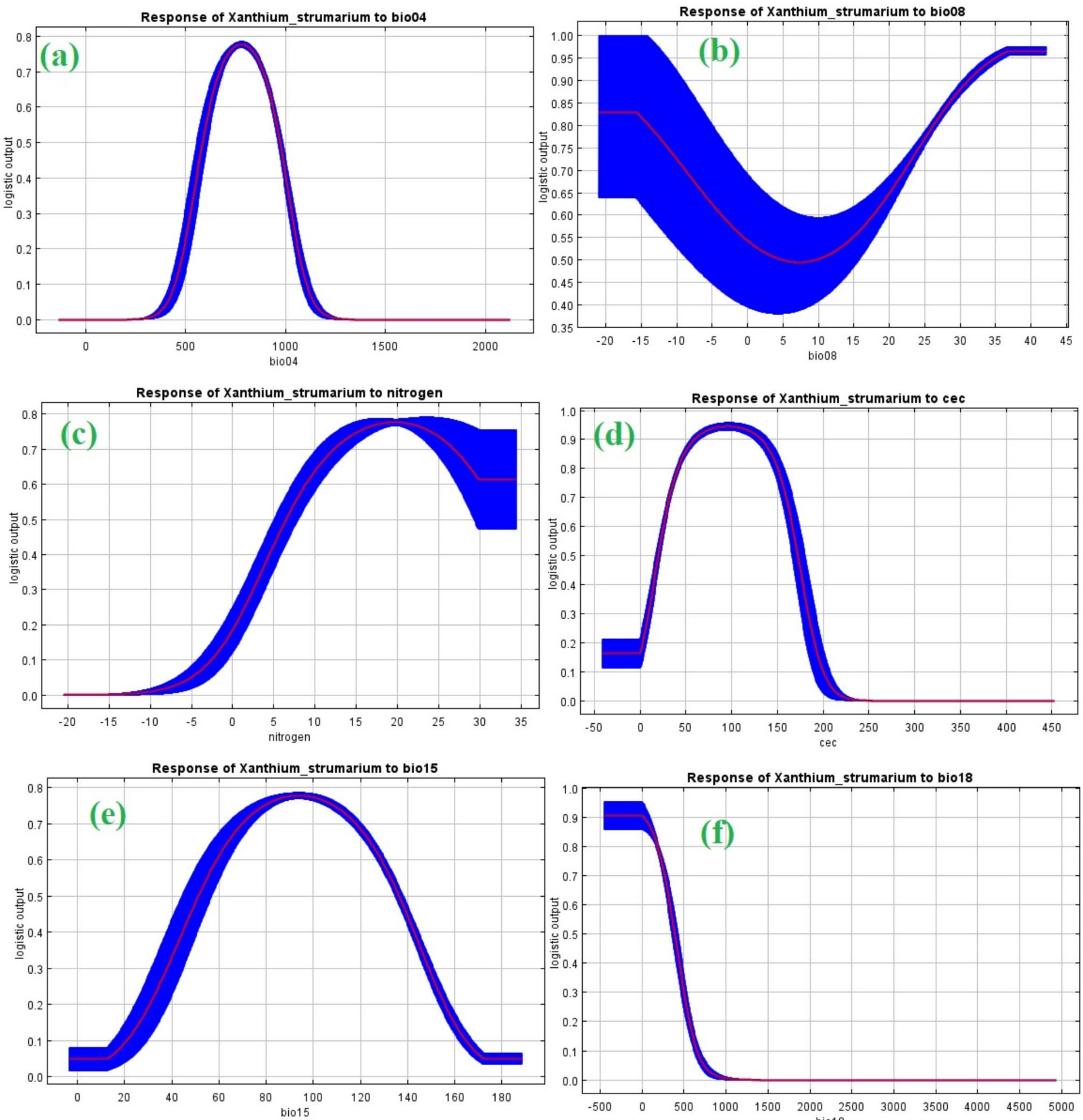

Fig. 7 A significant impact on *Xanthium strumarium* distribution patterns include: **a**) seasonality of temperature (bio04); **b**) mean temperature of the wettest quarter (bio08); **c**) total nitrogen content (nitrogen); (**d**) Cation exchange capacity (CEC); (**e**) seasonality of precipitation (bio15); (**f**) precipitation of the hottest quarter (bio18)

emergence of a continuous distribution of particularly suitable locations in the upper regions of Punjab and neighboring areas, especially in Punjab and Khyber Pakhtunkhwa towards the northeast, as shown in Fig. 9. These changes in geographical distribution are a direct result of the upcoming climatic conditions.

Based on the comprehensive results of this study, it is prudent to assume a significant expansion of the total potential habitat suitability for Pakistan in the foreseeable future. This expansion under various common socio-economic scenarios (SSPs) in the 2050s and 2070s has significant implications for the distribution and ecological impact of *X. strumarium* in this region. In particular, the analysis shows that the potential habitat suitability for *X. strumarium*, defined as areas with a suitability probability greater than 0.4, is expected to increase significantly.

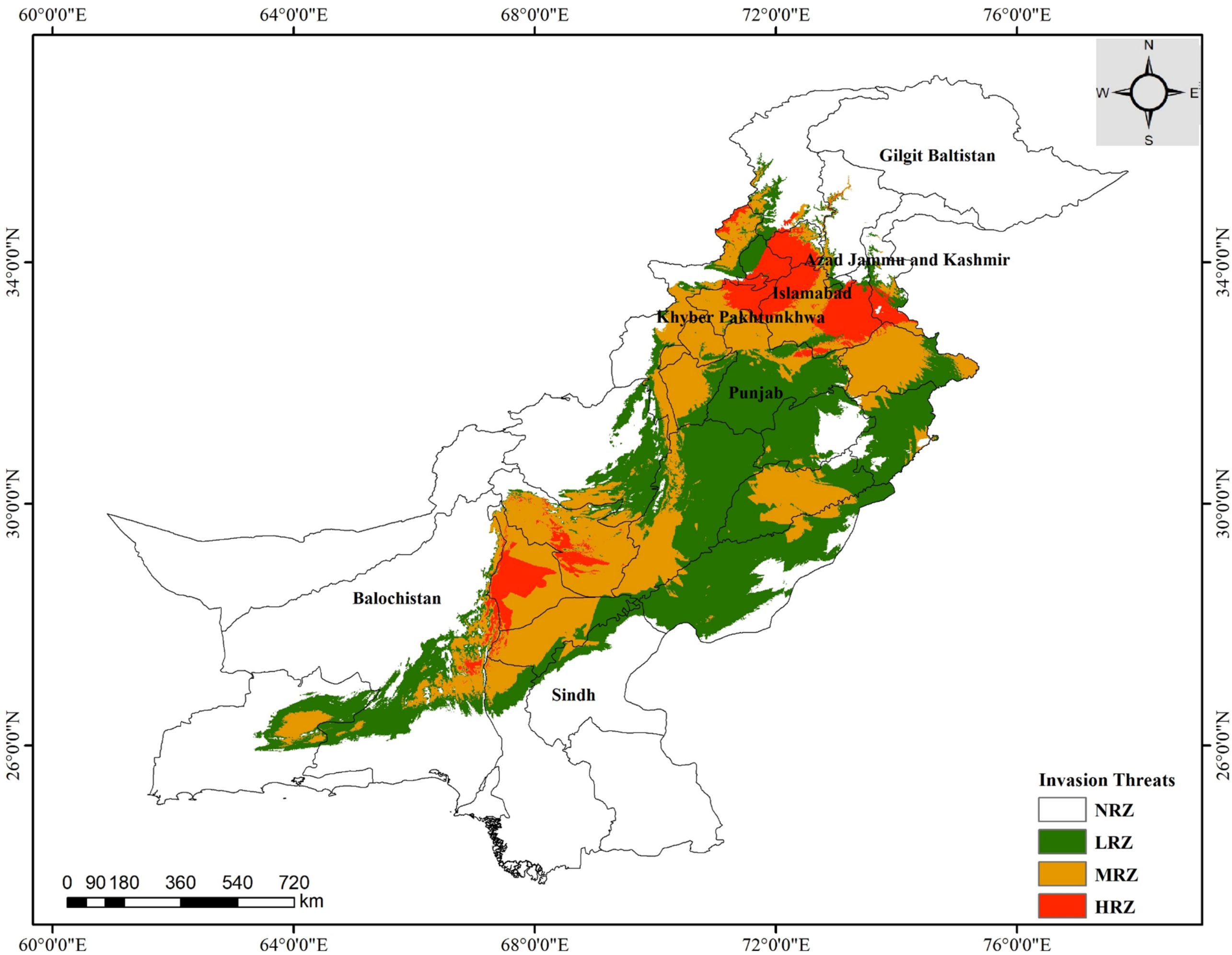

Fig. 8 In the context of current climatic conditions (1970–2000 s), the MaxEnt predictive map illustrates the potential habitat suitability of *X. strumarium* in the study area. (Legend: NRZ; No risk zones area, LRZ; Least risk zone area, MRZ; moderate risk zone area, HRZ; High risk zone area)

According to the SSP2-4.5 scenario for the 2050s, the estimated expansion rate is about 6.7% compared to the current range. This projection corresponds to a potential suitability area of 317,880 square kilometers (Fig. 9). In the more intensive SSP scenario for the same period, the rate of change is estimated to be up to 8.5%, resulting in an expanded suitability area of 331,637 km². Looking further into the future, the study predicts that the potential invasion risk areas under SSP2-4.5 will expand to 329,965 km² by 2070, which corresponds to a rate of change of 8.2%. Under the more stringent SSP5-8.5 scenario for the same period, this expansion is likely to be even greater, reaching 349,487 km², a rate of change of 10.8%, as shown in Fig. 10 of the study.

Deepening the analysis and focusing specifically on the high-risk zones (HRZs), the study shows that under SSP2-4.5 these high-risk zones will expand from their current extent of 60,256 km^2 to 96,356 km^2 in 2050, which corresponds to a rate of change of 4.7% (Fig. 9). Within these expanding HRZs, the estimated potentially suitable land area will increase to 106,351 km^2 (5.9%) under SSP5-8.5 for the 2050s, 122,325 km^2 (8%) under SSP2-4.5 for the 2070s, and 132,146 km^2 (9.3%) under SSP5-8.5 for the 2070s, as detailed in Table 2 of the research results.

After a thorough analysis of four different climate change scenarios, it becomes clear that the dynamics of risk zones related to the invasion of *X. strumarium* in Pakistan will change significantly as we move towards the 2070s. In particular, the study shows a remarkable trend in Balochistan and southern Punjab. Based on the model projections, the vulnerable areas are expected to gradually decrease and may cease to exist by 2070. This change represents a potentially positive development in these regions, where the ecological threat of *X. strumarium* could decrease over time.

Conversely, the western regions of Khyber Pakhtunkhwa in Pakistan, South Balochistan, Central Punjab and Sindh will see an expansion of risk zones for *X. strumarium* invasion. The study's models predict that these areas will include not only existing suitable habitats, but

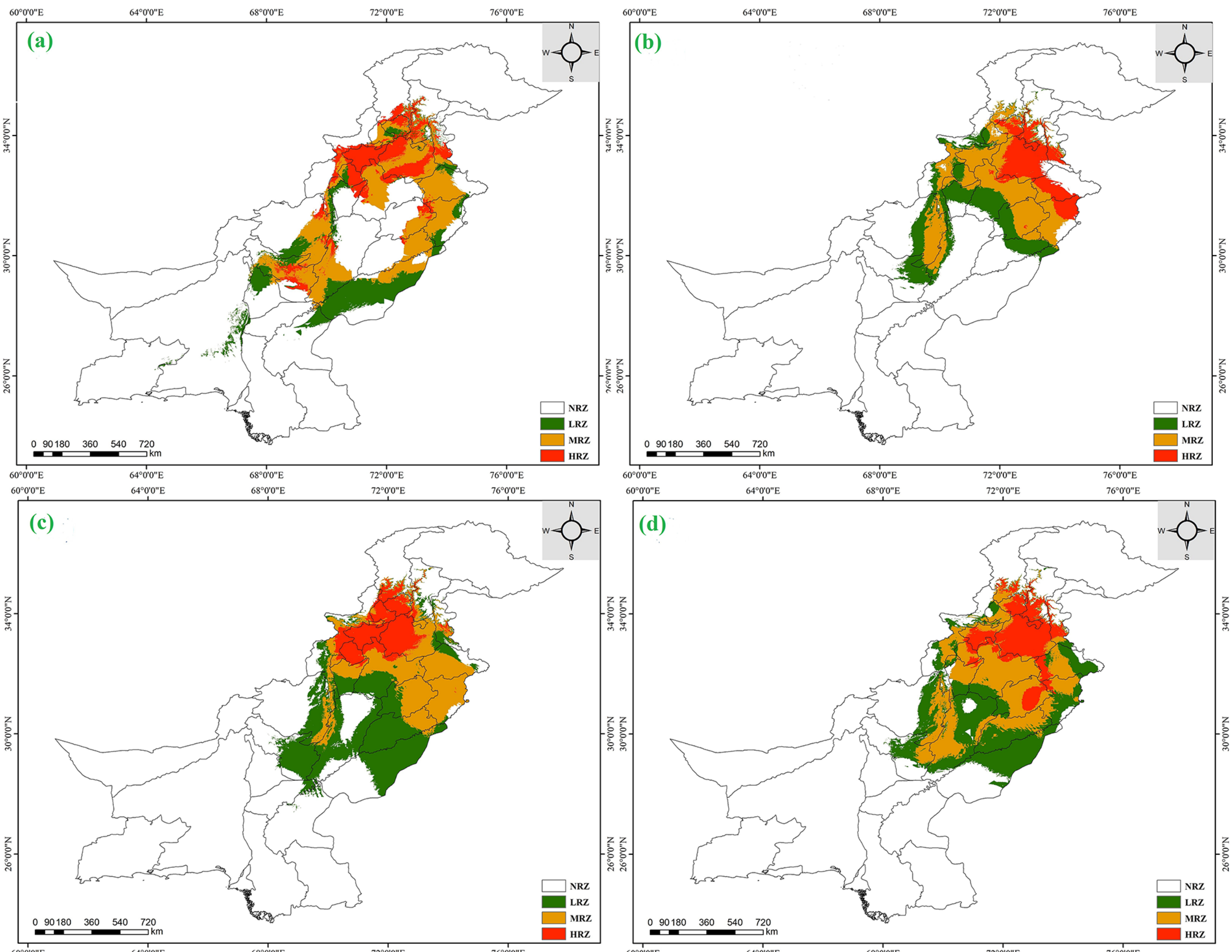

Fig. 9 Illustration of invasion risk categories on the MaxEnt prediction maps for different climate change scenarios: **A**) SSP2-4.5 for the 2050s, **B**) SSP5-8.5 for the 2050s, **C**) SSP2-4.5 for the 2070s, and **D**) SSP5-8.5 for the 2070s

also those classified as highly suitable in the 2050s and 2070s according to the SSP2-4.5 and SSP5-8.5 scenarios. This expansion indicates a growing ecological challenge in these regions, as *X. strumarium* is able to occupy ever larger areas. In addition, the study identifies certain regions such as the Upper Federal Territory, Peshawar, Murree Hills and Attock where areas of high risk in the dry landscape could emerge between 2050 and 2070. These areas, shown in Fig. 8, are projected to be increasingly vulnerable to *X. strumarium* invasion, increasing the complexity of the ecological landscape. In essence, this study demonstrates the dynamic nature of potential expansion and contraction of *X. strumarium* habitat in different regions of Pakistan in response to different climate change scenarios. These findings emphasize the urgency of proactive conservation and management strategies tailored to address the evolving ecological challenges that this invasive plant species will pose in the coming years.

Discussion

The MaxEnt model establishes statistical relationships by comparing background locations within the study area with predictor variables at locations where the species has been observed. These predictor variables, called trait classes (FCs), can influence the strength of these correlations. The inclusion of additional FCs increases the flexibility of the model and makes it possible to capture observed data in a more differentiated way. However, increased flexibility also carries the risk of overfitting, as Peterson et al. [45] emphasized. The MaxEnt model contains an automatic mechanism to determine the FCs to be used, considering the number of occurrence locations in the dataset. It also includes regularization techniques to avoid overfitting regardless of the FCs chosen, as described by Merwo et al. [39]. The user has the option to set the degree of regularization via a single parameter, the regularization multiplier (RM), with a default value of 1.0. The user can also specify allowable FCs. However,

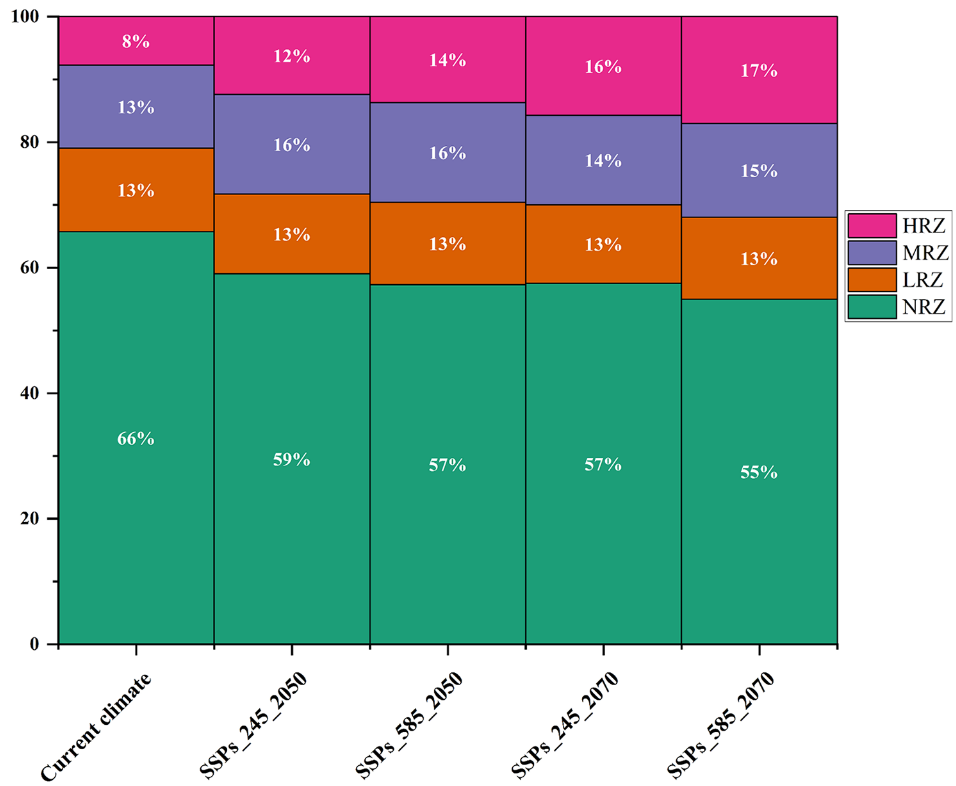

Fig. 10 Rate of change of areas at risk of *X. strumarium* invasion in different climate change scenarios: NRZ; area without risk zones, LRZ; area with low risk, MRZ; area with medium risk, HRZ; area with high risk

Table 2 Probability of habitat suitability of *X. strumarium* under different climate change scenarios

CClimate change scenario	Predicted probability of invasion of X. strumarium under considered invasion risks classes				
	(NRZ)	(LRZ)	(MRZ)	(HRZ)	Total land area (km^2) under invasion threats
	($p \leq 0.4$)	(p 0.41–0.6)	(p 0.61–0.8)	(p 0.81-1)	
Current climate	510,245	103,245	102,456	60,256	265,957
SSP2-4.5_2050	458,322	98,305	123,219	96,356	317,880
Rate of change (%)	-6.7	-0.6	2.7	4.7	6.7
SSP5-8.5_2050	444,565	102,134	123,152	106,351	331,637
Rate of change (%)	-8.5	-0.1	2.7	5.9	8.5
SSP2-4.5_2070	446,237	97,215	110,425	122,325	329,965
Rate of change (%)	-8.2	-0.8	1.0	8.0	8.2
SSP5-8.5_2070	426,715	101,214	116,127	132,146	349,487
Rate of change (%)	-10.8	-0.3	1.8	9.3	10.8

fine-tuning these parameters can be time-consuming, which is why many empirical studies rely on the default settings of algorithms or software packages. As Phillips and Dudík [46] point out, this reliance on default settings can lead to bias in evaluation methods.

The simulation accuracy was found to be high, which is consistent with previous studies in which MaxEnt model prediction indicators of over 0.90 were obtained, as shown by Chu et al. [47] and Xiong et al. [48]. However, it is important to emphasize that achieving a high goodness of fit of MaxEnt results does not guarantee an accurate representation of actual and potential species distributions, as many researchers have noted [49–51]. Nevertheless, this model remains very valuable for studying the distribution of species and plants under possible future climate scenarios.

The study of interactions between species and their environment is essential for understanding their ecological needs and spatial distribution [52]. In the case of the invasive plant *X. strumarium*, understanding its distribution is crucial for effective integration and management in ecosystems. Using the MaxEnt model, this study examines in detail the potential global habitats of *X. strumarium* under current and future climate conditions. While temperature and precipitation significantly influence the distribution of species, their impact may vary due to species-specific growth patterns [22]. The study identified crucial factors for the growth of *X. strumarium*, including specific bioclimatic factors such as seasonal temperature (bio04), mean temperature in the wettest quarter (bio08), seasonal precipitation (bio15), and precipitation in the warmest quarter. In addition, soil variables such as total nitrogen and cation exchange capacity (CEC) were found to play an important role in predicting the growth of *X. strumarium*. This plant thrives in warm, sunny conditions, but is susceptible to damage from freezing root systems in cold temperatures, which can ultimately lead to plant death. Conversely, adequate rainfall is critical for seedling survival and overall plant health, while too much water can disrupt the delicate water balance required for optimal growth and may even lead to plant death [53]. Remarkably, *X. strumarium* has a low rainfall requirement, as shown by the low rainfall in the warmest quarter (bio18) and the seasonal rainfall distribution (bio15).

The effects of bioclimatic variables on plant growth can vary greatly due to the unique characteristics of individual species. For example, the growth of *Sapindus mukorossi* is influenced by factors such as precipitation in the warmest quarter (bio18), minimum temperature in the coldest month (bio6), temperature dependence (bio4) and isothermality (bio3), as detailed by Li et al. [54]. Several important bioclimatic factors come into play when evaluating suitable habitats for species such as *Osmanthus fragrans* and *Pinus densiflora* using the MaxEnt model. *Osmanthus fragrans* relies on metrics such as UV-B seasonality, precipitation seasonality (bio15), annual temperature range (bio7) and mean daily temperature range (bio2), as shown by Kong et al. [55]. Conversely, the growth of *Pinus densiflora* is influenced by mean annual temperature (bio1), mean wettest seasonal temperature (bio8), temperature seasonality (bio4) and mean warmest seasonal precipitation (bio18), as shown by Duan et al. [56]. These results emphasize the need for further research on how bioclimatic factors affect different species and provide valuable insights for conducting cross-species comparisons.

Currently, the distribution of *X. strumarium* has been documented in several provinces and cities of Pakistan including Central Punjab, Upper Punjab, South Punjab, and Khyber Pakhtunkhwa. However, looking at the prediction results of the model (see Fig. 8), it is clear that the risk zones for *X. strumarium* under the current climate conditions extend over an even larger area, covering approximately 265,957 km^2 in Pakistan. This expanded high-risk zone indicates a greater extent of potential invasion of *X. strumarium* and emphasizes the need for proactive measures and strategies to effectively control and contain its spread in the region.

Ullah et al. [24] pointed out that invasive species such as *X. strumarium* have an inherent adaptability to different environmental conditions that allows them to thrive and expand their range. This adaptability, combined with the absence of native competitors, allows these species to colonize new geographic areas over time. Our predictive model predicts that the suitable habitat for *X. strumarium* will expand under future climate scenarios, which could lead to a loss of biodiversity and a decline in native vegetation. This expansion could harm the livelihoods of native pastoralists and agro-pastoralists, as well as on general societal well-being. As climate change favors invasive species, their competitive advantage over native species for ecosystem resources increases, exacerbating ecological impacts [57]. Climate change is expected to exacerbate the invasion of *X. strumarium* populations, possibly leading to local extinction. *X. strumarium* has invaded pastoral areas in several tropical regions and has had a negative impact on the economy, environment and biodiversity. This spread is exacerbated by the successful recruitment and densification of populations, which is exacerbated by climate change and local ignorance of its effects. Our study predicts an increase in particularly suitable habitats by 2050 and 2070, especially in the central and northern regions of Pakistan. Climate change is likely to play an important role in the invasion of *X. strumarium*, further endangering native species and rangelands [58]. This poses a significant threat to rangeland management and underscores the need for collaborative efforts among researchers, policy makers, resource managers and stakeholders to develop effective strategies to halt the spread of this invasive species and mitigate its detrimental impacts on rangeland livelihoods.

The specific biological characteristics of *X. strumarium*, together with temperature fluctuations and the environmental characteristics of the conquered habitats, play a decisive role in its effective establishment. Environmental changes can increase the susceptibility of plant populations to invasion [59]. For example, in arid locations, water availability fluctuates, leading to periods of resource scarcity, followed by periods when water is available through rainfall. Irregular water availability makes populations vulnerable to invasion by species such as the drought-tolerant *X. strumarium*. Climate change leading to higher temperatures and greater aridity in the research region [60, 61] could increase the invasive ability of *X. strumarium* as it originates from even drier areas [28]. This could also improve its competitive ability. Controlled competition trials between *X. strumarium* and native plants are necessary to better understand the future invasive potential of the plant. Our study shows that the introduction of *X. strumarium* leads to greater uniformity in subtropical ecosystems. The successful establishment and growth of *X. strumarium* populations suggest that this problem may be exacerbated in the future. Climate change and the lack of awareness among local communities of the impact of the invasion are expected to exacerbate this situation [62]. The uncontrolled regional spread of this plant, combined with its drought tolerance, poses the risk of further spread and disruption of the spatial diversity and ecosystem dynamics of native vegetation [63]. It can be assumed that this invasive species will dominate over time and exert a growing influence on the local environment.

The study assessed the average habitat suitability of *X. strumarium* in the subtropical region of Pakistan, which was categorized into low-risk zones (LRZ), medium-risk zones (MRZ) and high-risk zones (HRZ) (Figs. 7 and 8). The SSP5-8.5 projections showed transitions from the lowest suitability category to the moderate and high categories in Punjab, Balochistan and Khyber Pakhtunkhwa. In particular, in Punjab and Khyber Pakhtunkhwa, the moderate suitability category was higher at SSP5-8.5 than at SSP2-4.5, implying that *X. strumarium* can adapt over a wide range of temperatures, with even slight warming leading to tremendous expansion. These results emphasize the role of climate change in promoting the growth of *X. strumarium*, which is favored by increases in CO_2, temperature, and drought, resulting in a wider range [64–66]. In addition, these results have practical implications for the development of strategies to combat invasion risks in different regions. Furthermore, climate change is expected to create suitable habitats for *X. strumarium* at higher elevations. While no explicit elevational shifts were detected in this study, separate surveys in Khyber Pakhtunkhwa revealed that *X. strumarium* finds habitats at elevations up to 3000 m above sea level. This emphasizes that rising temperatures associated with climate change could promote the expansion of *X. strumarium* habitat to higher altitudes and latitudes.

In the context of future climate change, it is assumed that the spread of *X. strumarium* will increase considerably and reach northern regions. In particular, the habitats of *X. strumarium* are predicted to expand to all administrative districts of Khyber Pakhtunkhwa between 2050 and 2070, with the exception of Kohistan and Upper Der, which are located in the northwestern part of the country. These results are consistent with spatially explicit evidence and support the hypothesis that rising temperatures will drive the threat of invasions northwards. This trend is consistent with previous studies [67–75].

Furthermore, our study shows that districts in the southern and central regions of Punjab, with the exception of Bahawalpur, which had low to high habitat suitability in the period 2041–2060, will move up to the 'very high suitability' category by 2061–2080, as shown in Fig. 9. As global temperatures continue to rise, the habitat suitability of *X. strumarium* is expected to spread further into the central and northern regions, similar to other invasive species in Pakistan. This spread can be attributed to the removal of current climatic barriers, leading to a northward shift in the winter hardiness zones of the plants.

Various factors, including natural forces such as typhoons, wind, water dispersal, and wildlife, as well as human activities such as the importation of contaminated grain, plants, and pasture seeds, contribute to the spread of invasive species and pose a significant threat to the country. The invasive nature of *X. strumarium* negatively impacts agriculture and natural ecosystems by reducing crop yields, degrading pastures, and reducing the forage base for livestock and wildlife, thereby jeopardizing surrounding ecosystems. Regions with high agricultural activity, especially in Punjab, are particularly vulnerable to *X. strumarium* invasion, resulting in economic losses, compromised food security, and negative impacts on biodiversity and ecosystem services. To mitigate these risks, strict quarantine measures and concerted efforts by policymakers, land managers, and local stakeholders are essential to prevent and control further invasions of *X. strumarium*.

Dealing with the uncertainties inherent in the results derived from the MaxEnt model simulation requires a comprehensive assessment of the various factors that can lead to fluctuations and limitations. While the MaxEnt model is a valuable tool for clarifying the potential distribution of *X. strumarium*, uncertainties arise from several sources, including the quality of the input data used for model parameterization, inherent assumptions within the analytical process, and the complicated dynamics of ecological systems and species interactions. The spatial and temporal heterogeneity of environmental data, which includes variables such as climate parameters and soil properties, introduces variability into model predictions. In addition, uncertainties are compounded by the complexity of ecological dynamics and species responses. Despite efforts to optimize the model parameters and validate the results, it is important to acknowledge the inherent limitations of the MaxEnt method and to exercise caution when interpreting the results. Nevertheless, our approach ensures robustness by taking various factors into account and provides valuable insights into the distribution patterns of *X. strumarium*.

Conclusions

Agriculture, biodiversity, and natural ecosystems are severely affected by *X. strumarium*, which also has an impact on the country's economic prosperity. Seasonal temperature (bio04), mean temperature of the wettest quarter (bio08), and total nitrogen content of the soil were identified as important climatic factors influencing the suitability of the species as a habitat. The studies revealed that the potential habitat of *X. strumarium* in Pakistan is larger than its current range, indicating its probable spread throughout the country. This invasive species thrives mainly in the Punjab and Khyber Pakhtunkhwa regions and poses a threat to agriculture and biodiversity. The results of this study can help in the rapid detection and control of invasive species in suitable habitats. Essentially, this study demonstrates the dynamics of potential spread and habitat reduction of *X. strumarium* in different regions of Pakistan in response to different climate change scenarios in Asia, which need to be studied in detail using different representative concentration pathways. These findings emphasize the urgency of proactive conservation and management strategies tailored to address the evolving ecological challenges of this invasive plant species in the coming years. Further research is recommended to understand the adaptability of this species to unexplored areas.

Supplementary Information

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Supplementary Material 1

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Author contributions

Conceptualization, M.W. and S.M.H.; Methodology, F.A; software, M.W. and S.M.H.; validation, S.M.H., and F.A.; formal analysis, S.M.H; investigation, M.W.; resources, S.M.H. and R.W.B.; Data curation, F.A.; writing—original draft preparation, M.W.; writing—review and editing, S.M.H., I.V.K., M.W., A.H., E.F.A., R.W.B and F.A.; visualization, M.W.; supervision, F.A. and S.M.H.; project administration, F.A.; funding acquisition E.F.A., A.H. All authors having substantial contributions in research, read and agreed to the published version of the manuscript.

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Data availability

Data is contained within the article.

Declarations

Ethical approval and consent to participate

We secured permissions for our research activities within the subtropical region of Pakistan from both private landowners and public administrative authorities. These permissions granted authorization for our research team to conduct field studies and investigations concerning *X. strumarium* sampling. This ensured our strict adherence to ethical standards and local policies governing research conduct.

Consent for publication

Not applicable.

Competing interests

The authors declare no competing interests.

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