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Article

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Predicting the potential geographic distribution of the invasive ambrosia beetles, *Xylosandrus crassiusculus* (Coleoptera, Curculionidae) under climate change

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Abstract

Xylosandrus crassiusculus is a significant forestry pest that threatens healthy trees and timber quality across East Asia, North America, and parts of South America. As adults bore into branches and trunks, accurately assessing the species' distribution is essential for predicting its future impact on forestry and for developing effective management strategies. In this study, we used the MaxEnt model to evaluate the potential distribution of *X. crassiusculus* under two socioeconomic scenarios (SSP245 and SSP585) for the period 2061 - 2080. The results showed that the model exhibited high predictive accuracy, with mean AUC and TSS values of 0.9586 and 0.8701, respectively. Key environmental factors influencing its distribution include precipitation of the warmest quarter, precipitation of driest month, and mean temperature of driest quarter. Currently, *X. crassiusculus* is widespread across East Asia, Southeast Asia, North America, and South America, with notable populations in China and the United States. Under a medium-emission scenario (SSP245), highly suitable habitats were projected to increase by 1.79% by 2080, whereas the high-emission scenario (SSP585) predicts a smaller expansion of 0.52%. This findings underscores the need for enhanced monitoring and management efforts to mitigate the pest's impact under ongoing climate change.

Keywords: *Xylosandrus crassiusculus*, MaxEnt, Species Distribution Model, Ambrosia Beetle, Climate Change

Introduction

Insect pests pose significant threat to global forestry and biodiversity, leading to substantial ecological disruptions and economic losses[1,2]. The acceleration of international trade and transportation has inadvertently facilitated the spread of these species, creating new pathways for invasion and complicating management efforts[2]. Among these pests, the ambrosia beetle *Xylosandrus crassiusculus* (Motschulsky, 1866) (Coleoptera, Curculionidae) is of particular concern due to its ability to attack healthy trees and its potential for range expansion under changing climatic conditions[3,4].

Xylosandrus crassiusculus is widely distributed across the northeastern, mid-Atlantic, southeastern, southern, and midwestern United States, as well as in Hawaii and parts of Asia[5–7]. It is a polyphagous pest, infesting a broad range of hosts, including *Morus*

alba, *Camptotheca acuminata*, *Ziziphus jujuba*, *Quercus palustris*, and *Ligustrum lucidum*[3]. Unlike many secondary pests, *X. crassiusculus* is known to attack and damage healthy trees, typically boring into branches and trunks of 2.3–7.5 cm in diameter[4,8]. The larvae cohabitate with symbiotic fungi, which often cause rapid mortality or structural weakening in young or small-diameter trees, thereby reducing timber quality and economic value[9,10]. In recent years, *X. crassiusculus* has caused severe infestations in several Chinese provinces, including Jiangsu, Guizhou, Shanghai, Jiangxi, Guangxi, and Guangdong[5]. The situation is particularly acute in Guizhou Province, where large-scale cultivation of economically valuable fruit trees has coincided with rising damage from scolytine beetles[11]. Notably, *X. crassiusculus* has transitioned from a secondary pest to a primary threat, with a remarkable ability to infest and kill healthy saplings[8].

Ongoing climate is expected to further influence the distribution and abundance of insect pests such as *X. crassiusculus.* Rising temperatures, altered precipitation patterns, and increased frequency of extreme weather events can directly affect insect physiology, behavior, and population dynamics. Additionally, these climatic shifts may indirectly impact pest populations by altering the distribution and phenology of host plants, thereby modifying habitat suitability. Understanding how *X. crassiusculus* may respond to these environmental changes is crucial for developing effective pest management strategies and mitigating potential agricultural and forestry losses[12,13].

Species distribution models (SDMs) are widely recognized as powerful tools for predicting the geographical distribution of species by integrating climatic variables with species occurrence data[1,14]. Among these, MaxEnt is particularly effective for presence-only data and is known for its robust mathematical framework, ease of use, computational efficiency, and high predictive accuracy[15,16]. Researchers have successfully applied the MaxEnt model to predict suitable habitats for various bark beetle species, such as *Hylurgus ligniperda*, *Tomicus yunnanensis*, and *Xyleborinus saxesenii*[17]. Although previous studies have used MaxEnt to model the global habitat suitability of *X. crassiusculus*, the accuracy of these predictions remains limited due to outdated occurrence records[14,18]. To address this gap, our study incorporates the most recent occurrence records and climate datasets to project the current and future potential distribution of *X. crassiusculus* using the MaxEnt model. The goal is to provide a scientific foundation for global risk assessments and to support the development of targeted, evidence-based pest management strategies.

Results

Modeling Performance

The MaxEnt model for *X. crassiusculus* demonstrated strong predictive performance with a high mean cross-validated test AUC (0.9586) across replicate model runs (Supplementary Fig. 1), indicating the model's accuracy (AUC > 0.90). The True Skill Statistic (TSS) value of 0.8701 further validated model robustness, as values > 0.5 are considered reliable for distinguishing between presence and absence points. The Continuous Boyce Index of 0.90 also confirmed the model’s high predictive ability.

To further validate our MaxEnt predictions, we implemented an independent Boosted

Regression Trees (BRT) model. The BRT model achieved comparable performance, with an AUC of 0.9805 and TSS of 0.8945, both exceeding the thresholds for excellent model performance (Supplementary Table S1). The high consistency between these two independent modeling approaches (AUC difference = 0.0219, TSS difference = 0.0244) strongly supported the robustness and reliability of our distribution predictions.

Contribution of Bioclimatic Variables

The Jackknife test identified the most significant bioclimatic variables influencing the distribution of *X. crassiusculus*(Fig.1) . The top contributing variables were precipitation- and temperature-related (Table S2). Bio18 (precipitation of warmest quarter) contributing 39.17% on average across all scenarios, followed by Bio14 (precipitation of driest month) contributing 28.47%, and Bio9 (mean temperature of driest quarter) at 11.60%. Together, these three variables contributed for over 75% of the model's predictive ability. The response curves revealed optimal environmental conditions for *X. crassiusculus,* including moderate precipitation during the warmest quarter (Bio18: 200-600 mm), adequate precipitation during the driest month (Bio14: 50-200 mm), and suitable temperatures in the driest quarter (Bio9: 10-30℃) (Supplementary Fig. 2), providing insights into its climatic preferences and physiological tolerances.

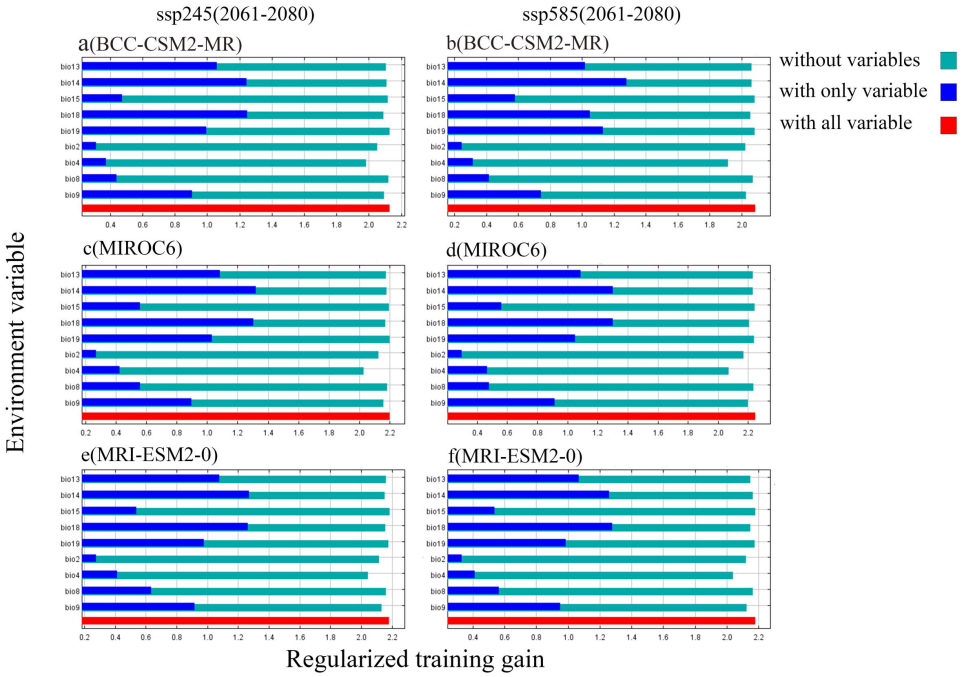


Figure 1 Jackknife test of variable importance for *Xylosandrus crassiusculus* under future climate scenarios (2061-2080).

Baseline Period Potential Distribution (1971–2000)

The MaxEnt model predicts the potential distribution of *Xylosandrus crassiusculus* extended beyond its known natural range across East Asia, Southeast Asia, North America, South America, and Oceania. All continents except Antarctica contain suitable habitats for the species during the baseline period (1971–2000).(Fig. 2). East

and Southeast Asia exhibited the highest habitat suitability, while Europe, northern North America, and northern Asia showed the lowest habitat suitability. The model's predictions suggested that baseline distribution was mainly dependent on precipitation and temperature variables (Table S2).

In East Asia, where the species was widely distributed in subtropical zones, the model identifies areas of very high suitability concentrated in southeastern China, southern Japan, and the Korean Peninsula. In North America, high suitability occured in the southeastern United States, particularly along the Atlantic and Gulf coasts. In South America, high-suitability areas are concentrated in southeastern Brazil, northern Argentina, and Uruguay. In Oceania, moderate suitability was predicted in eastern coastal Australia, particularly in Queensland and New South Wales.

Additionally, the model forecasts moderate to low climatic suitability in regions such as Central America, the Caribbean islands, parts of Southeast Asia (Indonesia, Philippines, Malaysia), Madagascar, and scattered areas in Africa. Globally, *X. crassiusculus* showed high suitability in East Asia (China, Japan, Korea), southeastern North America (United States), and southeastern South America (Brazil, Argentina), particularly within subtropical and warm-temperate regions (Fig. 2), while medium to low suitability was predicted in tropical regions and at higher latitudes. This indicated the species' ability to occupy a wide ecological range, especially in areas with moderate climate and adequate precipitation.

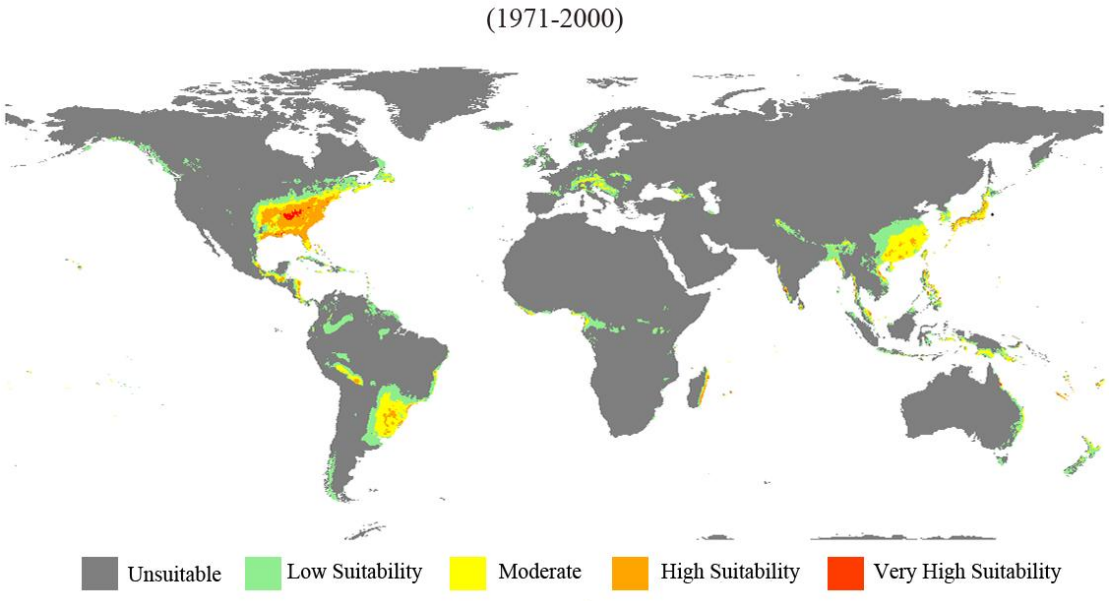


Figure 2 Global suitable habitats of *Xylosandrus crassiusculus* during the baseline period (1971-2000).

Predicted Future Distribution (2061–2080)

To assess the future distribution of *X. crassiusculus*, we used three Global Climate Models (GCMs: BCC-CSM2-MR, MIROC6, and MRI-ESM2-0) under scenarios SSP245 and SSP585 for the period 2061-2080 (Fig. 3). The results suggested moderate changes in habitat suitability under climate change, with suitable areas projected to expand slightly across all scenarios.

Under both emission scenarios, high suitability areas remained concentrated in

southeastern China, southern Japan, the southeastern United States, and southeastern South America (Brazil, Argentina). The three GCMs showed highly consistent distribution patterns, indicating that *X. crassiusculus* will maintain suitable habitats primarily in subtropical and warm temperate regions under future climate scenarios.

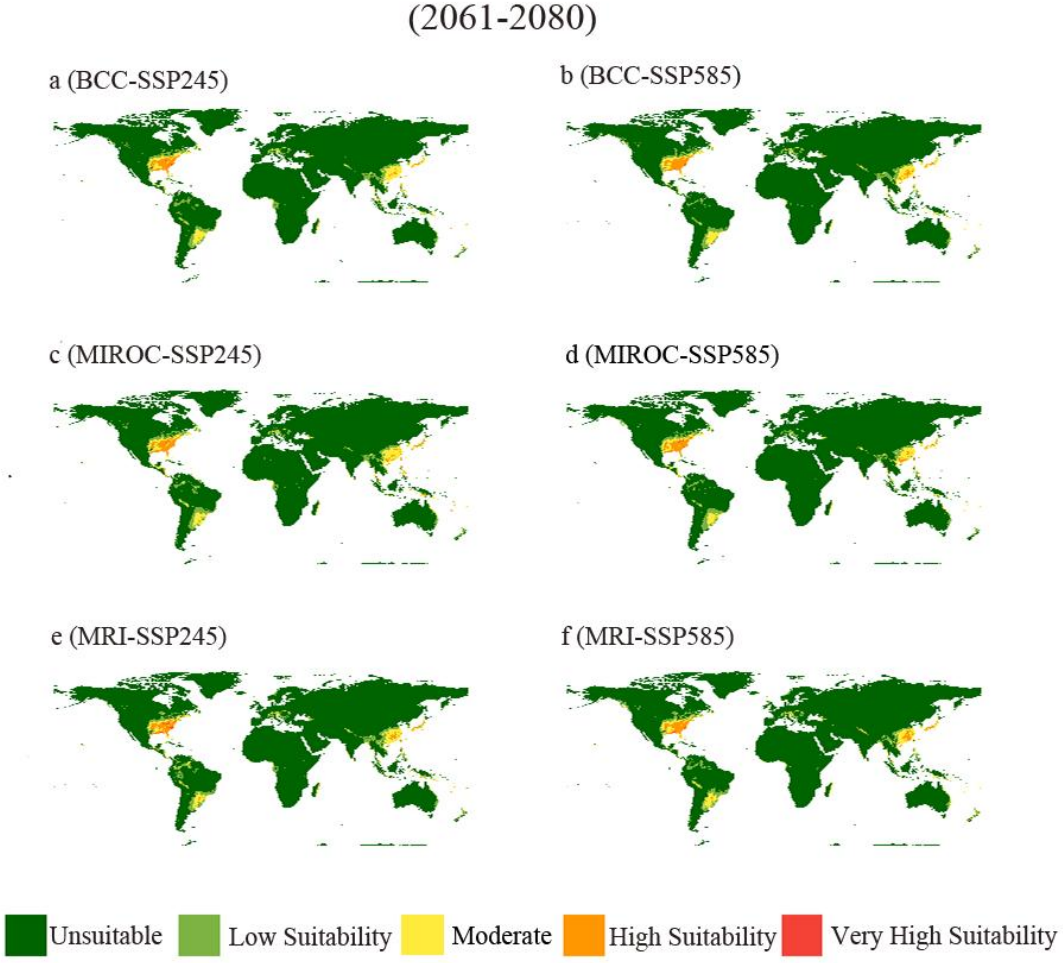


Figure 3 Future global suitable habitats of *Xylosandrus crassiusculus* under different climate scenarios (2061-2080).

Changes in Habitat Suitability

Quantitative analysis revealed that total suitable habitat area was projected to increase from 6991.06×10^4 km^2 during the baseline period (1971-2000) to 7116.13×10^4 km^2 under SSP245 ($+125.08 \times 10^4$ km^2, +1.79%) and 7027.44×10^4 km^2 under SSP585 ($+36.38 \times 10^4$ km^2, +0.52%).

Notably, habitat gains were highest in northern China, higher-elevation regions, and northeastern North America, indicating potential northward range shifts under a warming climate. SSP245 consistently showed larger expansion compared to SSP585, suggesting that more extreme climate change may limit habitat suitability in some currently suitable regions.

Conversely, certain regions, such as tropical Southeast Asia, parts of Central America, and scattered areas in Africa showed moderate to decreasing habitat suitability, particularly within tropical zones, as seen in the contraction areas (pink regions) in the habitat change maps (Fig. 4). This indicates that excessive warming or changes in

precipitation patterns may reduce suitability in some current range areas.

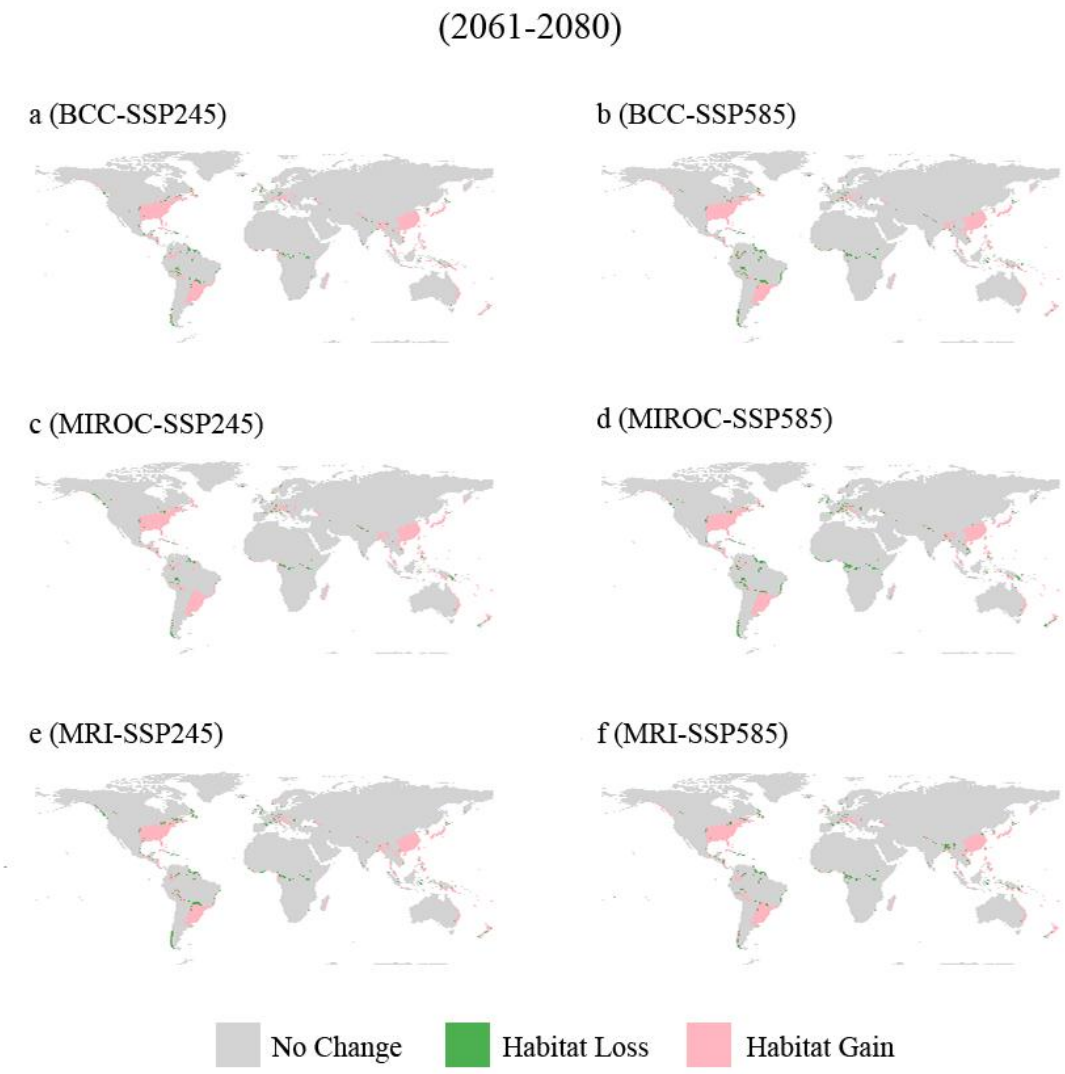


Figure 4 Habitat suitability change for *Xylosandrus crassiusculus* under future climate scenarios (2061-2080) compared to the baseline period (1971-2000).

Discussion

The accuracy of ecological niche model simulations depends critically on the appropriate selection of models, parameters setting, comprehensive species occurrence data, and representative environmental variables[1]. Among these factors, model choice significantly influences predictive reliability. The MaxEnt model, grounded in the principle of entropy maximization, has consistently demonstrated superior predictive accuracy compared to alternative modeling approaches[19]. Therefore, MaxEnt was chosen in this study to predict the potential global distribution of *X. crassiusculus* under both current and future climate scenarios, aiming to delineate its present range and anticipate spatial shifts in the future.

The MaxEnt model demonstrated excellent predictive performance for *X. crassiusculus* distribution, with AUC = 0.9586, TSS = 0.8701, and Continuous Boyce

Index = 0.90. These metrics exceed commonly accepted thresholds for species distribution models (AUC > 0.90, TSS > 0.5), indicating strong model reliability[20]. The high consistency between MaxEnt and our independent BRT validation (AUC difference = 0.0219) further supported the robustness of our predictions. The model accuracy obtained in this study matches the performance of prior MaxEnt-based researches on bark beetle distribution modeling.. For instance, Li et al[21]. MaxEnt reported AUC values of 0.950 and 0.952 for distribution modeling of *Euwallacea fornicatus* and *Euwallacea perbrevis*, respectively., while Huang et al[22].achieved AUC = 0.957 for *Tomicus yunnanensis*. Our higher AUC (0.9586) may be attributed to: The superior model performance is attributed to rigorous variable selection via VIF analysis, optimized regularization parameters, and strictly filtered high-quality occurrence data. Similarly, Urvois et al[18]. modeled two invading *Xylosandrus species* (*Xylosandrus compactus* and *X. crassiusculus*) with AUC = 0.88-0.91, but their study used older occurrence records and did not optimize model parameters, which may explain their slightly lower performance compared to our results.

The Jackknife test identified precipitation of warmest quarter (Bio18, 39.17%), the driest month (Bio14, 28.47%), and mean temperature of driest quarter (Bio9, 11.60%) as the top three variables influencing *X. crassiusculus* distribution. Together, these variables contributed 79.24% of the model's predictive ability, highlighting the species' strong dependence on water availability during critical periods.

The dominance of precipitation variables aligns with the biology of ambrosia beetles, which require adequate moisture for fungal symbiont cultivation and larval development[3,9]. This finding is consistent with previous studies on related species. For example, Ranger et al[9].reported increased dispersal activity of *Xylosandrus beetles* under wet conditions induced by rainfall, and Lizarraga et al[23]. further verified high relative humidity (the typical post-rain environment) maximizes their flight frequency.Similarly, Koontz et al[24]. demonstrated that climatic water deficit was a key driver of bark beetle-induced tree mortality across North America. However, our results differ from physiological and landscape-scale investigations of *Dendroctonus* bark beetles, which demonstrated that seasonal temperature regimes (winter minimum and summer maximum temperatures) dominate beetle development, overwinter survival and outbreak potential, while precipitation played a secondary regulatory role[25,26]. This discrepancy may reflect ecological differences: *Xylosandrus* species are ambrosia beetles dependent on fungal symbionts requiring high moisture, whereas *Dendroctonus* species are bark beetles with different host-finding strategies and fungal associations.

The response curves revealed optimal conditions at Bio18 = 200-600 mm and Bio14 = 50-200 mm, suggesting that *X. crassiusculus* prefers moderate precipitation levels sufficient to support fungal growth but not so high as to cause waterlogging or reduced wood quality. The temperature variable (Bio9) showed optimal range at 10-30°C, consistent with the species' subtropical and warm temperate distribution patterns.

During the baseline period (1971-2000), suitable habitats for *X. crassiusculus* were

concentrated in East Asia (southeastern China, southern Japan), southeastern North America (United States), and southeastern South America (Brazil, Argentina). These regions share similar climatic characteristics: subtropical to warm temperate climates with adequate precipitation during warm quarters. Our predictions align well with current known distributions from occurrence records and previous studies[5], validating the model's accuracy. The concentration of suitable habitats in East Asia (southeastern China, southern Japan) corresponds to the species' native range as documented by Wood and Bright and confirmed by recent surveys in China[3,5]. Similarly, the high climate suitability of southeastern North America predicted by our model aligns with long-term field trapping records of X. crassiusculus across the United States, where the species has established persistent invasive populations ranging from Florida in the south to New York in the north[4,8]. The predicted suitable areas in southeastern South America (Brazil, Argentina) are consistent with recent interception records at ports in these countries[11], suggesting established populations that warrant further investigation. However, our model also identified potentially suitable areas in Europe and Africa where current records are limited, which may indicate either under-sampling in these regions or that additional factors (e.g., host availability, biotic interactions) limit establishment despite climatic suitability.

Under future climate scenarios (2061-2080), total suitable habitat area is projected to expand slightly (+1.79% under SSP245, +0.52% under SSP585). This modest expansion contrasts with some previous studies predicting substantial range shifts for invasive pests under climate change[18,27].The smaller expansion under SSP585 compared to SSP245 suggests that more extreme climate change may limit habitat suitability in some currently suitable regions, potentially due to excessive warming or altered precipitation patterns. This modest expansion contrasts with numerous niche modelling forecasts which predict substantial latitudinal range shifts and dramatic suitable habitat enlargement for invasive scolytine pests under future warming scenarios[27,28], The smaller expansion in our study may be explained by: (1) *X. crassiusculus* already occupies most climatically suitable areas globally, leaving limited room for expansion; (2) the species' broad climatic tolerance buffers against moderate climate change; (3) habitat loss in tropical regions partially offsets gains at higher latitudes. Our results are more consistent with Urvois et al[27]. who projected modest (5-10%) range changes for *Xylosandrus* species under climate change, suggesting that ambrosia beetles may be less responsive to climate change than other forest pests due to their protected gallery lifestyle and fungal symbiont buffering effects.

Habitat gain areas were primarily identified in northern China, higher elevation regions, and northeastern North America, indicating potential northward range shifts under warming climate. This pattern is consistent with general expectations that climate warming will facilitate poleward and upward elevational expansions of insect pests[27–30] The northward shift in China aligns with observations by Zu et al[31]. who documented upward elevational migration of subtropical mountain species on the Gongga Massif. Similarly, the expansion into northeastern North America mirrors range shifts reported for other invasive bark beetles in this region[32]. Conversely,

habitat loss was observed in tropical Southeast Asia, parts of Central America, and scattered areas in Africa, particularly within tropical zones. These contraction areas likely reflect regions where future temperatures exceed the species' thermal tolerance or where precipitation patterns become unsuitable for fungal symbionts. The habitat loss in tropical Southeast Asia and Central America is consistent with predictions for heat-sensitive insect species[13,27,33], where future temperatures may exceed physiological tolerance thresholds. However, the magnitude of tropical contraction in our study (+0.52% net change under SSP585) is smaller than projected for some tropical insect pests (up to 50% loss)[34,35], possibly because *X. crassiusculus*' gallery-dwelling lifestyle provides microclimatic buffering against extreme temperatures.

The consistency of distribution patterns across three GCMs (BCC-CSM2-MR, MIROC6, and MRI-ESM2-0) provides confidence in these projections. All models agreed on the core suitable regions (southeastern China, southeastern United States, southeastern South America) and the general direction of range shifts (northward expansion, tropical contraction). This multi-GCM approach reduces uncertainty associated with individual climate model biases and strengthens the reliability of our management recommendations.

Despite the strong model performance, several limitations should be acknowledged. First, our model relies solely on climatic variables and does not incorporate host plant distribution, land use changes, or anthropogenic dispersal pathways, which may also influence the spatial distribution of *X. crassiusculus*[27,36]. Second, the model assumes equilibrium between the species and its environment, which may not hold for rapidly expanding invasive populations. Third, we focused on two emission scenarios (SSP245 and SSP585); intermediate scenarios could provide additional insights. Future studies should integrate host plant data, human-mediated dispersal models, and additional climate scenarios to refine distribution predictions.

Our results have important implications for pest management and biosecurity. The expansion into northeastern North America mirrors range shifts reported for other invasive bark beetles in this region[28]. Conversely, habitat loss was observed in tropical Southeast Asia, parts of Central America, and scattered areas in Africa, particularly within tropical zones. These contraction areas likely reflect regions where future temperatures exceed the species' thermal tolerance or where precipitation patterns become unsuitable for fungal symbionts. The habitat loss in tropical Southeast Asia and Central America is consistent with predictions for heat-sensitive insect species[33].

Our results have important implications for pest management and biosecurity. Regions projected to become suitable under future climate (habitat gain areas in northern China, northeastern North America) should be prioritized for monitoring and early detection programs. Quarantine measures should be strengthened in ports and trade hubs within these expansion zones to prevent human-mediated dispersal. In currently suitable regions experiencing habitat loss (tropical Southeast Asia, Central America), continued surveillance is necessary, as the species may shift to higher elevations or latitudes within these regions[27].

Conclusion

This study presents a comprehensive ecological niche model for *X. crassiusculus* and evaluates its potential distribution under baseline and future climate scenarios using MaxEnt. The model showed strong predictive performance (mean AUC = 0.9586; TSS = 0.8701), indicating reliable discrimination of suitable habitats. Precipitation-related variables, particularly precipitation of the warmest quarter (Bio18) and precipitation of the driest month (Bio14), along with temperature variables (mean temperature of driest quarter, Bio9), were identified as the key drivers shaping the species' distribution. Under baseline conditions (1971-2000), high habitat suitability is concentrated mainly in East Asia, Southeast Asia, southeastern North America, and southeastern South America, while Europe and northern Asia show limited suitability. Future projections reveal scenario-dependent responses with modest range expansions. Under the medium-emission scenario (SSP245), suitable habitats are projected to increase by 1.79% by 2080. In contrast, the high-emission scenario (SSP585) predicts a smaller expansion (0.52% increase), suggesting that more extreme climate change may limit habitat suitability in some currently suitable regions. Localized gains are projected in northern China, higher elevation regions, and northeastern North America, indicating potential northward range shifts. To increase utility for management, we recommend targeted surveillance in high-suitability and gain-prone areas; incorporation of host plant and anthropogenic variables in future models; and empirical monitoring to validate forecasts. Future research should combine systematic field surveys, host distribution data, and trade-pathway analyses to effectively validate model outputs and to inform adaptive, locally tailored integrated pest management strategies.

Methodology

Occurrence Records

Occurrence data for *X. crassiusculus* were sourced from multiple repositories to ensure comprehensive geographic coverage. Data were obtained from the Global Biodiversity Information Facility (GBIF) database (https://www.gbif.org), published literature accessed via China National Knowledge Infrastructure (CNKI,https://oversea.cnki.net), Web of Science (https://webofscience.com), ScienceDirect (https://sciencedirect.com), and field surveys conducted by our research team. To ensure data integrity and model accuracy, we implemented a rigorous data filtration process. Duplicate entries, georeferencing errors, and spatially redundant records were systematically removed using Microsoft Excel. Additionally, records without precise geographic coordinates or those located in unsuitable habitats (e.g., marine points) were excluded[7]. After rigorous filtering, 317 unique and validated occurrence records (from an initial 373) were retained for model development and validation (Figure 5). The final dataset represents the species' known distribution across East Asia, Southeast Asia, North America, South America, and Oceania.

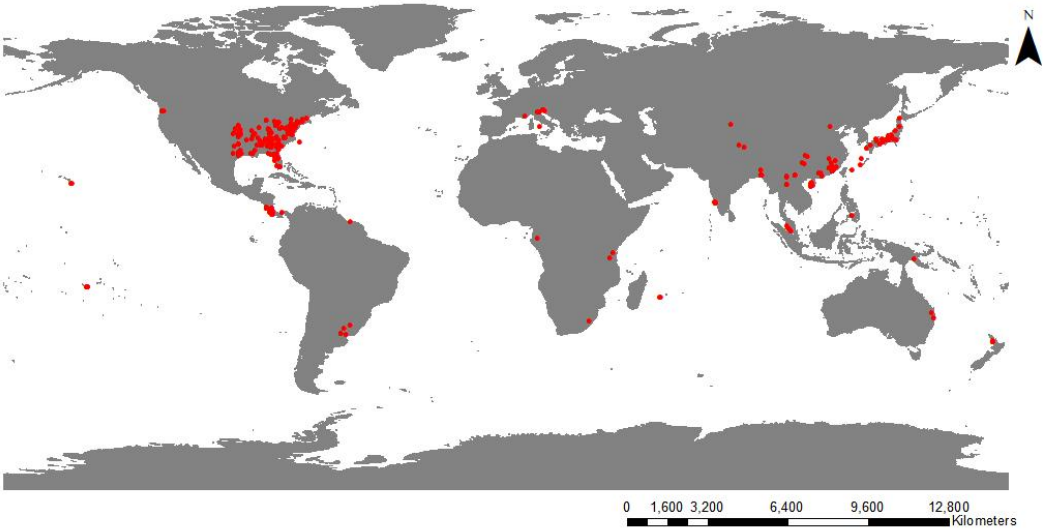


Figure 5 Distribution of *Xylosandrus crassiusculus* occurrence points globally during the baseline period (1971-2000).

Acquisition and Selection of Environmental Variables

Environmental variables were obtained from the WorldClim 2.1 database (https://www.worldclim.org) at a spatial resolution of 2.5 arc-minutes, including both baseline (1971–2000) and projected future (2061–2080) climate conditions. The initial dataset comprised 19 bioclimatic variables. Future climate data were derived from three Global Climate Models (GCMs): BCC-CSM2-MR (Beijing Climate Center), MIROC6 (Model for Interdisciplinary Research on Climate), and MRI-ESM2-0 (Meteorological Research Institute). We selected two Shared Socioeconomic Pathways (SSPs) representing contrasting emission scenarios: SSP245 (medium forcing) and SSP585 (high forcing). These scenarios were chosen to assess potential range shifts under moderate and extreme climate change conditions.

To address multicollinearity among environmental variables and improve model performance, we performed Variance Inflation Factor (VIF) analysis using the 'usdm' package in R[34,35]. Variables with VIF > 10 were sequentially removed until all remaining variables had VIF < 10, indicating acceptable collinearity levels. After VIF screening, 9 bioclimatic variables were retained as final model input (Table S2). All selected bioclimatic layers were converted to ASCII format and incorporated into the MaxEnt modeling to forecast habitat suitability under baseline and future climate scenarios.

Modeling Approach

MaxEnt (version 3.4.4) was used to model the baseline and future global distribution of *X. crassiusculus*. MaxEnt was selected for its effectiveness with presence-only data and its robust performance across various species distribution models. Occurrence records (n = 317) were used with 10-fold cross-validation to maximize calibration data while retaining an independent evaluation set. Key model settings included 10,000 background points, 500 iterations, and auto features (linear, quadratic, hinge, product, and threshold). To optimize model performance, we tested eight regularization multiplier (RM) values ranging from 0.5 to 4.0 and selected the optimal

RM of 1.0 based on the highest TSS value. Random seeds were used for each test to ensure reproducibility[14,19,39].

Suitability scores in the resulting models were classified into five categories: unsuitable (0.00–0.20), low (0.20–0.40), moderate (0.40–0.60), high (0.60–0.80), and very high (0.80–1.00). Suitability maps were converted to binary presence/absence layers using the optimal threshold of 0.20 determined by maximizing the True Skill Statistic (TSS), whereby grid cells with logistic values ≥ 0.20 were classified as suitable (presence = 1) and cells with values < 0.20 as unsuitable (absence = 0). Binarization was performed with the 'classify' function in the R package 'terra', producing a presence/absence matrix for each scenario and time period. Using binary matrices for the baseline and each future scenario, we compared cell values to identify spatial changes in suitability. Cells that were absent (0) under baseline but present (1) under a future scenario were recorded as 'habitat gain' areas. Cells that were present (1) under baseline but absent (0) under a future scenario were recorded as 'habitat loss' areas. Cells that remained present (1) or absent (0) in both periods were recorded as stable areas. These three classes were mapped and summarized.

Model Evaluation

Model performance was assessed using the Area Under the Curve (AUC), True Skill Statistics (TSS), and Continuous Boyce Index. AUC values range from 0 (random discrimination) to 1 (perfect discrimination), with values above 0.90 considered excellent for species distribution models[25]. Additionally, TSS values between -1 and +1 were used to measure model accuracy, where values closer to +1 indicate a strong relationship between the predicted and observed distributions. TSS values greater than 0.5 are regarded as reliable for distinguishing between presence and absence points[40]. The Continuous Boyce Index (ranging from -1 to +1) was also calculated to assess model predictions against presence-only data, with values above 0.8 indicating high predictive ability.

To ensure model robustness, we implemented an independent Boosted Regression Trees (BRT) modeling approach for validation. Both MaxEnt and BRT models achieved excellent performance metrics (MaxEnt: AUC = 0.9586, TSS = 0.8701; BRT: AUC = 0.9805, TSS = 0.8945). The high consistency between these two independent modeling approaches (AUC difference = 0.0219, TSS difference = 0.0244) strongly supports the robustness and reliability of our distribution predictions.

Data Analysis

All data analyses were conducted using R software (version 4.2.2) and MaxEnt (version 3.4.1). To address multicollinearity among environmental variables, Variance Inflation Factor (VIF) analysis was performed using the 'usdm' package in R. Variables with VIF values greater than 10 were sequentially removed until all remaining variables had VIF < 10.

Model performance was evaluated using three metrics: Area Under the Receiver Operating Characteristic Curve (AUC), True Skill Statistic (TSS), and Continuous Boyce Index. A 10-fold cross-validation procedure was applied to ensure model robustness. Parameter optimization was conducted by testing different regularization multipliers (RM), with RM = 1.0 selected based on the lowest AICc value.

Future habitat projections were generated using three Global Climate Models (GCMs: BCC-CSM2-MR, MIROC6, and MRI-ESM2-0) under two Shared Socioeconomic Pathways (SSP245 and SSP585) for the period 2061-2080. Changes in suitable habitat area were calculated using ArcGIS (version 10.8). All maps were refined using Adobe Photoshop (version 2023) for publication.

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Supplementary material

Supplementary material is available at Journal of Scientific Reports online.

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Competing interests

The authors declare no competing interests.

Data availability

The occurrence data analysed in this study were compiled from publicly available databases (Global Biodiversity Information Facility, https://www.gbif.org; Web of Science, https://webofscience.com; ScienceDirect, https://sciencedirect.com) and from published literature accessed via the China National Knowledge Infrastructure (CNKI, https://oversea.cnki.net). The field survey data generated during this study, together with the occurrence records compiled from the literature, are provided in the Supplementary Material 2.

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