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# Estimating global geographical distribution and ecological niche dynamics of *Ammannia coccinea* under climate change based on Biomod2

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Invasive alien plants pose a significant threat to biodiversity and the agricultural economy. The invasive weed (*Ammannia coccinea*) competes with rice in paddy fields, potentially threatening rice production. Despite the crucial need to estimate the global geographical distribution and ecological niche dynamics of *A. coccinea* for effective early warning, control strategies, and global rice security, relevant research remains scarce. This study utilized the Biomod2 platform, which integrates multiple single models into ensemble model, incorporating environmental and species data to analyze the distribution range shifts of *A. coccinea* under current and future climate scenarios. It also quantified and analyzed shifts in the species' ecological niche across these climate scenarios. The results indicated that the potential suitable areas for *A. coccinea* were mainly in Southern North America, northern and south-eastern South America, south-western Europe, the Middle East, central Africa, western Asia, south-eastern Asia, with a gradual increase in mid-high suitability habitat over time and radiation levels. While the overall ecological niche of *A. coccinea* remains stable, minor shifts are expected under future conditions. Temperature, precipitation, and the human impact index were the key factors influencing the future distribution of *A. coccinea*. Climate change contributes to the expansion of *A. coccinea*'s highly suitable areas and shifts its ecological niche. Organizations efforts should focus on preventing the spread of *A. coccinea* in regions where its potential distribution overlaps with key rice production areas. The findings of this study provide critical insights into the global distribution and ecological niche dynamics of *A. coccinea*, aiding in the development of early warning and control strategies to mitigate its impact on biodiversity, agriculture, and particularly rice production under future climate scenarios.

**Keywords** *Ammannia coccinea*, Biomod2, Climate change, Ecological niche, Habitat distribution

In recent years, with the acceleration of international exchanges and transnational trade, an increasing number of organisms have crossed spatial boundaries to reach other regions, where they have proliferated and caused adverse impacts on the local ecological ecosystems. As a result, the invasion of exotic organisms has emerged as a significant environmental concern for humanity in the twenty-first century<sup>1</sup>. Among these invasive species, plants play a major role, accounting for approximately 20% of the world's flora<sup>2</sup>. Invasive alien plants pose a serious threat to native species, biodiversity, ecological balance, agricultural production, and even economic stability<sup>3,4</sup>. For example, species like *Mikania micrantha* Kunth and *Eupatorium odoratum* L. have caused significant ecological and economic damages in regions such as China and Australia, contributing to billions in financial losses<sup>5-7</sup>. These losses include reduced crop yields, increased costs of management and eradication, and disruption of local ecosystems.

In the context of global warming, future climate change will alter the land surface temperature and precipitation pattern, significantly affecting invasive species distribution<sup>8</sup>. Higher temperatures typically

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accelerate their metabolism, development, and reproductive cycles, promoting their spread. For example, the red imported fire ant (*Solenopsis invicta*) has expanded into higher latitude regions as warmer climate allow it to thrive in new habitats<sup>9</sup>. Similarly, species are likely to shift to higher altitudes and latitudes under global climate change, accelerating the invasion process of exotic species<sup>10</sup>. In addition to temperature changes, alterations in precipitation patterns can also facilitate the invasion of alien plants. Some studies have shown that genetic alterations and accelerated evolution, triggered by changes in precipitation, contribute to the spread of invasive species. For example, two annual grass species, *Avena barbata* and *Bromus madritensis*, have shown reduced growth and reproduction in areas with decreased precipitation in the United States<sup>11</sup>. Human activities and land use further exacerbate these shifts by modifying habitats and ecosystems<sup>12,13</sup>. Once invasive species successfully colonize new areas, eradication becomes highly challenging. Therefore, it is crucial to investigate the global distribution of invasion plants under climate change conditions. Such research will provide the foundation for developing effective early warning and control systems to mitigate the threats posed by invasive species<sup>14</sup>.

To enhance the efficiency of invasive species control, predicting the potential distribution habitats of invasive plants using species distribution models (SDMs) has become a key focus in biological invasion research<sup>15</sup>. SDMs predict the actual and potential distribution of a species by using algorithms to determine its ecological requirements, projecting these results in a specific spatiotemporal context. This process considers both the known distribution points and the associated environmental variables<sup>16</sup>. Numerous SDMs are available, each differing in principles, algorithms, and predictive performance<sup>17</sup>. We applied 10 modelling algorithms from the Biomod2 platform, including Generalized Linear Model (GLM), Generalized Boosted Model (GBM), Generalized Additive Model (GAM), Classification Tree Analysis (CTA), Artificial Neural Network (ANN), one Rectilinear Envelope Similar to BIOCLIM (SRE), Flexible Discriminant Analysis (FDA), Multivariate Adaptive Regression Splines (MARS), Random Forest (RF), Maximum Entropy Models (MaxEnt)<sup>18</sup>. Biomod2 integrates results from multiple single models to improve the accuracy of species distribution predictions<sup>19</sup>. Ensemble model refer to the modeling approach where multiple individual models (often referred to as “single models”) are combined to make a final prediction. The greater reliability of ensemble model compared to single models has made them widely used for studying the potential suitable areas for invasive alien plants<sup>9</sup>, such as *Centaurea solstitialis* L.<sup>20</sup>, *Heracleum mantegazzianum*<sup>21</sup>, *Aegilops tauschii* and *Ambrosia artemisiifolia* (common ragweed)<sup>22–24</sup>.

*Ammannia coccinea* is a noxious weed that competes with rice and is frequently found in rice paddies. It also thrives in various wet environments including wet meadows, rivers, riverbanks, floodplains, ponds, lakes, and marshes<sup>25,26</sup>. Native to North and Central America, *A. coccinea* has been introduced to many countries, including France, Spain, Portugal, Italy, Bulgaria, Greece, Turkey, Australia, Africa, Morocco, and others<sup>25,27,28</sup>. It was introduced to China, Japan, Korea, Malaysia, and other Asian countries in the 1950s<sup>28,29</sup>. It is now one of the most widely distributed nuisance weeds in the region<sup>30,31</sup>. The seeds of *A. coccinea* are small and highly prolific, averaging 270 seeds per capsule and producing over 500,000 seeds per plant<sup>32</sup>. In shaded conditions, *A. coccinea* adapts by increasing the ratio and stem node length while reducing stem diameter, branch number, and stem node count<sup>33</sup>. *A. coccinea* contains flavonoids, such as quercetin, that are converted to protective compounds when exposed to UV-B radiation<sup>34</sup>. These flavonoids scavenge free radicals and improve the plant's resistance to fungal pathogens<sup>35</sup>. *A. coccinea* thrives in freshwater at a depth of up to 0.5 meters<sup>25,30</sup>. These biological characteristics traits enhance the competitiveness and invasiveness of *A. coccinea*<sup>32</sup>. In California rice fields, *A. coccinea* is highly competitive, outcompeting rice 45 days after sowing, with densities of 110 plants/m<sup>2</sup> causing a 39% reduction in rice yields<sup>33,36</sup>.

Given *A. coccinea*'s high competitiveness and its significant impact on paddy fields, predicting its global distribution patterns under climate change and understanding its niche dynamics are of critical importance. However, comprehensive research on this subject remains limited. This study addresses this gap by employing advanced species distribution models and niche analysis methods to examine *A. coccinea*'s distribution and niche shifts in globally suitable areas. This research reveals *A. coccinea*'s invasion dynamics, offering critical insights for developing effective biosecurity measures and management strategies to mitigate its impact on global agriculture.

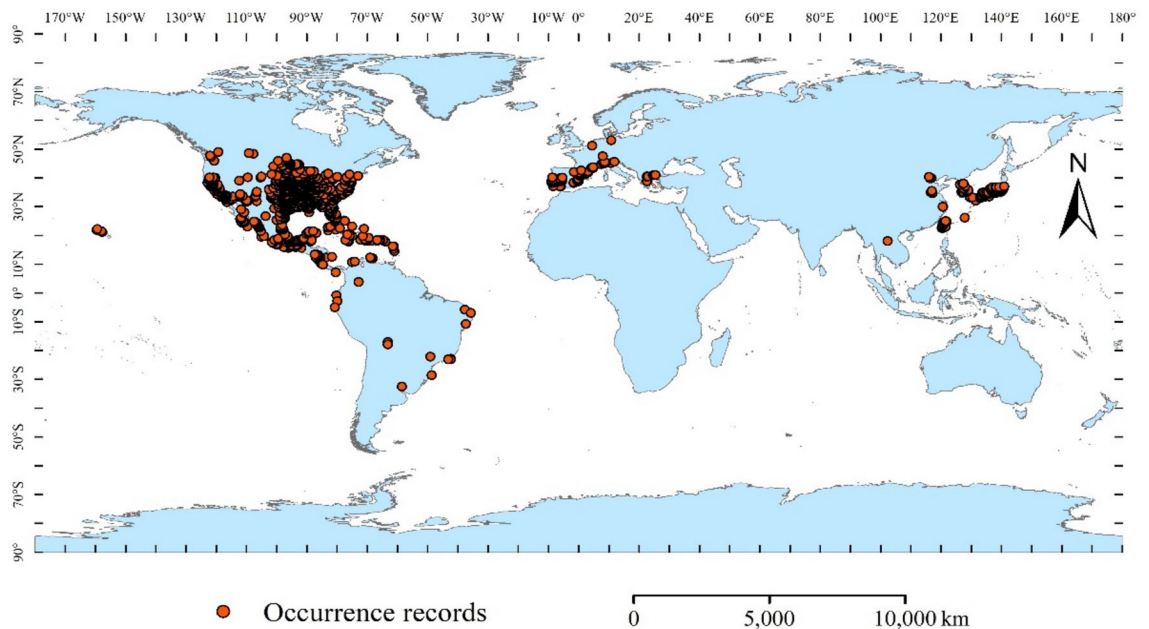
## Materials and methods

### Acquisition and screening of occurrence records

Occurrence records for *A. coccinea* were gathered from literature resource, field surveys, the Global Biodiversity Information Network (<http://www.GBIF.org>; <https://doi.org/https://doi.org/10.15468/dl.d9vykx>)<sup>37</sup>, China Plant Image Bank (<https://ppbc.iplant.cn>), and China Digital Herbarium (<https://www.cvh.ac.cn/index.php>). Once the occurrence locations were identified from China Plant Image Bank and China Digital Herbarium, the coordinate picker tool (<https://lbs.amap.com/tools/picker>) was used to retrieve latitude and longitude data. 2862 occurrences were collected after removing some duplicates. To ensure data accuracy and precision, occurrence records that were not on land or had incorrect coordinates were excluded. Concurrently, to ensure compatibility with the resolution of our environmental variables, we refined the occurrence data using ENMTools v1.4.4<sup>38</sup>. This process filtered the data to retain only one occurrence record per 10 × 10 km grid, effectively minimizing spatial autocorrelation. If unaddressed, spatial autocorrelation can skew results due to the clustering of data points<sup>39</sup>. Finally, 1138 occurrence records of *A. coccinea* were obtained for modeling its potential global distribution using Biomod2 (Fig. 1).

### Obtaining and filtering environment variables

Current climate data (1970–2000) and future climate data (2041–2060, 2061–2080, 2081–2100) were downloaded from WorldClim ([www.worldclim.org](http://www.worldclim.org))<sup>40</sup>. The current climate data come from WorldClim 2.1 and include 19 variables related to temperature and precipitation, along with digital elevation data (elev), all at a resolution of 5 arc-minutes. To account for the influence of human activities and land use on invasive plant distribution<sup>34,35</sup>,



**Fig. 1.** Screened global distribution occurrence records of *Ammannia coccinea*.

we included Human Impact Index (HII; 2.5 arc-minutes) and global land cover data (GlobCover 2009; [http://du.e.esrin.esa.int/page\\_globcover.php](http://du.e.esrin.esa.int/page_globcover.php); 2.5 arc-minutes). Both variables were resampled to 5 arc-minute resolution in ArcGIS. Future climate data for the 2050s, 2070s, and 2090s were derived from three shared socioeconomic pathways (SSPs) under CMIP6: SSP126, SSP245, and SSP585. These scenarios reflect different levels of radiative forcing in 2100: 2.6 W/m<sup>2</sup> in a sustainability-focused world (SSP126), 4.5 W/m<sup>2</sup> in a middle-of-the-road scenario (SSP245), and 8.5 W/m<sup>2</sup> in a high-growth, high-energy world (SSP585)<sup>41,42</sup>. Data from the BCCCSM2-MR model were used, which combines SSPs with Representative Concentration Pathways (RCPs) to project future climate trends<sup>43</sup>.

To prevent model misinterpretation due to multicollinearity between environmental variables<sup>44</sup>, we conducted a correlation analysis on the 22 bioclimatic variables using R. The variables were first extracted to the sample points using ArcGIS's multi-value extraction module and then analyzed for correlation using R. Variables with a correlation coefficient  $|r| > 0.8$  were removed, keeping the one with the higher contribution to the models based on jackknife importance values. This process reduced the 22 variables to 12 predictors, minimizing redundancy and enhancing model robustness (Table 1, Fig. 2). Correlation analysis is essential for identifying multicollinearity, preventing highly correlated variables from distorting model outcomes. Jackknife importance values assess each variable's independent contribution to the models. Combining these two approaches ensured the models remained both robust and interpretable.

### Construction and evaluation of ensemble models

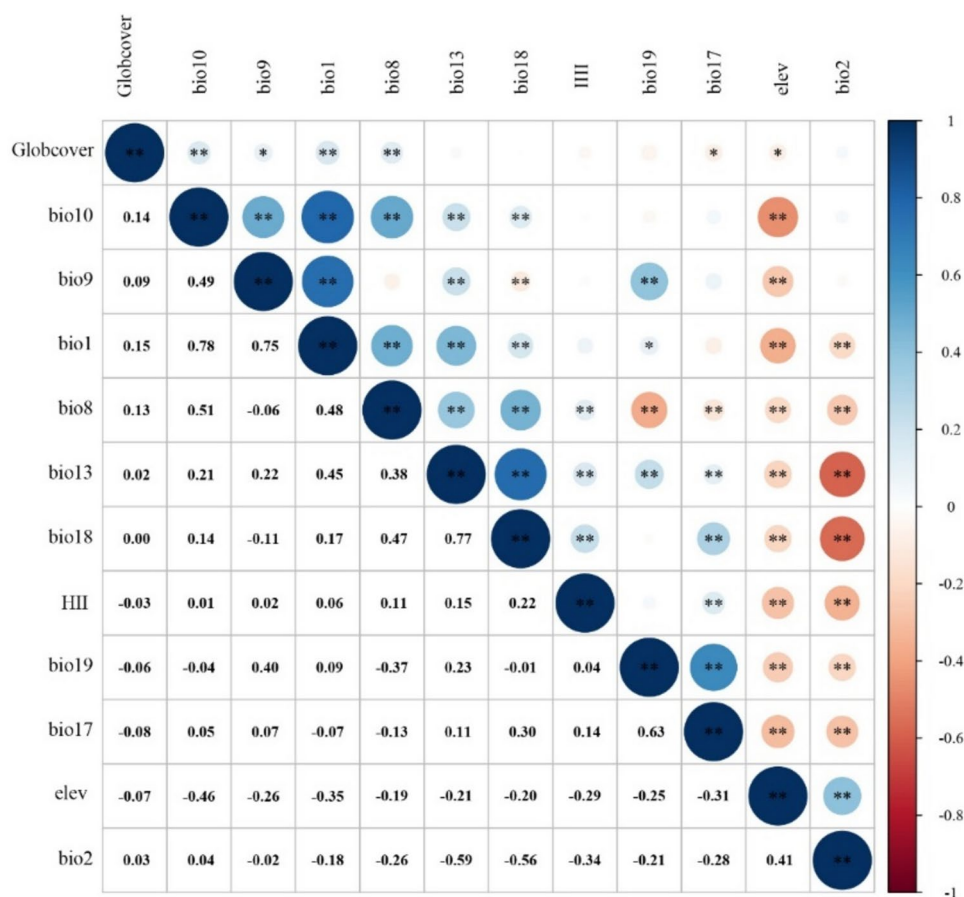
The Biomod2 includes 10 single models, enabling a wide range of configurations to meet diverse research needs<sup>45</sup>. By integrating these single models, we leverage their respective sensitivities and explanatory powers to enhance the diversity, robustness, and comprehensiveness of predictions. This ensemble approach reduces individual model bias, minimizes errors, and improves overall prediction accuracy by combining outputs, thereby better assessing uncertainty<sup>19</sup>. Studies have shown that combining multiple single models generally results in higher predictive accuracy than using a single model, thereby improving the reliability and practicality of scientific research<sup>17</sup>.

In this study, we used 10 single models (GAM, GBM, GLM, CTA, MARS, ANN, SRE, FDA, RF, MaxEnt) from the R package Biomod2 to predict potentially suitable areas for *A. coccinea* based on species occurrence records and environmental variables. We employed the disk method in Biomod2 to generate pseudo-absence samples equal in number to the presence points. This approach enhances the accuracy of classification algorithms like classification trees and random forests<sup>46</sup>. In each species distribution models setup, 75% of the data was used for training and the remaining 25% for testing to evaluate model accuracy and reliability<sup>47</sup>. The division of training and test data was repeated randomly 5 times and the models were repeated 10 times. Additionally, 500 pseudo-negative sample points were randomly selected<sup>46,48,49</sup> and repeated three times, resulting in a total of 150 modeled species distributions.

The true skill statistic (TSS), area under the receiver operating characteristic curve (AUC), and Cohen's kappa (Kappa) were used to evaluate model accuracy, with values closer to 1 indicating more reliable predictions<sup>50–52</sup>. The evaluation criteria for AUC, TSS and Kappa are presented in Table 2. Of the 150 constructed models, those with TSS and AUC values greater than 0.75 were selected to build the ensemble species distribution models. Model weighting in the ensembles was based on the evaluation score. Models with higher ratings received

Code	Description	Unit	Weather to use <i>A. coccinea</i> for modeling	Importance (Jackknife)
bio1	Annual mean temperature	°C	Yes	6
bio2	Mean diurnal range	°C	Yes	2.5
bio3	Isothermality	°C	No	2
bio4	Temperature seasonality	-	No	5.1
bio5	Maximum temperature of the warmest month	-	No	1.5
bio6	Minimum temperature of the warmest month	°C	No	0.4
bio7	Annual mean temperature range	°C	No	1.1
bio8	Mean temperature of the wettest quarter	°C	Yes	0.1
bio9	Mean temperature of the driest quarter	°C	Yes	0.1
bio10	Mean temperature of the warmest quarter	°C	Yes	10.9
bio11	Mean temperature of the coldest quarter	°C	No	0.9
bio12	Annual precipitation	mm	No	0.4
bio13	Precipitation of the wettest month	mm	Yes	1.3
bio14	Precipitation of the driest month	mm	No	0.6
bio15	Precipitation seasonality ( CV)	-	No	0.8
bio16	Precipitation of the wettest quarter	mm	No	0.2
bio17	Precipitation of the driest quarter	mm	Yes	3.6
bio18	Precipitation of the warmest quarter	mm	Yes	0.3
bio19	Precipitation of the coldest quarter	mm	Yes	7.8
HII	Human Influence Index	-	Yes	44.4
Globcover	Global land cover	Km <sup>2</sup>	Yes	8.6
elev	above sea level	M	Yes	1.3

**Table 1.** Selected climatic variables influencing the distribution of *Ammannia coccinea*.



**Fig. 2.** Correlation analysis of 12 selected environment variables.

Evaluation index	Fail	Bad	Medium	Good	Excellence
AUC	0.50–0.60	0.60–0.70	0.70–0.80	0.80–0.90	0.90–1.00
TSS	0.00–0.40	0.40–0.55	0.55–0.70	0.70–0.85	0.85–1.00
Kappa	0.00–0.40	0.40–0.55	0.55–0.70	0.70–0.85	0.85–1.00

**Table 2.** Evaluation standard for AUC, TSS and Kappa.

Evaluation index	MARS	RF	MAXENT	CTA	FDA	GAM	GBM	GLM	EMca	EMmean
TSS	0.844	0.992	0.857	0.882	0.828	0.836	0.883	0.807	0.891	0.876
ROC	0.967	0.997	0.944	0.972	0.961	0.974	0.986	0.958	0.983	0.982
KAPPA	0.847	0.991	0.832	0.884	0.831	0.844	0.892	0.816	–	–

**Table 3.** Evaluation metric values for individual models and ensemble models.

greater weighting in the combined models<sup>50</sup>. The importance of each environmental factor was assessed using Biomod2. Finally, the ensemble model was used to predict the potential global distribution of *A. coccinea* under climate change scenarios.

We employed multiple integrated methods to construct ensemble models for the potential distribution areas of *A. coccinea*, including EMmean (ensemble mean), and EMca (consensus average) etc. This multifaceted approach enabled a comprehensive evaluation of the models, ensuring the selection of the optimal ensemble model for accurate prediction.

### Division of the suitable areas

The critical value of ensemble model were used as the threshold to differentiate between suitable and unsuitable zones. The ASCII raster layer, ranging from 0 to 1,000 in the ensemble model, indicated the occurrence probability (p) of *A. coccinea*. A larger *P*-value indicates a higher probability of occurrence of *A. coccinea*<sup>9,20</sup>. We divided the potential global distribution of *A. coccinea* into four categories using ArcGIS: high-suitability habitat ( $600 \leq P \leq 1000$ ), moderate-suitability habitat ( $400 \leq P < 600$ ), low-suitability habitat ( $200 \leq P < 400$ ), and unsuitable habitat ( $0 \leq P < 200$ ). We used the raster map of suitable zones for *A. coccinea* to create binary maps through the reclassification function in ArcGIS 10.2, and applied the SDM Toolbox v2.0 plugin to calculate the spatial patterns of these suitable zones. When binarizing the prediction results, we used 0.2 as the boundary between suitable and non-suitable zones. We compared current and future projections of total suitable area and assessed changes by calculating areas of expansion, contraction, and rates of gain and loss.

### Ecological Niche comparison measures

We utilized the Principal Component Analysis (PCA) method from the ecospat software package<sup>53</sup> to investigate ecological niche shifts of *A. coccinea* under current and future climatic scenarios. This approach is widely used to analyze the ecological niche dynamics of invasive alien species<sup>54,55</sup>. We employed the Schoener's D metric was used to quantify ecological niche overlap, which ranges from 0 to 1, with larger values indicating greater overlap between the two areas<sup>56</sup>. This index is crucial for understanding how the ecological niche of *A. coccinea* changes or remains stable under current and future climate scenarios. Niche equivalency tests and similarity were conducted to evaluate the significance of niche overlap across geographic areas<sup>56,57</sup>. The niche equivalency test assessed whether the niches of the two entities were equal (full overlap), moderately similar (partial overlap), or distinctly different (no overlap). The niche similarity test assessed whether the niches of the two entities being compared were more similar (or different) than expected by chance, also considering the surrounding environmental conditions throughout the geographic area<sup>56,58</sup>. The test was repeated randomly 100 times, and the null hypothesis of ecological niche equivalence or similarity could be rejected if the observed niche values (D) were significantly lower than the overlap value from the null distribution ( $P \leq 0.05$ )<sup>57</sup>.

To assess niche dynamics, an environments was considered to indicate niche expansion if it is available in both current and future ranges but was only occupied in the future range<sup>56</sup>. Similarly, an environment indicated niche stability if occupied in both current and future ranges, while niche unfilling if it was used in the current range but available yet unexploited in the future range<sup>58</sup>. Values for expansion, stability, and unfilling ranging from 0 to 100% were deemed significant if greater than 10%. Niche expansion is regarded as the sole measure that accurately reflects shifts in a realized niche<sup>54,55</sup>.

## Results

### Evaluation of model accuracy

We evaluated the performance of 10 individual models (GAM, GBM, GLM, CTA, SRE, MARS, FDA, ANN, RF, and MaxEnt) using TSS, Kappa, and AUC as evaluation metrics (Table 3). Since the TSS values of SRE and ANN did not meet the threshold of greater than 0.75, they were not included in the construction of the ensemble models. Ultimately, we selected GAM, GBM, GLM, CTA, MARS, FDA, RF, and MaxEnt to construct the ensemble models. We found that the EMca version had the highest accuracy, with TSS and AUC values

greater than those of EMmean (Table 3). Therefore, we selected the EMca version for further visualization and analysis.

### Significance of environmental variables

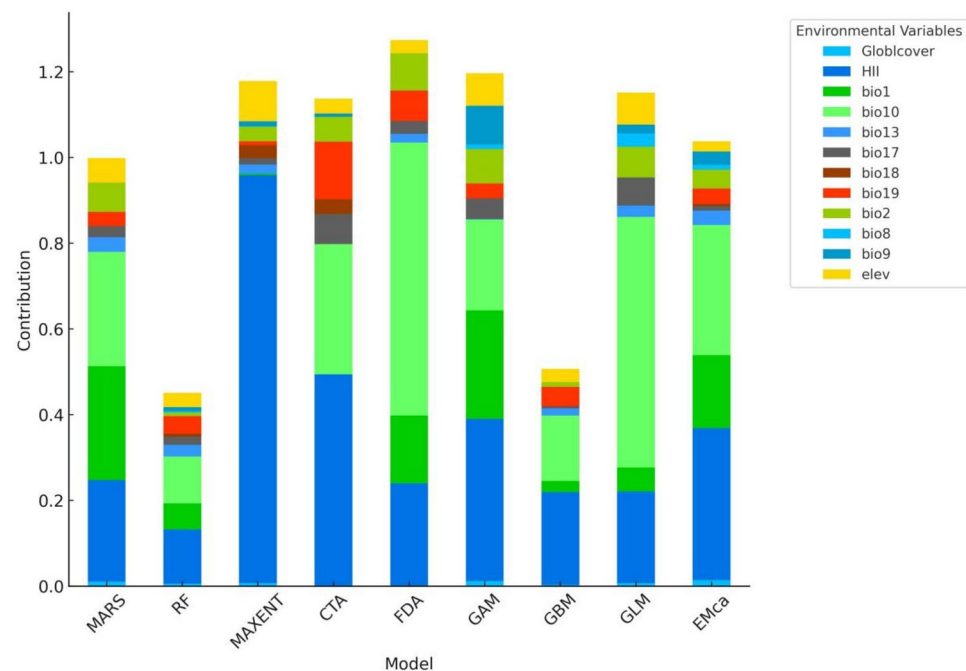
Eight single models were used to assess the contribution of environmental variables affecting the distribution of *A. coccinea*, and the results were shown in Fig. 4. The top contributing variables across different models varied slightly, but the most influential variables included the Human Impact Index (HII), mean annual temperature (bio1), mean temperature of the warmest quarter (bio10), and precipitation of the coldest quarter (bio19). Specifically, the ensemble model results (Fig. 3) confirmed that these four environmental variables were consistently the most influential across all models, indicating that two temperature variables, one precipitation variable, and one anthropogenic factor primarily drive the distribution of suitable habitats for *A. coccinea*. This highlights the central role of temperature and human influence in determining the species' suitable habitats.

### Ecological Niche analysis

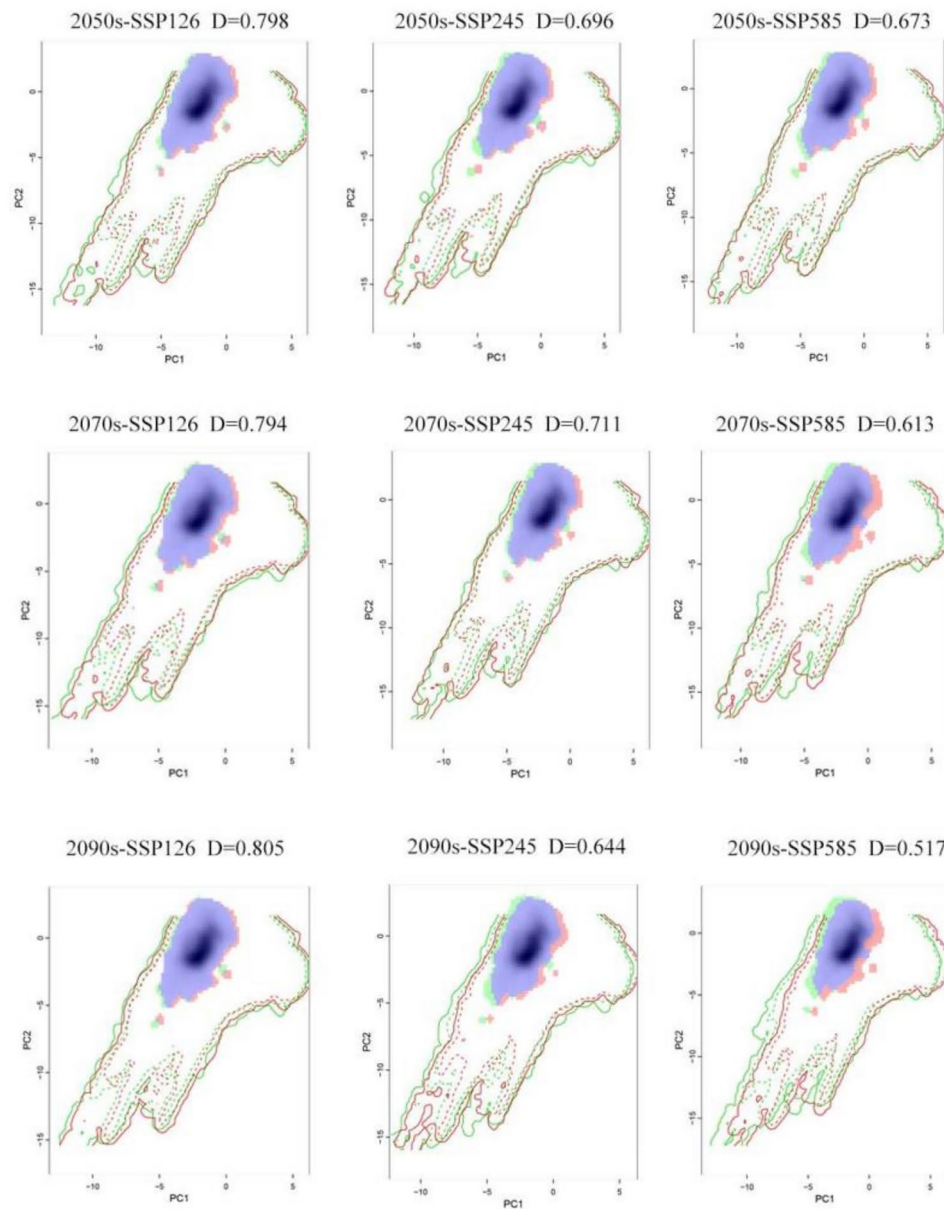
Niche analyses contrasting current and future climatic conditions revealed a moderate degree of similarity across all scenario comparisons, with Schoener's D values ranging from 0.518 for current vs SSP585-2090s to 0.805 for current vs SSP126-2050s (Fig. 4; Table 4). These Schoener's D values indicate moderate to high similarity between suitability distributions in different climatic scenarios. The pattern suggests a prospective shift in climatic suitability, with a potential reduction of *A. coccinea*'s current niche under future climate conditions. The results showed that the Schoener's D values for the SSP126 scenarios are all greater than the SSP245 scenarios, while the Schoener's D for the SSP245 scenarios are all greater than the SSP585 scenarios. In short, there was a decreasing trend in the Schoener's D values with an increasing radiation intensity over time. The results of the climatic background PCA have been presented in Table 4 and Figure S3. Across all PCA analyses, PC1 consistently captures the largest source of climatic variation, typically associated with temperature-related variables (e.g., bio1, bio10). PC2, on the other hand, reflects the second-largest variation in the climatic dataset, generally driven by precipitation variables (e.g., bio19). These principal components together provide a comprehensive summary of the key climatic factors influencing the environmental variation across different time periods and SSP scenarios. This result is consistent with the importance of environment variables in Biomod2.

Furthermore, we extended the exploration of niche equivalency and similarity. In pairwise analyses of climate ecological niches of species under current and future climate scenarios, the p-values for equivalence were less than 0.05, leading to the rejection of the null hypothesis of ecological niche equivalency and similarity in all pairwise comparisons (Fig. 4; Table 4). This suggested that *A. coccinea* may experience significant differences in its ecological niche characteristics under future climate scenarios (Fig. 5).

Red areas indicate expansion, green areas represent unfilling, and blue areas show overlap (Table 4). The values of ecological niche expansion and stability suggested that *A. coccinea* will experience minimal niche expansion (< 10%) in the future. However, as radiation intensity increases over time, the extent of ecological niche expansion and unfilling is expected to increase, while niche stability is likely to decrease.



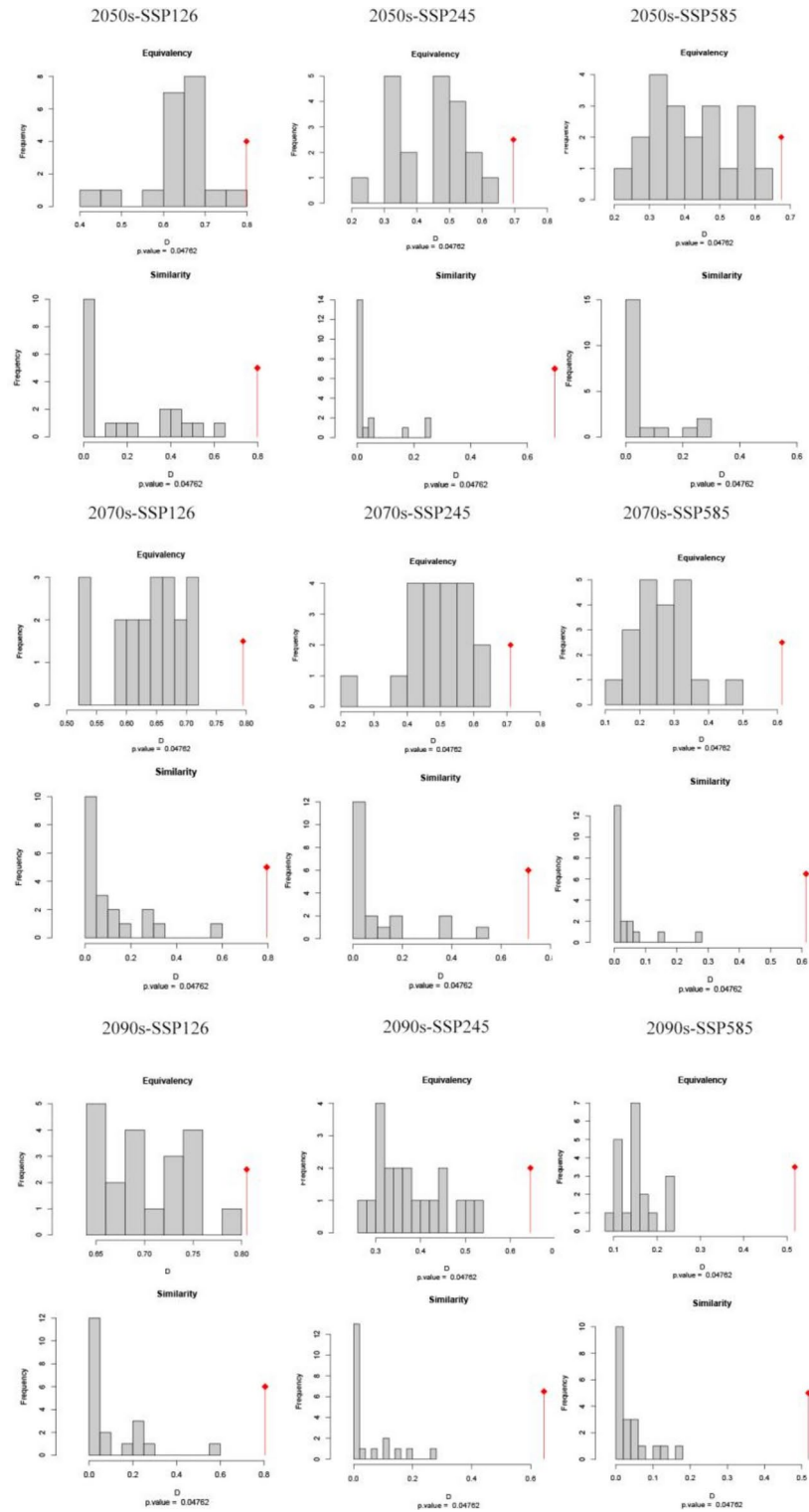
**Fig. 3.** Contribution values of environmental variables in single models and the ensemble model.



**Fig. 4.** Changes in the ecological niche of *A. coccinea* under different future climate scenarios compared to the current.

Niche comparison pairs	PC1 (%)	PC2 (%)	Niche overlap (D)	Niche expansion (%)	Niche stability (%)	Niche unfilling (%)
Current vs SSP126-2050s	38.08	23.21	0.799	0.008	0.992	0.004
Current vs SSP126-2070s	38.10	23.18	0.794	0.007	0.993	0.003
Current vs SSP126-2090s	38.01	23.32	0.805	0.006	0.994	0.003
Current vs SSP245-2050s	38.05	23.22	0.696	0.006	0.994	0.007
Current vs SSP245-2070s	37.91	23.18	0.711	0.009	0.991	0.007
Current vs SSP245-2090s	37.75	23.15	0.645	0.012	0.987	0.012
Current vs SSP585-2050s	37.78	23.20	0.673	0.01	0.99	0.008
Current vs SSP585-2070s	37.40	23.21	0.613	0.026	0.974	0.01
Current vs SSP585-2090s	37.11	23.01	0.518	0.037	0.963	0.022

**Table 4.** Niche comparisons and variation between the current and future projected distribution ranges of *A. coccinea*.

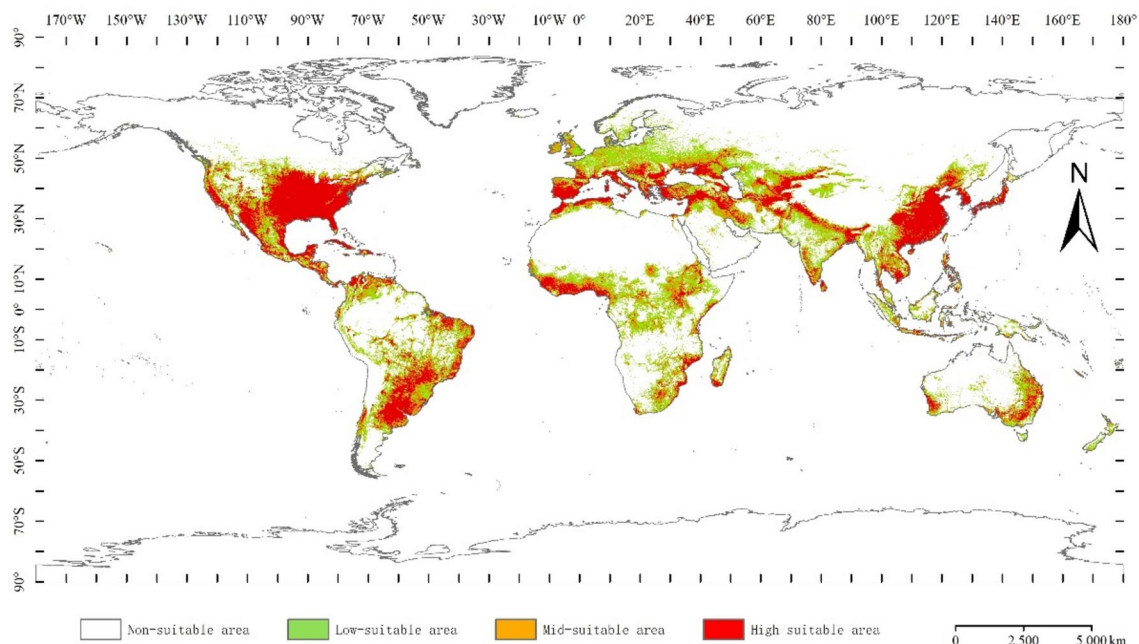


**Fig. 5.** The ecological niche equivalency and similarity of *A. coccinea* under different future climate scenarios compared to the current.

**Current potential global distribution of *A. coccinea***

We employed the ensemble model in Biomod2 to predict the potential global distribution of *A. coccinea* under current climate conditions (Fig. 6). Under current climatic conditions, the potential global geographic distribution of *A. coccinea* is concentrated in southern North America, northern and southeastern South America, southwestern Europe, the Middle East, central Africa, western Asia, Southeast Asia, etc. (150 °E–120 °W, 40 °S–60 °N). Specifically, the high suitable habitat area was  $1,759.12 \times 10^4$  km<sup>2</sup>, accounting for 11.81% of the global





**Fig. 6.** Potential global distribution of *A. coccinea* under current climate conditions.

land area, covering regions such as the United States, Mexico, Cuba, Puerto Rico, Jamaica, northern Colombia, northern Venezuela, Portugal, the eastern coast and south of Brazil, northeastern Argentina, Paraguay, Spain, Italy, Greece, Turkey, the southwestern corner of Russia, Iran, India, northern China, Cambodia, Vietnam, the Philippines, Korea, Japan, southeastern Australia, Guinea, Liberia, the southern coast of Nigeria, and other areas. North, southeastern China, Cambodia, Vietnam, Philippines, Korea, Japan, southeastern Australia, Guinea, Liberia, southern coast of Nigeria and other regions. The moderately suitable habitat area was  $101.76 \times 10^4$  km<sup>2</sup>, accounting for 8.1% of the global land area, mainly surrounding the highly suitable area. The low-suitable habitat area was  $1920.86 \times 10^4$  km<sup>2</sup>, accounting for 12.89% of the global land area, covering regions such as the northwestern United States, central Mexico, Peru, Bolivia, central Colombia, Venezuela, Fatima, Germany, Poland, Hungary, Rome, Ukraine, Turkey, Iran, Uzbekistan, Pakistan, central India, Myanmar, Indonesia, Cameroon, Central Africa, the Congo, the Sudan, South Africa, Zimbabwe, Mozambique, Madagascar and other regions.

#### Future potential global distribution of *A. coccinea*

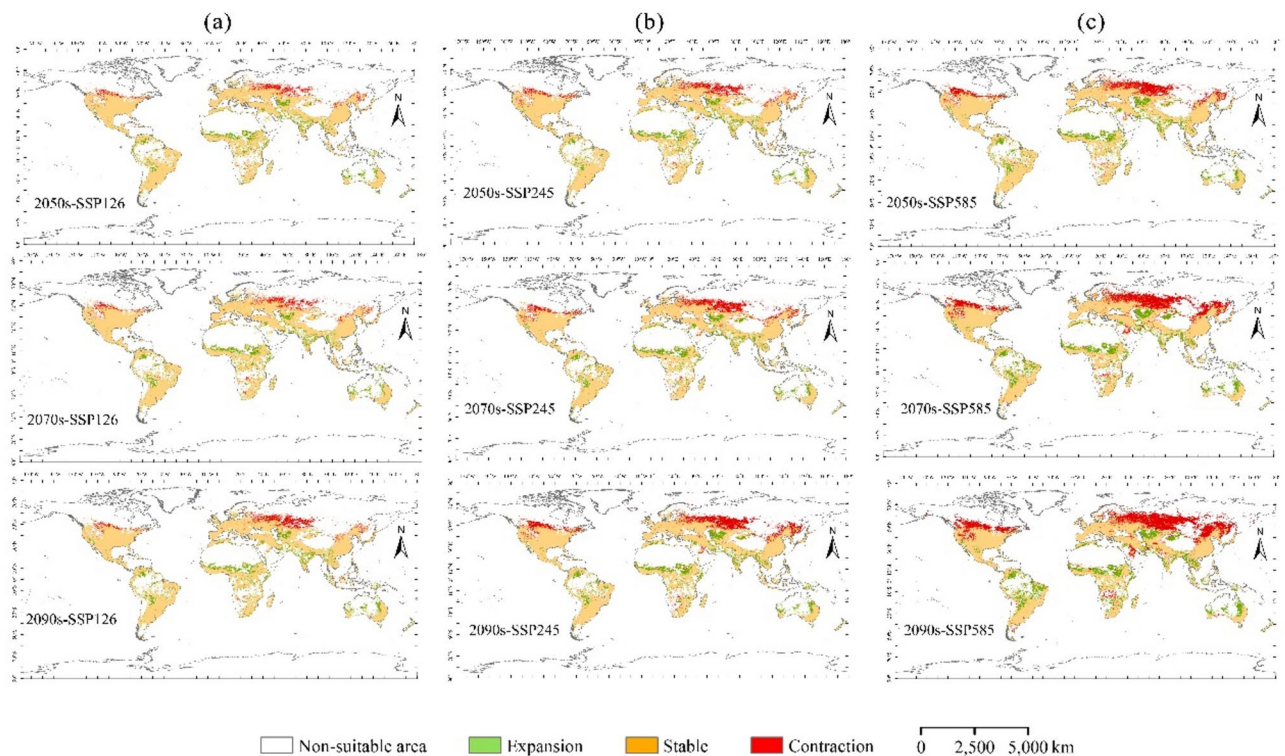
The potential geographic distribution and suitable area of *A. coccinea* under future climate conditions are presented in the supplemental materials (Figures S1 and S2, Table S1). The changes in the area of *A. coccinea* distribution under future climate change conditions compared to the current distribution are shown in Fig. 7.

Compared with the current conditions, mid-high suitable areas were expected to expand under future climate scenarios, with the most significant expansion observed under the SSP585 scenario in the 2090s (Figures S1, S2). While the distribution of suitable areas remains relatively stable in some regions, overall, significant geographical shifts are anticipated under future climate conditions. Except for SSP245 in 2090 and SSP585 in 2070 and 2090, habitat contraction exceeds expansion, and total suitable habitat area decreases under all other climate scenarios. Notable expansion were expected in regions such as northeastern Bolivia, eastern Colombia, central Brazil, Nigeria, South Sudan, Uzbekistan, central India, Myanmar, Thailand, northwestern China, and parts of Australia. The contractions areas of the suitable areas were mainly located in the southwestern Russia, northern Kazakhstan, southern Africa, northern China, and southern Canada.

## Discussion

### Accuracy of model predictions

Variations in the prediction process and parameter algorithms across individual models may lead to uncertainty in their prediction results<sup>9</sup>. Ensemble model constructed using the Biomod2 platform were applied to predict the potential habitat distribution of the invasive plant *A. coccinea*, effectively reducing the uncertainty and simulation bias with single models. To mitigate sampling bias, the occurrence records of *A. coccinea* were carefully screened. To avoid multicollinearity among environmental variables, Pearson correlation analysis and jackknife method were used to remove highly correlated and less importance factors. Nine climate factors, one terrain factor, one human disturbance factor, and one land type coverage factor were selected for the distribution models. The predicted values of AUC, TSS, and Kappa for the single models met the "excellent" standard, while the of AUC and TSS values for the ensemble model reached the standard of "excellent." This indicated that the



**Fig. 7.** Projected changes in potential global suitable habitats for *A. coccinea* under future climate scenarios compared to the current climate: (a) SSP126 for the 2050s, 2070s, and 2090s; (b) SSP245 for the 2050s, 2070s, and 2090s; (c) SSP585 for the 2050s, 2070s, and 2090s.

model predictions were accurate and reliable, and closely aligned with the species' actual distribution. Thus, these models can be utilized to analyze the global potential distribution of *A. coccinea*.

### Key environmental and anthropogenic factors influencing the global distribution of *A. coccinea*

The key environmental variables influencing the potential global distribution of *A. coccinea* included annual mean temperature (bio1), mean temperature of the warmest quarter (bio10), precipitation of the coldest quarter (bio19), and human impact index (HII). In summary, the potential global geographic distribution of *A. coccinea* was determined by the synergistic effects of three environmental variables: temperature, precipitation and anthropogenic impacts. In areas where *A. coccinea* has successfully invaded, favorable temperature and precipitation have facilitated its colonization and expansion. This has led to faster reproduction and greater adaptability in *A. coccinea*<sup>25,33,34</sup>. Research has shown that *A. coccinea* is photoblastic, requiring temperature above 15 °C and a soil burial depth of less than 3 cm for successful germination and seedling emergence<sup>29</sup>. Dormant *A. coccinea* seeds require at least 100 days of cold stratification, diurnal temperature fluctuations, and light for optimal germination<sup>59</sup>. Generally, *A. coccinea* thrives in warm environments, with temperatures above 28 °C favoring its growth<sup>32</sup>. Climate warming has increased *A. coccinea*'s environmental tolerance, expanding its invasive range. These studies support and validate our findings.

The coldest season precipitation (bio19) significantly influences the potential geographic distribution of *A. coccinea*. Precipitation plays a crucial role in determining the establishment and spread of invasive species, as it directly affects soil moisture levels and plant physiology<sup>51</sup>. For *A. coccinea*, adequate precipitation during colder months may promote germination and seedling survival, particularly in regions with moderate or seasonal droughts. Insufficient precipitation can limit the species' growth by reducing soil water availability, leading to lower reproductive success and slower population expansion<sup>60</sup>. Studies have shown that altered precipitation patterns, driven by climate change, have already begun reshaping the geographic distribution of invasive species globally, facilitating their spread into previously unsuitable areas<sup>11,61,62</sup>. Therefore, changes in precipitation patterns due to climate change could enhance the invasiveness of *A. coccinea* in regions with favorable conditions.

Anthropogenic influences have also partially shaped the potential geographic distribution of *A. coccinea*. Studies have shown that *A. coccinea* frequently occurs in rice fields, which are heavily impacted by human activities. Human influences have also facilitated multiple dispersal pathways of *A. coccinea*. The seeds of *A. coccinea* can be dispersed through various pathways, including agricultural trade, water flow, and attachment to mud or machinery tires used in cultivation<sup>22</sup>. The spread of *A. coccinea* is accelerated by human activities. Therefore, under suitable temperature, precipitation, and anthropogenic activity, *A. coccinea* will flourish.

### Changes in potential geographic distribution of *A. coccinea*

Our results showed that, under current climatic, the potential geographical distribution of *A. coccinea* is mainly in Southern North America, northern and southeastern South America, southwestern Europe, West Asia, and Southeast Asia. This was consistent with previous research<sup>32</sup>, indicating a strong agreement between the simulated potential geographic distribution of *A. coccinea* and its actual range under the current climatic scenarios. Research indicates that under future climate conditions, the potential areas of moderate to high suitability for *A. coccinea* are expected to expand. Furthermore, with ongoing climate change, particularly the rise in radiation intensity, the global invasion range of *A. coccinea* is expected to expand rapidly in moderate to high suitability zones. This suggests that different socioeconomic development pathways significantly impact the global spread of *A. coccinea*, with high fossil fuel consumption accelerating its spread<sup>63</sup>. Additionally, the Schoener's D values and niche analysis results indicate that as radiation intensity increases (e.g., in the SSP585 scenario), the climatic suitability of *A. coccinea*'s current niche gradually decreases. This reduction in suitability may drive the species to seek new habitats at higher latitudes where temperature and precipitation conditions are more favorable. Specifically, the declining trend in Schoener's D values suggests that *A. coccinea*'s current niche will become less suitable in the future, promoting a shift in its range to higher latitudes to find climates that match its tolerance thresholds.

### Ecological niche dynamics and adaptation of *A. coccinea*

Ecological niches are crucial for prediction invasive species, distribution. Invasive alien species adapt to new habitats in a variety of ways and expand their ecological niche space after colonisation, ultimately leading to differences between native and invasive ecological niches, such as thermal niche shifts<sup>64</sup>. For *A. coccinea*, the maximum ecological niche overlap (SSP126-2050s) was 0.805, indicating substantial similarity, while the minimal ecological niche overlap (SSP585-20900 s) decreased to 0.518, indicating greater differentiation in extreme future climate scenarios. This suggests that *A. coccinea* has broad ecological adaptability to various environments.

Despite overall niche stability for *A. coccinea* under future conditions, we observe increased niche expansion and unfilling as radiation intensity rose (e.g., SSP585), suggesting *A. coccinea* will exploit more diverse habitats and expand its range. As its current niche becomes less suitable, it is likely to migrate to higher latitudes in search of favorable conditions. Additionally, the PCA analysis showed significant shifts in the species' niche under future scenarios, with niche equivalency being rejected ( $p < 0.05$ ). This supports the potential for *A. coccinea* to expand its distribution as temperatures rise and precipitation patterns change. As the suitable areas expand, *A. coccinea* is likely to face competition with local species for resources and space. This competition could negatively impact local biodiversity, as invasive species often suppress or replace native species by occupying resources and altering habitats<sup>33,35</sup>. Therefore, as climate change intensifies, managing the expansion of *A. coccinea* will become a critical issue for ecological management.

### Targeted prevention and control strategies for *A. coccinea*

*A. coccinea* is a noxious weed that competes with rice in paddy fields and is spreading globally. Globalization and climate warming have promoted the invasion of alien species<sup>65,66</sup>. Managing *A. coccinea* is challenging due to climate change, with its global distribution influenced by temperature, precipitation, and human activities. The seeds can spread through water currents or agricultural machinery, such as rice harvesters<sup>34</sup>. Therefore, government should focus prevention and control efforts on regions where *A. coccinea* overlaps with key rice production areas, rather than only targeting highly suitable habitats for the weed. Tailored prevention strategies are crucial, especially in areas where rice production and *A. coccinea* overlap, as these regions face significant threats to food security.

Control measures should combine mechanical, chemical and biological measures. Mechanical techniques like early removal and tilling can eliminate the weed, while herbicides provide chemical control. Biological control through natural enemies like insects or pathogens can offer long-term suppression. Early and intensive control usually yields better outcomes<sup>62</sup>. Thus, agencies should conduct surveys in high-risk areas to assess the weed's impact and provide a scientific basis for implementing effective control measures. These efforts will improve global knowledge of invasive species management and reduce the impact on rice production.

### Existing deficiencies and future development directions

Our analysis of *A. coccinea*'s potential distribution is more comprehensive and accurate compared to previous studies. The key advantages are: (1) Using the latest species distribution data, which improves accuracy and geographic coverage; (2) Implementing a stricter environmental variable selection, considering factors like the human impact index (HII) and Globcover; (3) Using the Biomod2 platform to integrate multiple models, enhancing prediction reliability; (4) Expanding the study to a global scale, predicting future distributions across different climate scenarios; (5) Quantifying niche dynamics like expansion, unfilled areas, and stability, offering deeper insights into the species' ecological adaptability.

Despite efforts to improve model accuracy, species distribution is a complex result of biotic and abiotic interactions. Our study focused on climate, HII, and Globcover, but factors like species interactions, infrastructure development, and trade activities also influence invasive species spread, highlighting limitations in our model<sup>43</sup>. Future research should include a wider range of variables, especially species interactions, native biota, and socioeconomic factors, to better understand distribution patterns of *A. coccinea* and other invasive species under changing environmental conditions. Although our research offers valuable insights into the species' distribution, future studies should incorporate more comprehensive factors for deeper understanding and more effective management strategies.

## Conclusions

The habitats of *A. coccinea* are highly susceptible to climate change, resulting in shifts in suitable areas and alterations the species, ecological niches. Using the ensemble model constructed from the best-performing single models, we achieved high accuracy in predicting the potential global distributions of *A. coccinea*. Under current climatic conditions, the species is predominantly found in Southern North America, northern and south-eastern South America, south-western Europe, the Middle East, central Africa, western Asia, and south-eastern Asia. Future climate scenarios predict an expansion of mid-to-high habitability areas for *A. coccinea*.

While the overall ecological niche of *A. coccinea* remains stable, minor shifts are expected under future conditions. Key environmental drivers—temperature, precipitation and human impact index (HII) -played a key role in facilitating its invasion and expansion globally. Given these findings, organizations efforts should focus on preventing the spread of *A. coccinea* in regions where its potential distribution overlaps with key rice production areas, rather than solely targeting the species' highly suitable habitats. Strengthening prevention and control measures in such regions is crucial, as *A. coccinea* poses a threat to food security. Taking proactive measures will not only safeguard agricultural production but also contribute to achieving the United Nations Sustainable Development Goals, particularly those related to food security and environmental sustainability.

## Data availability

The datasets generated and/or analysed during the current study are not publicly available due (our experimental team's policy) but are available from the corresponding author on reasonable request.

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## Author contributions

YanJing Zhang wrote the main manuscript text; Jie Hu and ChenBin Wang provided Formal analysis, investigation and Writing–review & editing; YaQiong Wan & Mulan Ji prepared Writing – review & editing; FangZhou Ma and YiQing Lu provided Funding acquisition, Methodology and Writing–review & editing. All authors reviewed the manuscript.

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## Declarations

### Competing interests

The authors declare no competing interests.

### Additional information

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