SUITE HABITAT AREA ANALYSIS AND NICHE ASSESSMENT OF THE INVASIVE EMERALD ASH BORER (AGRILUS PLANIPENNIS) IN NATIVE AND INVASIVE RANGES


1College of Economic Management, Xinjiang Agricultural University, Urumqi 830052, China
2Forestry and Prairie Bureau of Xinjiang Uyghur Autonomous Region, Urumqi 830011, China
3Institute of Plant Protection, Xinjiang Academy of Agricultural Sciences, Urumqi 830091, China
4Key Laboratory of Nation Forestry and Grassland Administration on Northeast Area Forest and Grass Dangerous Pest Management and Control, Fushun 113122, China
5College of Forestry and Landscape Architecture, Xinjiang Agricultural University, Urumqi 830052, China
6Center for Forestry and Grassland Development and Guarantee, Huludao 125300, China
7Urumqi Botanical Garden, Urumqi 830013, China
8Institute of Forest Ecology, Xinjiang Academy of Forestry, Urumqi 830063, China

*Corresponding authors
e-mail: zhangluyou8183@126.com, lijiangui001@163.com
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Abstract. The emerald ash borer, Agrilus planipennis, is a bark beetle native to Asia that has caused significant forest resource losses in North America since its introduction in the early 21st century. In this study, we used the niche assessment R package “ecospat” and the integrated model “biomod2” to compare 19 bioclimatic variables for A. planipennis in its native range (China) and part of its invasive range (the United States). Future data predicted for the 2050s and 2070s were utilized to forecast potential habitat regions for A. planipennis in China and the United States under two representative climate scenarios (SSP126 and SSP585). We revealed low niche overlap between A. planipennis populations in these ranges, with significant differences in bioclimatic variables. This indicates that A. planipennis has adapted to a range of climatic conditions in the United States. In upcoming times, the suitable habitat region for A. planipennis is expected to significantly decrease in the United States but considerably increase in China. Our study provides insights that can be used to prevent further A. planipennis spread, for economic loss assessment of and developing management strategies against A. planipennis, and as a methodological reference for niche analysis of other invasive species.

Keywords: Agrilus planipennis, niche analysis, potential distribution, biomod2, biological invasion

Introduction

Invasive species have become a major issue in global agricultural, forestry, and fisheries production (Cuthbert et al., 2022). Many species that are not highly detrimental in their native habitats have caused significant economic and ecological losses upon invading new areas (Olden et al., 2006; Wen et al., 2024). It can be difficult to prevent the spread of invasive species because there is limited knowledge of when, where, and which species will invade. It is thought that species distribution is the result of
interactions among multiple environmental factors, and all species on Earth have finite geographic ranges beyond which they do not occur (Bates and Bertelsmeier, 2021). Species can persist within a certain suitable range, and this range, along with the species’ adaptive potential, constitutes its niche within the environment (Thuiller et al., 2015). However, accurately assessing the niche of invasive species is challenging.

The emerald ash borer (*Agrilus planipennis*) is a globally recognized invasive pest and is responsible for one of the costliest bioinvasions in North America (Aukema et al., 2011; McCullough, 2020). *A. planipennis* is a bark beetle that originates from East Asia, where it causes only minimal damage and leads to the demise of only a few Manchurian ash (*Fraxinus mandshurica* Rupr.) and Chinese ash (*F. chinensis* Roxb.) (Klooster et al., 2014). However, since its introduction to the United States in 2002, it has caused extensive tree mortality throughout North America (Herms and McCullough, 2014). In 2003, this beetle also invaded the European parts of Russia and spread westward into Ukraine, posing a significant threat to the safety of European ash (*F. excelsior* L.) (Peterson et al., 2023). Additionally, *A. planipennis* was reported to expand its range at rates of 2.5 to 80 km per year in North America and 13 to 41 km per year in European Russia (Valenta et al., 2017). Because of the current rate of expansion, analyzing the potential future spread areas of *A. planipennis* and implementing proactive prevention measures are crucial for safeguarding the health of ash trees in North America and Europe.

Species distribution modeling (SDM) is a primary method based on niche theory that uses known species population distribution points and associated climate factors to deduce the possible effects of climate change on species range (Schipper et al., 2014). One key assumption of applying niche models is that a species’ niche is conserved over time and space (known as “niche conservatism”); therefore, the species occupies similar environmental conditions in new spatial or temporal contexts (Pearman et al., 2008). However, there is an ongoing debate in the scientific community regarding the niche conservatism hypothesis (Sax et al., 2013; Guisan et al., 2014; Sexton et al., 2017) that challenges the notion that a species’ niche is truly conserved over time and space. However, biological invasions offer a valuable opportunity to investigate the niche conservatism hypothesis on a global scale. Recently, integrated analyses of invasive species showed that a conserved niche both improves the credibility of model predictions for the distribution of invasive species in new environments and supports the application of niche models for predicting species responses to climate change (Liu et al., 2020). Therefore, niche conservatism of an invasive species can help to improve our ability to forecast the range of that species in unfamiliar habitats and elucidate their potential responses to climate change.

Earlier research has shown that large ecological scales, species ranges are most affected by environmental factors, especially alterations in temperature and rainfall, can influence the reproductive potential, growth, and competitive prowess of invasive organisms (Thomas, 2010; La Marca et al., 2019). These changes can subsequently alter the susceptibility of ecosystems to invasive organisms, thereby indirectly impacting the geographic distribution and level of harm caused by invasive species (Tang et al., 2021). Therefore, it is essential to elucidate the implications of climate change on invasive species, explore the spatiotemporal coupling between climate change and the mechanisms of invasive species spread, and identify high-risk areas for invasive species under changing climatic conditions. This is crucial for developing effective prevention and control strategies (Mainka and Howard, 2010; Bertelsmeier et al., 2013; Cai et al., 2023).
We investigated *A. planipennis* in this study. We employed the latest ensemble modeling approach, biomod2, and the niche assessment R package, ecospat, to analyze the suitable habitat areas and niche shift characteristics of *A. planipennis* in its native range (China) and in a part of its invasive range (the United States). We compared the variations in bioclimatic factors associated with *A. planipennis* across different regions and assessed the degree of niche overlap. Additionally, we generated current and future potential distribution maps of *A. planipennis*. These findings will contribute to early *A. planipennis* prevention efforts in relevant regions and provide valuable insights and references for future research on invasive species ecology.

**Materials and methods**

**Occurrence data of *A. planipennis***

We gathered data on occurrences for *A. planipennis* in the continental United States and China. We sourced the occurrence data for the United States from the Global Biodiversity Information Facility (GBIF) database, specifically the GBIF Occurrence Download (https://doi.org/10.15468/dl.vd6vc2, 11 September 2023). The presence data for China were gathered from the GBIF database, published literature, and the third National Forest Pest Survey of China. Because of the lack of latitude and longitude coordinates for some data, we employed Google Earth to extract the coordinates matching the named locations (Li et al., 2011).

Using these methods, we collected a total of 2,027 occurrence records for *A. planipennis*, with 1,902 records from the United States and 125 records from China. The substantial disparity in the number of records is attributed to the few recorded reports on the distribution of *A. planipennis* in East Asia, where it has a relatively minor impact (Herms and McCullough, 2014). We loaded the data into ArcGIS 10.4.1 (Esri, Redlands, California) and procured the administrative boundary maps for China and the United States from the Database of Global Administrative Areas (http://www.gadm.org/country). Using this information, we generated occurrence maps that illustrated the distribution of *A. planipennis* in China and the continental United States (Fig. 1).

**Selection and juxtaposition of climate variables**

We retrieved climatic variables from the WorldClim database (http://www.worldclim.org) (Fick and Hijmans, 2017). This dataset comprised 19 bioclimatic variables at a 30 arc-second spatial resolution, roughly equal to 1 km². For upcoming climate projections, we opted for two representative models from CMIP6:SSP126, which corresponds to a radiative forcing of 2.6 W/m² by 2100, and SSP585, which corresponds to a radiative forcing of 8.5 W/m² by 2100 (Eyring et al., 2016). These scenarios represent low and high radiative forcing levels, respectively, and indicate different levels of future climate change.

To avoid multicollinearity issues and the subsequent overfitting of models, we used ArcGIS to extract the Bio1 to Bio19 values for *A. planipennis* and calculated the Pearson correlation coefficient for each climate variable (Wang et al., 2023). If two variables had a Pearson correlation coefficient greater than 0.8, we excluded one of the correlated variables to maintain the precision of the model’s simulation (Wen et al., 2022). When removing variables because of excessively high correlation, we carefully
considered the contribution and ecological significance of the variables in the default model. Ultimately, we selected seven climate variables for China and 10 climate variables for the United States (Table 1). These selected climate variables were used for niche comparison and the construction and analysis of integrated models. Furthermore, we performed a unique two-way analysis of variance (ANOVA) with SPSS v27.0.1 to assess the average values of the 19 climatic variables. Additionally, we applied a bootstrapping method to ascertain if variations in sample size influenced univariate comparisons (Lee and Rodgers, 1998).

Figure 1. Distribution of records of A. planipennis. (a) Continental United States; (b) China
Table 1. Climate variables selected in this study

<table>
<thead>
<tr>
<th>Type</th>
<th>Variables</th>
<th>Description</th>
<th>UNITS</th>
<th>CHN</th>
<th>USA</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bioclimatic</td>
<td>Bio1</td>
<td>Annual mean temperature</td>
<td>℃</td>
<td>Y</td>
<td>Y</td>
</tr>
<tr>
<td></td>
<td>Bio2</td>
<td>Mean diurnal range</td>
<td>℃</td>
<td>Y</td>
<td>Y</td>
</tr>
<tr>
<td></td>
<td>Bio4</td>
<td>Temperature seasonality</td>
<td>℃</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Bio5</td>
<td>Max temperature</td>
<td>℃</td>
<td>Y</td>
<td>Y</td>
</tr>
<tr>
<td></td>
<td>Bio6</td>
<td>Min temperature of coldest month</td>
<td>℃</td>
<td>Y</td>
<td>Y</td>
</tr>
<tr>
<td></td>
<td>Bio8</td>
<td>Mean temperature of wettest quarter</td>
<td>℃</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Bio9</td>
<td>Mean temperature of driest quarter</td>
<td>℃</td>
<td>Y</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Bio12</td>
<td>Annual precipitation</td>
<td>mm</td>
<td>Y</td>
<td>Y</td>
</tr>
<tr>
<td></td>
<td>Bio13</td>
<td>Precipitation of wettest month</td>
<td>mm</td>
<td></td>
<td>Y</td>
</tr>
<tr>
<td></td>
<td>Bio15</td>
<td>Precipitation seasonality</td>
<td>-</td>
<td>Y</td>
<td>Y</td>
</tr>
<tr>
<td></td>
<td>Bio18</td>
<td>Precipitation of warmest quarter</td>
<td>mm</td>
<td>Y</td>
<td></td>
</tr>
</tbody>
</table>

Y indicates that the variable was chosen to predict suitable areas in the United States and China

We randomly selected data on invasive species equal to the count of the original distribution points, computed the average and variance for every variable, and carried out this method 1000 times. As a result, we obtained a 95% confidence interval for each climatic variable ($\alpha = 0.05$). This study aimed to evaluate the climatic similarities and disparities between the native and invaded territories.

**Bioclimatic niche shift**

To compare the differences in the seven selected climate variables between the native and invaded ranges of *A. planipennis*, we chose a reference niche in China, where the species is native. First, we used the Wallace program in R to establish a 50-km buffer zone around each distribution point in China and the United States (Crego et al., 2022). These buffer zones were combined to create an overall buffer zone that encompassed all distribution points. From this combined buffer zone, we randomly selected 10,000 points as background data. Second, to separate, quantify, and compare the climatic and spatial environmental conditions within the study areas, we used ArcGIS to extract the climate data that corresponded to each background point. Next, we employed the “ecospat” R package to create a kernel density distribution map based on the dispersion rate of *A. planipennis* and conducted a PCA-env analysis (Cruz et al., 2023). Finally, we analyzed the niche shift of *A. planipennis* by examining the niche overlap index (D), niche equivalence, and niche similarity (Broennimann et al., 2012).

The niche overlap index (D) indicates the extent of shared ecological space between populations of a species across two areas. Its values can range from 0 to 1, where a higher value suggests greater overlap. To test for niche equivalence, we collected all distribution points and randomly selected a new set of distribution points that were equal in number to the original origin and invaded points in each region. Then, we calculated the value of D (Vaissi and Rezaei, 2023).

Niche similarity compares the observed niche overlap within each region to the overlap between observed small habitats in one region and randomly selected small habitats in the other region (Suárez-Mota et al., 2015). Niche equivalence and similarity
tests were conducted 100 times at random, and the mean niche occupancy profile was deduced using individual bioclimatic factors (Evans et al., 2009). Chosen variables such as Bio1, Bio2, Bio4, Bio5, Bio6, Bio12, and Bio15 were utilized to encapsulate the yearly conditions of the species’ environment.

**Suitable habitats of A. planipennis in China and the United States**

To create a suitable habitat area model for *A. planipennis*, biomod2 was used. The distribution data of *A. planipennis* were divided into 70% for modeling and 30% for model validation. The ensemble models with a TSS value greater than or equal to 0.7 were obtained through integration using the weighted averaging method (Cheng et al., 2023). The above steps were achieved using the BIOMOD_tuning-optimized model parameters. A 0/1 cutoff was obtained from the model results. Areas with values below the cutoff were considered nonsuitable habitat areas, and values exceeding the threshold were segmented into three equal portions, denoting areas of low, medium, and high suitability (Gao et al., 2023).

To assess the changes in the niche area over time, the “Distribution change between binary SDMs” tool in the SDM Tools plugin in ArcGIS was used. Additionally, the BIOMOD_RangeSize function in biomod2 was employed to calculate the spatial pattern changes in the suitable habitat area of *A. planipennis* under future climate change scenarios (Zhao et al., 2021). Finally, the matrix of habitat changes was loaded into ArcGIS to visualize the spatial pattern changes in the suitable habitat area of *A. planipennis*.

**Results**

**Contribution rate of variables**

The chief environmental determinants affecting *A. planipennis* distribution in China included the annual average temperature (Bio1), minimum temperature of coldest month (Bio6), mean diurnal range (Bio2), and temperature seasonality (Bio4). These four environmental factors together accounted for 91.4% of the relative contribution to the predictive factors (Table 2).

**Table 2. Contribution rate of bioclimatic variables in prediction of current suitable areas**

<table>
<thead>
<tr>
<th>Variable</th>
<th>Contribution rate of China (%)</th>
<th>Variable</th>
<th>Contribution rate of USA (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bio1</td>
<td>33.6</td>
<td>Bio1</td>
<td>9.4</td>
</tr>
<tr>
<td>Bio2</td>
<td>16.5</td>
<td>Bio2</td>
<td>18.9</td>
</tr>
<tr>
<td>Bio4</td>
<td>13.9</td>
<td>Bio5</td>
<td>2.9</td>
</tr>
<tr>
<td>Bio5</td>
<td>1.9</td>
<td>Bio6</td>
<td>2.5</td>
</tr>
<tr>
<td>Bio6</td>
<td>27.4</td>
<td>Bio8</td>
<td>0.1</td>
</tr>
<tr>
<td>Bio12</td>
<td>5.5</td>
<td>Bio9</td>
<td>1.9</td>
</tr>
<tr>
<td>Bio15</td>
<td>1.3</td>
<td>Bio12</td>
<td>17.8</td>
</tr>
<tr>
<td>-</td>
<td>-</td>
<td>Bio13</td>
<td>3.5</td>
</tr>
<tr>
<td>-</td>
<td>-</td>
<td>Bio15</td>
<td>34.0</td>
</tr>
<tr>
<td>-</td>
<td>-</td>
<td>Bio18</td>
<td>8.9</td>
</tr>
</tbody>
</table>
In the United States, the main factors that influenced *A. planipennis* distribution were precipitation seasonality (Bio15), mean diurnal range (Bio2), annual precipitation (Bio12), and annual mean temperature (Bio1). These elements constituted more than 80% of the relative significance in the prediction factors. It is worth noting that Bio1 and Bio2 influenced the *A. planipennis* distribution in both China and the United States.

**Direct comparison of environmental variables**

There were significant differences (P < 0.001) in all environmental factors between the *A. planipennis* distribution areas in China and the United States (Fig. 2). In the United States distribution area, the maximum temperature of the driest quarter (Bio5) was higher than that in China (ΔT = 5.50°C). Consequently, *A. planipennis* experiences significantly higher summer temperatures in its invaded range in the United States than in its native environment; this suggests that *A. planipennis* may have adapted to the warmer conditions found in the eastern United States. Moreover, the lowest temperature (Bio6) in the invasion area was also significantly higher than that in the native range (ΔT = 6.74°C). This demonstrates the potential of *A. planipennis* to spread to colder regions. In terms of humidity, the precipitation indicators in the United States distribution area were generally lower than those in the native range. However, there were only slight increases in three indicators related to dry season rainfall (Bio14, Bio17, Bio19) compared with China. This indicates that *A. planipennis* does not require high rainfall in its invaded areas.

This section may be divided by subheadings. It should provide a concise and precise description of the experimental results, their interpretation, as well as the experimental conclusions that can be drawn.

**Climatic niche overlap, equivalency, and similarity**

The results of the climate niche analysis for *A. planipennis* are presented in Figures 3 and 4. Principal component analysis (PCA) revealed that the first two principal components accounted for 74.74% of the variation in the selected climatic variables (PC1 = 50.07%, PC2 = 24.67%) (Fig. 3c). The first axis (PC1, 50.07%) was negatively correlated with climatic variation, whereas the second axis (PC2, 24.67%) was positively correlated with climatic variation.

Based on these two principal components, *A. planipennis* exhibited overlap in the majority of the background habitats across both China and the United States (Fig. 3). The ecological niche overlap between its native and invaded territories was 15.76%, and the trend in niche movement varied from that of the overall environment (Fig. 3d). Furthermore, the invasive range (the United States) exhibited many unfilled areas compared with the niche in China.

The pairwise comparisons of niche equivalence and niche similarity between the United States and China did not support the fundamental assumption of niche equivalence, and niche similarity tests could not be conducted (P > 0.05). These niche equivalence and niche similarity results indicate significant changes in the *A. planipennis* niche during invasion (Fig. 3a and b).

Notably, there was a substantial shift in the climate niche (Fig. 3d). The bioclimatic variable analysis and resulting predicted niche occupancy curve revealed substantial differences in the climate requirements of *A. planipennis* between its native and invaded ranges (Fig. 4).
Figure 2. Comparison of A. planipennis environmental variables between native (China) and invasive ranges (the United States). In the figure, Bio1 represents annual mean temperature, Bio2 represents mean diurnal range, Bio3 represents isothermality, Bio4 represents temperature seasonality, Bio5 represents max temperature, Bio6 represents min temperature of coldest month, Bio7 represents temperature annual range, Bio8 represents mean temperature of wettest quarter, Bio9 represents mean temperature of driest quarter, Bio10 represents mean temperature of warmest quarter, Bio11 represents mean temperature of coldest quarter, Bio12 represents annual precipitation, Bio13 represents precipitation of wettest month, Bio14 represents precipitation of driest month, Bio15 represents precipitation seasonality, Bio16 represents precipitation of wettest quarter, Bio17 represents precipitation of driest quarter, Bio18 represents precipitation of warmest quarter, and Bio19 represents precipitation of coldest quarter.

Current distribution of suitable habitat areas for A. planipennis

Under current climate conditions, the highly suitable area for A. planipennis in the United States covered 25.58 × 104 km², which accounted for 3.06% of the total land area. The moderately suitable area covered 96.36 × 104 km², which represented 11.52%
of the total land area. The slightly suitable area was 59.66×104 km², which accounted for 7.13% of the total land area. The suitable habitat for *A. planipennis* was primarily located in the northeastern United States, from New Hampshire to Virginia. Additionally, highly and moderately suitable areas were identified in Ohio, Michigan, Indiana, and Illinois.

![Ecological niche of A. planipennis](image)

**Figure 3.** Ecological niche of *A. planipennis* in its original range (China) compared to its invasive range (the United States) based on climatic factors. (a) and (b) Graphs showcase the results of the niche equivalence and similarity tests for both regions, respectively. (c) Highlights the contribution of individual variables to each primary component axis. (d) Displays the overlap between the niches in the native and invaded territories. Blue points to areas of niche overlap, green to unfilled ecological spaces, and red signifies areas of expansion. The red arrow denotes Schoener’s D estimate. The continuous and dotted contour lines represent 100% and 50% of the total accessible environmental space, respectively.

In China, the total suitable habitat area for *A. planipennis* was 120.19×104 km². The proportions of highly and moderately suitable areas were 27.11% and 28.65%, respectively. The main suitable habitat areas were distributed in Northeastern and North China regions, with a small amount in Xinjiang (Fig. 5).
Future changes in suitable habitat area

The changes in suitable habitat areas for *A. planipennis* in the United States and China under two future climate scenarios (SSP126 and SSP585) are depicted in Figures 6 and 7. Compared with the current suitable habitat areas, we predict there will be a clear northward shift in the highly suitable areas for *A. planipennis* in both its native and invaded ranges in the future. In the United States, both climate scenarios were predicted to lead to reduced suitable habitat area for *A. planipennis*. This is particularly the case for SSP585, which predicted significantly decreased distribution of highly suitable areas. Conversely, the forecasted trend in its original habitat in China was entirely distinct; future climate change is predicted to cause substantial increase in the highly suitable areas for *A. planipennis*, with expansion mainly predicted to occur in Heilongjiang Province in northeastern China.

![Figure 4](image_url)

*Figure 4. Forecasted ecological niche patterns. The blue area represents the predicted niche occupancy in the native range (China), whereas the pink area represents the predicted niche occupancy in the invasive range (the United States)*

The highest radiative forcing scenario, SSP585, had a pronounced effect on reducing the suitable habitat area for *A. planipennis* in the invasive range. In the United States,
the predicted moderate and highly suitable areas in the 2050s and 2070s were significantly smaller than those of the lowest radiative forcing scenario, SSP126. In China, the native range, the predictions differed except for SSP126 in the 2070s; the moderate and highly suitable areas under SSP585 exceeded those of SSP126 (Fig. 8).

Figure 5. Current suitable distribution range of A. planipennis. (a) Continental United States; (b) China
Figure 6. Predicted A. planipennis distribution under different climate scenarios in the continental United States

Figure 7. Predicted A. planipennis distribution under different climate scenarios in China
Figure 8. Variations in areas apt for A. planipennis in China and the continental U.S. based on distinct climate models. (a) Areas in China with high suitability; (b) Areas in China with moderate suitability; (c) Highly suitable zones in the U.S.; (d) U.S. areas with medium suitability

Discussion

Currently, the distribution range of A. planipennis in both China and the United States is primarily located between latitudes 32° and 47°, and the regions share similar temperature and humidity conditions. Based on existing biological research and observational records (Jones et al., 2020; Orlova-Bienkowskaja andBienkowski, 2020), we believe that temperature is likely the primary climatic condition influencing A. planipennis spread. To assess the potential invasion of A. planipennis in the future, the similarity of temperature conditions between northeastern China and the eastern United States will be crucial for determining invasion risk in different regions. Although it is not surprising that the environments in China and the eastern United States are similar, direct comparison between the two countries revealed that there were significant differences in the suitable bioclimatic variable ranges (excluding the mean diurnal range, Bio2) during A. planipennis invasion. In addition to the expected increase in the adaptability of globally invasive insects to the environment (MacFarlane and Meyer, 2005; Tang et al., 2021), we speculate that bioclimatic variables may also be related to the different species of host trees in China and the United States (Knight et al., 2013).

In addition to temperature, annual precipitation (Bio12) and precipitation seasonality (Bio15) are also common factors that influence suitable areas across China and the United States both. The difference in annual precipitation between the two countries was not significant, but the seasonal precipitation is influenced by monsoons. China
experiences higher summer precipitation, whereas the eastern United States receives more rainfall in winter and spring. The peak emergence period of *A. planipennis* in the United States is concentrated from late June to July (Poland et al., 2011; Herms and McCullough, 2014), which coincides with the summer season in the United States. The relatively lower precipitation during this period may be unfavorable for nutrient replenishment and reproduction of *A. planipennis*.

The niche outlines the set of conditions essential for a species’ survival (Lambea-Camblor et al., 2023), encompassing various environmental elements (such as temperature, humidity, and resource availability) and the species’ adaptability to the environment (Rodríguez-Merino et al., 2019; Bernery et al., 2022). The niche is crucial in elucidating ecological variations within a species and its ability to adapt to diverse areas and habitats. Previous studies found that species often expand or modify their niches when invading new areas (Simard et al., 2009; Pyron et al., 2015).

Our study revealed significant differences in the *A. planipennis* niche space between its native and invaded ranges. The niche overlap results indicated low overlap between the occurrence areas of *A. planipennis* in the United States and China; this indicates that the *A. planipennis* niche has changed under adaptation to the new environmental conditions in the invasive range. Niche equivalence analysis showed that the environmental niche of *A. planipennis* was not consistent under the climatic conditions of China and the United States. Moreover, niche similarity analysis also revealed that there was not significant climate niche conservatism between the occurrence areas of *A. planipennis* in China and the United States. These results indicate that the *A. planipennis* niches in China and the United States are similar but not identical. For many species, niche changes often correspond to changes in geographic space (Breiner et al., 2017). This may be why there were significant differences in *A. planipennis* niches between different regions.

Compared with a previous study that used Maxent and GARP (Sobek-Swant et al., 2012), our integrated model predicted a smaller current suitable habitat area for *A. planipennis*, but the regional locations were generally consistent. This further supported the reliability of our predictions. Currently, the highly suitable areas for *A. planipennis* in the United States are primarily located in the eastern coastal regions of Pennsylvania and Virginia, which is highly consistent with the current extent of *A. planipennis* damage in the United States (Lewis and Turcotte, 2015; Gould et al., 2022).

In the future, we predict that there will be distinct trends in the suitable habitat areas of *A. planipennis* between its native and invaded ranges. We predict that the invaded range will show a drastic reduction in suitable habitat area, whereas the native range will experience a substantial increase in suitable habitat area. This overall pattern aligns with the expected northward shift in species distribution due to future climate change (Lin et al., 2020). However, it is important to note that the two scenarios we simulated are highly specific carbon emission scenarios. Further observation is needed to determine whether the predicted decline in the suitable habitat area for *A. planipennis* in North America will occur as projected 50 years from now.

Although we employed a more sophisticated ensemble model and ecospat analysis to assess the suitable habitat area and niche of *A. planipennis*, similar to all modeling studies, there are some challenges that could not be avoided but need to be addressed. First, the availability of comprehensive species distribution points is crucial for accurate modeling. Despite the current existence of global databases such as GBIF, invasive species such as *A. planipennis* often receive little attention in their native range because
they cause minimal harm. This poses significant challenges in obtaining important information from the native range. Furthermore, the processes of invasions and species migrations are multifaceted and dynamic. Factors like natural catastrophes, human actions, and competition both within and between species play pivotal roles in determining species distributions. This study only included environmental factors, which may have limited the predictive accuracy by not accounting for these additional factors.

Conclusion

In this study, we used ecospat and biomod2 to analyze the niche differences of A. planipennis, the most dangerous invasive species living in North American forests, in its native range (China) and an invaded range (the United States) to predict the current and future distribution of its suitable habitat areas. The strikingly comparable annual average temperature and daily temperature range in both China and the United States are important factors that supported the successful invasion of A. planipennis. The notable disparities in other bioclimatic factors, coupled with the minimal niche overlap between China and the United States suggest that A. planipennis may have the ability to rapidly adapt to new environments during invasion. Increasing solar radiation in the future is predicted to reduce the A. planipennis distribution in the invaded range but increase its suitable habitat area in the native range. The highly suitable habitat area is predicted to shift northward and potentially lead to A. planipennis invasion at higher latitudes, such as Canada and the Russian Far East. Our study helps elucidate the patterns of spread and dispersal of invasive species and provides valuable insights for economic loss assessment and management policies of A. planipennis in relevant regions.

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