THE CHANGES AND INFLUENCING FACTORS OF CURRENT AND FUTURE POTENTIAL DISTRIBUTION OF *MATSUCOCCUS MATSUMURAE* (HEMIPTERA: MARGARODIDAE) IN CHINA

SHI, M. J.[1] – GAO, X.[1] – DAI, L. L.[2] – CHEN, M. J.[3] – QIU, H.[3] – ZHAO, M. Z.[1*]

[1]*Key Laboratory of Vector Biology and Pathogen Control of Zhejiang Province, College of Life Science, Huzhou University, Huzhou, Zhejiang 313000, China*

[2]*Co-Innovation Center for Sustainable Forestry in Southern China, College of Forestry, Nanjing Forestry University, Nanjing 210000, Jiangsu, China*

[3]*Huzhou Ecological Forestry Protection Research Center, Huzhou, Zhejiang 313000, China*

**Corresponding author*
e-mail: 02864@zjhu.edu.cn

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Abstract. *Matsucoccus matsumurae,* an invasive alien species in China, primarily infests *Pinus densiflora*, *Pinus massoniana*, and *Pinus tabulaeformis*. This study addresses the lack of information on its current distribution, influencing factors, and potential future distribution under different Representative Concentration Pathways (RCPs). Utilizing the MaxEnt model, the research aimed to ascertain the current distribution of *M. matsumurae* and its hosts, identify key factors influencing distribution, forecast potential distribution under current and future climate conditions, and analyze centroid distributional shifts under climate change. Key findings include the influence of precipitation variables, elevation, temperature seasonality, and history of invasion from Japan on the species' distribution in China's eastern coastal regions. This study predicts a northward shift in high suitable areas and a significant decrease in the Middle-Lower Yangtze Plain's suitability due to rising temperatures. These insights provide essential guidance for managing *M. matsumurae* and conserving *Pinus* species.
Keywords: *Matsucoccus matsumurae, climate change, potential distribution, distribution forecast, core distributional shift*

Introduction

The genus *Matsucoccus* (Hemiptera: Margarodidae) contains 34 species that mainly infect *Pinus* species (Pinales: Pinaceae) (Mech et al., 2013). The Japanese pine blast scale (*Matsucoccus matsumurae*) is a representative species of the genus *Matsucoccus*, which is also one of the most ancient insects (Beardsley, 1968; Booth and Gullan, 2006; Koteja and Azar, 2008). *M. matsumurae* is native to Japan and has been introduced into China, the Korean Peninsula, North America, and Northern Europe (Choi et al., 2019a).

M. matsumurae was originally found in Japan in 1905 (Xie et al., 2014). Subsequently, it was first identified in 1942 in Lushun City, Liaoning province, China, after being introduced to China from Japan in the 1940s (Liu et al., 2014a). Since then, it has caused significant damage to hundreds of thousands of hectares of pine trees in northern China (Zhao et al., 1990). It was introduced to Korea, infecting the country's *Pinus thunbergii*, twenty years later (Hong et al., 2021). *M. matsumurae* poses significant harm to *Pinus* species as a forestry pest and has a wide range of host species, including *Pinus massoniana* and *P. thunbergii* (Choi et al., 2019a; Liu et al., 2014a). In China, its host species are expanding, with newly introduced exotic species such as *Pinus sylvestris* and *Pinus banksiana* (Li et al., 2016) rapidly spreading to the southern

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regions of the country, causing extensive damage. *M. matsumurae* has now spread widely throughout Shanghai, Jilin, Liaoning, Jiangsu, Zhejiang, Guizhou, and other provinces (Tian et al., 2021), significantly impacting China's forestry and economy. The alien invasive species list issued by the Ministry of Agriculture and Rural Affairs, Ministry of Natural Resources, Ministry of Ecology and Environment, Ministry of Housing and Urban–Rural Development, General Administration of Customs, and State Forestry and Grass Administration in China on December 20, 2022, included *M. matsumurae* as one of the 59 invasive alien species prioritized for management in China.

The primary hosts of *M. matsumurae* in China have been identified as *Pinus* species, including *Pinus tabuliformis*, *Pinus densiflora*, and *P. massoniana* (Choi et al., 2019b; Liu et al., 2014b). Due to the significant damage caused to *Pinus* trees, many local governments have placed a strong emphasis on controlling this pest. Monitoring programs have been initiated to better understand the pest situation, preserve local *Pinus* species, and prevent the further spread of *M. matsumurae* (Hong et al., 2021; Choi et al., 2019b). Various effective measures have been promptly implemented to prevent *M. matsumurae* from causing additional harm to local forestry. Furthermore, researchers have conducted studies comparing the efficacy of different pest control strategies, such as chemical treatments and the use of natural enemies (Liu et al., 2015).

The geographic distribution of species populations is expected to be significantly influenced by climate change, leading to changes in suitable habitats (Gao et al., 2021). These changes may result in the expansion, reduction, or even extinction of species populations, as well as alterations to the genetic characteristics of the same species across different regions (Wells and Tonkyn, 2018). In recent years, global climate warming, driven by substantial greenhouse gas emissions, has been observed. This warming trend is affecting insect populations worldwide, impacting the invasion patterns of pests and posing threats to agricultural production in invaded areas (Biber-Freudenberger et al., 2016). Furthermore, climate change is anticipated to influence pest distribution by altering the geographical ranges of their host species, consequently affecting the suitable habitats of these insects (Wells and Tonkyn, 2018; Peng et al., 2022; Huang et al., 2021).

While many mealybug populations are known to be influenced by increasing temperatures (Frank et al., 2021), further research is required to ascertain whether the distribution of *M. matsumurae* is similarly affected. Studies have shown that the development and dispersal of *M. matsumurae* can be influenced by changes in meteorological conditions (Wang et al., 2016). Additionally, variations in the population differentiation of *M. matsumurae* have been observed in different locations concurrently (Yang et al., 2013). Further investigation into the potential impact of rising temperatures and changing climatic conditions on *M. matsumurae* distribution is necessary to understand the dynamics of this invasive pest species.

Mathematical models like the CLIMEX model (Early et al., 2022; Byeon et al., 2020) and the Maximum Entropy model (MaxEnt model) are commonly employed to assess the potential geographic distribution of target species and predict future distribution areas under changing climatic conditions. The MaxEnt model is a popular approach that is less sensitive to data quantity and errors, making it simpler to analyze and offering more advantages compared to other models (Phillips et al., 2006). The MaxEnt model utilizes the species' fundamental climate requirements and is frequently utilized to project the potential distribution of target species populations and assess the

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influence of future climate change on species distribution for predictive purposes (Gao et al., 2021). This modeling approach has been applied to various species, including *Sirex nitobei* (Fischbein et al., 2019), *Icerya aegyptiaca* (Liu and Shi, 2020), *Cicadella viridis* (Wei et al., 2023), and many others, to investigate potential distribution shifts in response to changing environmental conditions.

Modeling the impact of climate change on pests is crucial for developing effective strategies to manage their spread (Wei et al., 2020). However, current research progress on the influence of future climate on the population distribution of *M. matsumurae* in China is limited, with most studies focusing on local areas (Li et al., 2005). Understanding the distribution of biological populations and how it may change with changing temperatures is vital for controlling *M. matsumurae*, and gaining insights into population distribution is a crucial initial step before implementing control measures. To improve our understanding of the population distribution of this invasive species and develop effective control strategies, our study aims to survey the distribution of *M. matsumurae* in China and predict this species' potential distribution using the MaxEnt model. This approach will allow us to make projections about how climate change could impact the species' spread, providing valuable data to enhance monitoring and control efforts. By investigating the potential distribution shifts of *M. matsumurae* in response to changing climatic conditions, we can better prepare for and mitigate the potential impacts of this invasive pest species.

Materials and methods

Collection of P. densiflora, P. tabulaeformis, P. massoniana, and M. matsumurae distribution data

In this study, the distribution of *P. densiflora*, *P. tabulaeformis*, *P. massoniana*, and *M. matsumurae* was investigated by compiling reports from every Chinese provincial- and prefecture-level city Forestry Bureau, as well as through field observations conducted by research teams. A total of 141 sites for *P. densiflora*, 398 sites for *P. tabulaeformis*, 303 sites for *P. massoniana*, and 338 sites for *M. matsumurae* were initially collected through these methods. These data were then reviewed and refined using a buffer zone analytical approach in the ArcMap software (Gorshkov and Novikova, 2018; Feng et al., 2019). After the screening process, a final dataset of 87 sites for *P. densiflora*, 303 sites for *P. tabulaeformis*, 276 sites for *P. massoniana*, and 145 sites for *M. matsumurae* were selected for further analysis. The distribution sites for *P. densiflora* were spaced more than 20 km apart, similar to those for *P. tabulaeformis* and *P. massoniana*. In contrast, the distribution sites for *M. matsumurae* were spaced more than 10 km apart. The species name, longitude, and latitude of each distribution site for these four species were recorded in CSV format for subsequent analysis using the MaxEnt software. This comprehensive dataset will serve as the basis for conducting predictive modeling of the potential distribution of these species in response to changing climatic conditions.

Environmental variables

Climatic variables are the main factors determining the ecological niche of species, which are often used in insect niche models (Wei et al., 2018). For the MaxEnt model to best simulate the prediction of the potential future distribution area of *M. matsumurae*,

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19 climatic variables (Bio1, Annual mean temp (°C); Bio2, Mean diurnal range (°C); Bio3, Isothermality; Bio4, Temperature seasonality; Bio5, Maximum temp of warmest month (°C); Bio6, Minimum temp of coldest month (°C); Bio7, Temperature annual range (°C); Bio8, Mean temp of wettest quarter (°C); Bio9, Mean temp of driest quarter (°C); Bio10, Mean temp of warmest quarter (°C); Bio11, Mean temp of coldest quarter (°C); Bio12, Annual precipitation (mm); Bio13, Precipitation of wettest month (mm); Bio14, Precipitation of driest month (mm); Bio15, Precipitation seasonality (mm); Bio16, Precipitation of wettest quarter (mm); Bio17, Precipitation of driest quarter (mm); Bio18, Precipitation of warmest quarter (mm); Bio19, Precipitation of coldest quarter (mm)) downloaded from www.worldclim.org (accessed on 15 April 2023) were utilized in this study. Elevation variables were obtained from the United States Geological Survey (http://edcdaac.usgs.gov/gtopo30/gtopo30.html (accessed on 1 April 2021)). A total of 20 environmental factors were considered, with a spatial resolution of 30 s (~1 km^2). The variable layers were converted into ASCII format using ArcMap 10.4.1. The National Map was sourced from the National Fundamental Geographic Information System (http://www.ngcc.cn (accessed on 15 May 2023)). Future climate databases were acquired from the Climate Change, Agriculture, and Food Security program (http://ccafs-climate.org/ (accessed on 15 May 2023)) to forecast the future potential distribution of *M. matsumurae* under different climate scenarios. Low levels of greenhouse gas emissions (RCP2.6), moderate levels of greenhouse gas emissions (RCP4.5), and a high-risk future scenario (RCP8.5) were employed in this study to model the future distributions of *M. matsumurae* in the 2050s and 2070s. To prevent overfitting, the correlations among the 20 environmental variables were analyzed using ArcGIS and SPSS (Ning et al., 2021a; Graham, 2003). By utilizing 145 valid distribution data points and the 20 environmental variables, specific values of the environmental variables for the 145 data points were extracted using ArcGIS, and the output was converted from TXT to CSV format. Pearson correlation analysis was conducted on the 20 variables using SPSS, and the correlation coefficient matrix between variables was calculated. A correlation coefficient with an absolute value greater than 0.9 was considered highly correlated (Ning et al., 2021a; Graham, 2003). In cases of high correlation, variables with relatively low biological significance were removed, and only independent variables with significant biological relevance were retained. Additionally, the contribution percentage of environmental variables to the model was calculated.

Species distribution modeling

MaxEnt v.3.3.1 (http://www.cs.princeton.edu/wschapire/MaxEnt (accessed on 10 May 2022)) was utilized to predict both the current potential distribution and the future potential distribution of *M. matsumurae* in the 2050s and 2070s. Due to the distribution sites originating from various observers and collectors, a ten-percentile training presence logistic threshold was implemented to mitigate sampling bias (Bean et al., 2012). All environmental layers were converted to ASC format using the Arc Tools function in ArcGIS, and the obtained ASC format layers, along with the distribution data, were inputted into the MaxEnt model. Then, 75% of the distribution data were randomly selected for model training, while the remaining 25% were reserved for model validation (Phillips et al., 2006). The output layer was configured as Logistic, and the remaining parameters were set to the default values of the model (Phillips and Dudík, 2008). The area under the curve (AUC) of the receiver operating characteristic (ROC) is

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widely employed to assess the predictive performance of different models (Mc Pherson et al., 2004; Thuiller et al., 2005; Allouche et al., 2010). The AUC value represents the index of sensitivity and specificity calculated at different thresholds, with a value range from 0 to 1. A higher AUC value indicates better model performance. The default parameter settings in MaxEnt often lead to significant differences in actual species distribution; hence, parameter optimization is crucial for prediction accuracy and result reliability (Tamura et al., 2011). The ENMeval tool (https://github.com/marlonecobos/kuenm (accessed on 5 October 2022); https://www.r-project.org/ (accessed on 5 October 2022)) was employed for parameter optimization (Kass et al., 2021). Akaike information criterion correction was utilized to evaluate the fitting degree and complexity of different parameters (Warren and Seifert, 2011). The fitting degree of various parameters was assessed by comparing the training and testing AUCs, 10% training omission rate, and minimum training presence omission rate. The most suitable parameter combination was determined through the method described above.

This threshold was utilized to define potential suitable habitat areas for *M. matsumurae*, categorizing suitable areas into four grades: unsuitable area (0–0.07), low suitable area (0.07–0.25), moderate suitable area (0.25–0.5), and high suitable area (0.5–1) (França and Cabral, 2019; Ning et al., 2021b; Zhao et al., 2023). By multiplying the number of existing grid units with different suitability levels on the distribution map using spatial resolution, the areas and percentages of different suitability areas for *M. matsumurae* under current and future climate scenarios were calculated.

Centroid distribution changes of M. matsumurae

The Species Distribution Modeling (SDM) toolbox (http://www.sdmtoolbox.org (accessed on 15 May 2023)) was used to forecast the centroid distribution changes of *M. matsumurae*.

Results

Current distribution sites of three main host pine trees and M. matsumurae

According to *Figure 1*, *P. massoniana* is primarily distributed in the provinces and cities south of the Qinling Mountains, while *P. tabulaeformis* is primarily distributed in the northern areas. *P. densiflora* has the smallest distribution range of any of the species and is the most common in Shandong and other northern coastal provinces. The host range of *M. matsumurae* that can survive in China is quite vast, while all three *Pinus* species are less common in the west and are present in all eastern provinces and cities of China.

The occurrence area of *M. matsumurae* is shown in *Figure 2*. Compared to the wide distribution of its hosts pines, *M. matsumurae*'s distribution range is relatively small, and it is primarily concentrated in the provinces of Zhejiang, Shandong, Liaoning, and Jilin, with less distribution in the Jiangsu, Anhui, and Guizhou provinces.

Performance and variable selection of the MaxEnt model

The AUC in the MaxEnt model is used to indicate to researchers whether the model's predictions are accurate. The accuracy and reliability of the predictions can be

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assessed based on the high or low AUC values. The AUC value ranges from 0 to 1, with a value closer to 1 suggesting more accurate predictions. A higher AUC value implies that the predicted distribution area of the target species aligns well with the future suitable areas, making it more reliable. On the other hand, an AUC value below 0.6 indicates that the results from the dataset do not meet the criteria, while a value exceeding 0.9 is considered highly compliant (Li et al., 2005). Upon analyzing the results of the MaxEnt model for predicting the future suitable areas of *M. matsumurae*, we obtained an AUC value of 0.969 (*Fig. 3*), indicating a very satisfactory prediction with a high level of trustworthiness. Through Pearson correlation analysis and the percentage contribution (*Table 1*), five environmental variables were selected for use in the MaxEnt model.

Present potential distribution area of M. matsumurae

Based on the modeling of the current potential areas of *M. matsumurae* in China (*Fig. 4*), it is evident that the invasion range of *M. matsumurae* is situated along the east coast of China. The severely affected areas primarily include the provinces of Liaoning, Shandong, Zhejiang, and Anhui, with Liaoning province exhibiting the largest area of high suitable habitat. The moderate suitable areas are predominantly found in the Jilin, Hebei, Jiangsu, Jiangxi, Hubei, and Hunan provinces.

In comparison to the occurrence records of *P. densiflora*, *P. massoniana*, and *P. tabulaeformis* in China (*Fig. 1*), the hosts of *M. matsumurae* were widely distributed in central and eastern China. However, *M. matsumurae* itself was primarily distributed along the east coast and the Middle-Lower Yangtze Plain.

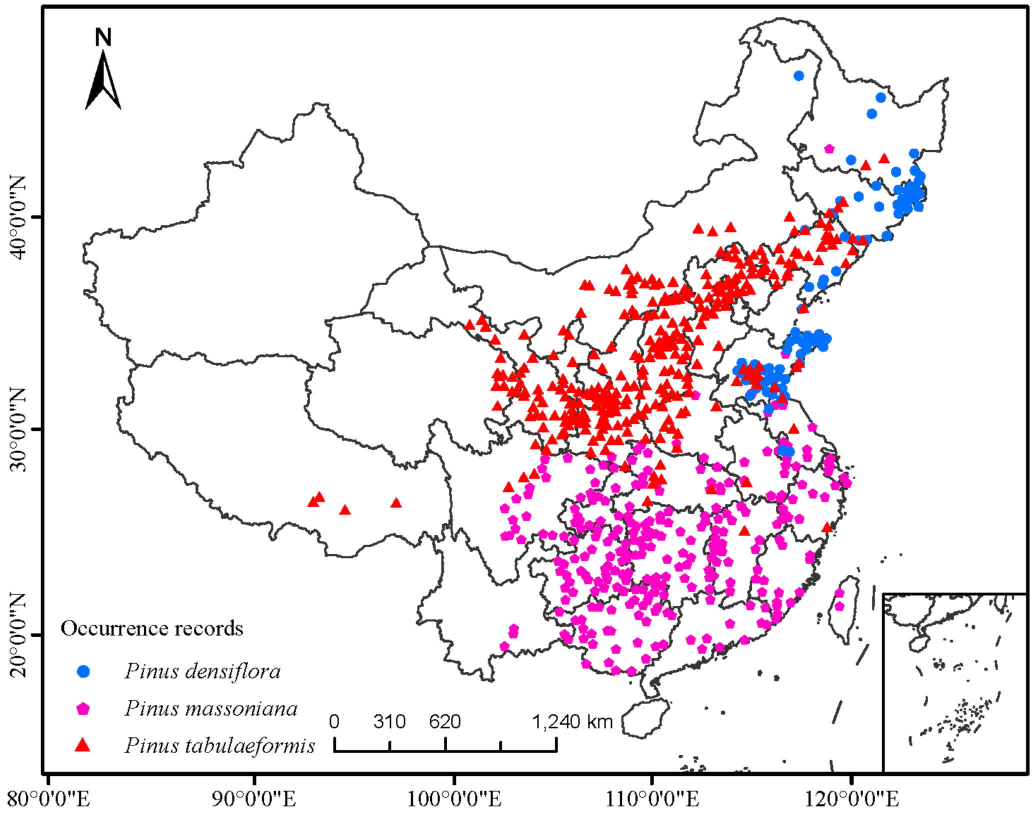

Figure 1. *Occurrence records of Pinus densiflora, Pinus massoniana, and Pinus tabulaeformis in China*

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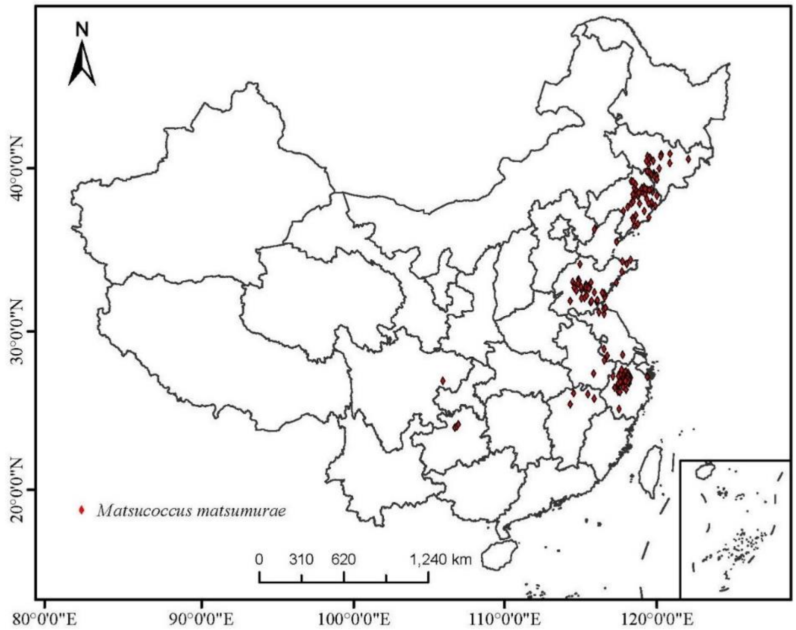

Figure 2. *Occurrence records of Matsucoccus matsumurae in China*

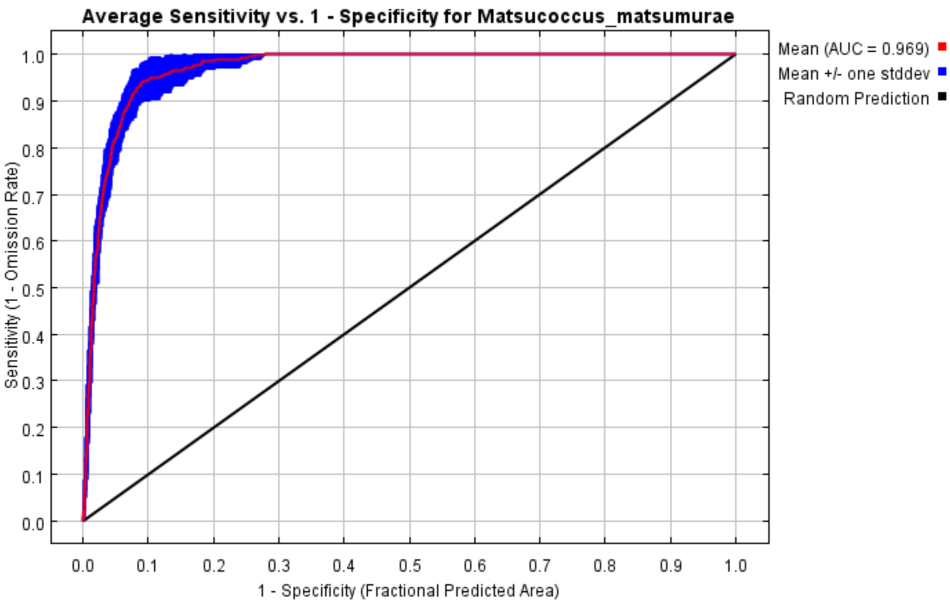

Figure 3. *AUC value of test on applicability of the MaxEnt model*

Table 1. *Five environmental variables were chosen for predicting the distribution of M. matsumurae in the MaxEnt model*

Abbreviation	Environmental variables	Percent contribution
Elev	Elevation	22.2
Bio13	Precipitation of wettest month (mm)	18
Bio14	Precipitation of driest month (mm)	15.6
Bio4	Temperature seasonality	14.7
Bio18	Precipitation of warmest quarter (mm)	11.1

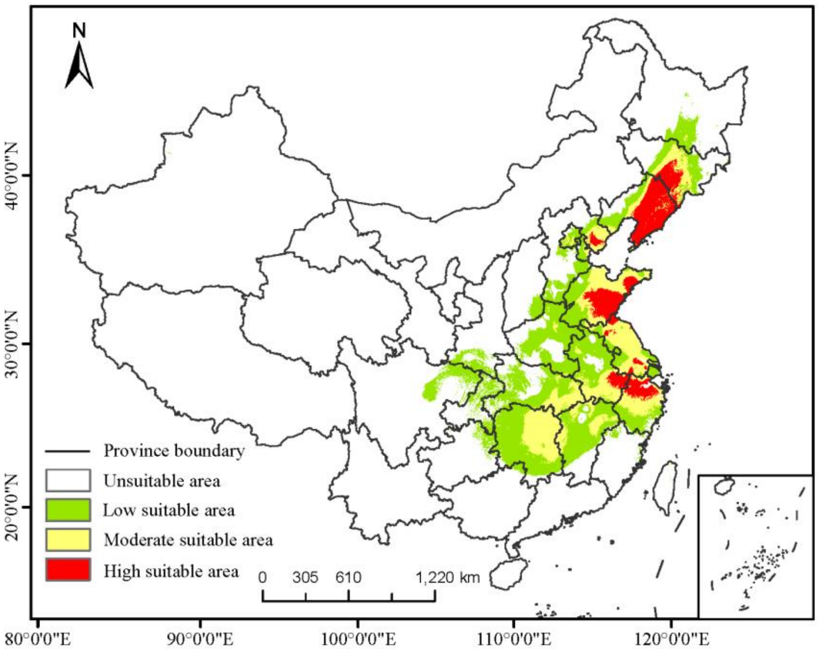

Figure 4. *Present potential distribution area of Matsucoccus matsumurae in China*

Future potential distribution area of M. matsumurae

The potential future distribution of *M. matsumurae* was predicted for the 2050s and 2070s under RCP2.6, RCP4.5, and RCP8.5 and exhibits some changes with the current potential distribution of *M. matsumurae* (*Figs. 5* and *6*). Under RCP2.6 in the 2050s, the high suitable areas are located in the Jilin, Liaoning, Shandong, Jiangsu, and Zhejiang provinces (*Fig. 5A*). The high, moderate, low, and total suitable areas occupying the land in China are 23.17 × 10^4 km^2, 27.38 × 10^4 km^2, 103.44 × 10^4 km^2, and 153.99 × 10^4 km^2, respectively. Under RCP2.6 in the 2070s, the high suitable areas are located in the Jilin, Liaoning, and Shandong provinces (*Fig. 5*B). The high, moderate, low, and total suitable areas occupying the land in China are 21.82 × 10^4 km^2, 26.98 × 10^4 km^2, 104.19 × 10^4 km^2, and 152.99 × 10^4 km^2, respectively. Under RCP4.5 in the 2050s, the high suitable areas are located in the Jilin, Liaoning, Heilongjiang, and Shandong provinces (*Fig. 5C*). The high, moderate, low, and total suitable areas occupying the land in China are 24.36 × 10^4 km^2, 32.87 × 10^4 km^2, 104.24 × 10^4 km^2, and 161.47 × 10^4 km^2, respectively. Under RCP4.5 in the 2070s, the high suitable areas are located in the Jilin, Liaoning, Heilongjiang, and Shandong provinces (*Fig. 5D*). The high, moderate, low, and total suitable areas occupying the land in China are 26.83 × 10^4 km^2, 30.18 × 10^4 km^2, 91.91 × 10^4 km^2, and 148.92 × 10^4 km^2, respectively. Under RCP8.5 in the 2050s, the high suitable areas are located in the Jilin, Liaoning, Heilongjiang, and Shandong provinces (Fig. 5*E*). The high, moderate, low, and total suitable areas occupying the land in China are 28.31 × 10^4 km^2, 32.53 × 10^4 km^2, 75.72 × 10^4 km^2, and 136.56 × 10^4 km^2, respectively. Under RCP8.5 in the 2070s, the high suitable areas are located in the Jilin, Liaoning, and Heilongjiang provinces (*Fig. 5F*). The high, moderate, low, and total suitable areas occupying the land in China are 45.51 × 10^4 km^2, 27.89 × 10^4 km^2, 68.79 × 10^4 km^2, and 142.19 × 10^4 km^2, respectively. Under RCP2.6, the high suitable areas increased from the present day to 2050 (increased by 8.56%) and decreased from 2050 to 2070

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(decreased by 5.81%); the moderate suitable areas decreased from the present day to 2050 (decreased by 35.23%) and decreased from 2050 to 2070 (decreased by 1.40%); the low suitable areas increased from present to 2050 (increased by 19.91%) and increased from 2050 to 2070 (increased by 0.65%); the total suitable areas increased from present to 2050 (increased by 2.75%) and decreased from 2050 to 2070 (decreased by 0.69%) (*Fig. 6A*). Under RCP4.5, the high suitable areas increased from the present day to 2050 (increased by 14.41%) and increased from 2050 to 2070 (increased by 9.84%); the moderate suitable areas decreased from the present day to 2050 (decreased by 22.27%) and decreased from 2050 to 2070 (decreased by 8.19%); the low suitable areas increased from present to 2050 (increased by 20.80%) and decreased from 2050 to 2070 (decreased by 11.88%); the total suitable areas increased from present to 2050 (increased by 7.75%) and decreased from 2050 to 2070 (decreased by 7.85%) (*Fig. 6B*). Under RCP8.5, the high suitable areas increased from the present day to 2050 (increased by 32.88%) and increased from 2050 to 2070 (increased by 60.68%); the moderate suitable areas decreased from the present day to 2050 (decreased by 22.95%) and decreased from 2050 to 2070 (decreased by 14.16%); the low suitable areas decreased from present to 2050 (decreased by 12.24%) and decreased from 2050 to 2070 (decreased by 9.13%); the total suitable areas decreased from present to 2050 (decreased by 8.84%) and increased from 2050 to 2070 (increased by 4.15%) (*Fig. 6C*).

Changes in the centroid distributional shifts

The analysis of the changes in the distribution core of *M. matsumurae* under climate change is depicted in *Figure 7*. Currently, the distribution center of *M. matsumurae* is situated in Suzhou City, Northern Anhui province. However, under different RCP scenarios and timeframes, the distribution centers of *M. matsumurae* are projected to shift to different locations. Under RCP2.6 in the 2050s, the distribution center is expected to gradually move to Yantai City in eastern Shandong province. Subsequently, by the 2070s under RCP2.6, there will be a southwestward shift towards Weifang City in the middle of Shandong province. For RCP4.5, in the 2050s, the distribution center is forecasted to move to the Bohai Sea region near west Dalian City in Liaoning province. By the 2070s under RCP4.5, the center is predicted to shift southward to southwest Dalian City in Liaoning province. Under RCP8.5, in the 2050s, the distribution center is anticipated to move to north Dalian City in Liaoning province. By the 2070s under RCP8.5, there will be a northeastward shift towards Shenyang City in Liaoning province. These findings highlight the dynamic nature of the distribution core of *M. matsumurae* under climate change scenarios, with significant shifts projected in the coming decades based on different levels of greenhouse gas emissions.

Discussion

This study provides a basis for predicting the distribution range of *M. matsumurae* in the future from the perspective of host distribution. From the occurrence records for *M. matsumurae* (*Fig. 2*), the northeast of China (Jilin and Liaoning provinces), Shandong and Zhejiang provinces will be the main area affected by this pest. According to the above information, we carried out further investigations on the affected area. In the field investigation, we found that (1) *M. matsumurae* mainly invades *P. tabulaeformis* in

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northeast China; (2) *M. matsumurae* mainly invades *P. densiflora* in Shandong province, and rarely invades *P. thunbergii*; and (3) *M. matsumurae* mainly invades *P. massoniana* in Zhejiang province. A further investigation was carried out to determine the distribution range of these three kinds of *Pinus* species in China. From the survey results (*Fig. 1*), *P. tabulaeformis* was primarily found in the east-central region, *P. massoniana* was primarily found in the provinces south of the Qinling Mountains, and *P. densiflora* had a relatively small geographic range located on the northeast coast. In general, the three favorite hosts of *M. matsumurae* were mainly distributed in central and eastern China.

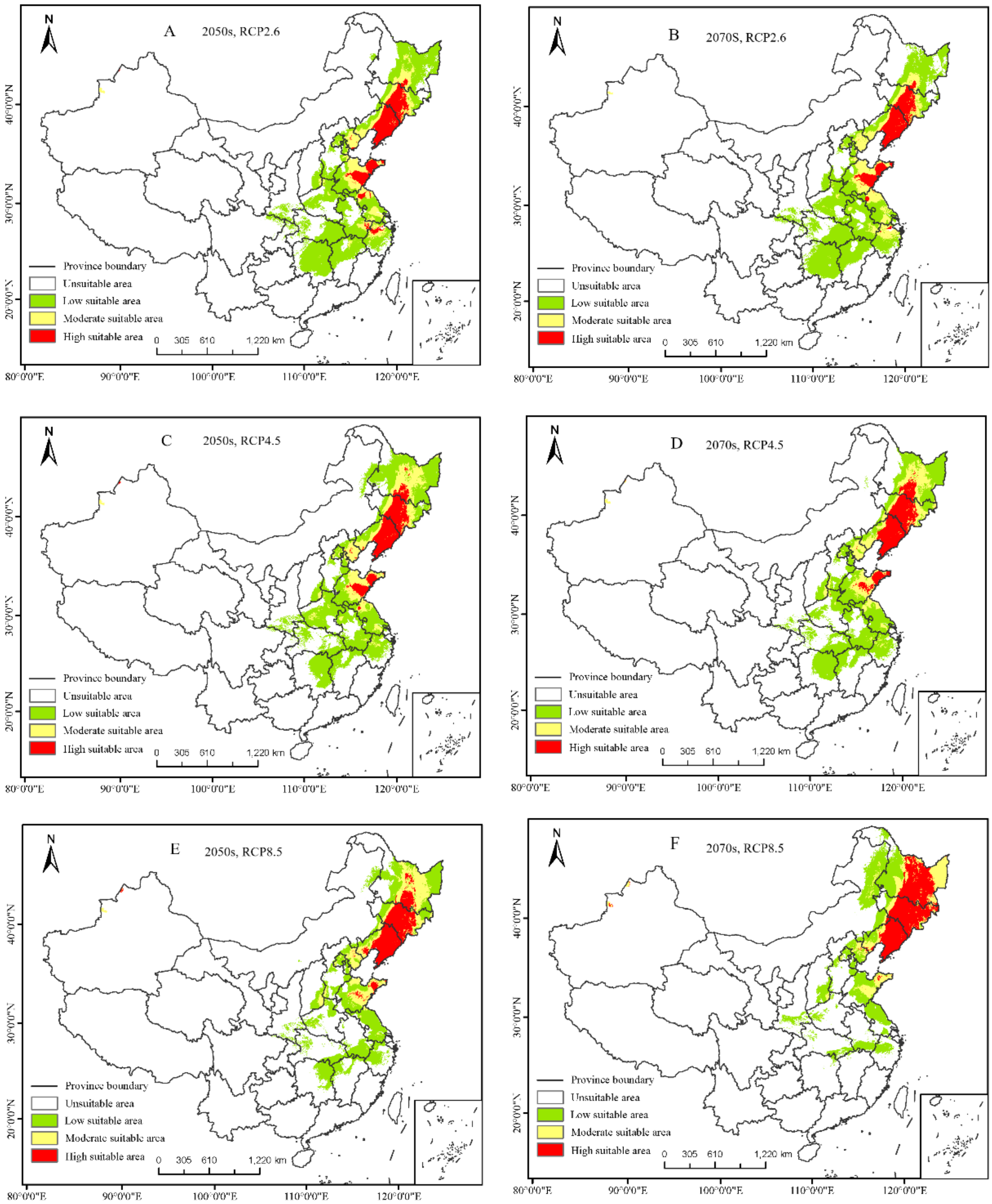

***Figure 5.** Future potential distribution area of Matsucoccus matsumurae under RCP2.6, RCP4.5, and RCP8.5 during the 2050s and 2070s in China*

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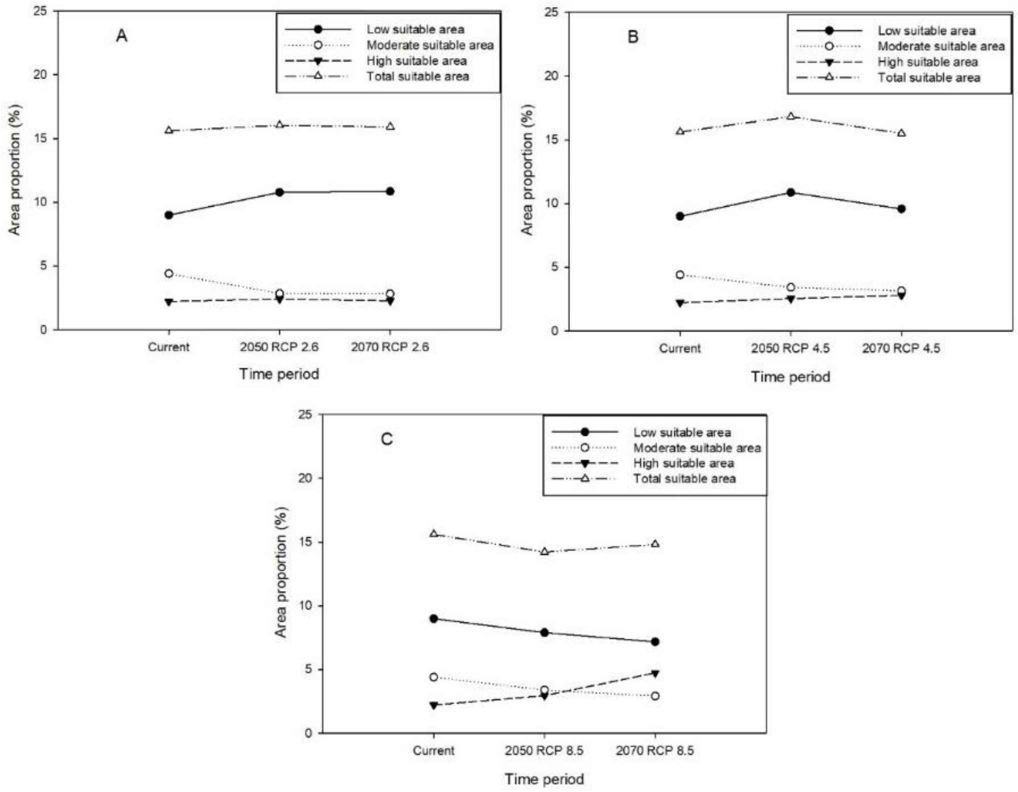

Figure 6. *Change in area proportion (%) from present day to 2070s under RCP2.6 (A), under RCP4.5 (B), and under RCP8.5 (C)*

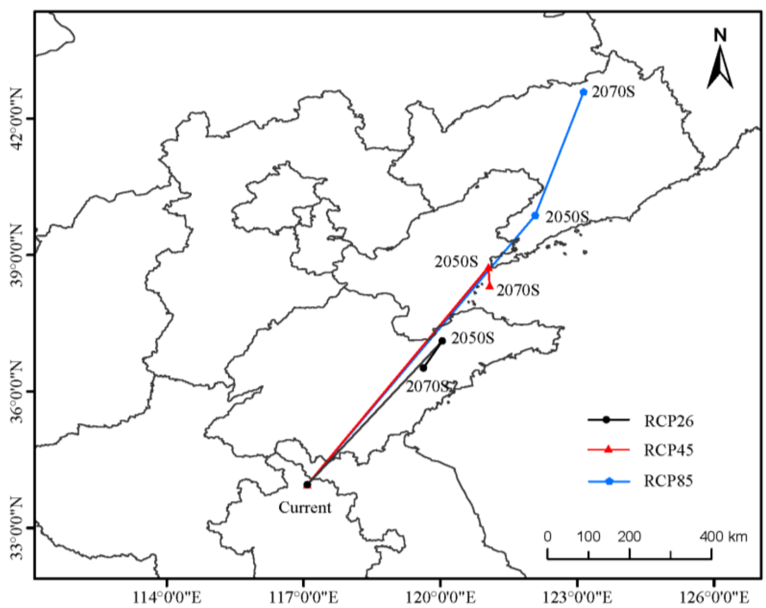

Figure 7. *Changes in the centroid distributional shifts of Matsucoccus matsumurae under climate change*

The current distribution of *M. matsumurae* in China is primarily concentrated in the latitudes 27N-41N and the longitudes 114E-121E, mainly in the coastal provinces

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(*Fig. 2*). The narrow distribution range of *M. matsumurae* (*Fig. 2*) compared to the distribution range of its host pines (*Fig. 1*) suggests that host distribution is not the main factor. When studying the distribution of target species, many researchers have found that the host's effect is not very obvious, and it may not be a significant influencing factor (Hanspach et al., 2014; Wang et al., 2020). Further, according to the combined results of 20 environmental variables (*Table 1*), precipitation factors (precipitation of wettest month, precipitation of driest month, and precipitation of warmest quarter) exhibit the largest contribution rate at 44.7%. Moreover, elevation accounts for 22.2% and temperature seasonality accounts for 14.7%. Temperature factors (Bio2, Bio3, Bio8) were the main influencing factors in *Pseudaulacaspis pentagona* (Lu et al., 2020), a finding that differs from the study of *M. matsumurae*.

The main distribution range for the Jilin and Liaoning provinces was located in the medium temperature zone, the main distribution range for Shandong province was located in the warm temperate zone, and the main distribution range for Zhejiang province was located in the subtropical zone. From the information above, it can be inferred that temperature seasonality is an important factor. However, since most of China's land area falls within the medium temperature zone, warm temperate zone, and subtropical zone, temperature seasonality is not the main factor affecting the distribution of *M. matsumurae*. Based on the above information, we can infer the reason why *M. matsumurae* mainly congregates in the eastern coastal area of China. Firstly, this geographical location is close to Japan, the birthplace of *M. matsumurae*. Provinces such as Zhejiang, Shandong, and Liaoning, which are in close proximity to Japan and have significant trade relations with the country. Secondly, the eastern coastal area of China receives abundant rainfall, which ensures the growth and development of the species. Thirdly, *M. matsumurae* prefers lower altitudes, and the eastern coastal area is mostly flat with low altitude.

Based on the results of the MaxEnt model depicting the current potential distribution suitability of *M. matsumurae* (*Fig. 4*), the high suitable areas were primarily concentrated in the Jilin, Liaoning, Hebei, Shandong, Jiangsu, Zhejiang, and Anhui provinces. The regions of Jilin, Liaoning, Shandong, and Zhejiang with high suitability cover a significant proportion, aligning with the occurrence records of *M. matsumurae* (*Fig. 2*). In the northern affected areas, the limited spread of *M. matsumurae* westward may be influenced by factors such as climate, geography, and other environmental conditions. Generally, as we move from north to south, *M. matsumurae* tends to expand further westward. A notable difference between the occurrence records and the current potential distribution of *M. matsumurae* is the possibility of a large undiscovered area of *M. matsumurae* in the Middle-Lower Yangtze Plain.

By comparing the current potential distributions with all of the studied future climate scenarios, three notable features stand out, as follows: (1) The high suitable area shows a general northward shift under RCP2.6, RCP4.5, and RCP8.5 during the 2050s and 2070s in China. (2) The moderate suitable area in the middle region of the Yangtze Plain almost completely disappears under RCP2.6, RCP4.5, and RCP8.5 during the 2050s and 2070s in China. Additionally, the low suitable area in the middle region of the Yangtze Plain significantly decreases under RCP2.6, RCP4.5, and RCP8.5 during the 2050s and 2070s in China. Furthermore, the higher the temperature rises in the future, the more the area of low suitability will decrease. (3) The high and moderate suitable areas in the low region of the Yangtze Plain will diminish with the temperature rise (from RCP2.6 to RCP4.5 to RCP8.5) and the passage of time (from 2050s to 2070s).

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The results from the above analysis indicate that climate change can have a significant impact on the geographical distribution of *M. matsumurae*, as supported by a considerable amount of evidence for other species (Ziter et al., 2012; Maclean and Wilson, 2011; Roth et al., 2014), and the strength of this influence has a strong correlation with the location of the species (Stoeckli et al., 2020). At the same time, the distribution of insects is generally affected by climate on a large scale, and is mainly influenced by species interactions on a small scale (Hortal et al., 2010). In the context of climate change, the potential habitat areas of other insects also tend to shift northward, for example, those of *Anoplophora chinensis* and *Apocheima cinerarius* (Zhou et al., 2022; Ding et al., 2022), while the potential habitat area of some insects is shrinking in the south (Chen et al., 2017; Wei et al., 2022). Climate change has had a significant impact on scale insects, expanding their range of suitable areas, increasing the number of pest generations, and raising the risk of alien pest invasion (Skendžić et al., 2021).

Further analysis was conducted to explore the reasons for the strength of the influence of climate change. The northern migration of *M. matsumurae* in the high suitable area under future climate scenarios was consistent, and a similar trend has been observed in predictive studies of many other species (Cheng et al., 2022). Under future climatic scenarios, the high suitable area of *Ceroplastes japonicus* (Japanese wax scale, also an invasive alien species from Japan) showed a tendency to shift northward in China, while the high suitable area of *Pseudococcus comstocki* (an East Asian native pest and invasive alien species in Europe, Central Asia, and North America) exhibited an expansion trend to the north (Cheng et al., 2022). The distribution area of *M. matsumurae* in the Middle Yangtze Plain did not show a tendency to shift or expand northward; instead, it decreased as temperatures rose. Conversely, the suitable areas of *C. japonicus* and *P. comstocki* in central China did not experience significant reductions (Cheng et al., 2022). This was attributed to the fact that the distribution area of *M. matsumurae* in the Middle Yangtze Plain was primarily composed of moderate suitable and low suitable areas, with the moderate suitable areas evolving into low suitable ones and then these areas becoming unsuitable with future climate change. On the other hand, the suitable areas of *C. japonicus* and *P. comstocki* in central China were mainly high and moderate suitable areas, which may evolve into moderate suitable and low suitable areas with future climate change, resulting in no significant changes in their distribution areas in central China. These research findings indicate that the activity range of scale insects is increasing in the north and decreasing in the south under future climate change models in China.

In the Middle Yangtze Plain area, there is a significant disparity between the current prediction results and occurrence records. Particularly in the Chongqing municipality directly under the central government, Hubei, Hunan, and Henan provinces, no occurrence records have been found, despite the extensive presence of moderate and low suitable areas. Further investigations should be conducted in the future to determine the presence of *M. matsumurae* in these areas.

The changes in the damage area caused by *M. matsumurae* will have implications for the control strategies of this pest in China in the future. In northeast China, Heilongjiang province is expected to gradually experience the emergence of moderate and high suitable areas, while the suitable areas of Jilin and Liaoning will further expand. Enhanced monitoring and prevention efforts will be necessary to control *M. matsumurae* in northeast China in the future. On the other hand, the damage caused by *M. matsumurae* in Shandong province is projected to persist under RCP2.6 and 4.5

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scenarios, but weaken under extreme weather conditions (RCP8.5). Therefore, continuous monitoring and prevention measures for *M. matsumurae* in Shandong province are still crucial. In the border area of the Zhejiang, Anhui, and Jiangsu provinces, the high suitable area is expected to considerably decrease. As a result, more relaxed prevention and control strategies can be implemented in the future, primarily focusing on surveillance activities.

Based on the analysis of the area proportion change from the current period to the 2070s under RCP2.6, RCP4.5, and RCP8.5 (*Fig. 6*), it is evident that the high suitable area for *M. matsumurae* populations is projected to increase over time under all future climate scenarios, particularly in the three northeastern provinces of China. Climate change is identified as a key driver in the change of suitable areas, presenting significant challenges for the control and monitoring of *M. matsumurae* in the future in China. Moreover, the changing temperature conditions in the Middle-Lower Yangtze Plain have created unsuitable conditions for the survival of *M. matsumurae*, leading to a northward shift in the suitable distribution area. The moderate suitable area has shown a significant decrease from the current period to the 2070s under all future climate scenarios, with variations between the Middle-Lower Yangtze Plain and northeast China. This is primarily due to the gradual evolution of the moderate suitable area into one of high suitability in northeast China, while transitioning into low suitability or unsuitability in the Middle-Lower Yangtze Plain. The influence of climate warming on *M. matsumurae* is characterized by a general trend of the northward migration of suitable areas. This highlights the importance of focusing on forestry practices in the three northeastern provinces of Liaoning, Jilin, and Heilongjiang. The monitoring of all suitable areas is deemed crucial to effectively manage the impact of *M. matsumurae* in the face of changing climatic conditions.

The relationship between population density and suitability values indicates that low population densities can be found in areas with both low and high suitability values, while high population densities are typically concentrated in areas with better suitability (Tôrres et al., 2012; Oliver et al., 2012). The continuous improvement in the high suitable area for *M. matsumurae* from the current period to the 2070s under all future climate scenarios suggests an expansion of geographic areas conducive to high population densities of this pest. This trend increases the likelihood of outbreaks of *M. matsumurae*, highlighting the need to further enhance prevention and control strategies to effectively address the significant challenges that lie ahead. The transition from zero or low population levels to high population densities can potentially trigger sudden outbreaks, especially in areas that are ill-prepared for the management and control of *M. matsumurae*. To mitigate the risk of sudden outbreaks, it is crucial for local forestry bureaus, particularly in the three provinces of northeast China, to include *M. matsumurae* in their regular investigations and monitoring efforts. By incorporating *M. matsumurae* into routine surveillance activities, local authorities can better prepare for and prevent potential outbreaks of this pest in the future. This proactive approach is essential in safeguarding forest health and biodiversity in the face of increasing challenges posed by *M. matsumurae*.

The analysis of the centroid distribution of *M. matsumurae* reveals a notable shift tendency from the current position towards the northeast under all future climate scenarios. Additionally, the centroid distributional shifts are projected to move increasingly northward with the rise in RCP values. Specifically, the centers of RCP2.6 and RCP4.5 are forecasted to reach their respective northernmost positions in the 2050s,

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after which they are expected to shift southward again. An unexpected finding is that the center of RCP8.5 continues to move northward continuously, ultimately reaching the northern Liaoning province. This observation underscores the significant influence of RCP values on the centroid distributional shift of *M. matsumurae*. The results suggest that the trajectory of the centroid distribution of this pest will be substantially impacted by the specific RCP scenarios considered, with varying patterns of movement over time. Regardless of the mode of impact of different RCP scenarios, the current distribution center shows a significant northeastern shift. Therefore, in the future, the northeastern region may be a severely affected area, while the forests in the central and southern regions may experience reduced harm. Understanding and monitoring these centroid distributional shifts are crucial for predicting the potential spread and impact of *M. matsumurae* under different climate change scenarios. This information can inform targeted management and control strategies to mitigate the consequences of the shifting distribution of this pest in forested areas.

The development of insects depends on the host (Skidmore and Hansen, 2017), making host distribution a crucial factor influencing pest distribution. The distribution of the three main hosts of *M. matsumurae* has been observed to change with climate change, showing a trend of expanding their range (Wen et al., 2021; Chi et al., 2023; Duan et al., 2022). This expansion of host plant distribution further supports the northward shift trend of suitable areas for *M. matsumurae*. While it is speculated that changes in host suitable areas may not be the primary driver of *M. matsumurae*'s distribution shifts, investigating the species' host habitat changes under specific climatic conditions remains important. There are numerous uncertainties in the forecast, particularly stemming from human factors such as widespread control measures and trade interactions with Japan. Therefore, it is crucial to control the spread of *M. matsumurae* given the influence of climate change on its suitable areas.

Different SDMs showed variations in the species' distribution forecasts (Elith et al., 2006; Marmion et al., 2009). Despite drawing conclusions from our results, our study still has certain limitations, as some factors other than climatic conditions (such as human activities, geography, and natural enemies) are challenging to incorporate into the analysis (Mattia et al., 2019; Niemczyk et al., 2021; Terry et al., 2021). Therefore, altitude was included as the twentieth environmental variable in this research. Additionally, the geographical factors influencing the spread of *M. matsumurae* from Japan to China were taken into consideration in the analysis. However, the MaxEnt model used in this study is faster and more reliable than other conventional models (Yang et al., 2021), and it offers advantages in processing small sample sizes of data (Wisz et al., 2008). Some of this study's limitations were: (1) despite MaxEnt's advantages in handling small datasets, the small size may still impact result accuracy; (2) while the ENMeval tool is used to optimize MaxEnt's default parameter settings, the predicted outcomes may vary when using alternative SDMs.

Conclusions

M. matsumurae primarily infests *P. tabulaeformis* in northeast China, *P. densiflora* in Shandong province, and *P. massoniana* in Zhejiang province. These three preferred hosts of *M. matsumurae* are widely distributed in China, laying the groundwork for the pest's expansion. Precipitation factors (such as the precipitation of the wettest month, driest month, and warmest quarter), elevation, and temperature seasonality were

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identified as the main influencing factors in the distribution of *M. matsumurae*, rather than host plant distribution. Based on the history of invasion from Japan and the information provided, the reasons *M. matsumurae* tends to concentrate in the eastern coastal area of China can be inferred: (1) due to their closer proximity to the origin of *M. matsumurae*, the eastern coastal provinces are more likely to be invaded first; (2) the eastern coastal regions of China receive more abundant rainfall compared to the central and western regions; (3) the eastern coastal regions have lower elevations. Comparing the current potential distributions with future climate scenarios, climate change is projected to have a significant impact on the geographical distribution of *M. matsumurae*, including a general northward shift of high suitable areas and a decrease in the suitable area of the Middle-Lower Yangtze Plain with rising temperatures. The increase in high suitable areas for *M. matsumurae* populations will pose challenges for prevention and control efforts over time, particularly in the three northeastern provinces. In northeast China, Heilongjiang province is expected to gradually emerge as a moderate to high suitable area, while the suitable areas of Jilin and Liaoning provinces are projected to further extend. Enhanced monitoring and prevention measures will be necessary to control *M. matsumurae* in northeast China in the future. Due to the northeastern shift in the distribution center of *M. matsumurae*, the degree of damage in central and southern regions of China is relatively reduced. In the future, the monitoring efforts in these regions can be gradually decreased. Additionally, the centroid distribution of *M. matsumurae* is predicted to shift significantly towards the northeast under all future climate scenarios. This study fills a research gap regarding the potential impact of temperature changes on the distribution of *M. matsumurae* and provides a theoretical foundation for more effective pest control measures. Understanding the potential distribution area of *M. matsumurae* is crucial for devising efficient pest control strategies and safeguarding its host plants.

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