Evaluating the Impact of Climate Change and Human Activities on the Potential Distribution of Pine Wood Nematode (Bursaphelenchus xylophilus) in China

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Abstract: Bursaphelenchus xylophilus is a pest that interferes with the health of forests and hinders the development of the forestry industry, and its spread is influenced by changes in abiotic factors and human activities. The potential distribution areas of B. xylophilus in China under four shared-economic pathways were predicted using the optimized MaxEnt model (version 3.4.3), combining data from a variety of environmental variables: (1) prediction of natural environmental variables predicted under current climate models; (2) prediction of natural environmental variables + human activities under current climate models; and (3) prediction of natural environmental variables under the future climate models (2050s and 2070s). Meanwhile, whether the niche of B. xylophilus has changed over time is analyzed. The results showed that human activities, precipitation in the driest month, annual precipitation, and elevation had significant effects on the distribution of B. xylophilus. In the current conditions, human activities greatly reduced the survival area of B. xylophilus, and its suitable distribution area was mainly concentrated in the southwestern and central regions of China. Under the influence of climate change in the future, the habitat of B. xylophilus will gradually spread to the northeast. In addition, the ecological niche overlap analysis showed that B. xylophilus in future climate was greater than 0.74. This study provides important information for understanding the ecological adaptation and potential risk of B. xylophilus, which can help guide the decision making of pest control and forest protection.

Keywords: Bursaphelenchus xylophilus; climate change; human activity; MaxEnt model; habitat suitability

1. Introduction

The spatial distribution of organisms is a fundamental spatial characteristic influenced by prolonged interactions between species and their environment [1]. Currently, the impacts of global climate change and human interference on biodiversity and ecosystems are important research priorities in the fields of ecology, environmental science, and conservation biology [2]. As societies evolve, human activities alter land use patterns and create novel landscape interfaces, which in turn influence the spatial distribution and diversity of species. Numerous examples can be given to illustrate the above points: activities such as urbanization, agricultural expansion, and deforestation can result in the loss and fragmentation of habitats, thereby impeding the ability of numerous species to locate suitable living environments, which in turn affects their survival and reproduction [3]. Furthermore, climate change can affect temperature and precipitation patterns, as well as increase the frequency of climatic extremes. These changes will inevitably alter the geographical distribution of species and the stability of ecosystems [4]. Since the advent of the Industrial Revolution, the global climate has been warming due to the greenhouse
effect caused by human activities [5]. According to the Fifth Assessment Report (AR5) of the Intergovernmental Panel on Climate Change (IPCC), the average temperature of the Earth will have risen by 0.3 to 4.5 °C by the end of the 21st century [6]. In order to respond to these challenges, scientists are engaged in research aimed at elucidating the impact of climate change and human activities on the geographic distribution patterns of species [7]. These studies help elucidate species’ responses to environmental changes and potential future distribution.

Forests are the largest terrestrial ecosystems on Earth and play an irreplaceable role as carbon sinks and in combating climate change [8]. Pine trees, as an important silvicultural species, are widely planted globally, and they not only provide timber and other forest products but also play key roles in ecosystem services, such as fixing soil and reducing erosion and wind and sand control, which have important economic, cultural, and ecological values [9]. Nevertheless, pine trees are susceptible to pine wilt disease (PWD), a significant global quarantine forest disease caused by *Bursaphelenchus xylophilus*, which is highly detrimental to pines; once infected, pines typically succumb within a few months [10]. The species was initially identified in North America and subsequently disseminated to Japan, China, Korea, Portugal, and other countries [11]. A recent report by the National Forestry and Grassland Administration (NFGA, 2024) indicates that PWD has spread northward and westward to Jilin and Gansu Provinces; this epidemic has shown a rapid proliferation and spread, posing a serious threat to the ecological security, biosecurity, and economic development of forest ecosystems [12].

Under the background of intensified global climate change, the area of China’s forests infested by PWD has been gradually increasing, and the scope of transmission has been expanding [13]. Analyzing the characteristics of the evolution of the geographical distribution of *B. xylophilus* and the prediction of the future development trend under the influence of climate change and human interference can provide the theoretical basis and technical support for the government and the forestry management department to effectively monitor, predict and control PWD in a timely manner.

Species distribution modeling is an important tool for studying the geographical distribution of species and their response to climate change and human activities [14,15]. Models predict the potential distribution of species under different environmental conditions by analyzing their current distribution data and environmental variables (e.g., climate, topography, vegetation, etc.). The MaxEnt model is widely used; it is based on the principle of maximum entropy as conceptual information, which means that in the absence of more information, the model will tend to choose the most uniform probability distribution. It is able to infer the potential distribution of a species from limited data on the presence points of the species and still maintains a high predictive accuracy when dealing with incomplete data [16–18]. In addition to MaxEnt, other models such as CLIMEX, GARP, and ENFA have their own characteristics and applications [19–21]. These models have applications in several fields, including conservation planning for endangered species, habitat assessment for wildlife, estimation of potential acreage for crops, and monitoring and control of quarantine pests [22]. In particular, in the context of pest management, ecological niche modeling can help to predict the potential distribution areas of pests, thus providing a scientific basis for monitoring and controlling their spread [23,24].

In this study, we compare predictions based on different environmental factors using the MaxEnt model, which can reveal how human activities and climate change individually or jointly affect the distribution of *B. xylophilus*. We aimed to (1) identify the most critical factors affecting the distribution of *B. xylophilus* within China; (2) compare the differences in the distribution and size of *B. xylophilus* habitats under scenarios with and without anthropogenic disturbance in the current period; (3) explore changes in the size of potential geographic distribution areas of *B. xylophilus* under different future climate scenarios; and (4) clarify the pattern of spatial evolution and development trend of *B. xylophilus*. The results of this study can provide a scientific basis and reference for localities and governments to
formulate reasonable prevention and control strategies, which can help protect forestry resources, maintain ecological balance, and promote ecological civilization.

2. Materials and Methods

2.1. Data

To generate the occurrence records of *B. xylophilus* used in the modeling, we collected data from multiple sources, specifically the following: (1) information regarding endemic regions affected by *B. xylophilus* was obtained from the National Forestry and Grassland Administration (http://www.forestry.gov.cn, accessed on 2 June 2024); (2) book materials and online references (CNKI, https://www.cnki.net, accessed on 20 May 2024; WOS, https://www.webofscience.com/wos, accessed on 19 May 2024) [25,26]; and (3) two online public databases, the Global Biodiversity Information Facility (GBIF) (https://doi.org/10.15468/dl.uvs3yu, accessed on 18 May 2024) and an iNaturalist (https://www.inaturalist.org, accessed on 20 May 2024). For available record locations without specific latitude and longitude coordinates, we instead used Google Earth software (http://ditu.google.cn, accessed on 3 June 2024) to obtain this information. Ultimately, through these sources, a total of 1385 occurrence points were collected for this study (Figure 1). These records provided the necessary database for modeling.

In order to prevent model overfitting, the “ENMTools” package was employed to guarantee the quality of the dataset utilized for model construction and to minimize potential biases in spatial clustering due to data duplication, thereby enhancing the accuracy and reliability of the model [27]. The tool automatically identifies the cell size of the environmental factor grid and eliminates redundant data within the same grid, which in this study was set to 2.5 arcmin (~21 km² at the equator). This approach is rapid and effective, and the results of the analysis are more meaningful. Consequently, the resulting occurrence records are necessarily smaller than the actual distribution area. Ultimately, 963 occurrence data points for *B. xylophilus* were retained for the construction of the MaxEnt model.

![Figure 1. Occurrence records of *B. xylophilus* within China.](image)

In this study, in order to analyze and predict the potential distribution area of *B. xylophilus*, we initially selected 31 environmental variables that may affect the distribution of *B. xylophilus* (Table 1). These variables cover a wide range of aspects, including bioclimatic,
topographic, normalized difference vegetation index, ultraviolet radiation, and human activities [28]. Climate data at a resolution of 2.5 arcmin from the 1970s to 2000s were downloaded from WorldClim version 2.1 for the current period. Future climate data for the 2050s and 2070s were simulated under four shared socioeconomic pathways (SSPs) using the BCC-CSM2-MR global circulation model. Elevation data at 2.5 arcmin resolution were downloaded from WorldClim, and slope and aspect were extracted using ArcGIS Map software (version 10.8.1). We downloaded the normalized difference vegetation index (NDVI) data from the Center for Resource and Environmental Sciences and data from the Chinese Academy of Sciences (https://www.resdc.cn/, accessed on 19 January 2024). In addition, we have downloaded ultraviolet radiation data (https://www.ufz.de/gluv/index.php?en=32367, accessed on 19 January 2024). Human activity data were downloaded from the Socioeconomic Data and Applications Center (https://sedac.ciesin.columbia.edu, accessed on 15 January 2024), including the global human influence index and global human footprint. Finally, we used the “Resample” and “Extract” tools in the ArcGIS Map software to standardize the 31 environmental variables into a consistent format for subsequent analysis and modeling [29]. These data provide a comprehensive environmental background for studying the distribution of *B. xylophilus* in China, helping to understand the relationship between the species and its environment and to predict the possible effects of future climate change on the distribution of the species.

The selection and treatment of environmental variables is a crucial step when constructing a species distribution model, as the interconnections between variables may lead to autocorrelation and multicollinearity problems, which can reduce the predictive accuracy of the model [30]. To address these issues, we first assessed the contribution of the 31 environmental variables in the MaxEnt model using the Jackknife method, which identifies the variables that contribute most to the model predictions. Subsequently, a Pearson correlation analysis was conducted utilizing the “ENMTools” package (version 1.1.3) within the R platform (Figure S1). Environmental variables with correlation coefficients of $|r| \leq 0.9$ were selected for modeling to avoid multicollinearity issues. When the correlation coefficient $|r| > 0.9$ between two environmental variables was observed, the variable with the higher contribution was chosen for inclusion in the model. This implies that in the case of highly correlated variables, only those that contribute the most to the model are retained. Through the aforementioned steps, 13 bioclimatic factors were ultimately incorporated into the MaxEnt model (Figure 2). These variables were deemed to be the most crucial and mutually independent environmental factors in the model, thereby enhancing the predictive accuracy and reliability of the model.

**Table 1.** Screening of 31 environmental variables.

| Abbreviation | Environmental Variables                                      | Operation ($|r| > 0.9$) |
|--------------|-------------------------------------------------------------|------------------------|
| Bio1         | Annual mean temperature (°C)                               | Retain                 |
| Bio2         | Mean diurnal range (°C)                                    | Retain                 |
| Bio3         | Isothermality                                               | Retain                 |
| Bio4         | Temperature seasonality                                     | Retain                 |
| Bio5         | Maximum temp of warmest month (°C)                         | Eliminate              |
| Bio6         | Minimum temp of coldest month (°C)                         | Eliminate              |
| Bio7         | Temperature annual range (°C)                              | Eliminate              |
| Bio8         | Mean temp of wettest quarter (°C)                          | Eliminate              |
| Bio9         | Mean temp of driest quarter (°C)                           | Eliminate              |
| Bio10        | Mean temp of warmest quarter (°C)                          | Eliminate              |
| Bio11        | Mean temp of coldest quarter (°C)                          | Eliminate              |
| Bio12        | Annual precipitation (mm)                                  | Retain                 |
| Bio13        | Precipitation of wettest month (mm)                        | Eliminate              |
| Bio14        | Precipitation of driest month (mm)                         | Retain                 |
| Bio15        | Precipitation seasonality (mm)                              | Retain                 |
| Bio16        | Precipitation of wettest quarter (mm)                      | Eliminate              |
| Bio17        | Precipitation of driest quarter (mm)                       | Eliminate              |
Table 1. Cont.

| Abbreviation | Environmental Variables                                      | Operation (|r| > 0.9) |
|--------------|-------------------------------------------------------------|-------------|
| Bio18        | Precipitation of warmest quarter (mm)                       | Eliminate   |
| Bio19        | Precipitation of coldest quarter (mm)                       | Eliminate   |
| Bio20        | Elevation (m)                                               | Retain      |
| Bio21        | NDVI                                                        | Retain      |
| Bio22        | Slope                                                       | Retain      |
| Bio23        | Aspect                                                      | Retain      |
| Bio24        | Annual_mean_UV-B                                           | Eliminate   |
| Bio25        | UV-B_seasonality                                            | Eliminate   |
| Bio26        | Mean_UV-B_of_highest_month                                  | Eliminate   |
| Bio27        | Mean_UV-B_of_lowest_month                                   | Eliminate   |
| Bio28        | Sum_of_UV-B_radiation_of_highest_quarter                    | Eliminate   |
| Bio29        | Sum_of_UV-B_radiation_of_lowest_quarter                     | Eliminate   |
| Bio30        | Global human footprint                                      | Retain      |
| Bio31        | Global human influence index                                | Retain      |

2.2. Evaluation and Validation of MaxEnt Model

Regularized multipliers (RMs) and feature combinations (FCs) serve as crucial parameters within the MaxEnt model, and optimizing these parameters can substantially enhance the model’s accuracy [31]. The RMs and FCs parameters were optimally tuned using the “ENMeval” package in the R software (version 4.3.3). Feature combinations encompass 5 feature types, namely L (linear features), Q (quadratic features), P (product features), T (threshold features), and H (hinge features). Initially, RMs were configured from 0 to 4 at intervals of 0.5 based on the preserved distribution data and environmental variables. Additionally, 6 FCs were designated to identify the optimal parameter combinations: L, LQ, H, LQH, LQHP, and LQHPT. Subsequently, 48 models incorporating various RM and FC combinations were constructed, and the model with the lowest delta AICc value among the feature combinations was selected as the optimal model (Figure S2). Finally, under natural environmental variable conditions, RMs were set to 0.5 with the FCs specified as “LQHP” (Figure S2A). Under conditions incorporating both natural environment variables and human activities, RMs were set to 1 with the FCs specified as “LQHPT” (Figure S2B). The additional parameter settings for the optimal model were as follows: 25% of the distribution points for each species were selected as the test set, while 75% were used for training. The maximum number of iterations was set to 5000, the maximum number of
background points was limited to 10,000, and the repetitions were carried out 10 times. The closer the test omission rate is to the theoretical omission rate, the more accurate the model construction [32].

In ecological and environmental science research, the area under the curve (AUC) of the receiver operating characteristic curve (ROC) is an important metric for assessing the accuracy and predictive performance of modeling results [33]. The generalization ability of the model can be assessed by comparing the AUC values of the training and test sets and ensures that the model performs well on the training data and accurately predicts new and unseen data [34]. The AUC value determines the accuracy of the model, which ranges from 0 to 1. The larger the AUC value, the higher the accuracy of the model prediction. AUC values below 0.6 indicate a failure of the model performance, rendering the predictions unreliable. Values between 0.6 and 0.7 are considered poor, between 0.7 and 0.8 are considered fair, between 0.8 and 0.9 are considered good, and those above 0.9 are considered excellent. These values help to ensure the reliability and applicability of the findings.

2.3. Changes in the Potential Distribution Areas of B. xylophilus

The impact of natural environmental factors and human activities on the geospatial distribution pattern of B. xylophilus was investigated by developing three distinct models: (1) prediction of natural environmental factors (including bioclimate + topography + ultraviolet radiation + the normalized difference vegetation index) under the current climate model; (2) prediction of natural environmental factors (including bioclimate + topography + ultraviolet radiation + the normalized difference vegetation index) + human activity (including global human footprint + global human influence index) under the current climate model; and (3) prediction of natural environmental factors (including future bioclimate + topography + ultraviolet radiation + the normalized difference vegetation index) under the future climate model. Among them, model (1) and model (2) are based on current climate model projections, while model (3) is based on future climate model projections. Models (1) and (2) were employed to assess the influence of anthropogenic factors on the suitability of habitat for B. xylophilus, while models (1) and (3) were utilized to examine the potential effect of climate change on the suitability of habitat for B. xylophilus.

The average of the optimal MaxEnt model run through 10 repetitions was utilized as the final result, which was then evaluated based on the logistic value of the probability of species presence ($P$). The final results were converted to raster form and visualized using ArcGIS Map software, and the proportion of area in each suitable habitat was calculated. For comparison, the same thresholds were used for categorization in both the current and future climate models [35]. The suitability results for B. xylophilus were classified into two categories based on the natural breaks (Jenks) method in the ArcGIS Map software: unsuitable habitat ($P < 0.172121$) and suitable habitat ($P \geq 0.172121$).

2.4. Change in Potential Distribution Center Shift under Future Climate Scenarios

We applied the “Centroid Changes (Lines)” tool in SDMToolbox v2.6 to identify potential geographic distribution centers in areas of high probability of species presence in each time period. The locations of potential distribution centers were compared across time and under different carbon emission scenarios. This helps to understand how the distribution of species changes in response to different climate change scenarios [36]. In addition, connecting the calculated potential distribution center points for different time periods represents the route of spatial change in the main suitable growing areas for B. xylophilus under future climate conditions.

2.5. Dynamics of Potential Distribution Areas of B. xylophilus under Future Climate Scenarios

We applied the “Distribution Changes between Species Distribution Models (SDMs)” function in SDMToolbox v2.6 to create binary maps with a threshold value of 0.172121, and the binary maps of each category in different future climate change scenarios were compared with the current climate scenarios to assess the future changes in the distribution
Four results were obtained: “Expansion” (species range increases), “No occupancy” (species has no distribution under the new scenario), “Unchanged” (species range remains unchanged), and “Contraction” (species range decreases). In addition, we analyzed the extent of future climate change impacts on \( B. \ xylophilus \) in China using multivariate environmental similarity surfaces (MESSs) [38]. Environmental variables from contemporary potentially suitable areas were used as the reference layer to calculate the similarity between future climate conditions and the current one. The S value reflects the degree of similarity between the climate conditions at a point and the climate conditions in the reference layer during a given period. Negative values indicate that at least one of the environmental variables at the point has a value outside the range of the corresponding value in the reference layer, which is referred to as a climate anomaly, while a maximum value of 100 indicates that the climate at the point is completely normal. This operation is realized by running the “density.tools.Novel” tool in the “maxent.jar” file in the command window, and the ASCII file exported from the model was imported into ArcGIS Map 10.8.1 software for drawing.

### 2.6. Niche Dynamics Analyses

We conducted ecological niche quantification and overlap analyses using the “ecospat” software package (version 4.0.0) to explore climatic ecological niche changes between the ranges of \( B. \ xylophilus \) under contemporary and future climate scenarios [39]. Firstly, the presence and non-presence areas of \( B. \ xylophilus \) were binarised using ArcGIS Map software, with presence marked as 1 and non-presence marked as 0. Then, relevant environmental variables were extracted from each occurrence record. Subsequently, Schoener’s D index was employed to quantify the degree of overlap between ecological niches across climate scenarios, with values ranging from 0 (indicating no overlap) to 1 (representing complete overlap).

### 3. Results

#### 3.1. Model Accuracy and Evaluation

The AUC values were applied to assess the accuracy of the optimized MaxEnt model in the prediction of species distributions. The results of this study showed that under contemporary climatic conditions, the average training AUC value of 10 repetitions of natural environmental variables was 0.9338, and the average testing AUC was 0.9285, while the average training AUC value of the model for the coexistence of natural environmental variables and human activities was 0.9500 and the average testing AUC value was 0.9465, which suggests that human activities may play an important role in predicting the results of the potential distributional areas of \( B. \ xylophilus \) potential distribution areas. In addition, the mean training AUC values and mean test AUC values for the different future carbon emission scenarios under the four climate change scenarios were greater than 0.9 (Table 2). This indicates that the optimized MaxEnt model is more accurate and precise and confirms the stability of the model’s robustness and generalization ability.

<table>
<thead>
<tr>
<th>Shared Socioeconomic Pathways</th>
<th>Train AUC (Avg)</th>
<th>Test AUC (Avg)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Current-Environmental variables</td>
<td>0.9338</td>
<td>0.9285</td>
</tr>
<tr>
<td>Current-Environmental variables + Human activity</td>
<td>0.9500</td>
<td>0.9465</td>
</tr>
<tr>
<td>Future-SSP1.0-2.6 2040–2060</td>
<td>0.9345</td>
<td>0.9277</td>
</tr>
<tr>
<td>Future-SSP1.0-2.6 2060–2080</td>
<td>0.9338</td>
<td>0.9284</td>
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<tr>
<td>Future-SSP2.0-4.5 2040–2060</td>
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<td>Future-SSP2.0-4.5 2060–2080</td>
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<td>Future-SSP5.0-8.5 2060–2080</td>
<td>0.9351</td>
<td>0.9286</td>
</tr>
</tbody>
</table>
3.2. Main Environmental Variables Affecting Distribution of B. xylophilus

In this study, the effect of each variable on the geographic distribution of B. xylophilus was assessed using MaxEnt model outputs and Jackknife methods. This study found that the potential geographic distribution of B. xylophilus in the presence of only natural environmental factors was influenced by precipitation in the driest month (Bio14, 57.9%), annual precipitation (Bio12, 13.7%), elevation (Bio20, 10.6%), and the normalized difference vegetation index (Bio21, 6.2%), with a cumulative contribution of 88.4% (Figure 2). The main variables affecting the potential geographic distribution of B. xylophilus under a combination of natural environmental and human activities were precipitation in the driest month (Bio14, 44%), global human footprint (Bio30, 30.6%), and annual precipitation (Bio12, 7.1%), with a cumulative contribution of 81.7%. The variables with the largest changes in contribution were Bio14 (13.9% decrease), Bio12 (6.6% decrease), Bio20 (7.2% decrease), and Bio21 (4.4% increase) (Figure 2). This indicates that precipitation, the normalized difference vegetation index, elevation, and human activities are the main factors influencing the distribution of B. xylophilus.

3.3. Prediction of the Potential Distribution of B. xylophilus under Climate and Human Interference in the Current

The MaxEnt model was employed to predict the spatial extent and habitat of B. xylophilus with and without anthropogenic disturbance (Figure 3), and the results showed that it was mainly distributed in central and southeastern China, which was similar to the actual occurrence area, indicating that the optimized MaxEnt model was able to simulate the potential distribution area of B. xylophilus well. Under the influence of natural environmental conditions, the occurrence areas of B. xylophilus were mainly concentrated in Liaoning, Shandong, Zhejiang, Anhui, Jiangsu, Shaanxi, Henan, Hunan, Guangdong, Fujian, Chongqing, Sichuan, and Guangxi (Figure 3A). The suitable habitat covered an area of $138.58 \times 10^4 \text{ km}^2$, representing 14.59% of China’s total land area (Table S1).

![Figure 3. Distribution of suitable habitat for B. xylophilus without (A) and with (B) human activity under current climate models in China.](image-url)

Taking into account human activities, the combined suitable habitat area for B. xylophilus in China was $80.13 \times 10^4 \text{ km}^2$, making up 8.44% of China’s total land area. Conversely, unsuitable habitat covered $869.23 \times 10^4 \text{ km}^2$, comprising 91.56% of China’s total area (Figure 3B). Compared with the area affected by natural environmental factors alone,
there was a decrease of 42.18%, and the total area of suitable habitat for *B. xylophilus* decreased by $58.45 \times 10^4$ km$^2$, which represents 6.16% of China’s total land area (Table S1), indicating that human activities have reduced the area of suitable habitat for *B. xylophilus*.

### 3.4. Prediction of the Potential Distribution of *B. xylophilus* under Different Climate Scenarios in the Future

In the context of climate change, the projected suitable ranges of *B. xylophilus* were based on future climate change scenarios with different common socioeconomic pathways and representative concentration pathways. The results showed that under different future climate scenarios, the range of suitable habitats for *B. xylophilus* was generally consistent with the current climate scenario and was mainly distributed in northeast, central and southeastern China, including Liaoning, Shandong, Zhejiang, Anhui, Jiangsu, Shaanxi, Henan, Hubei, Hunan, Guangdong, Fujian, Chongqing, Sichuan and Guangxi (Figure 4). Under the future climate scenarios, the estimated area of suitable habitat for *B. xylophilus* ranges from $137.87 \times 10^4$ km$^2$ to $141.55 \times 10^4$ km$^2$, accounting for 14.52% to 14.92% of China’s total area (Table S1). Among them, SSP3.0-7.0-2070s predicted the largest area of suitable habitat, followed by SSP5.0-8.5-2070s, while SSP1.0-2.6-2050s predicted the smallest area of suitable habitat. Over time, the area of suitable habitat for *B. xylophilus* showed a decreasing and then increasing trend in the low greenhouse gas emission scenario (SSP1.0-2.6, SSP2.0-4.5) and the medium greenhouse gas emission scenario (SSP3.0-7.0), i.e., the area of suitable habitat decreased in the 2050s and increased in the 2070s. However, only the SSP5.0-8.5 scenario shows a continuous increase (Table S1).

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**Figure 4.** Suitable areas for *B. xylophilus* in China under different future climate scenarios. (A) SSP1.0-2.6-2050s; (B) SSP1.0-2.6-2070s; (C) SSP2.0-4.5-2050s; (D) SSP2.0-4.5-2070s; (E) SSP3.0-7.0-2050s; (F) SSP3.0-7.0-2070s; (G) SSP5.0-8.5-2050s; (H) SSP5.0-8.5-2070s.
Figure 4. Suitable areas for *B. xylophilus* in China under different future climate scenarios. (A) SSP1.0-2.6-2050s; (B) SSP1.0-2.6-2070s; (C) SSP2.0-4.5-2050s; (D) SSP2.0-4.5-2070s; (E) SSP3.0-7.0-2050s; (F) SSP3.0-7.0-2070s; (G) SSP5.0-8.5-2050s; (H) SSP5.0-8.5-2070s.

3.5. Relative Changes in the Potential Distribution Area of *B. xylophilus* under Future Climate Scenarios

Relative changes in the potential distribution of *B. xylophilus* were derived by comparing differences in current and future distribution areas (Figures 5 and 6). The results showed that under future climate scenarios, the expansion area ranged from $18.16 \times 10^4 \text{ km}^2$ to $29.82 \times 10^4 \text{ km}^2$, and the contraction area ranged from $6.71 \times 10^4 \text{ km}^2$ to $14.39 \times 10^4 \text{ km}^2$ (Table S2). The expansion is primarily observed in Liaoning, Jilin, Shandong, Henan, Hubei, Guangxi, Guangdong, Guizhou, Jiangxi, Jiangsu, Anhui, Shaanxi, and Fujian. Conversely, the contraction area is predominantly found in Guangxi, Guangdong, Guizhou, Jiangxi, Fujian, Jiangsu, Shandong, Jilin, Xizang, and Taiwan Island (Figure 5). Among them, the largest expansion area was predicted for the high greenhouse gas (GHG) emission scenario SSP5.0-8.5-2070s, followed by SSP3.0-7.0-2070s, while the smallest expansion area was predicted for SSP1.0-2.6-2070s, which was development-pattern- and climate-change-dependent. Whereas the largest contraction area is in the low greenhouse gas (GHG) emission scenario (SSP1.0-2.6-2050s), the smallest is in the medium greenhouse gas (GHG) emission scenario (SSP3.0-7.0-2070s). Furthermore, under future climate scenarios, Inner Mongolia, Shanxi, Ningxia Hui Autonomous Region, Gansu, Qinghai, and Shaanxi exhibit a high degree of similarity with the climatic conditions of their origins (Figure 6), indicating that the climatic zones of the potential distribution area of *B. xylophilus* differ significantly from the current climate reference layer (Table S3).
Jiangxi, Fujian, Jiangsu, Shandong, Jilin, Xizang, and Taiwan Island (Figure 5). Among them, the largest expansion area was predicted for the high greenhouse gas (GHG) emission scenario SSP5.0-8.5-2070s, followed by SSP3.0-7.0-2070s, while the smallest expansion area was predicted for SSP1.0-2.6-2070s, which was development- and climate-change-dependent. Whereas the largest contraction area is in the low greenhouse gas (GHG) emission scenario (SSP1.0-2.6-2050s), the smallest is in the medium greenhouse gas (GHG) emission scenario (SSP3.0-7.0-2070s). Furthermore, under future climate scenarios, Inner Mongolia, Shanxi, Ningxia Hui Autonomous Region, Gansu, Qinghai, and Shaanxi exhibit a high degree of similarity with the climatic conditions of their origins (Figure 6), indicating that the climatic zones of the potential distribution area of *B. xylophilus* differ significantly from the current climate reference layer (Table S3).

**Figure 5.** Relative changes in *B. xylophilus* within China under different future climate scenarios. (A) SSP1.0-2.6-2050s; (B) SSP1.0-2.6-2070s; (C) SSP2.0-4.5-2050s; (D) SSP2.0-4.5-2070s; (E) SSP3.0-7.0-2050s; (F) SSP3.0-7.0-2070s; (G) SSP5.0-8.5-2050s; (H) SSP5.0-8.5-2070s.
3.6. Potential Distribution Center Shifts of *B. xylophilus* under Different Scenarios in the Future

We applied the "Centroid Changes (Lines)" tool to compare changes in the center of distribution of *B. xylophilus* under different carbon emission scenarios, which allowed us to assess the potential impacts of different emission reduction strategies on the movement of the species.

**Figure 5.** Relative changes in *B. xylophilus* within China under different future climate scenarios. (A) SSP1.0-2.6-2050s; (B) SSP1.0-2.6-2070s; (C) SSP2.0-4.5-2050s; (D) SSP2.0-4.5-2070s; (E) SSP3.0-7.0-2050s; (F) SSP3.0-7.0-2070s; (G) SSP5.0-8.5-2050s; (H) SSP5.0-8.5-2070s.

**Figure 6.** MESS analysis for *B. xylophilus* under future climate scenarios in China. (A) SSP1.0-2.6-2050s; (B) SSP1.0-2.6-2070s; (C) SSP2.0-4.5-2050s; (D) SSP2.0-4.5-2070s; (E) SSP3.0-7.0-2050s; (F) SSP3.0-7.0-2070s; (G) SSP5.0-8.5-2050s; (H) SSP5.0-8.5-2070s.
3.6. Potential Distribution Center Shifts of *B. xylophilus* under Different Scenarios in the Future

We applied the “Centroid Changes (Lines)” tool to compare changes in the center of distribution of *B. xylophilus* under different carbon emission scenarios, which allowed us to assess the potential impacts of different emission reduction strategies on the movement routes and ecosystem stability of *B. xylophilus*. The current distribution center of *B. xylophilus* is located in Hubei Province at 113.18° N, 31.60° E (Figure 7 and Table 3). In the SSP1.0-2.6 pathway, the distribution center in the 2050s is located at 31.53° N, 113.49° E, and that in the 2070s is located at 32.35° N, 114.13° E, with the distribution center shifting 122.58 km to the northeast. In the SSP2.0-4.5 pathway, the distribution center was located at 31.71° N, 113.36° E in the 2050s and 31.75° N, 113.05° E in the 2070s, shifting the center of distribution by 20.86 km to the northwest. The distribution center in the SSP3.0-7.0 pathway was located at 31.63° N, 113.30° E in the 2050s and 31.55° N, 113.13° E in the 2070s and moved to the southwest by 7.20 km. In the SSP5.0-8.5 pathway, the distribution center for *B. xylophilus* was located at 31.87° N, 113.36° E in the 2050s and at 31.55° N, 113.40° E in the 2070s, with a southeast move of 21.02 km. As time goes on, the distribution center of *B. xylophilus* remained relatively stable between time points, suggesting that the MaxEnt model performs well in predicting the stability of the potential future range of the species, implying that the model’s selection and trade-offs of environmental variables were accurate (Figure 7 and Table 3).

![Figure 7](image-url)

**Figure 7.** (A) Moving trajectories of potential distribution center routes for *B. xylophilus* in China; (B) The *B. xylophilus* movement routes under different shared socio-economic path models; (C) SSP1.0-2.6; (D) SSP2.0-4.5; (E) SSP3.0-7.0; (F) SSP5.0-8.5.

**Table 3.** Trends in longitude, latitude, and migration distance of *B. xylophilus* in different periods.

<table>
<thead>
<tr>
<th>Shared Socioeconomic Pathways</th>
<th>Longitude (°E)</th>
<th>Latitude (°N)</th>
<th>Center Migration Distance (km)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Current</td>
<td>113.18</td>
<td>31.60</td>
<td>-</td>
</tr>
<tr>
<td>Future-SSP1.0-2.6 2040–2060</td>
<td>113.49</td>
<td>31.53</td>
<td>30.52</td>
</tr>
<tr>
<td>Future-SSP1.0-2.6 2060–2080</td>
<td>114.13</td>
<td>32.35</td>
<td>122.58</td>
</tr>
<tr>
<td>Future-SSP2.0-4.5 2040–2060</td>
<td>113.63</td>
<td>31.71</td>
<td>43.98</td>
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<tr>
<td>Future-SSP2.0-4.5 2060–2080</td>
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<td>31.75</td>
<td>20.86</td>
</tr>
<tr>
<td>Future-SSP3.0-7.0 2040–2060</td>
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<td>31.63</td>
<td>11.93</td>
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<td>113.40</td>
<td>31.55</td>
<td>21.02</td>
</tr>
</tbody>
</table>
3.7. Niche Dynamics of B. xylophilus

The ecological niche similarity of B. xylophilus was analyzed under different climatic scenarios using ecological niche overlap (Figure 8). The Schoene’s D index ranged from 0.74 (current vs. SSP5.0-8.5-2070s) to 0.89 (current vs. SSP1.0-2.6-2070s). The higher overlap values indicate that the ecological niche of B. xylophilus is highly similar under different climate scenarios. This implies that despite future changes in climatic conditions, the ecological needs and adaptations of B. xylophilus remain largely consistent with current climatic variables and may not change significantly in its future range because it is able to adapt to these changes.

Figure 8. Future analysis of B. xylophilus ecological niche dynamics under different climate scenarios. The blue areas show the stable habitats of B. xylophilus, the green areas show the habitats it will lose, and the pink areas show the habitats that are shifting. The red arrow shows the direction of niche migration for B. xylophilus in future climates. Solid and dashed lines connect the current and future distribution centers, with the dashed lines outlining the potential range of distribution changes.

4. Discussion

The accuracy of ecological niche model prediction results depends on the selection of input data and adjustment of model parameters, both of which directly affect the output of the results [40,41]. In this experiment, we used more distribution point data than online books and public online databases and obtained the most recent distribution point data through the National Forestry and Grassland Administration (NFGA) and the literature [25,26], which improved the accuracy and timeliness of the study. We also considered a variety of environmental factors, including climate change, terrain, ultraviolet
radiation, NDVI, elevation, and human activities, which are considered to be key factors influencing the distribution and dynamics of *B. xylostella*. In addition, in order to prevent model overfitting, the MaxEnt model parameter was adjusted in this study, which helped to improve the accuracy and precision of prediction. The results of this study pointed out that all average AUC values exceeded 0.92, indicating the high predictive reliability of the model and the reliability of the findings, which is crucial for the development of science-based management strategies.

In this study, the potentially suitable habitats of *B. xylophilus* were found to be limited by Bio14, Bio12, Bio20, and Bio21 under the influence of no anthropogenic disturbance through the combined analysis of the contribution rate, the sequence importance value, and the Jackknife method, which indicates that the combined effect of humid and thermal conditions plays an important role in the potential distribution of *B. xylophilus* [42,43]. With climate change, there will be a gradual decrease in precipitation in the future and a decrease in water content in the soil, thus exacerbating drought stress. Changes in temperature and precipitation patterns due to climate change may have significant impacts on the species. Global warming may cause species to expand their ranges to higher latitudes or higher altitudes, while changes in precipitation patterns may affect species’ food chains and habitats [44]. Thus, instability in precipitation and temperature may threaten the distribution of *B. xylophilus*, leading to changes in their range and thus spreading to form new distribution patterns [45]. With the involvement of human activities, the global human footprint (Bio30) and the global human influence index (Bio31) are important human factors influencing the distribution of *B. xylophilus*. Expression of agricultural work, road construction, and urbanization can all lead to fragmentation of natural habitats, which in turn reduces areas suitable for *B. xylophilus* survival.

The actual distribution of *B. xylophilus* and the potential distribution area predicted by the model are clustered in northern and central China. These areas have suitable geo-climatic conditions for *B. xylophilus* growth, providing a favorable environment for the survival, reproduction, and spread of *B. xylophilus* [46]. In addition, the transmission of *B. xylophilus* is mainly dependent on its insect vectors, *Monochamus alternatus* and *Monochamus saltuarius*. The larvae of these insects bore holes within the trunks of trees to form channels where *B. xylophilus* is usually found in the woody parts of pine trees. As the larvae of the family Cerambycidae develop within the pine tree, they may carry *B. xylophilus*, and when they develop into adults, they burrow out of the pine tree. Cerambycidae insects may transmit *B. xylophilus* to healthy pines as they search for new pines in which to lay their eggs [47,48]. Therefore, the range and number of these insect vectors play a key role in the spread of pine nematode dispersal. The climatic conditions in central and northern provide favorable conditions for the growth of pine trees, as well as suitable environments for the reproduction and activities of Cerambycidae [49]. These factors work together to make southern, central, and northeastern China high-risk areas for the spread and propagation of the PWD.

Climate change has altered the phenology and geographical distribution of the *B. xylophilus*, resulting in expansion and contraction of its range [50]. The results show that the expansion areas occur mainly in southern, central, and northeastern China, especially in Liaoning, Jilin, Shandong, Henan, Fujian, and Guangdong. These areas may become more suitable for the survival and reproduction of *B. xylophilus* due to changes in temperature and precipitation patterns caused by climate change. On the contrary, the contraction areas of *B. xylophilus* mainly occurred in Guizhou, Jiangsu, and Liaoning, which may be due to environmental conditions that are no longer suitable for *B. xylophilus* survival due to climate change [51]. Under the low–medium carbon greenhouse gas (GHG) emission scenarios (SSP1.0-2.6 and SSP2.0-4.5), the contracted area of *B. xylophilus* was larger than the expanded area, suggesting that suitable habitats for *B. xylophilus* will be continuously lost with climate change. However, under the medium-to-high carbon greenhouse gas (GHG) emission scenarios (SSP3.0-7.0 and SSP5.0-8.5), the contracted area of *B. xylophilus* was smaller than the expanded area, which may indicate that *B. xylophilus* is less dependent on its current
habitat and is able to adapt to a wider range of environmental conditions [52]. Similarly, it has been suggested that slight changes in the potential distribution of species as a result of climate change may be a consequence of the occurrence of their ecological amplitude and ecological niche width [53]. In this study, the ecological niche overlap analysis revealed that the ecological niche overlap of *B. xylophilus* was greater than 0.74 under different climatic scenarios, which indicates that *B. xylophilus* has a high ecological niche width and adaptability to maintain its ecological niche under different climatic conditions. In addition, the suitability areas of *B. xylophilus* did not change significantly under future climate change, which may imply that *B. xylophilus* has a strong adaptive capacity and can maintain its distribution range normally under the background of climate change.

Changes in temperature and precipitation patterns due to climate change can affect the geographic distribution of *B. xylophilus*, leading to a shift in its range center. This shift may occur towards higher or lower latitudes, depending on the different shared socioeconomic pathways (SSP) scenarios, which model the extent and rate of climate change [54]. Under the SSP1.0-2.6 and SSP2.0-4.5 scenarios, the *B. xylophilus* moves to higher latitudes, possibly because projected climate change under the low greenhouse gas (GHG) emissions scenario results in more favorable temperature and precipitation conditions at higher latitudes. In contrast, *B. xylophilus* migration to lower latitudes under the SSP3.0-7.0 and SSP5.0-8.5 scenarios may be due to the degradation of suitable areas at lower latitudes as a result of projected climate change under the medium–high greenhouse gas (GHG) emissions scenarios, forcing the species to search for new suitable habitats [55]. It is worth noting that migration to lower latitudes may be relative and does not necessarily mean that climatic conditions at lower latitudes become more favorable, but may simply be due to the degradation of suitable areas at higher latitudes [56]. In addition, geographical anomalies may also cause species to migrate to lower latitudes, suggesting that changes in species’ distributions may not only be due to climate change but may also be influenced by other factors, such as human activities that help certain species to overcome natural barriers and thus expand their ranges.

From the results of this study, we found that *B. xylophilus* is at risk of spreading to the northeast (Liaoning and Jilin) and central regions (Henan and Shandong) in the future, and that failure to prevent and control it in time may lead to the death of a large number of pine trees, which constitutes an ecological disaster. To address this challenge, China has taken a series of comprehensive control measures [57], which include the following: 1. timely detection of outbreaks through quarantine and monitoring to prevent the spread of the disease; 2. removal of infected trees to reduce the source of transmission of the pathogen; 3. control of insect vectors that transmit the *B. xylophilus*; 4. utilization of trunk injection techniques to inject insecticides into the tree, which distributes the drug throughout the tree by transpiration to kill the nematode; and 5. adoption of the natural enemies of the nematode, such as predatory nematodes or other microorganisms, to control pine nematode populations. A combination of the above measures can effectively control the spread of *B. xylophilus* and protect forest resources [58]. Nevertheless, due to the complexity and rapid spread of *B. xylophilus*, control requires sustained efforts and interdisciplinary cooperation to meet the challenges posed by *B. xylophilus* and thus protect China’s forest resources and ecological balance [59,60].

5. Conclusions

In this study, an optimized MaxEnt model was used to assess the potential distribution area and dynamics of *B. xylophilus* in China based on references and the latest distribution data published by the National Forestry and Grassland Administration, and a variety of environmental factors, including climate change, terrain, vegetation, ultraviolet radiation, and human interference. The prediction results showed that temperature, precipitation, NDVI, elevation, and human activities were the key factors affecting the distribution of *B. xylophilus*. Under current climatic conditions, suitable habitat areas are mainly distributed in Liaoning, Shandong, Zhejiang, Anhui, Jiangsu, Shaanxi, Henan, Hubei, Hunan, Guang-
dong, Fujian, Chongqing, Sichuan and Guangxi. Between 2050 and 2070, the potential range area of *B. xylophilus* is at risk of spreading to the northeast, suggesting that focused monitoring in the northeast is needed to prevent *B. xylophilus* from damaging pines in the region. Furthermore, the high ecological niche similarity indicates that *B. xylophilus* will be able to locate similar habitats under future climatic conditions, which may facilitate its spread and ability to adapt to new environments. The results of this study will provide valuable references for the development of sustainable management strategies for agriculture and forestry in China under the challenge of climate change, which will help to reduce economic losses and promote the healthy and stable development of ecosystems.

**Supplementary Materials:** The following supporting information can be downloaded at https://www.mdpi.com/article/10.3390/f15071253/s1, Figure S1: Correlation among the 31 bioclimatic variables; Figure S2: Tuning parameters for *Bursaphelenchus xylophilus* in predicting potential distribution regions using the MaxEnt model. Table S1: Area of *B. xylophilus* under current (with and without human activity disturbance) and future climate scenarios; Table S2: Relative change in potential range size of *B. xylophilus* under different future climate scenarios; Table S3: Multivariate environmental similarity surfaces (MESS) affecting the distribution of *B. xylophilus* under future climate conditions.

**Author Contributions:** Conceptualization, L.Z.; methodology, L.Z.; software, L.Z.; validation, L.Z. and P.W.; formal analysis, L.Z.; investigation, P.W. and G.X.; resources, W.W.; data curation, P.W. and G.X.; writing—original draft preparation, L.Z.; writing—review and editing, L.Z.; visualization, L.Z. and P.W.; supervision, W.W.; project administration, W.W.; funding acquisition, P.W. and W.W. All authors have read and agreed to the published version of the manuscript.

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