forests

Article

Habitat Suitability of Pine Wilt Disease in Northeast China under Climate Change Scenario

Jue Wang †, Jifeng Deng †, Wenfeng Yan and Yanan Zheng *

College of Forestry, Shenyang Agricultural University, Shenyang 110866, China; wjgz173@163.com (J.W.); jifeng-deng@syau.edu.cn (J.D.); yanwenfeng0303@163.com (W.Y.)
* Correspondence: rockyya@163.com; Tel.: +86-186-4040-3865
† These authors contributed equally to this work.

Abstract: Pine wilt disease (PWD), caused by *Bursaphelenchus xylophilus*, is one of the most severe forest diseases worldwide. PWD causes devastating disasters to Chinese pine trees, seriously threatening forestry production and the forest ecological environment, and causes economic losses of over ten billion yuan per year to China. Previous studies have shown that the spread of PWD is closely related to climate factors. Today, PWD is spreading rapidly owing to abnormal climate changes. In order to provide a reference for controlling the spread of PWD in China, in this study, we accurately assessed the risk of the continued spread of PWD in Northeast China; a correlative species distribution model (MaxEnt) (RM = 1, AUC = 0.9904) was used to evaluate China's climate suitability for PWD. The effects of climate factors on the spread of PWD in Northeast China were studied using Liaoning Province as an example by analyzing the relationship between the changes in average precipitation, average temperature, average relative humidity, average vapor pressure deficit, average wind speed, average sunshine duration and the area of the PWD epidemic over the past five years. These results suggest that with the change in climate, the areas suitable for PWD have expanded, and certain previously unsuitable areas for its distribution have become suitable. Temperature and precipitation were found to play key roles in the occurrence and damage of PWD, and hot and arid conditions favored the spread of PWD. It is recommended that for areas within the suitable range of PWD but not yet epidemic areas, quarantine should be strengthened to prevent the further spread of PWD. In addition, special attention should be paid to epidemic areas with high temperatures and arid while the monitoring of PWD should be strengthened to achieve the early detection and timely treatment of infected epidemic trees. Our results indicate that PWD undoubtedly poses a major threat to Northeast Chinese pine species if climate change proceeds as projected. In the future, more attention should be paid to monitoring the northward spread of PWD, and further studies should consider meteorological data forecasts, which could facilitate timely control measures.

Keywords: pine wilt disease; climate factors; Northeast China; MaxEnt; temperature; precipitation

Citation: Wang, J.; Deng, J.; Yan, W.; Zheng, Y. Habitat Suitability of Pine Wilt Disease in Northeast China under Climate Change Scenario. *Forests* **2023**, *14*, 1687. https://doi.org/10.3390/f14081687

Academic Editors: Jolanta Behnke-Borowczyk, Joanna Mucha and Radoslaw Witkowski

Received: 25 June 2023
Revised: 5 August 2023
Accepted: 11 August 2023
Published: 21 August 2023

1. Introduction

Pine wilt disease (PWD) is caused by *Bursaphelenchus xylophilus*. It is one of the most devastating forest diseases worldwide [1]. Since *B. xylophilus* was first detected to infect pine trees in 1905, it has been devastating millions of hectares of pine forests in parts of Asia and Europe for a hundred years and has been placed under global quarantine [2]. It is generally believed that *B. xylophilus* originates in North America [3]. Today, the disease mainly invades Asia, occurring in Japan, China, and South Korea [4]. In Asia, the disease was first recorded in Japan [5]. Spreading from Japan, *B. xylophilus* was subsequently detected in South Korea in 1988 [6]. The pine forests in China are the most damaged by the disease. In China, it was first spotted in 1982 in Nanjing, Jiangsu [7]. PWD has been prevalent in the most suitable areas of southern China for 35 years since its first occurrence in China [2]. In Dalian, Liaoning, *Pinus thunbergii* was discovered to be severely infected by PWD in 2016. In 2018, *P. tabuliformis* was also found to be infected with PWD in Fushun, northern Liaoning [8]. This indicated that PWD had spread northward to the mid-temperate regions of China. The disease caused by *B. xylophilus* now occurs in 19 provinces in China [9]; billions of pine trees have died due to *B. xylophilus* infection over the past 38 years, in the period from 1982 to 2020, and more than 1.81×10^4 km^2 of forests have been infected. As the most serious and costly invasive pest over the past 20 years, *B. xylophilus* has caused both direct and indirect economic losses reaching hundreds of billions of yuan [10].

B. xylophilus cannot spread by itself in nature and needs to be transmitted via vector insects from infested trees to healthy ones [11]. *Monochamus alternatus* and *M. saltuarius* are major vectors of *B. xylophilus* in Asia [2]. *M. saltuarius* is mainly distributed in mid-temperate regions and is a major vector of *B. xylophilus* in Northeast China [8,12]. Vector beetles transmit *B. xylophilus* mainly through wounds that are caused by feeding on healthy pine trees [13,14]. About 3–4 weeks after *B. xylophilus* infects a pine tree, the amount of pine resin decreases, and the release of volatiles attracts vector beetles to locate and oviposit on the pine tree [15]. Subsequently, *B. xylophilus* fourth-stage dispersal juvenile larvae (L_{IV}) in the dead tree enter the trachea of its vector again and complete the infection cycle [16] (Figure 1).

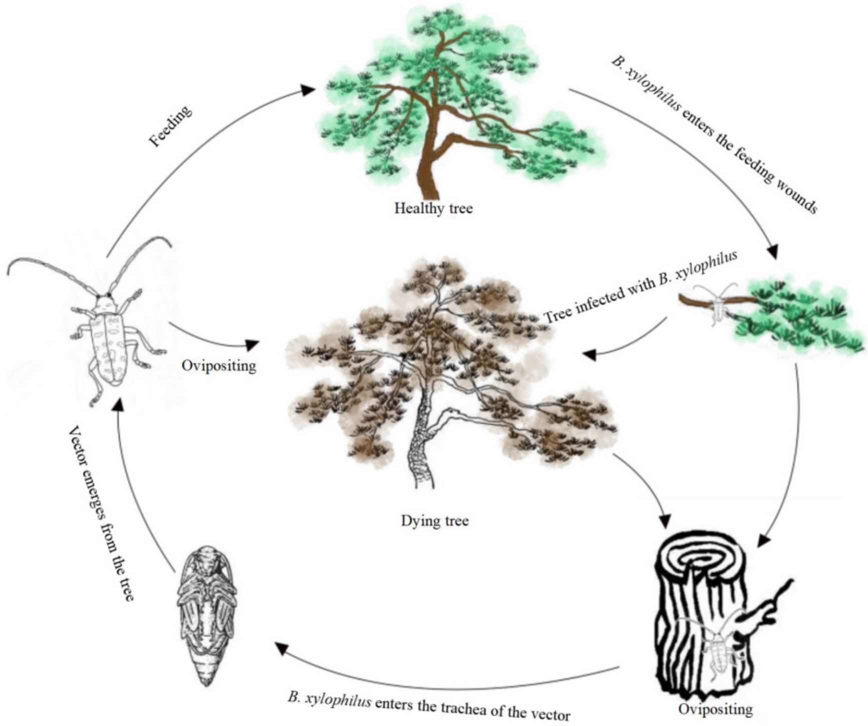

Figure 1. The infection cycle of *Bursaphelenchus xylophilus*.

In addition to affecting vector insects, climate change can affect the spread of *B. xylophilus* [17]. Whether pine trees die from PWD infection depends on host–vector–pathogen species interactions in combination with other factors [17], among which climate factors are one of the most important external factors affecting its infection cycle [18]. Among the climate factors, precipitation, light, and relative humidity can directly affect the survival and growth of the host pine trees, while temperature and humidity restrict the development and spread of vector insects [19]. High temperatures and dry climate conditions are conducive to the outbreak of PWD in new ecosystems [14]. The northward spread of PWD in China depends on *B. xylophilus*, *M. saltuarius*, and climate factors. Forecasting and analyzing suitable habitats are great reference values for controlling this spread. With the continuous development and improvement of climate simulation technology, the dispersal trend of invasive alien species under future climate conditions simulated by climate models has gradually become a new research direction [20,21]. Climate factors, biotic interactions, and species dispersal are the primary factors that determine a species' range in these models. Species distribution models (SDMs) have been developed to predict geospatial distribution by simulating the limiting effects of single or multiple factors on species distribution [22]. The most widely used models include CLIMEX, GARP, DIVA-GIS, and MaxEnt [23]. Among these, the MaxEnt model has already been widely used in the dispersal and distribution study of different plants, insects, and fungi [24] and, therefore, is applicable to our study. For example, MaxEnt has been used in multi-angle and fine-scale studies to predict the risk of PWD's continued spread in China [25]. The MaxEnt model was used in this study to identify the current and potential distribution and habitat suitability of three pine species and *B. xylophilus* in China [26]; MaxEnt was used to model PWD-damaged forest distributions during the period 1982 to 2020, and environmental factors included annual meteorological and human activity factors [27]. We used the MaxEnt model to evaluate the adaptability of PWD in the Liaoning Province, located in Northeast China and assessed the risk of the continued spread of PWD in this area. The MaxEnt model used the exact location of species occurrence and environmental variables to estimate the maximum entropy distribution of the species subjected to environmental constraints.

Climate factors are the key factors affecting species distribution on a large scale, and climate change has a significant impact on the distribution of pests [28]. We believe that PWD is also affected by climate factors. Global warming is the future trend of climate change [29], and modeling the future climate as accurately as possible is a prerequisite for predicting the potential geographic distribution of pests. In order to clarify the suitable range of PWD in China under current climate conditions and to clarify the impact of climate factors on the spread of PWD in China, in the present study, we first analyzed the current distribution of PWD in China. Then, we predicted the distribution of PWD in northern China under future climate conditions using the MaxEnt model. The effect of climate factors on the level of PWD morbidity was analyzed, and their effect on the northward spread of PWD in China was clarified. The research results provide a reference for controlling the spread of PWD in China.

2. Materials and Methods

2.1. Distribution Data

The related location data of PWD in China were first downloaded from the National Forestry and Grassland Administration of China (NFGA) (http://www.forestry.gov.cn/ (accessed on 12 September 2022)) with a total of 154 sample points. ENMTools software was used to screen distribution point data with an accuracy of 5 km, resulting in 148 valid distribution point data. We used Google Maps to determine the longitude and latitude of exact geocoordinates and altitude information. The occurrence points of PWD were visualized in ArcMap 10.6, and points within the study area were selected, exported, and used in the analysis (Figure 2). Data on the damage inflicted by PWD, including the number of epidemic areas, the number of dead pine trees, and damaged areas, were determined from the report on PWD published by the forestry bureaus and provinces in China. The distribution data of host pine trees were determined from the Plant Science Data Centre of the Chinese Academy of Sciences (https://www.plantplus.cn/cn (accessed on 20 October 2022)).

The first occurrence of PWD in an area with an average annual temperature below 10 °C was in Liaoning, China. This province was confirmed as an epidemic area for PWD, and most epidemic counties and cities are located in the mid-temperate region of eastern China (Figure 3).

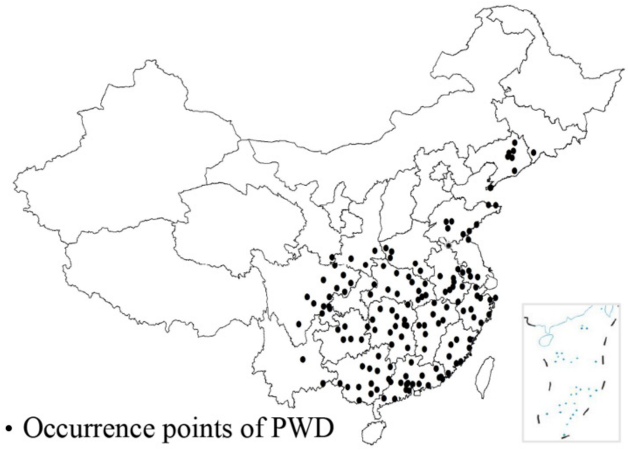

Figure 2. The occurrence points of pine wilt disease (PWD) used for MaxEnt modeling. The map was downloaded from the China Standard Map Service System (https://bzdt.ch.mnr.gov.cn/ (accessed on 12 September 2022)).

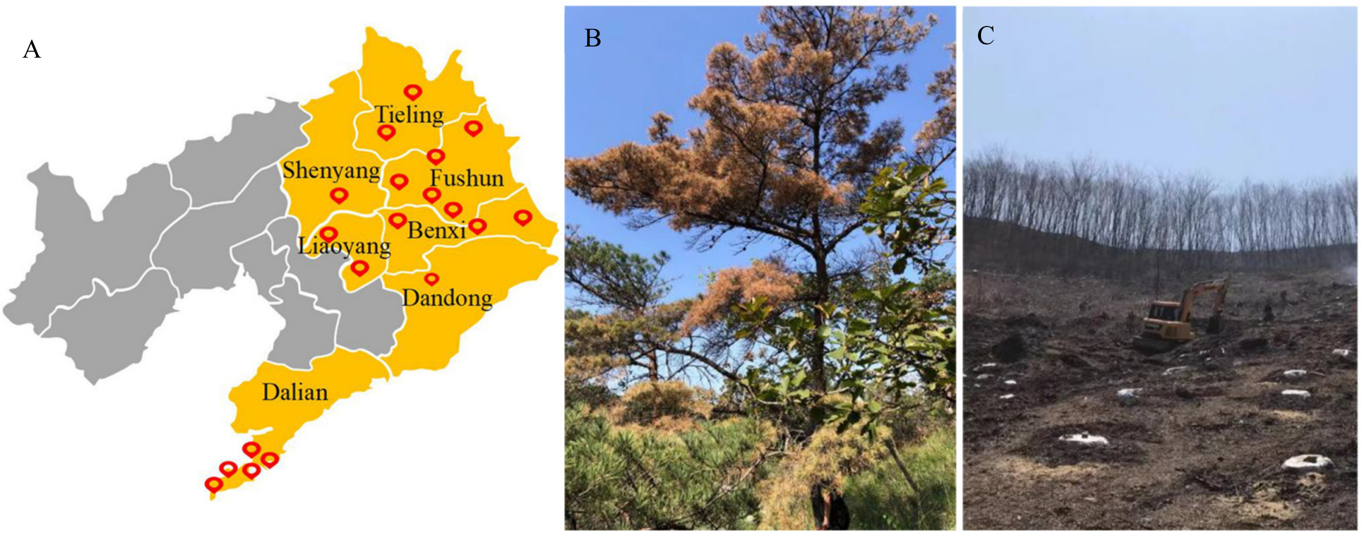

Figure 3. Pine wilt disease (PWD) distribution in Liaoning, China. (**A**) The occurrence points of PWD. (**B**) Pine trees that died from PWD (Data is current as of 2022). (**C**) Infected pine trees that were subsequently felled. The map was downloaded from the China Standard Map Service System (https://bzdt.ch.mnr.gov.cn/ (accessed on 12 September 2022)).

2.2. Climate Data

Current and future PWD suitable regions in China were simulated, in which 19 variables of environmental climate data, including current (1970–2000) and future (2021–2040) climate data at a 2.5 arc minute resolution, were downloaded from the Global Climate Database (WorldClim, http://www.worldclim.org (accessed on 14 September 2022)). The variance inflation factor was used to test the collinearity between climate variables, and finally six variables were selected to construct the species distribution model of PWD, including the precipitation of the warmest quarter, temperature seasonality, the precipitation of the wettest month, the mean temperature of the wettest quarter, the mean diurnal range, and precipitation seasonality were selected (Table 1).

General circulation models (CCSM4) under SSP5-8.5 Intergovernmental Panel on Climate Change (IPCC) emission scenarios (IPCC AR5) with 20 years on average for 2030 (average for 2021–2040) were used in this study. Climate data (including commonly used meteorological factors such as average precipitation, average temperature, average relative humidity, the average vapor pressure deficit, average wind speed, and average sunshine duration.) for Liaoning Province (2016–2021) were obtained from meteorological stations in the China Meteorological Administration (CMA, 2016–2021; http://data.cma.cn/ (accessed on 22 September 2022)). Environmental factor data were uniformly transformed from ArcGIS 10.6 into the ASCII format for convenient use. Regarding geographical data, the vector map of Chinese Administrative Regionalization at a scale of 1:60,000,000 was downloaded from the China Standard Map Service System (https://bzdt.ch.mnr.gov.cn/ (accessed on 12 September 2022)).

Table 1. Contributions of climate variables to the model of MaxEnt.

Climate Variables	Mean	Unit	Contribution (%)
Bio 1	Annual mean temperature	°C	0.38
Bio 2	Mean diurnal range	°C	3.87
Bio 3	Isothermality (Bio2/Bio7) (* 100)	%	0.51
Bio 4	Temperature seasonality (standard deviation * 100)	°C	19.10
Bio 5	Max temperature of warmest month	°C	0.27
Bio 6	Min temperature of coldest month	°C	0.15
Bio 7	Temperature annual range (Bio5-Bio6)	°C	0.20
Bio 8	Mean temperature of wettest quarter	°C	0.05
Bio 9	Mean temperature of driest quarter	°C	0.09
Bio 10	Mean temperature of warmest quarter	°C	5.76
Bio 11	Mean temperature of coldest quarter	°C	0.32
Bio 12	Annual precipitation	mm	0.01
Bio 13	Precipitation of wettest month	mm	8.61
Bio 14	Precipitation of driest month	mm	0.23
Bio 15	Precipitation seasonality (coefficient of variation)	mm	2.50
Bio 16	Precipitation of wettest quarter	mm	0.62
Bio 17	Precipitation of driest quarter	mm	0.20
Bio 18	Precipitation of warmest quarter	mm	56.88
Bio 19	Precipitation of coldest quarter	mm	0.25

* "bio" stands for "bioclimatic variables".

The vapor pressure deficit (VPD) was calculated by combining temperature (Ta) and relative humidity (RH), as follows:

$$\mathrm{VPD} = \mathrm{a} \times \exp[\mathrm{b} \times \mathrm{T_a}(\mathrm{T_a} + \mathrm{c})] \times (1 - \mathrm{RH})$$

where a is 0.61 kPa, b is 17.50, and c is 240.97 °C.

2.3. Data Analysis

The MaxEnt model was used to simulate and predict the future distribution of PWD. The collected 148 distribution coordinates of PWD (.csv) were converted into the ASCII format of China's bioclimatic layer with ArcGIS 10.6 software and were imported into MaxEnt 3.4.1 software. When using the MaxEnt model, 70% of the randomly selected occurrence data were used to build the model, and 30% of the data were retained for testing the model's performance. Other settinggs were set to default values for data simulation, the regularization multiplier (RM) was 1, and the simulation results were output in Cloglog format and ASC files. This process was repeated ten times. The area under the curve (AUC) of the receiver operating characteristic (ROC) curve was used to assess the accuracy of the model prediction. In general, a larger AUC value indicated better model accuracy, while an AUC value of 0.90~1.00 indicated very good models, 0.70~0.90 indicated better models, 0.50~0.70 indicated poor models, and less than 0.5 indicated worse than random models. The prediction results were visually transformed and reclassified using ArcGIS 10.6 software, and the fitness level of PWD was classified into four categories using Jenks' natural breaks, i.e., "unsuitable", ≤0.08; "low suitable", 0.08~0.27; "medium suitable", 0.27~0.55; and "high suitable", >0.55. In the ArcGIS 10.6 software, the weight of each level was calculated and then converted into the actual area of each level according to the actual area of each country's territory so as to obtain the actual area of China's suitable range in the future and analyze the trend of suitable range changes based on this result. All analyses and equation fitting were performed in SPSS 20.0, MaxEnt 3.4.1, and ArcGIS 10.6.

3. Results

3.1. Distribution of PWD in China

3.1.1. Spread Path and Spatiotemporal Distribution of PWD

PWD was first spotted in 1982 at the Sun Yat-sen Mausoleum in Nanjing, Jiangsu. It then spread to Anhui and Guangdong in 1988 and Taiwan in 1989, followed by Shandong in 1990 and Zhejiang in 1991. From 1992 to 1999, the disease was endemic in these six provinces of China. In 2000, it was recorded in Shanghai and Hubei, followed by Fujian, Chongqing, and Guangxi in 2001, Jiangxi, Hunan, and Guizhou in 2003, Sichuan and Yunnan in 2004 and Henan and Shaanxi in 2009. During the 35-year period from 1982 to 2017, PWD showed a predominantly southward-spreading trend with widespread prevalence in the warm temperate regions (Shandong, Shaanxi, Henan) and subtropical regions (Jiangsu, Anhui, Zhejiang, Hubei, Chongqing, Sichuan, Taiwan, Fujian, Jiangxi, Hunan, Guizhou, Yunnan, Guangxi, Guangdong) of China (Figure 4A). Liaoning is located on the border between the warm temperate and the mid-temperate regions of China, with Dalian in Liaoning in the warm temperate and most of the area, such as Fushun in Liaoning, in mid-temperate regions. In 2016, Liaoning was confirmed as an epidemic area for PWD. By 2018, PWD had spread northwards to Fushun in Liaoning, reaching the mid-temperate region. Subsequently, PWD continued to spread, reaching Tianjin in 2018 and Jilin and Gansu in 2021. It is worth mentioning that Liaoning, Jilin, and Gansu are occurrence areas with an average annual temperature below 10 °C. The westernmost occurrence area is Liangshan, Sichuan, and the northernmost point is Tonghua, Jilin. In China, PWD tends to spread northward and westward. To date, the disease has been recorded in 19 provinces (autonomous regions/municipalities) of China. Since PWD was first recorded in China in 1982, the number of epidemic provinces has been increasing year by year and has been gradually controlled with a slower growth rate since 2006 (Figure 4B).

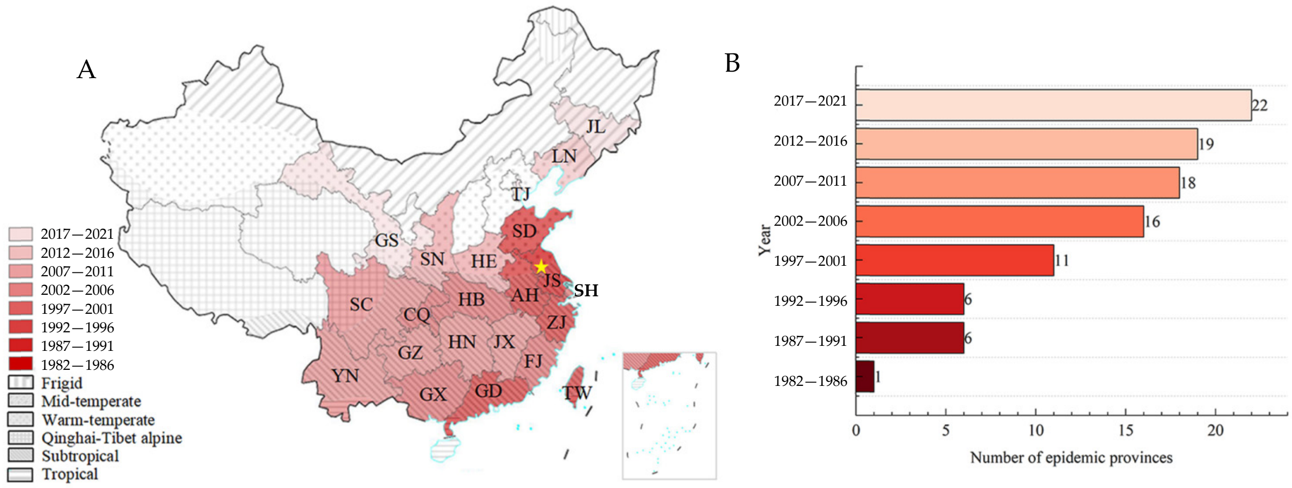

Figure 4. Distribution of pine wilt disease (PWD) in China. (**A**) Spatiotemporal distribution of PWD in China (The map was downloaded from the China Standard Map Service System (https://bzdt.ch.mnr.gov.cn/ (accessed on 12 September 2022)). The letters on the map show the abbreviations of each province. AH: Anhui, FJ: Fujian, CQ: Chongqing, GD: Guangdong, GS: Gansu, GX: Guangxi, GZ: Guizhou, HB: Hubei, HE: Henan, HN: Hunan, JL: Jilin, JS: Jiangsu, JX: Jiangxi, LN: Liaoning, SC: Sichuan, SD: Shandong, SH: Shanghai, SN: Shaanxi, TJ: Tianjin, TW: Taiwan, YN: Yunnan, ZJ: Zhejiang. The province marked with an asterisk is the center of the PWD epidemic in China. (**B**) The number of epidemic provinces in different years.

3.1.2. Climate Conditions and Host Tree Distribution in PWD Epidemic Areas

The main climate types in China include the tropical monsoon, subtropical monsoon, temperate monsoon, plateau mountain, and temperate continental climates. In China, PWD is predominantly found in subtropical monsoon climate areas, with a lower prevalence in tropical and temperate monsoon climate regions, while its presence is limited in temperate continental and highland mountain climate areas (Figure 5A). At present, PWD naturally infects 17 pine species in China, including *Pinus thunbergii*, *P. densiflora*, *P. massoniana*, *P. luchuensis*, *P. bungeana*, *P. taiwanensis*, *P. elliottii*, *P. kesiya*, *P. yunnanensis*, *P. taeda*, *P. tabuliformis*, *P. armandii*, *P. koraiensis*, *Larix olgensis*, *L. kaempferi*, *L. principis-rupprechtii*, and *P. sylvestris* var. *mongolica*. These pine tree species are widely distributed in China, typically with a variety of pines growing in the same area. Their distribution covers mainly the eastern region, which highly overlaps with the current distribution of PWD in China. The Northeast China forest region (including the Daxinganling, Xiaoxinganling, and Changbai Mountains) is the largest natural forest in China, with extensive pine forests. Therefore, the spread of PWD poses a potential threat to this region (Figure 5B).

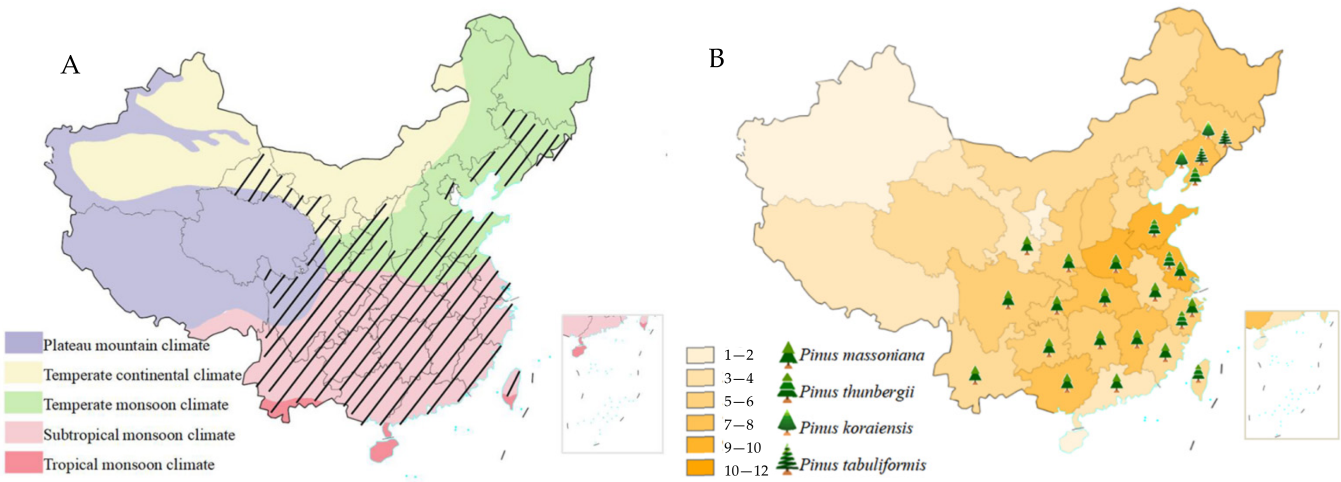

Figure 5. Distribution and host pine trees of *Bursaphelenchus xylophilus* in China. (**A**) Distribution of main climate types in China. Areas with oblique lines indicate the endemic areas of PWD. (**B**) Natural distribution of host pine trees in China. The different color blocks on the map show the number of *B. xylophilus* host species in each province, and the icons show the host pine species that are heavily infested by PWD in each province.

3.2. Relationship between PWD Epidemic Situation and Climate Factors

3.2.1. Damage Inflicted by PWD in China

From 2016 to 2021, the number of PWD epidemic counties in China annually increased. In 2019, the fastest growth rate was observed, while it was relatively steady during the other years (Figure 6A, Supplementary Data S1). From 2016 to 2020, both the area where PWD inflicted damage and the number of dead pine trees in China increased year by year. In 2021, the damaged area of PWD and the number of dead pine trees in China showed a downward trend for the first time, decreasing by 5.12% and 27.69%, respectively, compared with those in 2020 (Figure 6A). Data on the damage inflicted by PWD in China from 2016 to 2021 revealed the consistent pattern of its continued spread throughout the country (Figure 6B). Large areas of pine forests were infected, leading to the extensive mortality of pine trees and, thus, resulting in significant ecological damage.

3.2.2. Relationship between the Epidemic Area and Climate Factors

When PWD spread to Liaoning, China, in 2016, it was the first time that it had spread to an area with an annual average temperature below 10 °C in China. This indicates that PWD has the potential to continue spreading northward to areas with lower average annual temperatures. Thus, we analyzed the relationship between the occurrence areas of PWD and climate factors in summer (June to August) in Liaoning. The results showed that the change in the epidemic area during the year was positively correlated with the change in the average temperature (Figure 7B), average VPD (Figure 7D), and average wind speed (Figure 7E). The change in the epidemic area during the year was inversely correlated with average precipitation (Figure 7A), average relative humidity (Figure 7C), and average sunshine hours (Figure 7F). Hot and dry environments in summer were found to be conducive to the occurrence of PWD. However, high wind speed, short sunshine duration, and other environments that are not conducive to host tree growth also promoted the occurrence of PWD. Precipitation and temperature were the most critical climate factors affecting PWD occurrence in Liaoning.

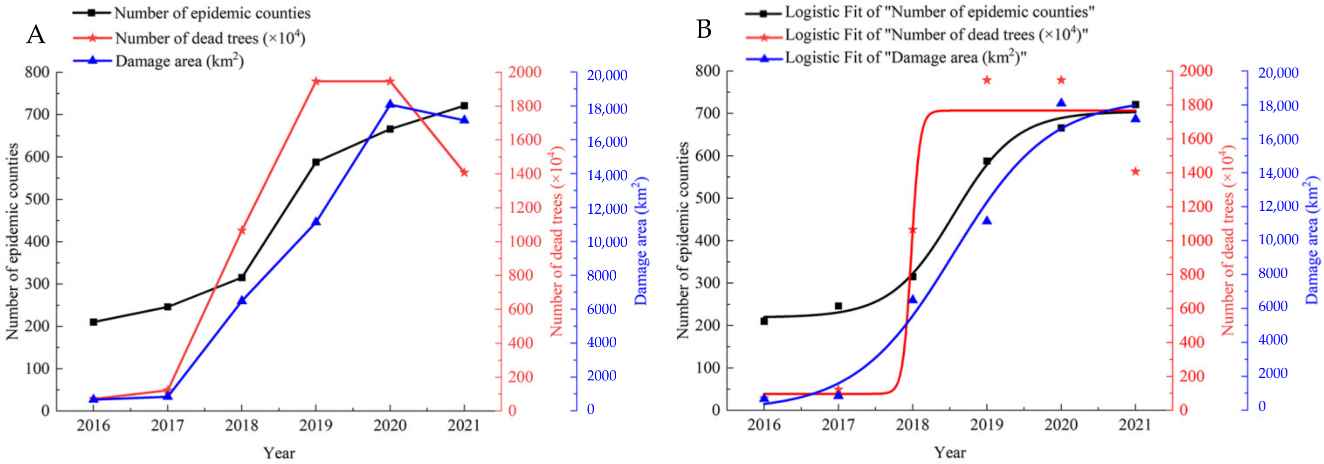

Figure 6. Damage inflicted by pine wilt disease (PWD) in China from 2016 to 2021. (**A**) Trends in the number of epidemic counties, the number of dead trees, and damaged areas infected by PWD in China. (**B**) Logistic fit of trends for the number of epidemic counties, the number of dead trees, and damaged areas infected by PWD in China.

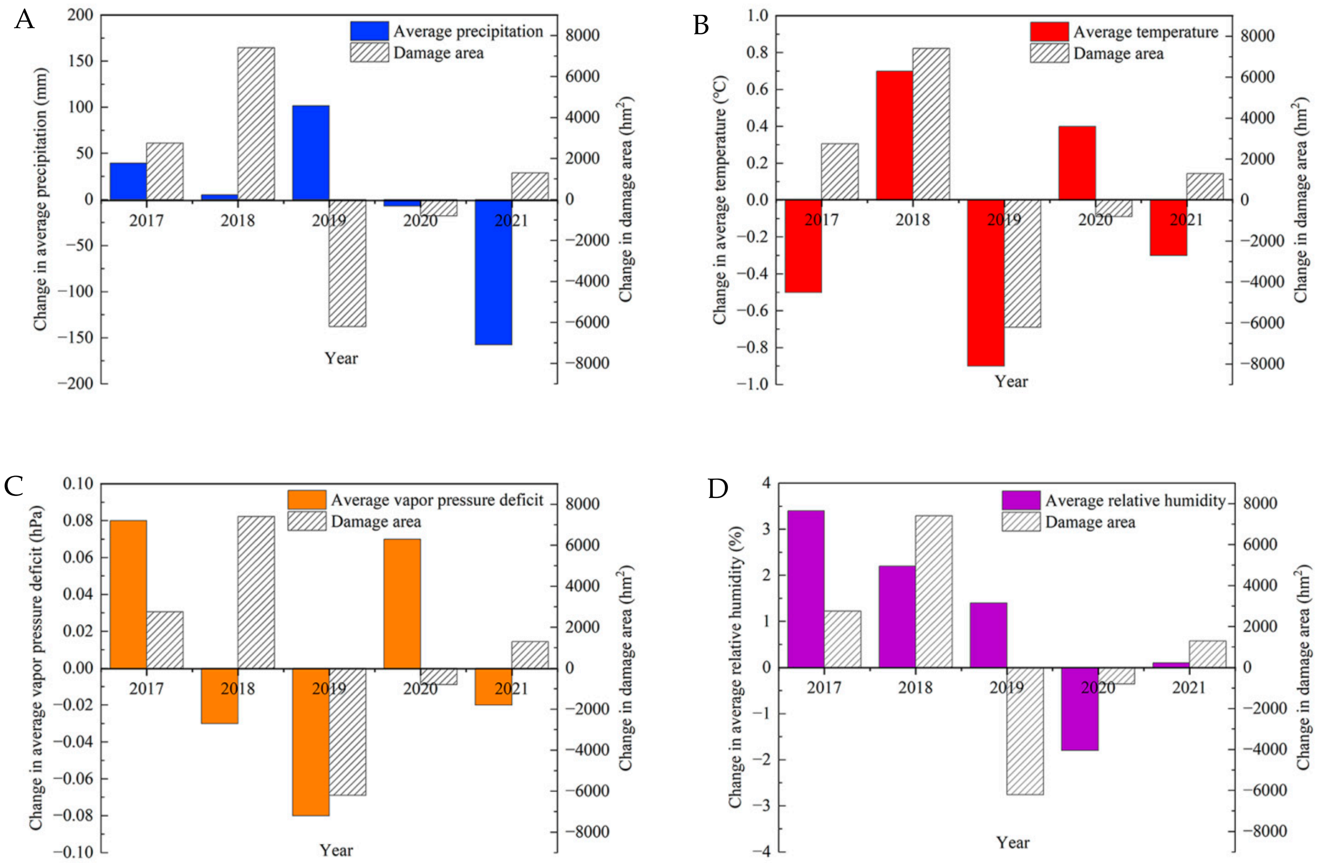

Figure 7. *Cont.*

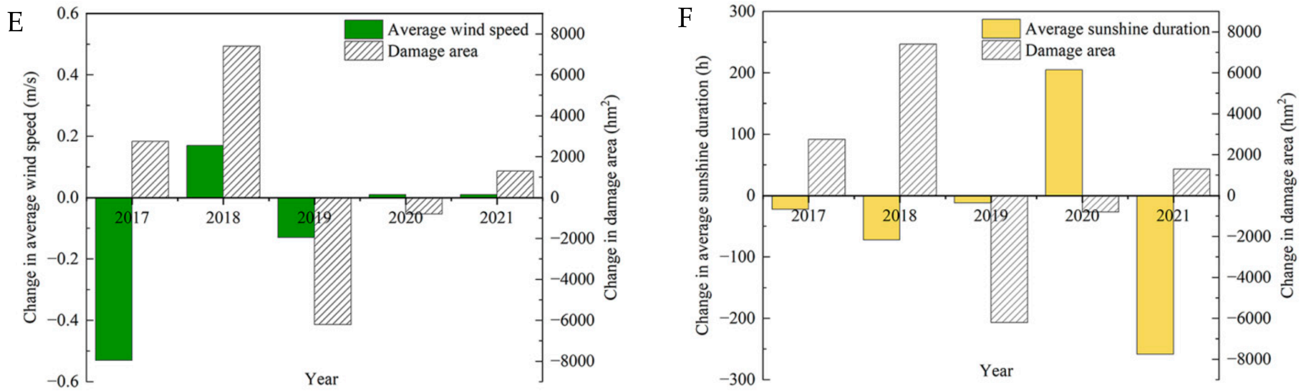

Figure 7. Relationship between the epidemic areas and climate factors in Liaoning, China. (**A**) Average precipitation, (**B**) Average temperature, (**C**) Average relative humidity, (**D**) Average vapor pressure deficit, (**E**) Average wind speed, (**F**) Average sunshine duration.

3.3. Predicted Geographical Distribution of PWD in China under Climate Warming

The AUC values of MaxEnt model training data were 0.9919 and 0.9923 in the present and future, respectively, and the test of AUC values in the present and future were 0.9915 and 0.9904, respectively, indicating that the model accuracy was excellent. Under current climate conditions, the areas suitable for PWD are mainly distributed in southeast China (Figure 8A). Under future climate conditions, the areas suitable for PWD are predicted to extend to most areas of Jilin, Heilongjiang, and Yunnan by 2030 (Figure 8B). The models show that the areas at risk from PWD infestation could increase and extend further north and west in China. Under current climate conditions, PWD has a relatively wide suitable range in China, covering an area from the southern boundary in Hainan and the northern boundary in Heilongjiang. The highly suitable range of PWD covers an area of 10.44%, primarily located in southeastern China, including Jiangsu, Anhui, Jiangxi, Hubei, Hunan, and Chongqing. The medium suitable range is smaller, covering 8.83% of the area, mainly located in Shandong, Guangxi, Guangdong, and surrounding areas of the highly suitable area. This low suitable range accounts for 13.86% of the area, extending as far north as Heilongjiang, as far south as Hainan, as far west as eastern Yunnan, and as far east as the eastern coast. The western areas of Inner Mongolia, Qinghai, and Xinjiang belong to unsuitable areas for the species.

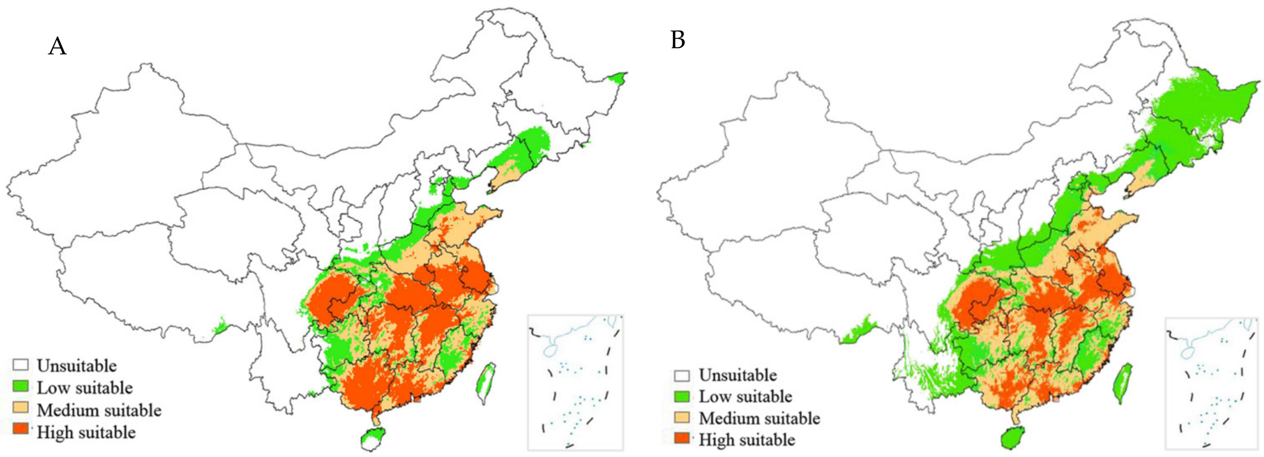

Figure 8. Ecological suitability of different areas in China for *Bursaphelenchus xylophilus*, as predicted using MaxEnt. (**A**) Ecological suitability under the current (1970–2000) climate assuming the RCP8.5 emissions scenario, (**B**) Ecological suitability under future (2021–2040) climate assuming the RCP8.5 emissions scenario.

4. Discussion

4.1. Spread and Hosts of PWD in China

The spread of PWD has caused significant damage to countries in East Asia, such as Japan, South Korea, and China. In Japan, PWD first spread in the warm temperate region and then northward to the mid-temperate region [14]. In South Korea, PWD occurred mainly in the south (Busan) area and spread northward, closer to Seoul [30]. In China, PWD first spread widely in the warm temperate region and then southward to the subtropical and tropical regions. In 2016, PWD spread northward to Dalian in Liaoning, which is still within the warm temperate region of China. By 2018, PWD had spread northward to Fushun in Liaoning, breaking through the lowest suitable temperature of 10 °C [12] and reaching the mid-temperate region of China. In the warm temperate and subtropical regions of China, the main host pines for *B. xylophilus* were *P. thunbergii* [7], *P. elliottii* [31], *P. massoniana* [32], *P. yunnanensis* [33], and *P. armandii* [34]. However, as the suitable area of PWD in China expanded northward, it established parasitic relationships with new host pine trees in northern China. In addition, *P. koraiensis* [8] and *Larix* spp. [35] have been identified as the main host pine trees in the mid-temperate region of China in recent years. PWD tends to spread rapidly and continuously infests new host pine trees, making them highly adaptable to environmental changes. Due to the high environmental adaptability of PWD, the large number of natural host pine species, and the abundance of pine resources in the northeastern forest area in China, PWD still poses a significant threat to the pine forests in that region, although it is currently less distributed in the mid-temperate region where most of the northeastern forest area in China is located. Therefore, it is necessary to enhance the monitoring and control of PWD in the Northeastern Forest Area.

4.2. Main Climate Factors Affecting the Ecological Suitability of PWD

The results of the present study show that temperature and precipitation play key roles in the occurrence of damage made by PWD. The population density of *B. xylophilus* was significantly increased by high temperatures. The inhomogeneous Poisson point process (IPP) model was constructed to predict potential PWD risk areas in Japan. The study showed that rainfall in the driest month (bio14) and the rainfall of the wettest quarter (bio16) had significant influences on PWD distribution [36]. The water stress experienced by the host trees was also a crucial climatic factor affecting PWD distribution; a severe drought might cause greater hazards to host plants than PWN; therefore, pine species affected by water scarcity are prone to PWD outbreaks [37]. Rainfall was studied as a crucial variable affecting the damage caused by PWD, reporting considerable pine death during a summer drought. Currently, it was agree that conditions of high temperatures and drought are conducive to the occurrence of PWD [38]. We speculated that climate factors affected the occurrence of PWD by affecting the growth potential of host trees as well as the activity of *B. xylophilus* and its vector species. A previous study on the effects of climate factors on trees showed that, among the effects of many climate factors, the effects of temperature and precipitation on tree growth potential were particularly prominent [39]. The height growth of pine trees during the growing season was found to be positively correlated with precipitation and negatively correlated with temperature [40]. Furthermore, higher temperatures can increase the activity of enzymes, the metabolism of endocrine hormones, and other physiological and biochemical activities, resulting in the increased activity of *B. xylophilus* and its vector species [18]. Precipitation directly determines air and soil humidity. When precipitation decreases are over a certain period of time in a given area, the relative humidity of the atmosphere decreases, which increases air dryness. This is conducive to an increase in the population density of *B. xylophilus*, which directly leads to PWD aggravation [14]. By contrast, large-scale precipitation during a certain period increases air humidity and easily results in the natural prevalence of parasitic bacteria, such as *Beauveria bassiana*, which has an obvious inhibitory effect on PWD vector species [18]. In the future, studies on the control of PWD should take into account meteorological data forecasts, which would be conducive to undertaking timely control measures.

4.3. The MaxEnt Model

Future suitable distribution areas of pests, such as *Bactrocera dorsalis* [20], *Contarinia nasturtii* [41], *Liriomyza huidobrensis* [21], and *Monacrostichus citricola* [42], have been predicted under climate warming scenarios, and these prediction results have an important reference value for controlling the spread of pests. It is an effective method to study various factors affecting the distribution of species using the MaxEnt model and geographic information system (GIS), combining biological and geophysical characteristics within the pest occurrence area and then predicting the areas suitable for species survival. The MaxEnt model is a valuable tool for analyzing species distribution patterns using species distribution and environmental data. It is beneficial for predicting the geographic distribution of species and has unique advantages, making it widely applicable in ecology [23]. It was reported that the MaxEnt model has several advantages, which include: (1) low data requirements—requiring only species occurrence coordinates and environmental variables; (2) low data bias—using the presence or absence data of species to construct conditional models; (3) high comprehensiveness—reflecting the interaction effects between different variables (including biotic and abiotic factors); and (4) high convenience—providing continuous and clear outputs [43]. This method has been widely used in the prediction and forecasting of pest risk analysis (PRA) [44,45], predicting the hazards caused by exotic species and their trends, and can be used for pest epidemic monitoring, analysis, and control [46]. Currently, there are many applications of the MaxEnt model for predicting the habitat suitability of PWD, such as MaxEnt, which has been used in multi-angle and fine-scale studies to predict the risk of PWD continuing to spread in China [25]. The MaxEnt model was used in this study to identify the current and potential distribution and habitat suitability of three pine species and *B. xylophilus* in China [26]; MaxEnt was used to model PWD-damaged forest distributions during the period 1982 to 2020 and environmental factors, including annual meteorological and human activity factors [27], using the MaxEnt model to assess the potential distribution of PWD in China based on actual distribution data and current and future climate information [47]. Previous research has shown that PWD might continue to spread toward northern China. Therefore, areas such as Hebei, Jilin, Heilongjiang, Inner Mongolia Autonomous Region, and Beijing are all at high risk of PWN invasion [47]. In terms of the driving forces of PWD outbreaks, the analysis results showed that high temperatures and arid climate aggravate PWD; abundant precipitation and high humidity can also alleviate PWD to a certain extent. The results of this study show that the MaxEnt model is a reliable tool for assessing the ecological suitability of PWD, with AUC values of 0.9919 and 0.9923. Currently, the PWD epidemic is primarily concentrated in southeastern China, such as Jiangsu, Anhui, and other areas. The MaxEnt model predicted that suitable areas for PWD were located mainly in southeastern China, including Jiangsu, Anhui, Jiangxi, Hubei, Hunan, and Chongqing, which is accurate. According to the MaxEnt model, Jiangsu was in highly suitable area, which also happened to be the main and earliest epidemic area of PWD in China, indicating that the MaxEnt model's prediction results are reliable.

4.4. Changes in PWD Distribution Areas under Future Climate Change

In the present study, the MaxEnt model predicted that under future climate change, most of China could become suitable for the spread of PWD, with only the plateau climate region of China (Inner Mongolia, Tibet, Qinghai, and Xinjiang) remaining unsuitable areas. Furthermore, we found that PWD tends to spread northward and westward in China. The predicted PWD suitable areas range from Liaoning (38°43′43°26′ N) and Jilin (40°52′46°18′ N) to Heilongjiang (43°25′53°33′ N), indicating that this disease can spread to higher latitudes. Previous research has shown that the suitable area for PWD is where the average annual temperature is above 14 °C, while a low suitable area is where the average annual temperature is 10–14 °C [17,48]. According to previous studies, suitable areas for PWD range from southern Liaoning to the Yellow River Basin, with the vast area south of the Yellow River Basin being in the low suitable area [49]. From 1982 to 2015, PWD was primarily concentrated in areas south of the mid-temperate region, which were highly suitable area for the disease [2]. However, in 2016, PWD was first discovered in Dalian, Liaoning, and in 2018, it was reported in Fushun, located in a mid-temperate region, where its severity is worse than before [8]. Based on the prediction in this study and the actual situation of PWD in China in recent years, most provinces and regions in China are now considered suitable areas for PWD. This indicates that most pine forests in China are at risk of infection by PWD, and more attention is required for PWD monitoring and control. As PWD continues to spread northwards in China, the cold tolerance of *B. xylophilus* continues to increase [50]. On the other hand, some currently cooler areas are predicted to become warmer under future climate assumptions due to a rising global mean temperature [26]. It is also one of the reasons at risk due to the northward spread of PWD in China. This study focused on changes in the suitable areas of PWD in China in the context of climate change. Therefore, further investigation is required to understand the environmental adaptation mechanism of this species. Future studies on PWD spread should also focus on vector insects and human activities because these are also considered to be primary facilitators for the spread of this disease.

5. Conclusions

According to the actual distribution data of PWD and current (1970 to 2000) and future (2021 and 2040) climate information, the MaxEnt model was employed to evaluate the potential distribution of PWD in China. The MaxEnt model predicted that suitable areas for PWD were located mainly in southeastern China, including Jiangsu, Anhui, Jiangxi, Hubei, Hunan, and Chongqing. We found that PWD tends to spread northward and westward in China. Furthermore, temperature and rainfall are the primary climatic elements affecting the possible geographic dispersion of PWD. By forecasting the potential diffusion of PWD, it is possible to establish a foundation for containment, supervision, and effective prevention and control.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/f14081687/s1.

Author Contributions: Conceptualization, Y.Z.; Formal analysis, J.W.; Funding acquisition, Y.Z.; Investigation, J.W. and W.Y.; Methodology, Y.Z. and J.D.; Project administration, Y.Z.; Resources, Y.Z.; Software, J.D.; Supervision, Y.Z.; Validation, J.W.; Visualization, W.Y.; Writing—original draft, J.W.; Writing—review and editing, Y.Z. and J.D. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by the Applied Basic Research Program of Liaoning Province [grant numbers: 2023JH2/101300130].

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: The data presented in this study are available on request from the corresponding author. The data are not publicly available due to their complexity.

Acknowledgments: We thank Haiyan Lv (College of Forestry, Shenyang Agricultural University, Shenyang 100866, China) for providing technical support with ArcGIS as well as Yushuang Song (Key Laboratory of Nation Forestry and Grassland Administration on Northeast Area Forest and Grass Dangerous Pest Management and Control, Shenyang 113122, China) for providing some data on the endemic area of PWD in our study.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Mota, M.; Vieira, P. *Pine Wilt Disease: A Worldwide Threat to Forest Ecosystems*; Springer: Berlin/Heidelberg, Germany, 2008; pp. 25–33.
2. Ye, J.R. Epidemic status of pine wilt disease in China and its prevention and control techniques and counter measures. *Sci. Silvae Sin.* **2019**, *55*, 1–10. (In Chinese)
3. Steiner, G.; Buhrer, E.M. *Aphelenchoides xylophilus* n. sp. A nemaode associated with blue stain and other fungi in timber. *J. Agric. Res.* **1934**, *48*, 949–951.

4. Li, M.; Li, H.; Ding, X.L.; Wang, L.C.; Wang, X.Y.; Chen, F.M. The detection of pine wilt disease: A literature review. *Int. J. Mol. Sci.* **2022**, *23*, 10797. [CrossRef]
5. Mamiya, Y. Hietory of pine wilt disease in Japan. *J. Nematol.* **1988**, *20*, 219–226.
6. Yi, C.K.; Byun, B.H.; Park, J.D.; Chang, K.H.; Yang, S. First finding of the pine wood nematode *Bursaphelenchus xylophilus* (Steiner et Buhrer) Nickle and its insect vector in Korea. *Res. Rep. For. Res. Inst.* **1989**, *38*, 141–149.
7. Sun, Y.C. Pine wood nematode found in Zhongshan Mausoleum Nanjing. *J. Jiangsu For. Sci. Technol.* **1982**, *4*, 27–47. (In Chinese)
8. Yu, H.Y.; Wu, H. New host plants and new vector insects of pine wood nematode found in Liaoning. *For. Pests Dis.* **2018**, *37*, 61. (In Chinese)
9. National Forestry and Grassland Administration. Pine Wilt Disease Epidemic Area in 2022. No.6. 2022. Available online: http://www.forestry.gov.cn/main/6206/20220406/151041215456755.html (accessed on 23 September 2022).
10. National Forestry and Grassland Administration. Five-Year Action Plan for the Prevention and Control of Pine Wood Nematode Disease in China. 2022. Available online: http://www.forestry.gov.cn/main/216/20210707/084935642722530.html (accessed on 23 September 2022).
11. Mamiya, Y.; Enda, N. Transmission of *Bursaphelenchus Lignicolus* (Nematoda: Aphelenchoididae) by *Monochamus Alternatus* (Coleoptera: Cerambycidae). *Nematologica* **1972**, *18*, 159–162. [CrossRef]
12. Zheng, Y.N.; Liu, P.X.; Shi, Y.; Wu, H.; Yu, H.Y.; Jiang, S.W. Difference analysis on pine wilt disease between Liaoning Province of northeastern China and other epidemic areas in China. *J. Beijing For. Univ.* **2021**, *43*, 155–160. (In Chinese)
13. Linit, M.J.; Edwards, O.R. Transmission of *Bursaphelenchus xylophilus* through oviposition wounds of *Monochamm carolinensis* (Coleoptera: Cerambycidae). *J. Nematol.* **1992**, *24*, 133–139.
14. Yang, B.J.; Pan, H.Y.; Tang, J.; Wang, Y.Y.; Wang, L.F. *Bursaphelenchus xylophilus*; China Forestry Publishing House: Beijing, China, 2003; pp. 12–125.
15. Futai, K. Pine wood nematode, *Bursaphelenchus xylophilus*. *Annu. Rev. Phytopathol.* **2013**, *51*, 61–83. [CrossRef] [PubMed]
16. Zhao, L.L.; Mota, M.; Vieira, P.; Butcher, R.A.; Sun, J. Interspecifific communication between pinewood nematode, its insect vector, and associated microbes. *Trends Parasitol.* **2014**, *30*, 299–308. [CrossRef] [PubMed]
17. Ikegami, M.; Jenkins, T. Estimate global risks of a forest disease under current and future climates using species distribution model and simple thermal model-Pine Wilt disease as a model case. *For. Ecol. Manag.* **2018**, *409*, 343–352. [CrossRef]
18. Roques, A.; Zhao, L.; Sun, J.; Robinet, C. Pine wood nematode, pine wilt disease, vector beetle and pine tree: How a multiplayer system could reply to climate change. In *Climate Change and Insect Pests*; CABI: Wallingford, UK, 2015; pp. 35–78.
19. Zhao, L.L.; Wei, W.; Kang, L.; Sun, J.H. Chemotaxis of the pinewood nematode, *Bursaphelenchus xylophilus*, to volatiles associated with host pine, *Pinus massoniana*, and its vector *Monochamus alternatus*. *J. Chem. Ecol.* **2007**, *33*, 1207–1216. [CrossRef] [PubMed]
20. Stephens, A.E.A.; Kriticos, D.J.; Leriche, A. The current and future potential geographical distribution of the oriental fruit fly, *Bactrocera dorsalis* (Diptera: Tephritidae). *Bull. Entomol. Res.* **2007**, *97*, 369–378. [CrossRef] [PubMed]
21. Mika, A.M.; Newman, J.A. Climate change scenarios and models yield conflicting predictions about the future risk of an invasive species in North America. *Agric. For. Entomol.* **2010**, *12*, 213–221. [CrossRef]
22. Shabani, F.; Kumar, L.; Ahmadi, M. A comparison of absolute performance of different correlative and mechanistic species distribution models in an independent area. *Ecol. Evol.* **2016**, *6*, 5973–5986. [CrossRef]
23. Xu, W.L.; Li, Q.K.; Yang, X.; Wang, J.S. Prediction of potential distribution of the invasive plant *Tagetes minuta* L. (Wild Marigold) in Tibet under climate change. *Acta Ecol. Sin.* **2022**, *42*, 7266–7277. (In Chinese)
24. Moat, J.; Williams, J.; Baena, S.; Wilkinson, T.; Gole, T.W.; Challa, Z.K.; Demissew, S.; Davis, A.P. Resilience potential of the Ethiopian coffee sector under climate change. *Nat. Plants* **2017**, *3*, 17081. [CrossRef]
25. Hao, Z.; Fang, G.; Huang, W.; Ye, H.; Zhang, B.; Li, X. Risk Prediction and Variable Analysis of Pine Wilt Disease by a Maximum Entropy Model. *Forests* **2022**, *13*, 342. [CrossRef]
26. Tang, X.; Yuan, Y.; Li, X.; Zhang, J. Maximum entropy modeling to predict the impact of climate change on pine wilt disease in China. *Front. Plant Sci.* **2021**, *12*, 652500. [CrossRef] [PubMed]
27. Wang, W.; Peng, W.; Liu, X.; He, G.; Cai, Y. Spatiotemporal Dynamics and Factors Driving the Distributions of Pine Wilt Disease-Damaged Forests in China. *Forests* **2022**, *13*, 261. [CrossRef]
28. Volney, W.J.A.; Fleming, R.A. Climate change and impacts of boreal forest insects. *Agric. Ecosyst. Environ.* **2000**, *82*, 283–294. [CrossRef]
29. Walther, G.R.; Roques, A.; Hulme, P.E.; Sykes, M.T.; Pyšek, P.; Kühn, I.; Zobel, M.; Bacher, S.; Botta-Dukát, Z.; Bugmann, H.; et al. Alien species in a warmer world: Risks and opportunities. *Trends. Ecol. Evol.* **2009**, *1146*, 686–693. [CrossRef] [PubMed]
30. Shin, S.C. Pine Wilt Disease in Korea. In *Pine Wilt Disease*; Zhao, B.G., Futai, K., Sutherland, J.R., Takeuchi, Y., Eds.; Springer: Tokyo, Japan, 2008.
31. Wang, Y.Y. Pine-wilting nematode disease. *Plant Quar.* **1986**, *3*, 46–51. (In Chinese)
32. Cheng, H.R.; Ge, J.J.; Zhou, G.L.; Sun, J.L.; Zhou, Y.S.; Ge, M.H.; Sun, Y.C. Survey on the occurrence and distribution of *Bursaphelenchus xylophilus* in China. *Jiangsu For. Sci. Technol.* **1988**, *2*, 28–30. (In Chinese)
33. Ren, W.; Zhou, D.Q.; Jin, H. Preliminary study of *Bursaphelenchus xylophilus* on the branch of *Pinus Yunnanensis*. *Yunnan For. Sci. Technol.* **1991**, *3*, 59–63. (In Chinese)
34. Wu, S.L.; Ma, L.; Lu, Q.; Liang, J.; Liu, Z.Y.; Zhang, X.Y. Identification of nematode isolated from *Pinus armandii* and its pathogenicity on *P. massoniana* in Tianzhu Mountain in Shaanxi Province. *For. Pest Dis.* **2013**, *32*, 5–9. (In Chinese)

35. Yu, Y.; Chi, Z.; Zhang, J.; Sun, P.; Wang, C.; Pan, X. Assessing the invasive risk of bark beetles (Curculionidae: Scolytinae and Platypodinae). *Ann. Entomol. Soc. Am.* **2019**, *112*, 451–457. [CrossRef]
36. Matsuhashi, S.; Hirata, A.; Akiba, M.; Songji, T.; Oguro, M.; Takano, K.T.; Nakao, K.; Hijioka, Y.; Matsui, T. Developing a point process model for ecological risk assessment of pine wilt disease at multiple scales. *For. Ecol. Manag.* **2020**, *463*, 118010. [CrossRef]
37. Rebetez, M.; Dobbertin, M. Climate change may already threaten Scots pine stands in the Swiss Alps. *Theor. Appl. Climatol.* **2004**, *79*, 1–9. [CrossRef]
38. Kanzaki, N.; Giblin-Davis, R.M. Diversity and plant pathogenicity of *Bursaphelenchus* and related nematodes in relation to their vector bionomics. *Curr. For. Rep.* **2018**, *4*, 85–100. [CrossRef]
39. Gao, H.; Gao, R.X. Review on the Impacts of Meteorological Factors on the Gymnosperms Growth Survey. *For. Eng.* **2014**, *2*, 6–9. (In Chinese)
40. Zhou, Y.; Lei, Z.; Zhou, F.; Han, Y.; Yu, D.; Zhang, Y. Impact of climate factors on height growth of *Pinus sylvestris* var. *mongolica. PLoS ONE* **2019**, *14*, e0213509. [CrossRef] [PubMed]
41. Mika, A.M.; Weiss, R.M.; Olfert, O.; Hallett, R.H.; Newman, J.A. Will climate change be beneficial or detrimental to the invasive swede midge in North America? Contrasting predictions using climate projections from different general circulation models. *Glob Chang. Biol.* **2008**, *14*, 1721–1733. [CrossRef]
42. Ni, W.L.; Chen, H.J.; Qu, W.W.; Wan, F.H.; A.M.; Pu, C.; Li, Z.H. The potential geographical distribution of the *Monacrostichus citricola* Bezzi based on the CLIMEX, in China. *Plant Quar.* **2010**, *24*, 20–25. (In Chinese)
43. Zhou, Y.T.; Ge, X.Z.; Zou, Y.; Guo, S.W.; Wang, T.; Tao, J.; Zong, S.X. Prediction of the potential geographical distribution of *Hylurgus ligniperda* at the global scale and in China using the MaxEnt model. *J. Beijing For. Univ.* **2022**, *44*, 90–99. (In Chinese)
44. Yu, H.Y.; Wu, H.; Zhang, X.D.; Wang, L.M.; Zhang, X.F.; Song, Y.S. Preliminary study on *Larix* spp. Infected by *Bursaphelenchus xylophilus* in natural environment. *For. Pests Dis.* **2019**, *38*, 7–10. (In Chinese)
45. Morey, A.C.; Venette, R.C. Minimizing risk and maximizing spatial transferability: Challenges in constructing a useful model of potential suitability for an invasive insect. *Ann. Entomol. Soc. Am.* **2020**, *113*, 100–113. [CrossRef]
46. Li, C.; Liao, J.H.; Ya, Y.K.; Liu, J.; Li, J.; Yu, G.W. Analysis of potential distribution of *Spodoptera frugiperda* in western China. *J. Asia-Pac. Entomol.* **2022**, *25*, 101985. [CrossRef]
47. Ouyang, X.H.; Chen, A.L.; Li, Y.; Han, X.X.; Lin, H.P. Predicting the Potential Distribution of Pine Wilt Disease in China under Climate Change. *Forests* **2022**, *13*, 1147. [CrossRef]
48. Mamiya, Y. Pathology of the pine wilt disease caused by *Bursaphelenchus xylophilus*. *Annu. Rev. Phytopathol.* **1983**, *21*, 201–220. [CrossRef]
49. Song, Y.S.; Zang, X.Q. Fitness analysis and quarantine countermeasures of pine wood nematode in China. *For. Pest Dis.* **1989**, *4*, 38–41. (In Chinese)
50. Huang, R.F.; Gao, R.H.; Shi, J.; Song, D.W.; Li, Z.M. Cold tolerance of *Bursaphelenchus xylophilus* in the Three Gorges Region of Hubei Province. *J. Northeast For. Univ.* **2014**, *42*, 138–141. (In Chinese)