



OPEN Projecting the global spread of *Xylella fastidiosa* under climate change using maxent modeling

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Xylella fastidiosa, a virulent plant pathogen native to the Americas, presents considerable risks to economically valuable crops and ornamental flora. It is a highly virulent bacterium that causes the most critical plant infections. Many regions around the world such as the European Union countries posed the strongest constraints to prevent the introduction and spread of *Xylella fastidiosa*, including obligatory surveillance, and removal measures for new outbreaks. This research utilizes Geographic Information Systems (GIS) and maximum entropy modeling (Maxent) to forecast the worldwide dissemination of *Xylella fastidiosa* across different climate change scenarios. We gathered occurrence data from various sources, yielding 113 distinct sites, and employed 19 bioclimatic variables from the WorldClim database to ascertain four principal factors—precipitation seasonality, precipitation of the driest month, mean temperature of the warmest quarter, and minimum temperature of the coldest month—that affect habitat suitability. The Maxent model exhibited superior performance, with an Area Under the Curve (AUC) of 0.91 and a True Skill Statistic (TSS) of 0.66, signifying its efficacy in forecasting suitable environments. Current distribution maps indicate high-risk areas predominantly in subtropical and tropical regions, particularly in the Americas and Mediterranean Europe. Forecasts for 2050 and 2070 based on Representative Concentration Pathways (RCP) suggest a significant expansion of these high-risk areas, implying that climate change may intensify the proliferation of this pathogen especially under elevated emissions scenarios. These findings highlight the critical necessity for proactive management techniques to alleviate the dangers associated with *Xylella fastidiosa*, protecting global agricultural systems and biodiversity.

Keywords Climate change, Geographic information systems (GIS), Maxent modeling, Plant pathogens

Xylella fastidiosa, a bacterium native to the Americas, has recently garnered significant attention due to its capacity to induce severe illnesses in numerous commercially vital crops¹. It is a very virulent bacteria responsible for severe plant infections, resulting in numerous fatal diseases in various commercially important crops and ornamental plants². It is a gram-negative, xylem-restricted bacterium capable of infecting over 500 plant species globally³. *X. fastidiosa*-related diseases, including Pierce's disease in grapes, citrus variegated chlorosis, and olive quick decline syndrome, can result in substantial economic repercussions, potentially incurring billions of euros in annual production losses throughout the European Union and threatening hundreds of thousands of jobs⁴.

The disease comprises various recognised subspecies, including *fastidiosa*, *pauca*, *multiplex*, and *sandyi*, each capable of infecting distinct host plants⁵. *X. fastidiosa* is mostly spread by xylem-feeding insect vectors, rendering it a challenging pathogen to manage⁶. The global distribution of *X. fastidiosa* exemplifies its capacity to adapt and survive. This disease was initially identified in the United States and has since been reported in several regions, including South America, Europe, and Asia, highlighting the need for a cooperative global effort to understand and manage its spread⁷.

The European Union has implemented rigorous regulations to avert the introduction and dissemination of *X. fastidiosa*, encompassing obligatory surveillance, eradication strategies for new outbreaks, and containment measures in regions where this bacterium is already present⁸. Extensive research endeavours are underway to further the understanding of the bacteria and to formulate suitable management strategies. Due to the destructive capacity of *X. fastidiosa*, it is imperative that any suspected cases be promptly reported to the relevant authorities to provide rapid and effective measures to mitigate the threat posed by this formidable plant disease, particularly in light of climate change⁹.

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Climate change is profoundly altering the global natural environment, creating conditions that increasingly promote the growth and establishment of *X. fastidiosa*¹⁰. Rising temperatures, modified precipitation patterns, and shifts in seasonal timing are creating conditions favourable for the development of the bacteria and its insect vectors¹¹. Warmer winters are associated with a heightened occurrence of *X. fastidiosa* in insect vectors such as *Philaenus spumarius* (the meadow spittlebug), suggesting that increasing temperatures enhance the survival and expansion of the bacterium. Furthermore, altered precipitation patterns may affect the availability of host plants and the behaviour of insect vectors, hence facilitating the spread of the disease¹².

The impact of *X. fastidiosa* on agricultural economics and plant health is intricate¹³. In regions where the bacteria is widespread, significant economic losses have been recorded due to reduced agricultural yields, increased management costs, and the requirement for rigorous quarantine measures. Moreover, the presence of *X. fastidiosa* may provoke enduring ecological changes, affecting biodiversity and ecosystem health³.

Geographic Information Systems (GIS) serve as a powerful tool for analysing the spatial distribution and potential spread of *X. fastidiosa* across various climatic conditions¹⁴. GIS models can predict the climatic suitability of different locations for *X. fastidiosa* and its vectors by integrating bioclimatic characteristics such as the minimum temperature of the coldest month, the mean temperature of the coldest quarter, and yearly precipitation¹⁵. These models can also integrate other critical factors, such as the accessibility of host plants, the distribution of insect vectors, and human activities that may facilitate the spread of the bacteria¹⁶.

This work aims to utilise GIS analysis to forecast the global dissemination of *X. fastidiosa* under potential climate change scenarios. This study seeks to provide critical insights for risk assessment and management strategies by examining the relationships between climate variables, the prevalence of *X. fastidiosa* in insect vectors, and the potential range shifts of the bacterium. The following objectives will be addressed: (1) Climate Suitability Mapping: To identify geographical regions currently favourable to *X. fastidiosa* and to predict potential changes in these areas under different climate change scenarios in the future; (2) Analysis of which bioclimatic variables predominantly influence the distribution of this bacterium throughout its range. The findings of this study will significantly assist in developing proactive strategies to regulate the spread of *X. fastidiosa*, hence mitigating its impact on global plant health and agricultural economies. This research provides a thorough framework for predicting and managing the dissemination of this bacterium, assisting policymakers, agricultural professionals, and researchers in efficiently preparing for and tackling the challenges posed by *X. fastidiosa* in a dynamic setting.

Results

Model evaluation and bioclimatic factor contribution

An excellent Area Under the Curve (AUC) of 0.91 and a True Skill Statistic (TSS) of 0.66 show that the model employed to forecast the possible distribution of *X. fastidiosa* performed admirably. The model's ability to distinguish between regions that are suited and those that are not for the presence of this plant pathogenic bacterium is demonstrated by these metrics, which demonstrate strong discriminatory power. In order to understand the environmental parameters that drive the spread of *X. fastidiosa*, the response curves for the four most relevant bioclimatic variables were analyzed (Fig. 1). The appropriateness of the distribution of the species was mainly affected by Bio_15 (Precipitation Seasonality). According to the response curve, *X. fastidiosa* does best in habitats that experience clear wet and dry seasons, and it is most commonly found in regions with moderate to high seasonal precipitation. Bio_14 (Precipitation of Driest Month): *X. fastidiosa* prefers locations with relatively large amounts of precipitation during the driest month of the year, according to the response curve for this variable. It appears that the bacterium needs a specific amount of moisture to live and multiply. *X. fastidiosa* has an ideal range of mean temperatures during the warmest quarter of the year, according to the response curve for Bio_10 (Mean Temperature of Warmest Quarter). These points to the fact that the bacterium thrives in slightly warm environments, which are probably essential for its maturation and expansion. *X. fastidiosa* is sensitive to cold temperatures, as shown by the response curve for Bio_6 (lowest Temperature of Coldest Month). As the lowest temperature of the coldest month lowers, the appropriateness of the organism diminishes. This suggests the bacterium might not be able to withstand frigid temperatures for very long. Bio_15 (Precipitation Seasonality) is the most important of these four bioclimatic variables (Fig. 1e), which together show how *X. fastidiosa* has evolved to adapt to its environment. Targeted monitoring, prevention, and management measures can be developed to address the threats presented by this plant pathogenic bacterium if we have a better understanding of the factors that drive the species' dispersal.

Current distribution of *X. fastidiosa*

The generated risk map of Maxent illustrates the anticipated global distribution of *X. fastidiosa* (Fig. 2a). The map employs a color-coded approach to denote the differing levels of appropriateness or danger for the presence of *X. fastidiosa*, ranging from low (green) to excellent (red). The analysis of the map indicates that areas of high risk and optimal suitability for *X. fastidiosa* are predominantly located in subtropical and tropical regions globally. Across the Americas, Extensive areas of the eastern United States, especially the Southeastern states, are depicted in red and orange, signifying excellent to very high suitability for the bacteria. Regions of Central America, encompassing Mexico, Guatemala, and Honduras, along with certain areas of the Caribbean islands, exhibit comparable high-risk zones. Substantial regions of South America, including Brazil, Argentina, and Colombia, are classified as possessing excellent to very high suitability. In Europe, the Mediterranean basin, encompassing countries such as Italy, Spain, and Greece, is identified as a region of exceptional and superior adaptability. High-risk areas are also evident in many regions of Southern Europe. The northern areas of Africa, encompassing nations such as Morocco, Algeria, and Tunisia, demonstrate excellent to very high adaptability. Specific regions of East Africa, including Ethiopia and Somalia, are categorized as high-risk zones. The Indian subcontinent, especially the southern areas, has excellent to very high suitability for *X. fastidiosa* in Asia.

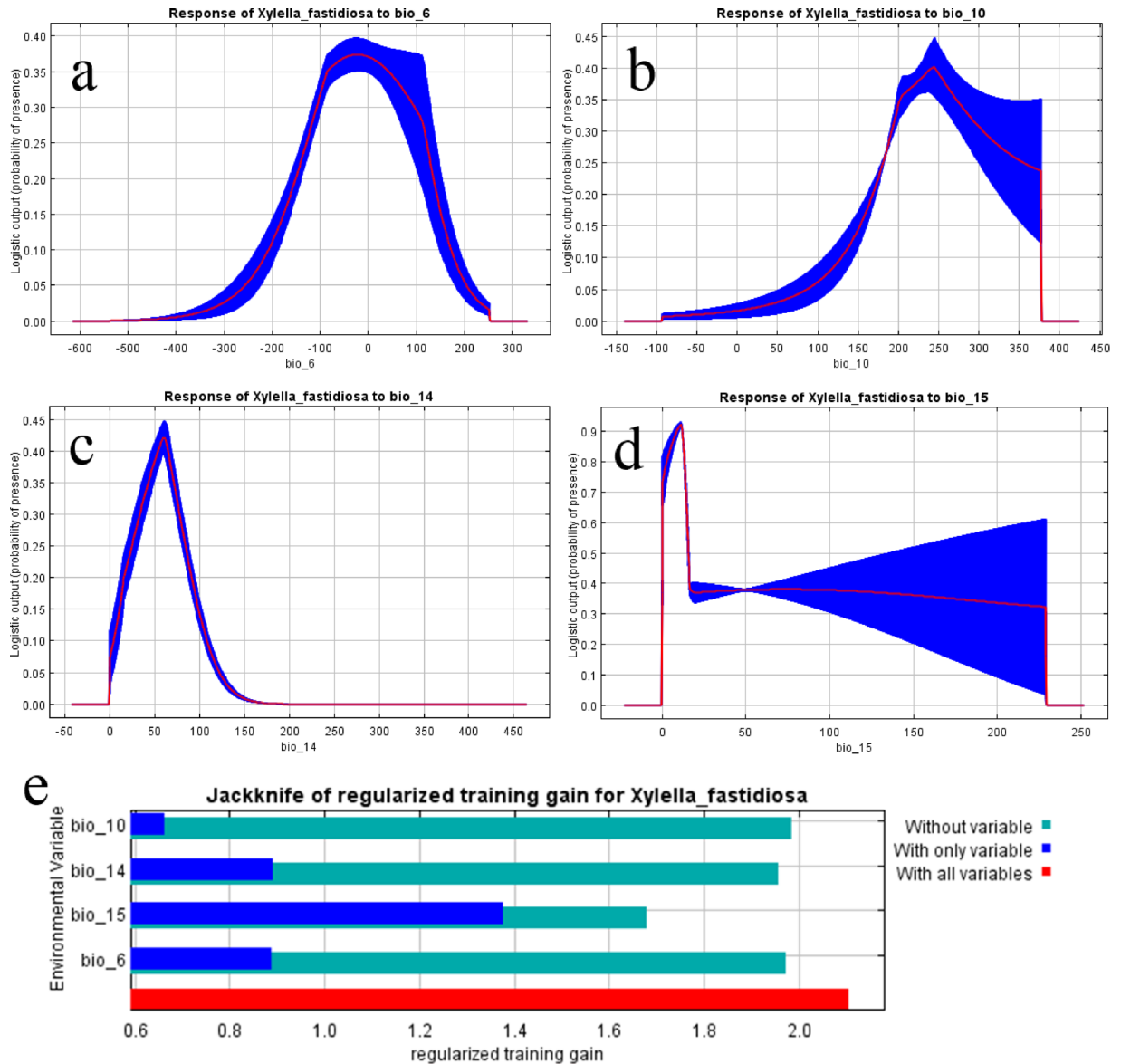


Fig. 1. Response curves of the four under investigation bioclimatic variable: (a) bio_6, (b) bio_10, (c) bio_14, (d) bio_15; (e). Jackknife test for the four variables.

Regions of elevated risk are evident across Southeast Asia, particularly in the Philippines and Indonesia. The data indicate that *X. fastidiosa* possesses the capacity to disseminate and establish itself in many places, especially those with climatic circumstances conducive to its survival and growth. This poses a considerable threat to agriculture and plant health, as the bacterium can infect numerous commercially vital crops and decorative plants, potentially resulting in huge economic and environmental consequences.

The predicted suitability map generated by the DIVA-GIS (Distributional Information and Visualization Analysis using a Geographic Information System) bioclimatic model reveals a clear gradient of environmental suitability across the study area, ranging from completely unsuitable to highly favorable conditions. Large portions of the region fall into the low to medium suitability categories, suggesting that while the species or variable of interest could persist in these areas, growth or survival may be limited by suboptimal environmental factors. However, scattered pockets of high and very high suitability stand out as prime zones where conditions align perfectly with the species' requirements, especially in Europe and the Mediterranean basin, making these areas critical for this pathogen. The unsuitable areas, likely constrained by extreme climatic conditions or other limiting factors, serve as natural boundaries for potential distribution. These results provide valuable insights for ecological planning, emphasizing the need to prioritize high-suitability regions while further investigating marginal zones to understand the specific factors influencing their lower suitability provided by DIVA-GIS. (Fig. 2b).

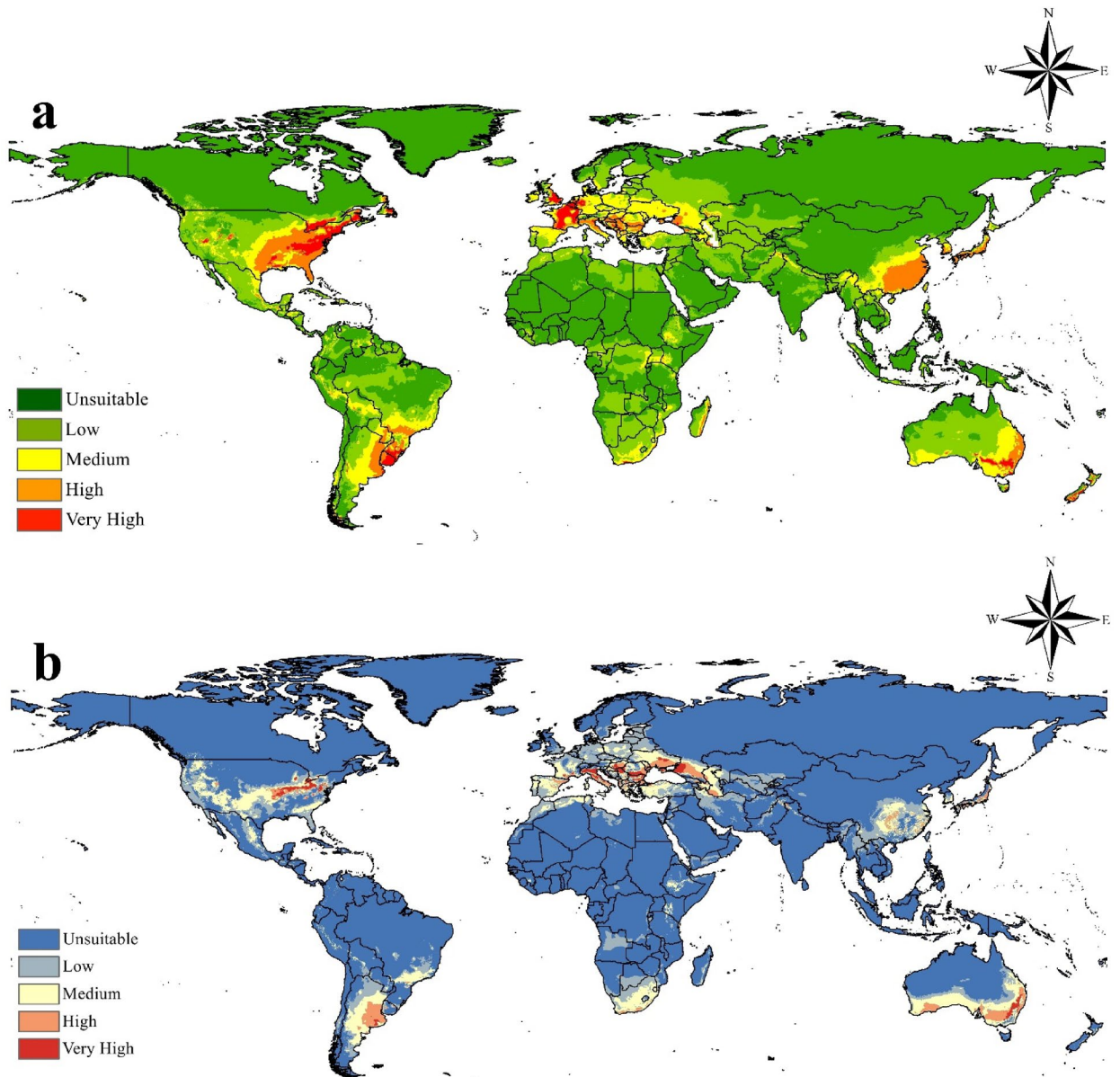


Fig. 2. Current prediction for spatial distribution of *X. fastidiosa*: (a) Maxent Modeling (The map was generated using the species distribution modeling technique based on Maxent software version 3.4.4 https://biodiversityinformatics.amnh.org/open_source/maxent/); (b) Bioclim Modeling based on DIVA-GIS.

Future prediction for *X. fastidiosa* under different climate change scenarios

The produced maps illustrate the anticipated future distribution of *X. fastidiosa* across various climate change scenarios for the years 2050 and 2070. In 2050, RCP 2.6 (reduced emissions scenario) (Fig. 3a): The map indicates a general increase in the high-risk and extremely high-risk zones for *X. fastidiosa* relative to the existing distribution. Regions such as the eastern United States, certain sections of Central and South America, the Mediterranean basin in Europe, and specific locations in Africa and Asia exhibit heightened suitability for the bacterium's presence. Although most of the world falls within the low to medium suitability range, the rise in high-risk zones indicates the likelihood of an expanded geographic distribution of *X. fastidiosa* by 2050 under this lower emissions scenario could be effective. At RCP 8.5 (higher emissions scenario) (Fig. 3b): The map illustrates a substantial increase in the high-risk and extremely high-risk zones these encompass significant regions of the Americas, Europe, Africa, and Asia, suggesting a broader potential dissemination of the bacterium under the elevated emissions scenario. The regions of concern, including the eastern United States, Mediterranean basin, and certain areas of Asia, seem to be at more risk than the RCP 2.6 scenario indicates. The prevailing trend indicates that the elevated emissions scenario may result in a more extensive and severe threat of *X. fastidiosa* by 2050.

On the other hand, in 2070, at RCP 2.6 (lower emissions scenario) (Fig. 3c): The map shows a further expansion of the high-risk and very high-risk areas compared to the 2050 projection. The regions of concern

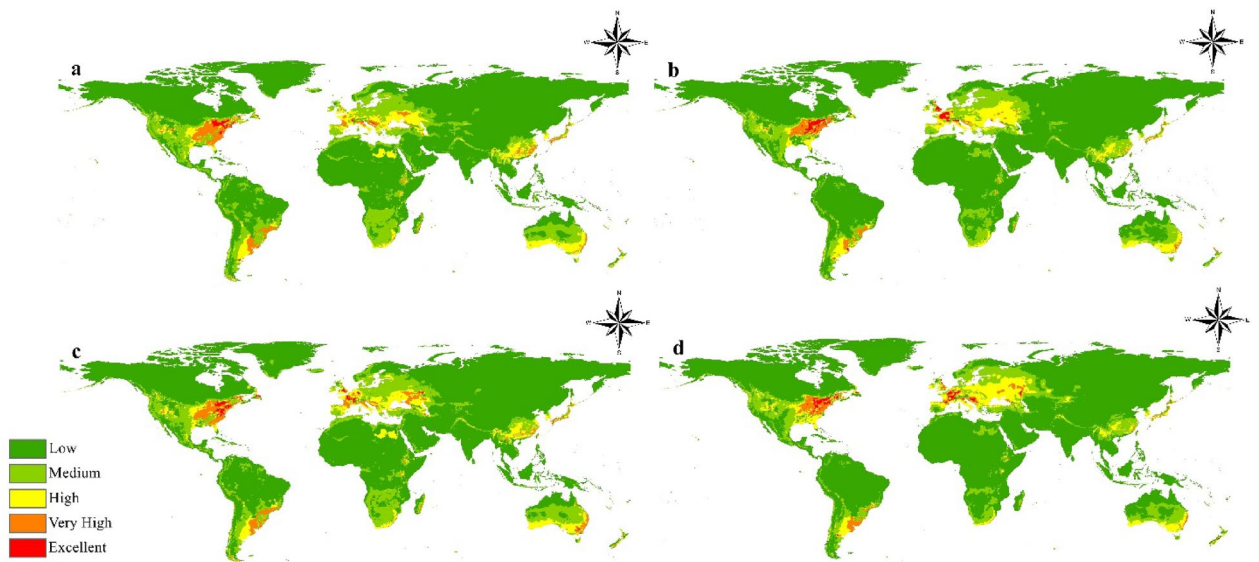


Fig. 3. The future prediction of *X. fastidiosa* distribution: (a) 2050 RCP 2.6, (b) 2050 RCP 8.5, (c) 2070 RCP 2.6 and 2070 RCP 8.5. The map was generated using the species distribution modeling technique based on Maxent software version 3.4.4 https://biodiversityinformatics.amnh.org/open_source/maxent/.

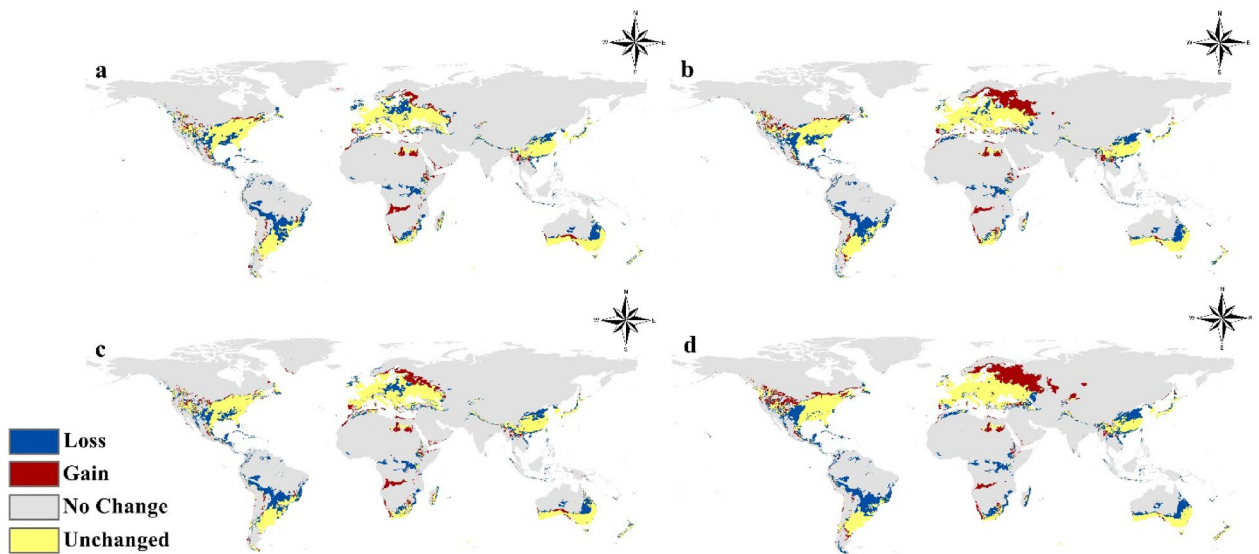


Fig. 4. The calibration map of the future situation of *X. fastidiosa* showing the gain and loss in habitat suitability: (a) 2050 RCP 2.6, (b) 2050 RCP 8.5, (c) 2070 RCP 2.6 and 2070 RCP 8.5. The map was generated using the species distribution modeling technique based on Maxent software version 3.4.4 https://biodiversityinformatics.amnh.org/open_source/maxent/.

continue to expand, with more areas in the Americas, Europe, Africa, and Asia falling into the high-risk and very high-risk categories. While the low to medium suitability regions still dominate, the increasing prevalence of high-risk zones indicates a growing potential for the spread and establishment of *X. fastidiosa* by 2070 under the lower emissions scenario. For RCP 8.5 (higher emissions scenario) (Fig. 4d): the results show more significant expansion of the high-risk and very high-risk areas for *X. fastidiosa*. The high-risk and very high-risk regions cover larger portions of the globe, with more areas in the Americas, Europe, Africa, and Asia falling into these categories. The extent of the high-risk and very high-risk zones suggests that the higher emissions scenario could lead to a more severe and widespread distribution of *X. fastidiosa* by 2070, posing a greater challenge for plant health and agriculture. The calibration maps show clearly the gain and loss in habitat suitability for through its range and area under risk of invasion appears obviously (Fig. 4).

Limitation factor map and envelope test

The map (Fig. 5) serves as a representation of the restrictive influences of the four bioclimatic factors (bio6, bio10, bio14, and bio15) on the possible distribution of *X. fastidiosa*. The diverse hues indicate the extent to which each environmental condition may inhibit the bacterium's growth and dissemination throughout various global locations. The examination of the limitation factor map revealed that the primary limiting variables influencing the potential dispersion of *X. fastidiosa* were BIO6 (minimum temperature of the coldest month) and BIO10 (mean temperature of the warmest quarter). These data indicate that temperature significantly influences the distribution of this bacterium within its habitat. Regions exhibiting reduced minimum temperatures in the coldest month and elevated mean temperatures in the warmest quarter are predisposed to more conducive conditions for the development and growth of *X. fastidiosa*. This underscores the significance of temperature in establishing the regional boundaries of this pathogen's dissemination.

The envelope test, which examines the two-dimensional correlation between BIO1 (Annual Mean Temperature) and BIO12 (Annual Precipitation), suggests that the occurrence data for this analysis is fairly homogeneous. The findings indicate that 88% of the 83 observations under consideration of the test are contained inside the defined envelope, implying a strong correlation between the species' distribution and the interplay of these two bioclimatic variables. This discovery aligns with the cosmopolitan distribution of the *X. fastidiosa* bacteria, recognized for its ability to thrive in diverse conditions. The extensive variation in annual mean temperatures and precipitation levels recorded in the data substantiates the adaptability of this plant disease to various environmental settings. The significant proportion of observations within the bioclimatic envelope indicates that the interplay between annual mean temperature and annual precipitation is a crucial determinant of the possible distribution of *X. fastidiosa*. This information is essential for comprehending the environmental limitations and appropriateness of various places for the establishment and proliferation of this bacteria, which is vital for focused monitoring, risk evaluation, and the formulation of effective management plans.

Discussion

This study employs Geographic Information Systems (GIS) and maximum entropy modelling to predict the worldwide dissemination of *X. fastidiosa* across various climate change scenarios. This research provides critical insights into the potential spread and establishment of this harmful plant pathogen, highlighting the urgent need for proactive management strategies¹⁷.

This comprehensive analysis provides a robust understanding of the current and future global distribution of *X. fastidiosa* under several climate change scenarios. The amalgamation of advanced modelling techniques, high-quality occurrence data, and carefully selected bioclimatic variables has enabled the development of a reliable predictive model to guide risk assessment and management strategies for this very harmful plant pathogen¹⁸. The Maxent model's exceptional performance, demonstrated by the AUC and TSS values, underscores its ability to accurately differentiate between suitable and unsuitable areas for the establishment and dissemination of *X. fastidiosa*. An analysis of the response curves for the four principal bioclimatic variables offers essential insights into the key environmental parameters affecting the distribution of this bacterium¹⁹.

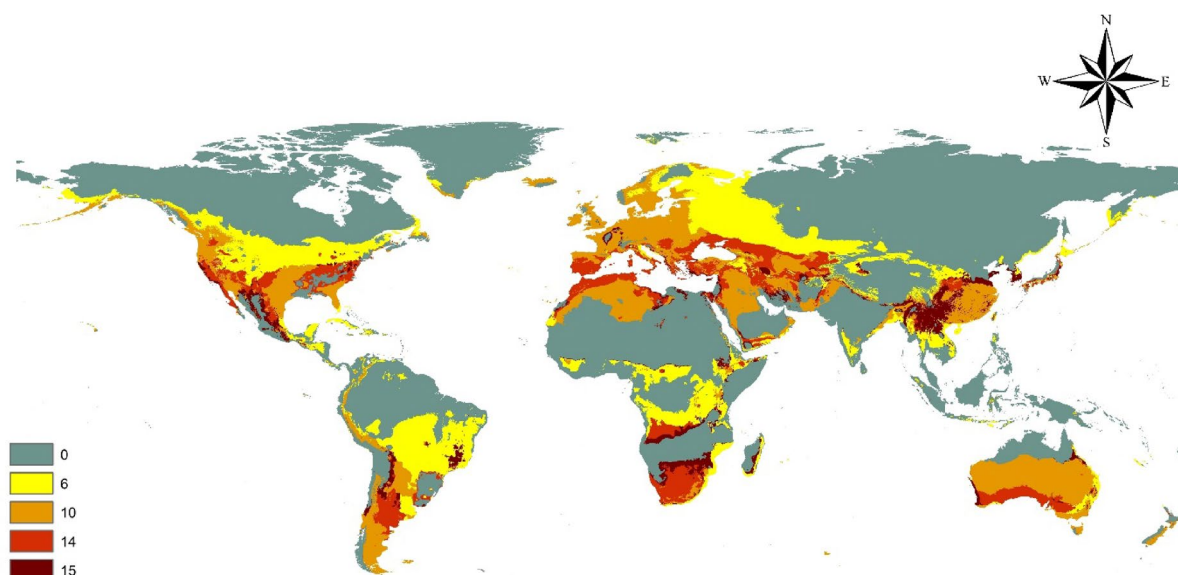


Fig. 5. Limitation factor map of *X. fastidiosa* showing the four bioclimatic variables that contribute to the presence of this bacterium and its limiting impact through the present range. The number represents the bioclimatic variable, and 0 indicates an unsuitable range. The map was generated using the species distribution modeling technique based on Maxent software version 3.4.4 https://biodiversityinformatics.amnh.org/open_source/maxent/.

The finding that precipitation seasonality (Bio_15) is the principal factor influencing *X. fastidiosa*'s habitat adaptation suggests that the bacteria thrives in environments marked by significant wet and dry periods. This aligns with the literature, which has highlighted the bacterium's preference for regions characterised by a Mediterranean climate, marked by cool, humid winters and hot, dry summers¹². The importance of precipitation during the driest month (Bio_14) and the average temperature of the warmest quarter (Bio_10) highlights the bacterium's necessity for a balanced moisture environment and temperate temperatures for optimal development and survival²⁰.

The present distribution maps of both models reveal that high-risk and extremely high-risk areas for *X. fastidiosa* are primarily situated in subtropical and tropical regions, notably within the Americas, the Mediterranean basin in Europe, and select portions of Africa and Asia. This spatial pattern corresponds with the documented prevalence of the disease in these regions and the suitability of the climatic conditions for the bacteria and its insect vectors²¹. The future projections under different climate change scenarios (RCP 2.6 and RCP 8.5) for the years 2050 and 2070 indicate a gloomy outlook. The maps illustrate a significant expansion of high-risk and very high-risk areas, with the increased emissions scenario (RCP 8.5) resulting in a more marked increase in the potential dissemination of *X. fastidiosa*. This suggests that climate change, particularly anticipated changes in temperature and precipitation patterns, may exacerbate the risk posed by this bacterium and facilitate its spread to new regions¹⁷.

The limitation factor map produced by the BIOCLIM modelling method offers significant insights into the environmental variables that may restrict the potential distribution of *X. fastidiosa*. The research indicated that the primary limiting factors were BIO6 (minimum temperature of the coldest month) and BIO10 (mean temperature of the warmest quarter)^{22,23}. This indicates that temperature, especially extremes in both the coldest and warmest seasons, is crucial in defining the geographic boundaries of this plant pathogen's dissemination and establishment. The significance of temperature as a limiting factor for *X. fastidiosa* is extensively documented in the literature. Research indicates that the bacteria exhibits sensitivity to low temperatures, with its growth and viability impeded in areas subjected to extended periods of minimal temperatures^{24,25}. Conversely, elevated mean temperatures during peak periods can also present a constraint, as *X. fastidiosa* may find it challenging to flourish in conditions of extended heat stress²⁶.

The envelope test, which examined the correlation between annual mean temperature (BIO1) and annual precipitation (BIO12), corroborates the conclusions drawn from the limitation factor map. The substantial proportion (88%) of observations within the defined envelope indicates a strong correlation between the species' distribution and the interplay of these two bioclimatic variables²⁷. This suggests that the yearly temperature and precipitation patterns are significant factors influencing *X. fastidiosa*'s potential distribution, as the bacterium seems to be suited to a wide range of climatic circumstances.

X. fastidiosa's adaptability to various annual mean temperatures and precipitation levels aligns with its established worldwide distribution²⁸. Nonetheless, the constraints identified by the modelling technique indicate that extreme temperature circumstances, especially during the coldest and warmest intervals, may impede the ongoing proliferation of this plant pathogen.

The implications of these discoveries are substantial, as *X. fastidiosa* has the ability to cause severe economic and ecological repercussions in affected areas. Precisely forecasting the bacterium's potential dissemination across diverse climate change scenarios is crucial for implementing targeted surveillance, early detection, and efficient management techniques to alleviate hazards to agricultural output, biodiversity, and ecosystem health²⁹.

The findings of this work align with the growing body of literature on the application of species distribution modelling to understand and predict the spread of plant diseases, such as *X. fastidiosa*, in the context of climate change. Previous studies have highlighted the necessity of including bioclimatic attributes and future climate projections to anticipate potential range alterations and the emergence of various plant diseases e.g.^{30–32}.

Our analysis utilizes the robust Maxent modelling technique and a comprehensive set of bioclimatic predictors, enhancing the previous information by providing a detailed worldwide evaluation of the current and future suitability for *X. fastidiosa*. Emphasising the identification of critical environmental elements, such as precipitation seasonality, improves the understanding of the complex interactions between climate variables and the distribution of the bacterium.

An intricate plan will be crucial to alleviate the anticipated impacts of climate change on *X. fastidiosa*. Improving global surveillance and early detection capabilities is crucial for promptly identifying and addressing potential outbreaks, particularly in regions expected to become more favourable under future climatic conditions³³. This requires the augmentation of international collaboration, information sharing, and capacity building among plant health authorities and research institutes.

Secondly, the development and implementation of adaptive management strategies that account for potential range shifts of *X. fastidiosa* and its insect vectors will be crucial. This may include the strategic execution of quarantine protocols, the exploration of biological management alternatives, and the evaluation of climate-resilient crop varieties and agricultural methods that can endure the impacts of this plant pathogen³⁴. Ultimately, further research is needed to improve the understanding of the complex interactions among climate change, *X. fastidiosa*, its host plants, and vectors. This may involve integrating additional biotic and abiotic factors into the modelling framework, validating predictions through field measurements, and exploring potential synergistic interactions among different plant diseases in a changing environment.

Through the execution of a thorough, multi-faceted strategy that incorporates sophisticated predictive modelling, targeted surveillance, adaptive management, and continuous research, the international community can mitigate the threats presented by *X. fastidiosa* and secure the enduring sustainability of agricultural systems and natural ecosystems.

Conclusion

This study offers an in-depth examination of the possible worldwide distribution of *X. fastidiosa* across different climate change scenarios, emphasizing the considerable threats presented by these harmful bacteria. By integrating Geographic Information Systems (GIS) with maximum entropy modeling (Maxent), we found essential bioclimatic variables that affect habitat suitability for *X. fastidiosa*. Our data demonstrate that precipitation seasonality, in conjunction with temperature and moisture variables, is crucial in influencing the dispersion of the bacterium. The present risk assessment identifies high-risk and very high-risk zones predominantly located in subtropical and tropical regions, including within the Americas, the Mediterranean basin, and certain sections of Africa and Asia. Forecasts for 2050 and 2070 across various Representative Concentration Pathways (RCPs) suggest a considerable enlargement of these high-risk areas, especially under elevated emissions scenarios. This concerning trend highlights the capacity of climate change to promote the dissemination of *X. fastidiosa*, jeopardizing agricultural output and environmental integrity. Due to the significant economic and ecological consequences of *X. fastidiosa*, it is essential for stakeholders to adopt proactive management techniques. Augmented surveillance, expedited reaction strategies, and flexible agricultural methodologies are crucial to alleviate the hazards linked to this bacterium. Furthermore, continuous study is essential to enhance our comprehension of the connections among climate change, *X. fastidiosa*, and its vectors, ensuring preparedness to tackle the problems presented by this developing threat. By promoting collaboration among researchers, politicians, and agricultural practitioners, we can formulate effective solutions to protect global food security and preserve biodiversity amid climate change.

Materials and methods

Compilation of occurrence data

The occurrence records for *X. fastidiosa* were obtained from online archives, especially Global Biodiversity Information Facility (GBIF)³⁵. To ensure data accuracy, duplicates were removed, yielding 113 unique sites. Subsequently, the data were transformed into comma-separated values (CSV) format (Supplementary material 1) in preparation for analysis.

Climatic information

The WorldClim global climate database, with a spatial resolution of 2.5 arc-min or 5 km² at the equator (accessed in December 2023), was utilised to extract nineteen bioclimatic variables (Supplementary material 2). Fifteen bioclimatic variables were transformed into ASCII format utilising ArcGIS version 10.7. Spatial artefacts required the omission of bioclimatic layers 8–9 and 18–19³⁶. Four non-correlated bioclimatic variables were selected for further investigation to reduce multicollinearity, as demonstrated by the Pearson correlation coefficient ($|r| \geq 0.8$). The test was conducted using the Species distribution modeling tool (SDMTools) within ArcGIS 10.3 (Universal tool; Remove highly correlated variables) to exclude variables with high correlations that lack biological value for the species³⁷. Bio_6 (minimum temperature of the coldest month), Bio_10 (mean temperature of the warmest quarter), Bio_14 (precipitation of the driest month), and Bio_15 (precipitation seasonality) were the influential variables employed to examine the distribution of *X. fastidiosa*. Furthermore, future predictions for two representative concentration pathways (RCPs 2.6 and 8.5) for the years 2050 and 2070 were sourced from www.worldclim.org and converted to ASCII format utilising ArcGIS 10.7³⁸.

Maximum entropy modelling

The maximum entropy approach, Maxent v3.4.3e, was employed to assess the biological niches and habitat appropriateness of *X. fastidiosa*. This strategy is acknowledged for its statistical efficacy and ability to generate reliable predictive models using presence-only data³⁹. To ensure the model's accuracy, 75% of the occurrence records were allocated for training, while the remaining 25% were designated for testing⁴⁰. Establishing the maximum quantity of background elements at 10,000 and the maximum number of iterations at 1,000 was important to the modelling process. To enhance the model's performance, a fivefold cross-validation was conducted^{36,41,42}.

Bioclimatic modelling

The species distribution modelling was performed using the DIVA-GIS software⁴³, which utilises the BIOCLIM approach. BIOCLIM is a presence-only modelling method that identifies the environmental factors associated with the recorded occurrences of the species. The BIOCLIM approach first creates a “climatic envelope” based on the bioclimatic parameters associated with the occurrence records of *X. fastidiosa*⁴⁴. This climatic envelope defines the range of environmental conditions that the species can tolerate and thrive in. The program then assesses the climatic conditions of each grid cell in the study area against the defined climatic envelope, assigning a suitability score based on the extent of conformity between the grid cell's conditions and the species' preferred environmental parameters. BIOCLIM utilises a presence-only modelling approach, obviating the necessity for real absence data, which can be challenging to obtain for several species. The concept is that the recorded occurrences accurately represent the environmental conditions the species can tolerate, allowing for extrapolation of this data to a broader geographic area.

Evaluation of the model

The anticipated habitat range of *X. fastidiosa* was forecasted utilising the Maxent model, which was executed with 113 presence-only sites and five chosen bioclimatic factors. Two separate types of occurrence records were produced, with 75% allocated for model training and 25% for testing^{45,46}. The model's efficacy was evaluated by the area under the curve (AUC), where values surpassing 0.9 denote outstanding performance⁴⁷. The jackknife

83 observations with 73 (88%) in this envelope: (50 (60.2%) overall)

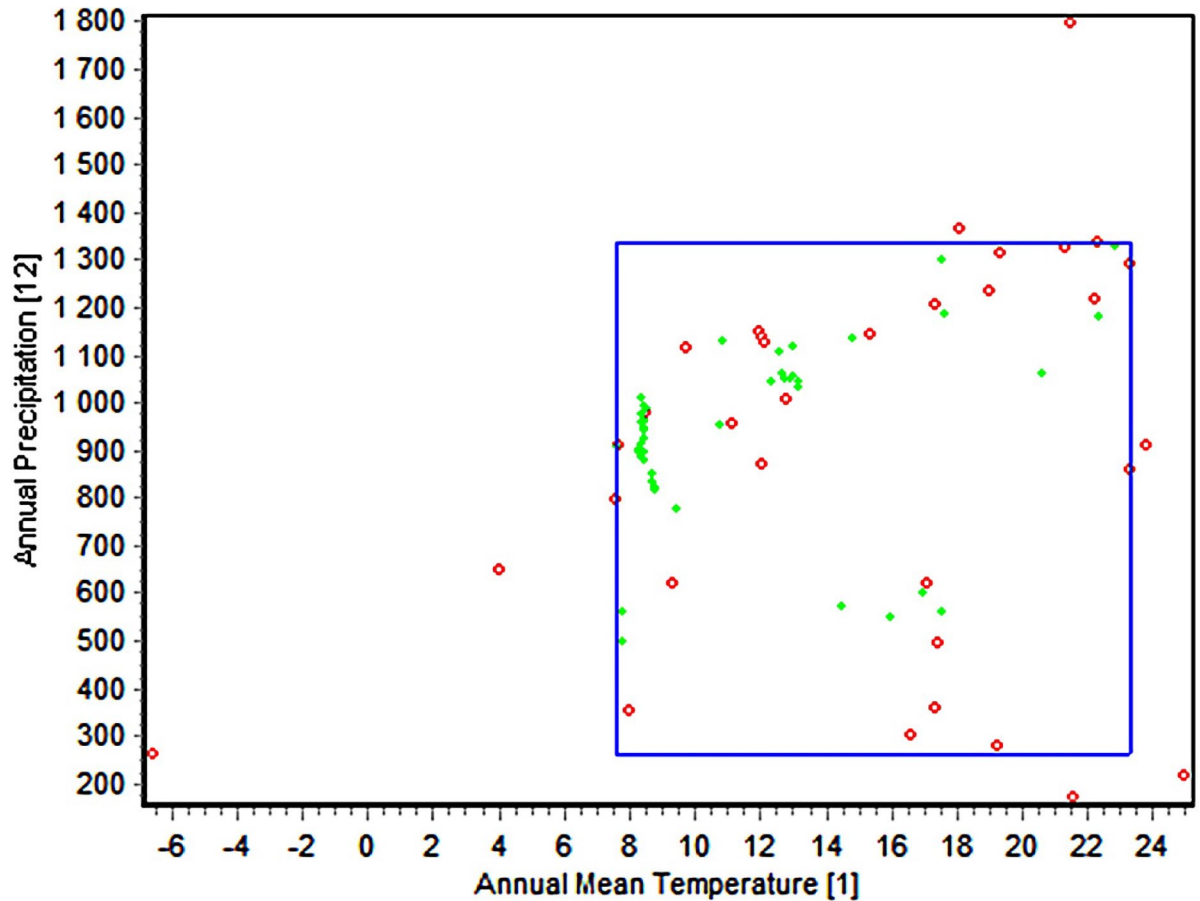


Fig. 6. The enveloped test indicates the wide range of the two factors bio_1 & bio_12; the green points indicate the occurrence records that fall in the envelope for the 19 bioclimatic factors while red points indicate the occurrence of this record outside the envelope for at least one of the 19 bioclimatic factors.

test was employed to identify the essential bioclimatic variables influencing the species' distribution^{38,48}. Additionally, the accuracy of the predicted models was assessed using true skill statistics (TSS). The projected model and the species' distribution exhibit a good correlation when TSS values are positive and close to 1, within a range of -1 to 1^{49} .

Envelope test and limitation factor map

We utilised Diva-GIS software to examine the two-dimensional niche of *X. fastidiosa*. The Envelope test was performed, focusing on two primary climatic variables: annual mean temperature (bio_1) and annual precipitation (bio_12) (Fig. 6)^{50,51}. This test allowed us to assess the relevance and suitability of these parameters for the species. Additionally, we employed the bioclimatic statistical modelling functionality in Diva-GIS to generate a limiting factor map based on the selected variables^{52–54}. This research enabled us to identify and specify the traits that most significantly constrain the dissemination of *X. fastidiosa*, providing essential insights into the ecological limits affecting the species.

Data availability

All the data are included in the manuscript.

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Declarations

Competing interests

The authors declare no competing interests.

Additional information

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