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Species distribution models predicting climate suitability for the psyllid *Trioza erytreae*, vector of citrus greening disease

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ABSTRACT

The African citrus psyllid, *Trioza erytreae* (Hemiptera: Triozidae), is a vector of citrus greening (Huanglonbing - HLB), a bacterial citrus disease caused by *Candidatus liberibacter* spp. Native to Africa, *T. erytreae* was detected in the Canary Islands and Madeira in the early 2000s and then in northwestern Spain in 2014. Since then, *T. erytreae* has become established along the Atlantic coastal areas of the Iberian Peninsula. Therefore, an accurate assessment of the potential long-term establishment of *T. erytreae* in major citrus-growing regions of Europe and the world is urgently needed to design adapted control strategies. I calibrated correlative species distribution models to understand the bioclimatic characteristics that determine the distribution of *T. erytreae*, and to assess the climatic suitability of the world's major citrus-growing regions for the psyllid under current and future climate conditions. I calibrated the models using only distribution data from Africa (its native range), the Canary Islands, and Madeira, and evaluated them using available data from the invaded area in continental Europe. This approach aims to avoid spurious good measures of model accuracy arising from spatial autocorrelation between the calibration and evaluation datasets. The models identify mild summer and winter temperatures and high levels of precipitation as optimal conditions for long-term psyllid establishment, consistent with its physiology. In Europe, models predict only the Atlantic coastal regions of the Iberian Peninsula as highly climatically suitable, a spatial pattern that corresponds exactly to the area currently invaded by the psyllid. Models predict that most of the important citrus-growing areas in the world are, and will remain in the future, poorly adapted to *T. erytreae* except in case of future physiological adjustments. These results are crucial for the design of appropriate pest management strategies and are timely for Europe where the African citrus psyllid has recently been detected.

1. Introduction

Greening disease (i.e. Huanglongbing in Chinese - HLB), induced by the bacterium *Candidatus liberibacter* spp., is a destructive pathology affecting citrus worldwide (Bové, 2006). The disease is currently present in Asia, the Americas, Africa, and a few Indian Ocean islands (EFSA et al., 2019). In these regions, it is considered the most important limiting factor for citrus cultivation. Common symptoms associated with HLB include leaf yellowing, defoliation, decreased root abundance, twig dieback, production of small, irregularly shaped and bitter fruits, and a general decline health, eventually leading to plant death. The disease causes enormous economic costs associated with substantial decreases in production as well as the use of plant protection products, and the implementation of costly control strategies (Hodges and Spreen, 2012; Spreen et al., 2014). There is no treatment to cure HLB-infected trees, so control strategies rely primarily on controlling competent vectors, removing infected trees, controlling plant nurseries, and using pathogen-free planting material.

The pathogen *C. liberibacter* spp. is mainly transmitted from one plant to another by insects. Two main vectors of HLB are currently recognized, the Asian citrus psyllid *Diaphorina citri* Kuwayama (Hemiptera: Liviidae) and the African citrus psyllid *Trioza erytreae* Del Guercio (Hemiptera: Triozidae). The Asian citrus psyllid is native to Asia and has invaded most of the major citrus-growing regions of the world - including North America, the Caribbean, the Middle East, and South America - where it is responsible for severe HLB outbreaks (CABI, 2021). The African citrus psyllid is native to Africa, where it is responsible for severe HLB outbreaks (Schwarz, 1967), and has invaded some Indian Ocean islands, the Canary Islands, Madeira, and continental Europe (CABI, 2021). However, *T. erytreae* is still absent from the main citrus-growing regions located in the Americas, Asia, and Australia. In continental Europe, the African citrus psyllid was first detected in 2014 in the northwestern

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parts of the Iberian Peninsula (Otero et al., 2015). Since then, the insect has remained confined to the Atlantic coastal regions of northern Spain and Portugal and has not spread to other citrus-growing regions of the Mediterranean basin (Arenas-Arenas et al., 2019).

The African citrus psyllid feeds mainly on plants belonging to the Rutaceae family (Moran, 1968). The species does not diapause and can reach a total of 6–8 generations when environmental conditions are optimal (Catling, 1972; Tamesse and Messi, 2004). However, under suboptimal conditions, the annual number of generations decreases sharply (Tamesse and Messi, 2004). Depending on temperature conditions, eggs hatch in 1–2 weeks, while 2–8 weeks are required to complete the five nymphal stages. Eggs and nymphs are thought to be the most temperature- and humidity-sensitive life stages; in particular, populations normally experience high mortality of eggs and early nymphal stages when conditions are hot and dry (Catling, 1969; der Merwe, 1923; Green and Catling, 1971; Moran VC & Blowers, 1967; Samways, 1987). Adults can live for several months and are able to cope with adverse conditions of drought and heat (Samways, 1987).

Risk assessment of a vector-borne plant disease ideally involves independently predicting the environmental tolerances of the plant pathogen and associated key competent vectors (Gimenez-Romero et al., 2022; Godefroid et al., 2021). Given the invasion of *T. erytreae* into regions beyond its native range and the threat posed by HLB, there is an urgent need to assess the potential risk of long-term establishment of *T. erytreae* in major citrus-growing regions in Europe and the rest of the world. Among the various factors determining the spatial distribution of a species, climate is obviously crucial. Therefore, the objective of this study is to understand the bioclimatic factors that determine the spatial distribution of the African citrus psyllid and to predict the climatic suitability of the world's major citrus growing regions for this species. To achieve this goal, I collected distribution data on *T. erytreae* and calibrated bioclimatic species distribution models (SDMs; Peterson et al., 2011) to depict the environmental tolerances of this species. Correlative SDMs are powerful tools that rely on distributional data and high-resolution bioclimatic rasters to depict the realized climatic niche of species, and to forecast the potential distribution of invasive species or the response of species to global change (Peterson et al., 2011). Despite their promise, the reliability and practical importance of SDMs has often been questioned due to weaknesses inherent in correlative niche modelling approaches, particularly when the goal is predicting the range of invasive species (Araújo and Peterson, 2012; Jiménez-Valverde et al., 2008, 2011). Among the various caveats of SDMs, the lack of spatial and/or temporal independence between calibration and evaluation datasets is a major potential source of errors sometimes leading to artifactual inflation of the perceived accuracy of the models (Elith and Burgman, 2002; Randin et al., 2006). To avoid this problem, it is therefore strongly recommended that model predictions be validated with data that are spatially and/or temporally independent of the calibration dataset, which will enhance the credibility of models and ensure that the models are transferable across space and time (Elith and Burgman, 2002; Randin et al., 2006). I therefore calibrated the bioclimatic models using data from Africa (the native range of this species), the Indian Ocean islands, the Canary Islands and Madeira, and then evaluated them using available data from the invaded range in continental Europe.

2. Material and methods

2.1. Occurrence data

I extracted presence data from the scientific literature and the freely available GBIF (Global Biodiversity Information Facility database (Gbif.org, 2021). I also obtained occurrence records from online reports available on the websites of the Province of Galicia (Xunta de Galicia, 2020) and the Portuguese Directorate General of Food and Veterinary Medicine (Direção-Geral de Alimentação e Veterinária, 2021). I checked the reliability of each record and discarded unreliable occurrences (e.g., records with lack of information to assign reliable GPS coordinates). A total of 2807 presence records were obtained (Fig. 1). After removing duplicate records (i.e., allowing only one presence record in each pixel of the bioclimatic rasters used for modeling), the final dataset included 1525 occurrences (133 records situated in Africa, Indian Ocean Islands, Canary Islands and Madeira and 1392 records situated in mainland Europe).

2.2. Bioclimatic data

I extracted global bioclimatic rasters from the CHELSA database, which reflects historical climate trends for the period 1979–2013 (Karger et al., 2017). Thes bioclim variables were built The rasters were downscaled to a resolution of 2.5 arc minutes (approximately 5 km^2). Four bioclimatic descriptors thought to reflect putative climate stress for this species were used in the modeling framework, namely the mean temperature of the warmest quarter of the year (bio10), the mean temperature of the coldest quarter of the year (bio11), the precipitation of the warmest quarter of the year (bio18), and the precipitation of the coldest quarter of the year (bio19). I ensured that these four covariates were not highly correlated in the calibration area (i.e., a Pearson's correlation index <0.7).

To predict the impact of climate change on the potential distribution of *T. erytreae*, I used estimates of future climate conditions for the period 2040–2060 simulated by two global climate models provided by the Intergovernmental Panel on Climate Change Fifth Assessment Report, namely the Model for Interdisciplinary Climate Research version 5 MIROC5 and the Canadian Earth System Model version 2 (CanESM2) (Swart et al., 2019; Watanabe et al., 2011). I used a moderate scenario of future greenhouse gas emissions (rcp45 scenario).

2.3. Calibration and evaluation of models

I used the algorithm Maxent to model the environmental tolerances of the African citrus psyllid (Phillips et al., 2006). This algorithm is a widely used presence-only approach that ranks among the best performing SDM techniques. (Wisz et al., 2008). I allowed only linear and quadratic features to ensure easy interpretation of the models and to avoid fitting overly complex species-covariate relationships and overparameterizing the models (Merow et al., 2013). I calibrated the models using only available occurrences in Africa, the Indian Ocean Islands, the Canary Islands and Madeira. I randomly generated 20,000 background points for model calibration (i.e., localities with unknown species presence status) generated in Africa, Indian Ocean Islands, Canary Islands and Madeira using the R package 'dismo' (Hijmans et al., 2017). (Appendix A). Although the selection of background selection may affect modelling outputs and evaluation metrics (Barve et al., 2011), I used a large continental-scale approach in the present modelling procedure. Models were fitted using a subset of 90% of these data (calibration dataset) and evaluated using the remaining 10% of data (evaluation dataset). I evaluated the models by calculating the area under the receiving operator characteristic curve (AUC) (Fielding and Bell, 1997), the True Skill Statistics (TSS) (Allouche et al., 2006) and the Boyce index (Hirzel et al., 2006). Before fitting the final models, I first evaluated the best-predicting parameters among different values of regularization multipliers (RMs) ranging from 0.5 to 4 with an increment of 0.5 (Radosavljevic and Anderson, 2014). I selected the RM value associated with the highest average AUC. The final models were also evaluated using the available occurrence records in continental Europe and 1000 background points generated in the western part of the Iberian Peninsula (latitude ranging between 36 and 44°; longitude ranging between −10 and −7.5°). This approach can be considered as a spatially independent evaluation procedure The models were replicated 5 times and the average climatic suitability between model replicas was mapped. The importance of each variable in models was estimated following the

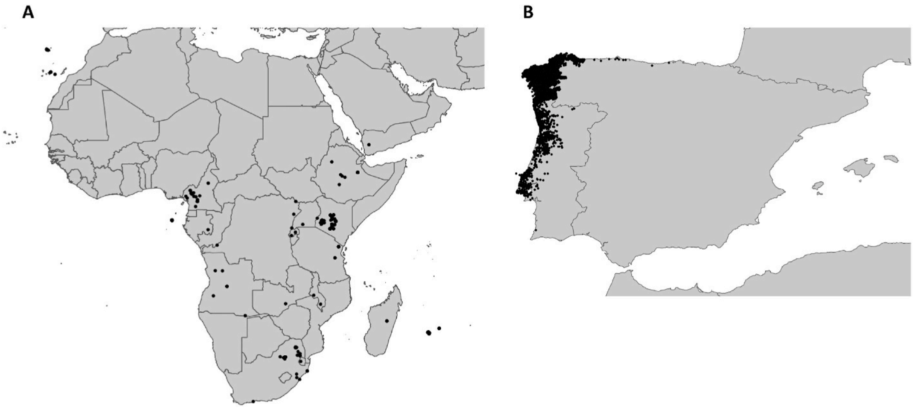

Fig. 1. Presence records for the African citrus psyllid *Trioza erytreae* in (A) Africa, Indian Ocean Islands, Atlantic Ocean Islands and (B) mainland Europe. Presences of *T. erytreae* are represented by black dots.

approach proposed by Thuiller et al. (2009). We finally transformed the climatic suitability estimates in predicted presence/absence binary maps by applying a threshold maximizing the sum of sensitivity and specificity (Fielding and Bell, 1997). We assigned a presence to each pixel for which more than half of the models predicted a presence. Models were fitted and evaluated using the *biomod2* R package (Thuiller et al., 2016). To assess similarity/dissimilarity between calibration and projected climatic spaces, I measured the multivariate environmental similarity surfaces (MESS; Elith et al., 2010). The MESS index reflects how similar a point in the projected area is to the set of calibration points, with respect to the set of predictor variables. The MESS index was measured with the R package ‘dismo’ (Hijmans et al., 2017).

3. Results

A value of 0.5 for the regularization multiplier produced the best evaluation measure. The final models produced excellent evaluation measures (mean AUC = 0.83 ± 0.07; mean TSS = 0.58 ± 0.16; mean Boyce index = 0.76 ± 0.08) when evaluated with the evaluation dataset built with data from the calibration area. The models also provided excellent evaluation metrics when evaluated with the spatially independent evaluation dataset built with data from continental Europe (mean AUC = 0.86 ± 0.01; mean TSS = 0.44 ± 0.07; mean Boyce index = 0.97 ± 0.01). The MESS maps suggest that most of major economically important citrus-growing areas of the world are not climatically very different from the calibration dataset under current and future climate conditions (MESS values > 0; Appendix B). Areas the most climatically different from the calibration dataset (MESS index <0)

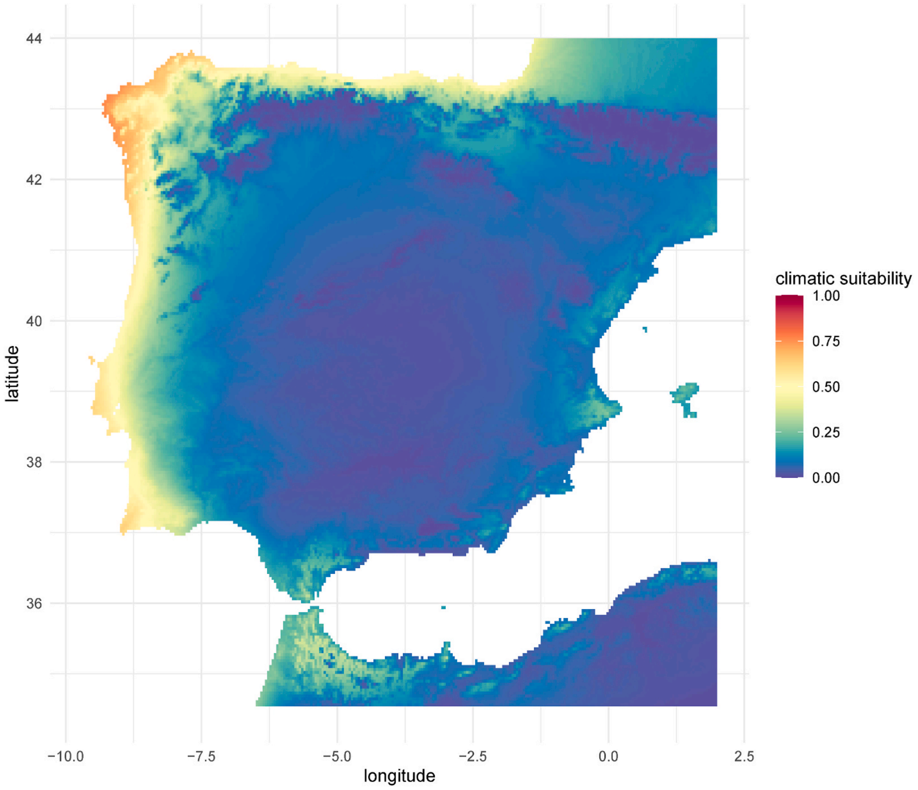

Fig. 2. Maxent-derived predictions of current climate suitability in the Iberian Peninsula for the African citrus psyllid *Trioza erytreae*. Maps represent the average predictions among 5 replicates.

mainly include cold temperate regions where citrus are not grown, desertic regions (Sahara region) and very dry and warm regions (i.e. Middle east, southern California; Appendix B).

Bioclimatic models identified summer average temperature (bio10) as the most important covariate in explaining the distribution data (mean variable importance = 0.7 ± 0.03), followed by winter average temperature (bio11; mean variable importance = 0.14 ± 0.03) and precipitation in the warmest quarter of the year (bio18; mean variable importance = 0.09 ± 0.01). Precipitation in the coldest quarter of the year (bio19) made a negligible relative contribution to the model (mean variable importance = 0.008 ± 0.007). The models modeled unimodal responses of African citrus psyllid to winter and summer temperatures (Appendix C). The models modeled a positive linear-like effect of increased rainfall during the warmest and coldest quarters of the year on the probability of *T. erytreae* occurrence (Appendix C).

Bioclimatic models have predicted that a very small part of Europe is currently highly climatically suitable for *T. erytreae*, which ideally matches the invaded range of this species in the Iberian Peninsula (Fig. 2). In Europe, the regions predicted to be most suitable encompass the cool, humid areas of the northern parts of the Iberian Peninsula, i.e.

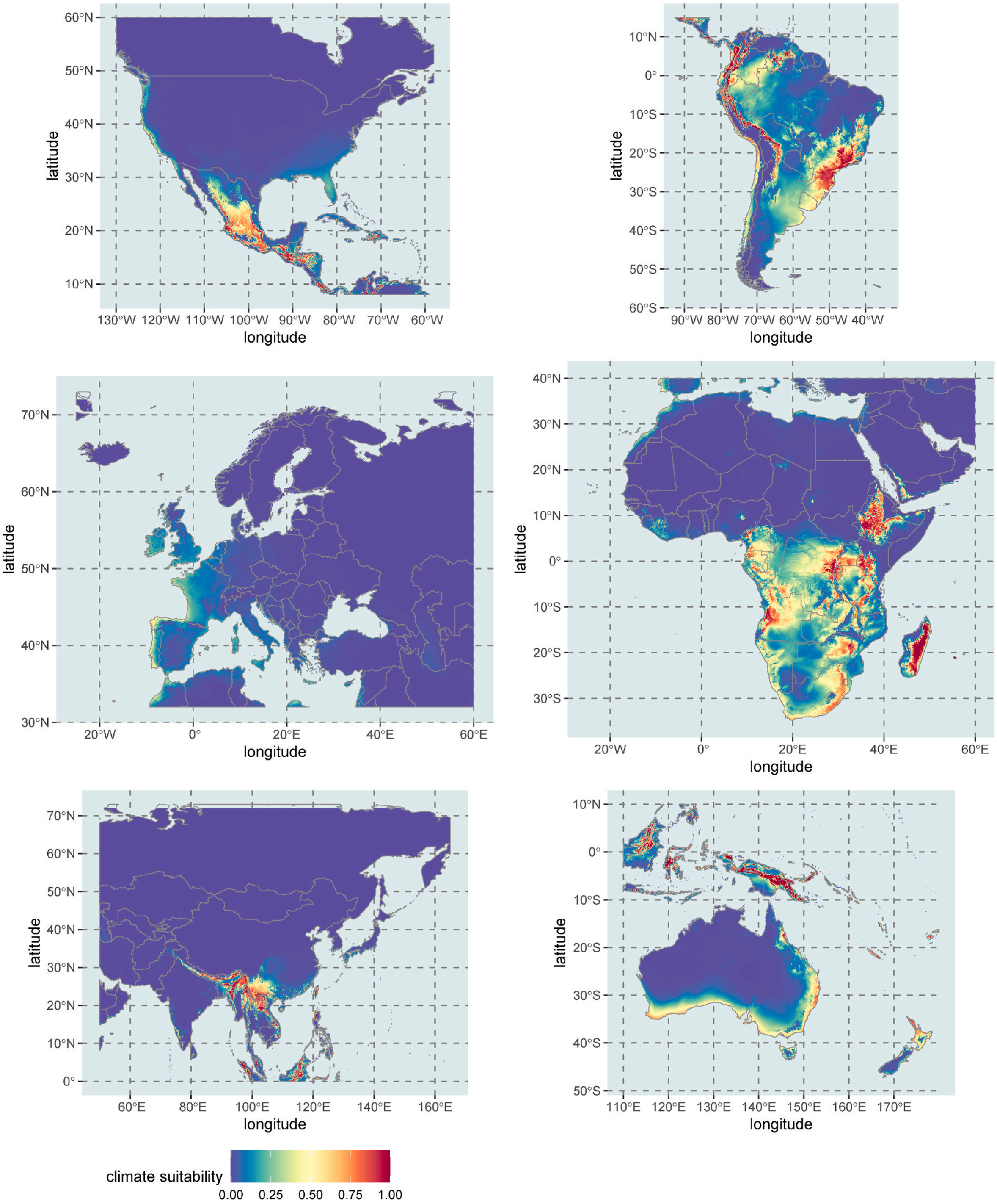

Fig. 3. Maxent-derived predictions of current climate suitability of some of the major citrus-growing regions of the world for the African citrus psyllid *Trioza erytreae* (A: North America; B: Europe and North Africa; C: South Africa; D: Australia; E: Asia; F: South America). Maps represent the average predictions among 5 model replicates.

the Atlantic coastal regions of Portugal and Spain (Figs. 2 and 3). The dry and hot regions of the Mediterranean basin, where economically important citrus cultivation is generally practiced (e.g., lowlands of southern and eastern Spain, lowlands of southern Italy and Greece) were considered moderately or poorly suitable (Figs. 2 and 3). Bioclimatic models did not predict a significant increase in climatic suitability for *T. erytreae* in these European citrus-growing regions for the period 2040–2060 regardless the global circulation model considered (Figs. 4 and 5; Appendix D).

Major economically important citrus-growing areas in the rest of the world (FAO, 2019) were predicted to be poorly suitable, e.g. Florida and California (USA), lowlands in southeastern China, India, lowlands in Mexico, lowlands in tropical Brazil, and coastal regions in southern Turkey or Egypt (Figs. 3 and 5). Bioclimatic models did not predict a significant increase in climate suitability for *T. erytreae* in most of these regions for the period 2040–2060 regardless the global circulation model considered (Fig. 5; Appendix D).

4. Discussion

4.1. Reliability of models' outputs

The Maxent-derived modeled response curves to bioclimatic covariates are consistent with currently available knowledge of the physiology of *T. erytreae*. Indeed, Maxent models identified a negative effect of high temperatures on the probability of occurrence of African citrus psyllid, which is consistent with early field observations (Green and Catling, 1971; Moran VC & Blowers, 1967; Samways, 1987) and recent laboratory evidence that this species is heat-sensitive (Aidoo et al., 2022b). Similarly, models have identified a negative correlation between low winter temperatures and the likelihood of occurrence of African citrus psyllid, consistent with the apparent lack of cold-induced diapause in this psyllid and the long-standing assertion that a temperature of 10 °C is the lower threshold for development of the various life stages of this species (Catling, 1969, 1973). Similarly, no complete development of *T. erytreae* has been observed in climatic chambers constantly maintained at 10 °C (Aidoo et al., 2022b). Bioclimatic models also suggest that high amounts of precipitations during the warmest and coldest periods of the year favor the presence of *T. erytreae*, confirming that moist conditions are optimal for the multiplication of this species (Green and Catling, 1971; Moran VC & Blowers, 1967; Samways, 1987).

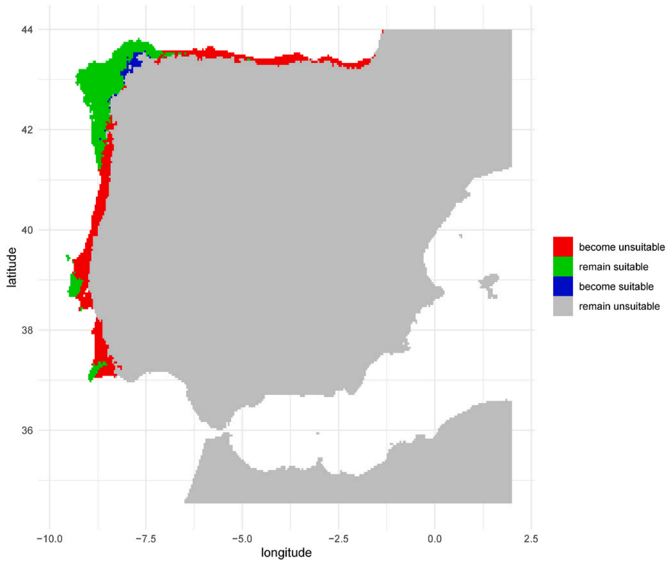

Fig. 4. Maxent-derived binary maps of predicted presence-absence of the African citrus psyllid *Trioza erytreae* under current and future climate conditions in the Iberian Peninsula i.e. the period 2040–2060 under the rcp45 scenario of future climate conditions (MIROC5 global circulation model). Predicted presence-absence were obtained by implementing a threshold maximizing the sum of sensitivity and specificity of models. The maps identified pixels that are predicted as suitable under current and future climate conditions ("remain suitable"); predicted as unsuitable under current and future climate conditions ("remain unsuitable"); predicted as unsuitable under current climate conditions and suitable under future climate conditions ("become suitable"); predicted as suitable under current climate conditions and unsuitable under future climate conditions ("become unsuitable").

The estimates of climatic suitability presented in this study are consistent with the known distribution of African citrus psyllid outside of continental Europe, i.e., this species is abundant in cool, humid highland areas and absent or at least rare in the warm lowlands of sub-Saharan Africa (Aidoo et al., 2019; Aubert et al., 1988; Tamesse et al., 1999) and Reunion Island (Aubert et al., 1980). The models are also congruent with expert knowledge and the scientific literature on psyllid distribution in citrus-growing regions of South Africa. Indeed, the models predict that the citrus-growing regions of Transvaal and Natal areas are highly suitable for the psyllid, confirming observations from field surveys (Schwarz, 1967). Conversely, bioclimatic models predict that the citrus-growing regions of Western cape and Northern cape are moderately and poorly suitable, respectively, which is also consistent with field observations provided by Schwarz (1967). Indeed, these regions have historically been relatively free from high psyllid populations and severe HLB outbreaks (Schwarz, 1967).

The models predicted the area invaded by *T. erytreae* in continental Europe with some accuracy (Fig. 2). It is promising since the continental European distribution data were not considered in the model calibration and were only used as an independent evaluation dataset. This promising accuracy in predicting a spatially independent evaluation dataset lends great credibility to the SDM-derived climate suitability estimations presented here (Elith and Burgman, 2002; Randin et al., 2006). According to the models, the current spatial pattern of *T. erytreae* spread along the Iberian Atlantic coast likely reflects the unique climatic conditions encountered in these regions i.e., mild temperatures in both summer and winter (Godefroid et al., 2016) and sufficient moisture conditions, which ideally match the environmental tolerances of the African citrus psyllid.

To my knowledge, the present study represents the second attempt to provide a global map of current and future potential climatic suitability for the African citrus psyllid by fitting correlative bioclimatic SDMs based on the occurrence data available in its native range (see Aidoo et al., 2022a). The Maxent-derived predictions proposed by Aidoo et al. (2022a), however, are derived from modeled response curves that do not match the physiology of the psyllid. For example, in their Maxent models, extremely high average temperatures during the driest month of the year are predicted to be suitable for the psyllid (see Fig. 6 in Aidoo et al., 2022a), which does not reflect the well-known heat sensitivity of this species. Similarly, in their Maxent models, extremely low temperatures in both the coldest quarter of the year and the warmest month of the year, are predicted to be very favorable for the psyllid (see Fig. 6 in Aidoo et al., 2022a), which is not ecologically realistic. For the Iberian Peninsula, my models provide different results from two recently published SDM-derived predictions (Benhadi-Marín et al., 2020, 2022). I argue that the present study provides a more reliable SDM-derived estimate of the climate niche of *T. erytreae*. On the one hand, the study published by Benhadi-Marín et al. (2020) has two major methodological caveats that may explain why their SDM-derived climatic suitability estimates do not ideally match the currently observable spread pattern of the psyllid in Portugal and Spain. Firstly, the calibration and evaluation of their models were both based solely on available distribution data from the recently invaded Iberian Peninsula, which may result in a risky loss of information (Elith et al., 2010). Second, their models were calibrated with only one explanatory climatic covariate (i.e. precipitation in the coldest quarter of the year) and thus do not account for the thermal tolerances of the psyllid, which are crucial to explain its

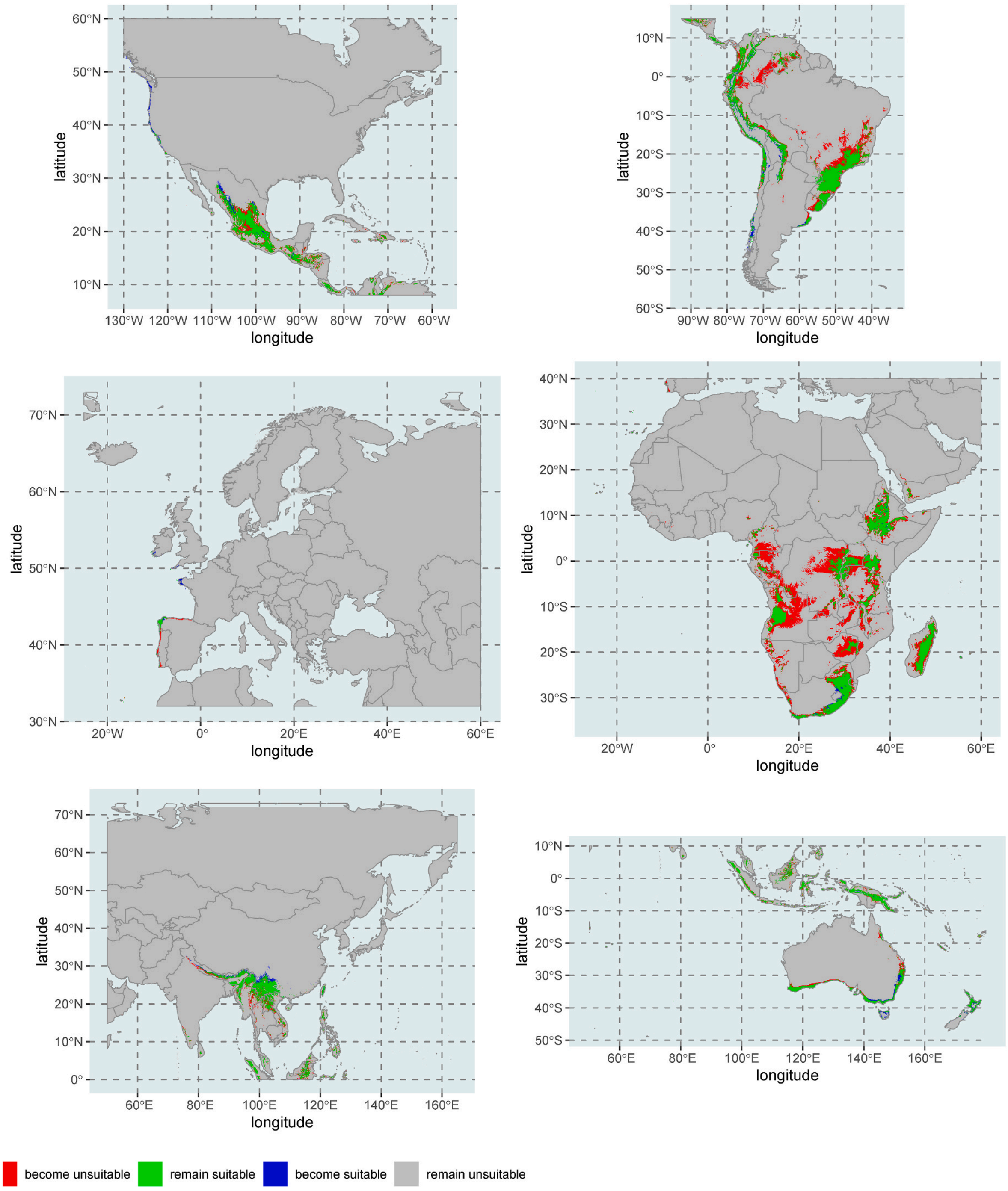

Fig. 5. Worldwide Maxent-derived binary maps of predicted presence-absence of the African citrus psyllid *Trioza erytreae* under current and future climate conditions i.e. the period 2040–2060 under the rcp45 scenario of future climate conditions (MIROC5 global circulation model). Predicted presence-absence were obtained by implementing a threshold maximizing the sum of sensitivity and specificity of models. A: North America; B: Europe and North Africa; C: South Africa; D: Australia; E: Asia; F: South America.

geographical range. On the other hand, the study published by Benhadi-Marín et al. (2022) has an important caveat, namely that the authors used a SDM-derived estimate of the climatic suitability of *Citrus* spp. as a proxy for the potential distribution of *T. erytreae* in the Iberian Peninsula. As noted in this study and published references provided here, *T. erytreae* and *Citrus* spp. do not have equivalent climatic tolerances.

I warrant caution in interpreting the climatic suitability estimates presented here due to the correlative nature of the modelling technique (Peterson et al., 2011). Furthermore, we modeled the distribution of *T. erytreae* by implementing relatively simple model features to promote model transferability and interpretability and to avoid model overfitting. I emphasize that low value of predicted climatic suitability should not be interpreted as a prediction of “no risk of local establishment at all”. However, I argue that these SDM-derived climate suitability estimates are a very promising proxy for predicting differences in potential psyllid population densities and identifying the citrus-growing regions most likely to allow long-term establishment of this species.

4.2. *Risk of establishment in economically important citrus-cropping regions*

In Europe, four Mediterranean countries are economically important citrus producers, namely Spain, Italy, Portugal and Greece (EFSA et al., 2019). Model predictions suggest that most citrus-growing regions in these countries are of low climatic suitability for African citrus psyllid long-term establishment (Figs. 2 and 3). In coastal Portugal, which was predicted to be highly suitable for *T. erytreae*, citrus cultivation is not economically important and citrus plants are generally found in home gardens. In Portugal, most citrus production comes from the Algarve region located in the south of the country. According to the models, the climate of the Algarve region is predicted to be moderately adapted to the African citrus psyllid (Fig. 2). In Spain, economically important citrus-growing areas are mainly located in the provinces of Andalusia, Murcia, and Valencia (EFSA et al., 2019), which were predicted to be poorly suitable for *T. erytreae* (Fig. 2). Similarly, in Italy, citrus production is limited to the southern provinces, which were also predicted to be poorly suitable for the African citrus psyllid (Fig. 3). According to predictions taking into account global change simulations, the risk of long-term establishment of *T. erytreae* in these main citrus-growing regions of Europe is not expected to increase over the next decades (Figs. 4 and 5), which is not surprising for a species that is preferentially present in regions characterized by cool summer temperatures. Importantly, the range of *T. erytreae* in Atlantic coastal areas of the Iberian Peninsula is predicted to decrease due to climate change (Fig. 3).

In the rest of the world, many important citrus-growing regions are predicted to be little suitable for establishment of the African citrus psyllid, including the Mediterranean coastal regions of Turkey, the lowlands of tropical Brazil, southeastern China, India, the southern United States (especially Florida and California), and the lowlands of Mexico (FAO, 2019). The bioclimatic models suggest that global change will not cause an increase of climatic suitability in a near future (Fig. 5 & Appendix D). We recognize that a more accurate assessment of the local risk of establishment of *T. erytreae* in citrus-growing areas would require accurate, high-resolution maps of citrus orchard distribution. However, such information on a global scale is currently lacking. In addition, addressing the future distribution of citrus-growing regions under global change scenario is another research field that could improve assessment of the future distribution of *T. erytreae*. I finally remind that the maps provided here only reflect an assessment of climatic suitability for *T. erytreae* and do not focus on bacterial pathogens responsible for HLB neither citrus distribution.

5. Conclusions

Overall, this study highlights that there is a high degree of spatial variation in the potential climatic suitability for African citrus psyllid in Europe and the major citrus-growing areas of the world. The maps provided here are essential tools for assessing the risk of global HLB outbreaks. It should be noted that the climate suitability of the major citrus-growing areas of the world is relatively low and is expected to remain so in the near future. This result has crucial implication for the design of control strategies and risk assessment of HLB, especially in Europe where *T. erytreae* has been recently detected. In addition, this study provides a striking example of the promise of SDMs for assessing the potential range of invasive species.

Authors' contributions

MG designed the study, collected the data, performed statistical analyses, and wrote the manuscript.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be available upon request to the author once acceptance of the MS.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cropro.2023.106228.

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