RODRIGO SOARES RAMOS

RISK LEVELS OF *Bemisia tabaci* AND *TYLCV* IN AREAS OF SUITABILITY FOR OPEN FIELD TOMATO CULTIVATION UNDER CURRENT AND FUTURE CLIMATES

Tese apresentada à Universidade Federal de Viçosa, como parte das exigências do Programa de Pós-Graduação em Entomologia, para obtenção do título de *Doctor Scientiae*.

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ABSTRACT

RAMOS, Rodrigo Soares, D.Sc., Universidade Federal de Viçosa, July, 2018. **Risk levels of *Bemisia tabaci* and *TYLCV* in areas of suitability for open field tomato cultivation under current and future climates**. Adviser: Marcelo Coutinho Picanço.

The aim of this work was to model the risk of *Bemisa tabaci* and the virose *Tomato Yellow Virus Curl Virus* in tomato crops *Solanum lycopersicum* using the MaxEnt and identify the climatic factors that are associated with the distribution; in addition to determining the spatiotemporal dynamics of *B. tabaci* using CLIMEX (version 4). In order to do so, this work was divided into three chapters; in the first chapter, the risk of *B. tabaci* in open field tomato crops for the present and future (2050 and 2070) was modeled, and the climatic factors that are associated to the distribution of the pest was identified. In the second chapter we studied the risk of dispersal of the Geminivirus *(Tomato Yellow Leaf Curl Virus*) in tomato crops under four scenarios of climate change (RCPs 2.6, 4.5, 6.0 and 8.5). In the third chapter we determined the seasonal variation of *B. tabaci* in tomato crops as well as the influence of climate for the species. The models demonstrate reliability. The results indicate that climatic changes will impact the distribution of insect pest *B. tabaci*, host plant *S. lycopersicum* and virose *Tomato Yellow Leaf Curl Virus*. Several regions around the globe are projected to be favorable for *TYLCV* in areas of suitability for *B. tabaci* under optimum conditions of open field tomato cultivation. The dynamic spatial-temporal climatic models are in agreement with the seasonal variations of *B. tabaci*, and the seasonal variations influence the density of *B. tabaci* in commercial tomato crops, presenting higher intensities of nymphs and adults in the months of October to December. Thus, the results of this work contribute to the elaboration of strategies to avoid the introduction and establishment of *B. tabaci* and virose (*TYLCV*) in suitable places for tomato cultivation, as well as the implementation of management programs in areas of current occurrence of species, especially in locations under high-risk conditions, and in times of increased susceptibility to the pest.

RESUMO

RAMOS, Rodrigo Soares, D.Sc., Universidade Federal de Viçosa, julho de 2018. **Risk levels of *Bemisia tabaci* and *TYLCV* in areas of suitability for open field tomato cultivation under current and future climates**. Orientador: Marcelo Coutinho Picanço.

O objetivo deste trabalho foi modelar o risco de *Bemisa tabaci* e da virose *Tomato Yellow Vírus Curl Virus* em cultivos de tomate *Solanum lycopersicum* utilizando o MaxEnt e identificar os fatores climáticos que estão associados com a distribuição; além de determinar a dinâmica espaço-temporal de *B. tabaci* utilizando o CLIMEX (versão 4). Para tanto, este trabalho foi dividido em três capítulos, no primeiro capítulo foi modelado o risco de *B. tabaci* em cultivos de tomate em campo aberto para o presente e futuro (2050 e 2070), sendo identificado os fatores climáticos que estão associados a distribuição da praga. No segundo capítulo estudou-se o risco de dispersão do Geminivirus (*Tomato Yellow Leaf Curl Virus*) em cultivos de tomate sobre quatro cenários de mudanças climáticas (RCP's 2.6, 4.5, 6.0 e 8.5). No terceiro capítulo foi determinado a variação sazonal de *B. tabaci* em cultivos de tomate bem como a influência do clima para espécie. Os modelos demonstram confiabilidade. Os resultados indicam que as mudanças climáticas irão impactar a distribuição do inseto praga *B. tabaci*, da planta hospedeira *S. lycopersicum* e da virose *Tomato Yellow Leaf Curl Virus*. Várias regiões em todo o planeta estão projetadas a serem favoráveis para *TYLCV* em áreas de adequabilidade para a *B. tabaci* em condições ótimas de cultivo de tomate em campo aberto. Os modelos dinâmicos climáticos espaço-temporal estão de acordo com as variações sazonais de *B. tabaci*, sendo que as variações sazonais influenciam a densidade de *B. tabaci* em cultivos comerciais de tomate, apresentando maiores intensidades de ninfas e adultos nos meses de outubro a dezembro. Assim, os resultados desse trabalho contribuem no processo de elaboração de estratégias para evitar a introdução e estabelecimento de *B. tabaci* e da virose (*TYLCV*) em locais adequados para cultivo do tomateiro, bem como a implementação de programas de manejo em áreas de atual ocorrência da espécie, especialmente em locais sob condições de alto risco, e em épocas onde há maior grau de susceptibilidade para a praga.

INTRODUÇÃO GERAL

Estudos de distribuição espaço-temporal de espécies permitem determinar o padrão de distribuição da ocorrência atual e modelar previsões futuras dos organismos em diferentes regiões do nosso planeta. A modelagem é uma técnica quem vem sendo amplamente utilizada, capaz de indicar os locais de ocorrência de pragas, quando elas podem ocorrer, de que maneira bem como a adequabilidade climática (Thomson & Hoffmann 2011). Estas informações possibilitam o planejamento de estratégias e táticas de controle de pragas em locais onde se encontram as maiores densidades populacionais (Kumar et al., 2014a; Kumar et al., 2014b). Os principais fatores que afetam a dinâmica populacional de um inseto praga ou de um patógeno são a presença de hospedeiros susceptíveis e condições climáticas adequadas (Elith &Leathwick 2009; McDowell et al. 2014; Ward & Masters 2007; Bacon et al. 2014).

Os elementos climáticos são os principais fatores que impactam a distribuição e abundância de espécies de artrópodes, patógenos e plantas (Biber-Freudenberger et al. 2016; Shabani et al. 2016; da Silva et al. 2016). Os estudos dos efeitos climáticos na distribuição de espécies tem avançado e atingindo grande relevância nos últimos anos. Visto que, as mudanças climáticas previstas no nosso planeta venha a ter relevantes impactos na agricultura em vários países, por afetarem diretamente as culturas bem como populações de insetos e dispersão de patógenos em diversos ecossistemas (Shabani & Kotey 2016; Ramirez-Cabral et al. 2017; Aljaryian & kumar 2016; Cornelissen 2011; da Silva et al. 2016).

As mudanças climáticas podem ter importantes impactos na agricultura em todo o planeta, esses impactos podem ter efeito direto ou indireto (Bazzaz & Sombroek 1996; Adams et al. 1998; Deschenes & Greenstone 2007; Bentz et al. 2010). O efeito direto se deve ao fato do clima se tornar adequado ou inadequado para o crescimento e desenvolvimento de determinada cultura agrícola, já o efeito indireto está relacionado ao fato das mudanças climáticas favorecerem ou desfavorecerem a invasão de insetos pragas e de doenças em uma localidade. Uma vez que essas mudanças podem afetar o a duração do ciclo de vida, capacidade reprodutiva e o grau de mobilidade de espécies, que por consequência afetam a sua distribuição geográfica (Parmesan 2006).

Os modelos de distribuição de espécies são importantes pois podem indicar os locais de maior ocorrência de um determinado organismo e ajudar a entender a dinâmica da movimentação de uma espécie no ambiente (Peterson et al. 2011). No caso de uma espécie praga, esta ferramenta na prática é de grande valia, pois possibilita direcionar o esforço amostral e o controle desta praga em locais específicos (Ribes-Dasi et al. 2005). Estes modelos são uma ferramenta bastante usada para entender, sobretudo os efeitos das mudanças climáticas sobre os organismos, tal como indicar possíveis expansões de áreas de ocorrência das espécies e riscos potenciais que essas expansões podem gerar. Além disso, tais modelos são considerados uma técnica bastante eficiente para simulação de climas futuros sob diferentes cenários climáticos (Shabani et al. 2012; Shabani et al. 2016).

Existem inúmeras espécies invasivas que são consideradas grandes ameaças para a agricultura por causarem perdas diretas nos cultivos e consequentemente desencadeiam impactos significativos na economia dos países (Oerke et al. 2012; Paini et al. 2016; Cook et al. 2011). Os níveis de ameaças de invasão descrevem os riscos que uma espécie, seja ela um inseto praga ou um patógeno por exemplo, pode oferecer a alguma região na qual a ocorrência deste organismo não foi relatada anteriormente. O desafio dos estudiosos está em identificar e quantificar todos os possíveis caminhos pelos quais as espécies invasivas podem atingir uma determinada região (Paini et al. 2016). Essas informações podem contribuir bastante para evitar que certas espécies sejam introduzidas, estabelecidas e por fim acabarem causando danos. Dentre as principais espécies que levam a grandes perdas agrícolas, causando impacto negativo nos cultivos em várias regiões do planeta estão os insetos pragas e as doenças de plantas.

Neste contexto, a mosca branca *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae), um inseto sugador de seiva, altamente generalista e com ampla distribuição geográfica, tem sido considerado como uma das pragas mais invasivas e devastadoras de cultivos agrícolas, causando grandes prejuízos em várias regiões de todo o planeta (De Barro et al. 2011; Lowe et al. 2000). Estima-se que cerca de 600 espécies de plantas podem hospedar este inseto (Lowe et al. 2000; Markhan 1994; De Barro et al. 2011; Jiao et al. 2018). Dentre as espécies de plantas colonizadas pela mosca branca o tomateiro *Solanum lycopersicum* apresenta-se como uma das culturas mais infestadas por esta praga, com grande impacto socioeconômico em todo o mundo (Perring et al. 1993; Brown et al. 1995). Esse herbívoro causa danos severos diretos devido a sucção de seiva do floema e a injeção de toxinas e danos indiretos devido e transmissão de viroses que podem ocasionar morte das plantas e perdas de até 100% na produção. A mosca branca tem sido um dos principais problemas no cultivo de tomate, onde casos de ataques severos e elevadas perdas de produtividade tem sido cada vez mais frequentes, e a preocupação é ainda maior principalmente nos locais onde a mosca branca já ocorre, mas a virose ainda não foi reportada. Uma vez que a combinação da presença do inseto vetor, hospedeiro, patógeno e condições ambientais adequadas ocorra, poderá comprometer a produção agrícola no campo.

Dentre as viroses transmitidas pela mosca branca, o *Tomato Yellow Leaf Curl Virus* (*TYLCV*) (Familia: Geminiviridae; Genus: Begomovirus) é considerado como uma das viroses mais devastadoras que afeta a cultura do tomateiro (Czosnek & Laterrot

1997). Esse vírus pode levar grandes perdas, chegando até mesmo a comprometer por completo a produtividade dependendo do estádio de desenvolvimento em que a cultura for infectada (Pan et al. 2012). A severidade da infecção está diretamente ligado ao tamanho da população de mosca branca (Czosnek & Ghanim 2011). Desta forma a melhor maneira de prevenir perdas devido a *TYLCV* é controlar a mosca branca e evitar a introdução e o estabelecimento dessa virose em regiões em que o cultivo do tomateiro são importantes.

Apesar da importância da mosca branca por causar grandes prejuízos devido aos danos diretos e indiretos (sobretudo pela transmissão de viroses) e do grande número de estudos realizados com esta espécie, ainda não se conhece os impactos que as mudanças climáticas poderão causar na distribuição espacial de *B. tabaci* e da virose *TYLCV* nos cultivos de tomate. Estes estudos são essenciais para o desenvolvimento de estratégias que venham reduzir os possíveis impactos nas culturas agrícolas. Os modelos de distribuição atual e futura fornecem informações de grande valia para que medidas sejam tomadas a fim de evitar a introdução e o estabelecimento de espécies invasivas como o exemplo de *B. tabaci* e *TYLCV*. Com isso, essa tese foi dividida em três capítulos: no primeiro capítulo foi modelado o risco de *B. tabaci* em cultivos de tomate em campo aberto para o presente e futuro (2050 e 2070) utilizando o MaxEnt, identificou-se quais os fatores climáticos que estão associados a distribuição da praga. No segundo estudou-se o risco de dispersão do Geminivirus (*Tomato Yellow Leaf Curl Virus*) em cultivos de tomate sobre vários cenários de mudanças climáticas utilizando o MaxEnt. No terceiro capítulo foi determinada a variação sazonal de *B. tabaci* em cultivos de tomate bem como a influência do clima (mensalmente) para espécie usando o CLIMEX (versão 4).

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CHAPTER 1: Risk levels of *Bemisia tabaci* in areas of suitability for open field tomato cultivation under current and future climates

ABSTRACT

BACKGROUND: The whitefly, *Bemisia tabaci*, is a major threat to tomato *Solanum lycopersicum* and ranks as one of the world's 100 most invasive pests. This is the first study of *B. tabaci* (Biotype B and Q) global distribution, focusing on risk levels of this pest, in areas projected to be suitable for open field *S. lycopersicum* cultivation under climate change. This study aims to identify levels of risk of invasive *B. tabaci* (Biotype B and Q) for areas of suitability for open field *S. lycopersicum* cultivation for the present, 2050 and 2070 using MaxEnt and the Global Climate Model, HadGEM2_ES under RCP45. **RESULTS:** 5% of areas optimal for open field *S. lycopersicum* cultivation are currently at high risk of *B. tabaci*. Among the optimal areas for *S. lycopersicum*, the projections for 2050 compared to the current time showed an extension of 180% in areas under high risk, and a shortening of 67 and 27% in areas under medium and low risk of *B. tabaci*, respectively, while projections for 2070 showed an extension of 164, and a shortening of 49 and 64% under high, medium and low risk, respectively. **CONCLUSIONS:** These results may be used in designing strategies to prevent the introduction and establishment of *B. tabaci* for open-field tomato crops, and assist the implementation of pest management programs.

KEYWORDS: Climate change, MaxEnt, modeling, *Bemisia tabaci*, *Solanum lycopersicum,* Pest Risk Analysis

1. INTRODUCTION

Plant pest expansion increased in the last century, mainly due to international travel and the trading of plants around the world [1]. A pest species may be distributed in different regions of the planet, introduced either by natural or anthropic dispersion. After introduction, the pest species may establish and cause negative impact to local hosting ecosystem and economy. Many factors may influence expansion, such as the availability of hosts and appropriate climatic conditions [2,3,4,5].

Climate is a major factor impacting on the distribution and abundance of arthropod species [6,7]. Studies of climate effects on pests and host species have advanced significantly in recent years and attained greater relevance, in terms of impact on distribution, physiology, phenology, genetics and behaviors of many invasive species [8]. It is predicted that climate change will have a great impact on agricultural crops such as date palm [9], maize [10], wheat and cotton [11], rice [12], as well as insect populations, both in natural ecosystems and agroecosystems [13].

The term ‘climate change’ refers to both global-scale and regional climate alterations over time. It is an important concept in organism distribution studies, especially in the case of insects, which are classified as ectotherms [14]. As particular regions become warmer, colder, wetter or dryer, they may become more or less suitable for specific pests and hosts. For example, a mean temperature increase hastens the maturing of many insect species, consequently affecting life cycle length, reproductive capacity and the degree of mobility [8]. Thus, the distribution of a species is primarily dependent on climate, which generally defines its geographical distribution.

A species distribution model (SDM) is a tool widely used in understanding the effects of climate change on a species, as well as planning further expansion of agricultural species and potential risks this may entail [15,16]. Such models offer the most efficient techniques for simulation of future climates under a variety of climate scenarios. They offer a means to study the projected impact of climate change on pest distribution. The model generates categories of climate suitability and matches these to geographical regions, whether or not the species occurs there currently. Such research, based on modeling, can predict the distribution and abundance of pests, in addition to elucidating ecological interactions and abiotic factors affecting the natural mortality.

The whitefly *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae) has been shown to be one of the most invasive and devastating insect pests of agricultural and horticultural crops, causing enormous economic losses worldwide [17,18]. The species is sap-sucking, highly generalist and widely distributed, making it a pest of great significance in many tropical countries. *B. tabaci* is ranked globally as one of the top 100 most invasive pests and has the ability to colonize on more than 600 plant species [18,19]. Among the species of plants colonized by the *B. tabaci*, the tomato *Solanum lycopersicum* cultivated in many countries and one of the most valuable vegetable crops globally, is one of the crops worst affected by the pest [20,21,22]. The damage caused by *B. tabaci* can be either through direct feeding (phloem sap-sucking), or due to the injection of toxins and transmission of over 150 plant viruses, mainly of the genus Begomovirus (Family: Geminiviridae), which is significant in tomato crops [23,24,25]. Damage caused by this insect pest may lead to mortality of the plants, with losses of up to 100% of production [23,26,27,28]. Thus, *B. tabaci* is a major problem in tomato crops. Cases of productivity losses due to the presence of the pest in open field tomato cultivation are more and more frequent, and concern is even greater where the insect is already present but the viruses (i.e Geminivirus) have not yet been reported. The combination can make tomato production unfeasible in many production fields around the world.

Bemisia tabaci is considered a species complex containing more than 30 morphological indistinguishable cryptic species [29], between them there are two most invasive and destructive species, which are the Middle East-Asia minor I, and the Mediterranean species, also referred as Biotype B and Q, respectively [17,29,30]. *B. tabaci* may fly long distances and acquire new niches, mostly by international trade. It is well known that the biotypes of *B. tabaci* are very dynamic and acquire new properties, and may replace another within a few years (e.g. Biotype B replacing A in the USA, and Q replacing B in the Middle and Far East). For this reason, it is important to consider these two biotypes in the model because they are showing to be similar in many aspects beyond climate requirements, and they are the ones, so far, that have strongly suppressed other biotypes especially when they reach places where only wild biotypes are present. Hence these two biotypes are considered most invasive and important to tomato crops [17], and for being similar on their climate niches [31], we selected the occurrences of these two biotypes B and Q for undertaking the modelling in this study.

Despite the impact of the whitefly and the large body of research on the species, the potential impact of climatic change on the global distribution of *B. tabaci* in agricultural crops remains understudied, particularly in tropical regions such as Brazil. So far there are only two modelling studies, one assessing the risk presented by *B. tabaci* in Europe [32] and another a case study in Bundaberg, Australia as adaptive pest management for horticulture under climate change [33]. Reviewing related research, our study appears to be unprecedented in its focus on risk levels of invasive pest of *B. tabaci*, in areas suitable for *S. lycopersicum* cultivation under climate change. In this research, we modeled the risk of *B. tabaci* in *S. lycopersicum* cultivation for the present and years 2050 and 2070. Thereafter, we overlaid these results onto predicted *S.*

lycopersicum future distributions, to establish categories of highest, medium and lowest risk for areas highly conducive to the cultivation of *S. lycopersicum*. Predicting geographical distributions of *B. tabaci* facilitates the development of models and consequently the concentration of efforts in regions with higher risk of invasion or establishment. Furthermore, analysis of the potential impact of climate change on areas of suitability for *S. lycopersicum* open-field cultivation, for both present and future are essential for the continued success of producing an economically viable crop and the design of more efficient strategies for controlling whitefly in open-field tomato farming, in terms of *B. tabaci*'s global ranking as a threat and the difficulties in attempting to control it [17,18,34], particularly in tomatoes [35]. Though *B. tabaci* is present on all continents, it is not yet established worldwide in open field scenarios [36].

2. MATERIAL AND METHODS

2.1. Occurrence data

Occurrence data for both species examined in our research was collected from GBIF and other references (for *B. tabaci*: 878 locations from GBIF GBIF.org (2nd May 2017) (http://doi.org/10.15468/dl.mwb31) and 84 from other literature and for *S. lycopersicum*: 186 occurrences from literature). We confirmed that all locations were open field, as opposed to glasshouses. Eventually, we selected 627 occurrences for *B. tabaci* and retained the 186 occurrences for *S. lycopersicum*. The *B. tabaci* records were reduced to 421 and *S. lycopersicum* to 177 after spatial filtering in spThin, an R package for minimizing spatial autocorrelation [37]. This technique retains as many localities as possible and outperforms alternative methods [38]. All occurrence data points were >10 km apart after filtering [38,39]. This distance ensures that each cell has only a single occurrence point.

2.2. Scenario and Model

Potential distributions of pest and host were modelled using the HadGEM2_ES GCM under the RCP45, for the years 2050 and 2070. RCP45 was developed by the GCAM (Global Change Assessment Model) modeling team at the Pacific Northwest National Laboratory's Joint Global Change Research Institute (JGCRI) (http://www.globalchange.umd.edu/models/gcam/). The scenario is structured on the core assumption that the global irradiative force will be stabilized by 2100 through the introduction of greenhouse gas limiting technology [40]. A secondary assumption is that forest land cover will be extended and crop and grazing lands reduced to increase carbon storage. RCP45 was selected on the basis that it sets out to describe the minimum aggregated impact of climate change [41].

HadGEM2-ES is a product of the Hadley Centre Global Environmental Model associated cycle of the fifth phase of the CMIP5 (http://www.ipcc.ch/report/ar5/wg1/) [42]. The model incorporates dynamic data on the impact of greenhouse gas emissions, aerosols, solar irradiance, ozone and other pollutants on vegetation, ocean biology and atmospheric chemistry [43]. With a CO_2 doubling rate of approximately 4.68°C, it ranks near the top of the CMIP5 range for climate sensitivity [43,44]. The coupling of the atmospheric and ocean models simulates the uptake and retention of carbon dioxide according to ocean depth more realistically than its predecessors [45].

2.3. Environmental Data layers

We initially considered 19 bioclimatic parameter variables (Table 1), from the WorldClim dataset [46] (http://www.worldclim.org/), at 2.5min spatial resolution (~5Km). This is a high quality resolution, sufficient to support climatic variables at global scale [2,47]. Average temperature was based on monthly climate data for minimum, mean, and maximum temperature and precipitation on data covering 1960-1990. Other parameters were drawn from seasonal variables and climatic extreme indices [46].

SDMtools in ARCGIS software was used to remove variables with high correlation, such that only one variable from a group with high correlation was included (Pearson correlation coefficient, r ≥|0.75|) (Table A.1). Values exceeding 0.75 are described by Kumar et al. (2014) as relatively strong for variable selection [48]. Ultimately the inclusion of a variable was based on realistic biological relevance to both *B. tabaci* and *S. lycopersicum*, and six bioclimatic variables were finally selected (Table 1; Table S1).

2.4. Model development and validation

Global potential distributions of *B. tabaci* and *S. lycopersicum* were obtained from the maximum entropy based model or MaxEnt algorithm version 3.3.3k [49] . MaxEnt constitutes a machine learning method that forecasts the probability distribution based on maximum entropy [49]. MaxEnt requires only a small sampling of data on the presence of a species and the background data [48,50,51,52]. The program most suited our research which had only presence data available for pest and host [49]. MaxEnt generates a suitability index ranging between 0 for unsuitable and 1 for optimum suitability. 50,000 background points were randomly selected for each species representing areas of current occurrence. A sampling bias was generated in that the data was collected unsampled from external sources. This was generated using a kernel density estimate in SDMToolbox [53]. The bias surface offsets sampling intensity and potential sampling bias [54].

To optimize the model for both *B. tabaci* and *S. lycopersicum*, we made adjustments to the MaxEnt default settings for certain combinations of feature types, as well as the regularization multiplier (RM). [48,54,55]. Initially, we combined sets of linear [L], quadratic [Q], product [P], threshold [T], and hinge [H] features (Table 3 and 4) with the RM to control the number of parameters and thus the model complexity [55,56]. RM values of 1.0; 1.5 and 2.0 were used for both species (Tables 3 and 4). An RM below 1 is restrictive and inappropriate for global predictions, while an RM greater than 1 produces a broader potential distribution [49].

We used the MaxEnt 'fade-by-clamping' option to eliminate extrapolations outside the environmental range [57]. The predictive contribution of environmental variables was estimated using the 'jackknife' technique. MaxEnt generates response curves and we chose only those representing relationships between probabilities of presence for each species, in terms of each environmental predictor. All response curves were evaluated on the basis of sound biological logic and those failing this test were eliminated from further evaluations.

Test sensitivities of 0% and 10% training Omission Rates (OR) [52,58] and the AUC_{cv} (area under the receiver operating characteristic [ROC] curve) were used to compare performance of the models [59]. To calculate these, a 10-fold cross-validation was run in MaxEnt. AUC_{cv} was also used for discriminating presence from background data. An AUC_{cv} value of 0.5 indicates that predictions do not exceed random; values below 0.5 are below random; 0.5-0.7 represents poor performance; 0.7-0.9 represents satisfactory to moderate performance; and values above 0.9 rate as high performance [60]. In the case of Omission Rate, the anticipated value at 0% training OR is 0 and at 10% it is 0.10; poor performance is indicated when the value exceeds the anticipated rate [38]. We ranked our models on 10% training OR, 0% training OR, and AUC_{cv} [55,58,61].

ArcGIS 10.3.1 software was used to extract the risk levels for *B. tabaci* invasion of areas suitable for open field cultivation of tomatoes from the MaxEnt outputs.

2.5. Determining B. tabaci risk levels

Maximum Test Sensitivity Plus Specificity (MTSPS) threshold was chosen to ascertain from projected future distributions of *B. tabaci* and *S. lycopersicum* which areas optimal for open field cultivation of *S. lycopersicum* would be at risk for *B. tabaci* invasion, according to the categories of highest, medium and lowest risk. For overlaying, ‘optimal conditions’ were defined as areas of medium or high suitability. Projections for both species, as well as their overlaying to ascertain level of *B. tabaci* risk in areas of optimal risk, were made using the four suitability classes of unsuitable, low, medium and high.

3. RESULTS

The pest species *B. tabaci* (Biotype B and Q) and host open-field *S. lycopersicum* are distributed globally (Figure 1). Climatic variables most contributory to *B. tabaci* distribution were annual mean temperature (bio1; °C), precipitation seasonality (CV) (bio15), mean annual precipitation (bio12; mm), precipitation of driest month (bio14; mm), mean diurnal range in temperature (bio2; °C) and temperature annual range (bio7; °C) (Table 1), and *S. lycopersicum* (Table 2). Based on observed occurrences, *B. tabaci* (Biotype B and Q) occurs in areas with mean annual temperature of 23.8°C, and mean annual precipitation between 0 - 3516 mm (Table 1) and *S. lycopersicum* occurs in areas with mean annual temperature of 20.1°C, and mean annual precipitation from 3000 - 3200 mm (Table 2).

The performance of all MaxEnt models used to determine the two species potential distributions exceeded random, using AUC_{cv} test values higher than 0.5 (Table 3 and 4). Based on 10-fold cross validation, mean AUC_{cv} values varied from 0.882 - 0.900 for *B. tabaci* (Table 3) and 0.898 – 0.904 for *S. lycopersicum* (Table 4). These models also had low test omission rates, with values at 0% training OR, varying from 0.0024 - 0.0096, and 0.1086 - 0.1227 at 10% for *B. tabaci* (Table 3). For *S. lycopersicum*, values at 0% training OR varied from 0.0056 - 0.0173, and from 0.1016 - 0.1206 at 10% (Table 4). The best model for *B. tabaci* included a combination of six environmental variables, Linear, Quadratic, Product and Hinge (LQPH) features, regularization multiplier=1.0, produced the best model for *B. tabaci* and exhibited the lowest omission rate at 10% and 0% (Table 3). Similarly for *S. lycopersicum*, the best model had six environmental variables, Linear and Hinge (LH) features, regularization multiplier=1, and had lowest omission rate at 10% and 0% (Table 4).

MaxEnt predictions of the best *B. tabaci* model closely matched current known distributions (Figures 1 and 2). Highly suitable areas were predicted in South America, Africa, Europe, Asia and Oceania. The *S. lycopersicum* model also displayed agreement between known occurrences and projections, globally (Figure 1 and 3).

The current and projected climate results for *B. tabaci* risk levels in areas with optimal conditions (medium and high suitability) for *S. lycopersicum* open-field cultivations for 2050 and 2070 are shown in figure 4. Results indicated that 5% of optimal areas are currently at high *B. tabaci* risk. Currently, much of South and Central America has a low, medium or high risk levels for *B. tabaci* in areas with optimal conditions for open-field tomato. On the North American continent, Mexico and the USA states of California and Florida exhibit low, medium or high risk. In all the above regions, *B. tabaci* is already present. In Europe, Africa, Asia and Oceania all three risk categories for *B. tabaci* can be discerned. Many sites in Europe and southern China which are at high risk for *B. tabaci* in optimal conditions for tomato open-field require close attention (Figure 4 A).

However, a decrease in areas with low or moderate levels of *B. tabaci* is projected for 2050 and 2070, but an increase of areas with high risk for *B. tabaci* (Figure 4 B and C). Among the optimal areas for *S. lycopersicum*, the projections for 2050 compared to the current time showed an extension of 180% in areas under high risk, and a shortening of 67 and 27% in areas under medium and low risk of *B. tabaci*, respectively. By 2070, the projections indicate an extension of 164, and a shortening of 49 and 64% under high, medium and low risk, respectively. According to projected scenarios for 2050 and 2070 the risks levels for *B. tabaci* in China will increase from the east to the centre of the country when compared to the current levels (Figures 4 A, B C). In Europe, the current *B. tabaci* risk level is moderate and high in southern regions but will increase to more moderately suitable for *B. tabaci* in regions with optimal climatic conditions for open-field *S. lycopersicum*.

In large areas such as South America (for example Brazil), the current risk levels of *B. tabaci* are moderate and high (Figure 4A). However, most optimal regions already produce open-field tomatoes. Future predictions show large reductions of areas with *B. tabaci* risk levels due to the reduction of climatic conditions suitable for both species, but mostly for the host (Figure 4A, B and C).

The Jackknife test of variable importance indicated that mean annual temperature had the most impact on both species models (*B. tabaci* and *S. lycopersicum*) (Figure 2D,E and Figure 3D,E). The highest probability for *B. tabaci* presence exits in areas with annual mean temperatures of 23-24°C (Figure 5A), and 18-20°C for *S. lycopersicum* (Figure 6A). The probability of *B. tabaci* presence is higher in areas of low mean diurnal temperature range (Figure 5B) and higher in areas of medium mean diurnal temperature range for *S. lycopersicum* (Figure 6B). The probability for the presence of both species is higher in areas with low precipitation, decreasing with an increase in precipitation (Figure 5C and 6D), and when the precipitation seasonality is 130 -150 mm for *B. tabaci* (Figure 5D), and temperature annual range is low for *S. lycopersicum* (Figure 6C).

4. DISCUSSION

B. tabaci is distributed worldwide (Figure1) and has caused many losses in tomato crops over the past 20 years in North, Central and South America, Africa (West, Central and South), Asia (India and China) and Mediterranean Europe countries [62,63,64,65,66].

All models presented in this study show great degree of reliability. Both *B. tabaci* and *S. lycopersicum* models produced 90% (AUC) agreement with the current modeled global climate. Cross-validation indicated that all models performed much better than would be expected at random, and had a high validation statistic. The high percentage of accordance with the distribution of both species highlights the consistency of these models Thus, the model outputs and their overlaying may be considered reliable as a foundation of research on *B. tabaci* occurrence and risk in areas suitable for open-field tomato, globally.

While *B. tabaci* and *S. lycopersicum* occurrence has been reported for regions on all continents (Figure 1), the combination is more probable in tropical regions with high mean annual temperatures (Table 1, 2 and Figure 5A, 6A), including areas with wide variations of daily temperatures (Figure 5B and 6B), and a wider range in precipitation (Table 1, 2 and Figure 5C, 6D). These important characteristics confirm that *B. tabaci* has great potential for invasion [67,68,69] and that *S. lycopersicum* may be produced in open field conditions in several areas in the world. However, in certain regions where *B. tabaci* has already been reported in glasshouses, it has not been reported as causing problems in the open field. This is probably because climatic conditions are unsuitable for *B. tabaci* growth, development and therefore the establishment of the species in these areas.

Although *B. tabaci* can establish across a wide thermal range, the species can be affected by global temperature changes (Figure 2). Extreme temperatures (either high or low) may affect the development of the species. Furthermore, pests are dependent on the survival of the host. Thus, tomato crops may well suffer from climate change, which will have an impact on *B. tabaci* [70] (Figure 3).

If the increases in temperature predicted by the HadGEM2-ES climate model do occur, this may affect not only the pest but impose limitations on *S. lycopersicum* growth. Vegetable species generally show great sensitivity under extreme environmental conditions, particularly temperatures, high or low temperatures [71]. This was confirmed by the results of the future models (2050 and 2070), in which greater reductions in susceptibility are predicted in *S. lycopersicum* globally, than in *B. tabaci* (Figure 2, 3).

The current climate modeling showed predominantly medium and high risk in South, Central and North America for *B. tabaci* in areas with optimal climate conditions for growing open-field tomato (Figure 4A). Europe, Africa, Asia and Oceania displayed all three categories of risk of *B. tabaci*; with close attention for many sites in Europe, southern China (Asia) and Brazil (South America), which are at high risk for *B. tabaci* in optimal conditions for open-field tomato.

While the majority of studies on the impact of climate change on organisms predict increases in invasive species, the converse may be seen for *B. tabaci* in open field tomato in some regions. After the overlaying of the current models and future projections in areas with optimal conditions for open field tomato, we observed that in some regions with current high risk, *B. tabaci* risk will decrease in the years 2050 and 2070, mainly in tropical countries of South America and Africa. The main reason related to the predicted increase of temperature in the world, which will mainly affect the host. Conversely, in China (from east to central areas), and Mediterranean Europe (e.g. France, Italy and Spain) a great increase in susceptibility to *B. tabaci* is predicted in regions with optimal climatic conditions for open field tomato crops. In some areas along the coastlines of Brazil (south, southeast and northeast) and Australia (south and east), the same levels of susceptibility to, or risk of, the pest are maintained (Figure 4).

At high temperatures, the current B and Q *B. tabaci* biotypes exhibit lower fertility than at temperate climates [72]. However, new emerging biotypes that are much more resistant to heat may be selected during climatic warming. This is something that we cannot include in our model because we do not know how often new biotypes in the species will emerge, and if the resistance will occur at the same speed that climate change. The biological factors such as generation time and how climate change may influence the appearance of new biotypes are characteristics that are still not possible to be included as parameters in the construction of models via MaxEnt.

Mean annual temperature (bio1) was one of the most important variables associated with the distribution of *B. tabaci* and *S. lycopersicum* (Tables 1 and 2, Figures 2D, E and 3D, E respectively). Many studies have shown that mean annual temperature is the major variable contributing to distributions of species [73,74,75,76]. The models predicted a greater probability of presence of *B. tabaci* in temperatures around 23-24°C and around 18-20°C for *S. lycopersicum*. This may be the major reason that *B. tabaci* occurrence has been so high in areas having a mean temperature close to the optimal requirement for growth. However, a combination of major climate factors with other variables, such as a higher number of hosts, might be related to the success of the *B. tabaci* distributions [77,78]. Consequently, the decreased *B. tabaci* risk levels in some areas may be due to a reduction of climatic suitability factors for both species.

Tomato production becomes unviable in places where temperatures reach values above 40 °C. There are many studies that show that high temperature causes stress in tomato plants (for the most common tomato cultivars) such as reduced fruit set, reproductive number, pollen production and pollen viability [70,79,80]. *S. lycopersicum* shows a wide climatic tolerance and is grown in both tropical and temperate regions around the world, and thus high or low temperatures can impact negatively on this species [81]. As shown by our model, the mean annual temperature is an extremely important parameter that determines the distribution (occurrence and establishment) of the species. Although there are varieties more adapted for high temperature sites (e.g. in the Middle East) they can still yield at high temperatures, mostly due the manipulation of the environment (nethouses and glasshouses), using ventilation or air-conditioning. Obviously, with the advance in genetic studies, new cultivars could be introgressed by breeding and selection into current genotypes when needed to cope with increasing temperatures. The same has happened in countries where the mean temperatures are very low and tomato production is only possible due to the temperature control possible in the greenhouse (where it is possible to maintain higher temperatures than the external environment). Therefore, the evolution and emergence of adapted varieties in high temperature environments may succeed as long as productivity is not compromised. Even with the advent of current plant genotypes resistant to high temperatures, this is not yet a reality that extends to the entire planet and we do not know if those varieties will support high temperatures and if they would be an alternative to overcome the barriers to climate change. In our model, we used the occurrence points of tomato plants of current and most commonly used cultivars. However, the production of new cultivars resistant to high temperatures can make tomato production feasible in places where air temperatures are quite high. This is one of the uncertainties that we could not include in the MaxEnt configuration for building our model.

Our overlaying results should contribute to warning agricultural authorities in many locations to employ management strategies to prevent a decreased viability for open-field tomato. In areas of high *B. tabaci* risk and optimal conditions for open-field *S. lycopersicum*, both whitefly and tomato are already present. It would still be logical to introduce preventive measures for the spread of toxins and viruses into areas in which these have not yet been reported. Strategies such as inspection of seeding plant trade and phytosanitary regulations would be valid in locations with high and medium risk of *B. tabaci,* to lessen the risk.

Despite the inherent uncertainty of correlative niche models such as MaxEnt in regard to the quality of occurrence data, resolution of spatial data layers, sampling bias, species characteristics, and spatial autocorrelation [54,76,82,83,84], MaxEnt software has a great user interface, making the modeling process easier. MaxEnt does offer options for certain adjustments, which can improve the quality of specific models [54,61,76]. The adjustments used in our study were in the selection of feature types, value of regularization multiplies, selection of background points and extent [49]. Utmost care was devoted to model calibration to obtain model results adhering to the current occurrence of both species studied. The quality of the models can be seen in the biological validity of the response curves and strong validation results (Tables 2 and 3; Figures 2D,E; 3D,E; 5 and 6).

Our models were based only on climate parameters, executed using the currently available global broad-scale climate data, and thus only show broad-scale shifts. Only open field occurrence data for both *B. tabaci* and *S. lycopersicum* were taken into account. It should be noted that the predictions of suitable areas for tomato production were established based on the current climatic thresholds from current commercial cultivars. However, the production of new cultivars resistant to high temperatures, the production of tomatoes in protected crops with climatic control or the production of tomato in times of mild temperature in very hot places can enable the future production of tomato in other places. Although tomato cultivation is still mainly cultivated in the open field, the current trend in tomato cultivation is increasingly favouring nethouses (50-mesh nets to protect from insects) or closed glasshouses. In both cases, proper ventilation or air-conditioning can control inside temperatures. These systems control the microclimate of crops and modelling studies can not take this into account. For this reason, the problems with *B. tabaci* in protected and semi-protected environments may be diverse in several locations around the world but not pointed out by our model.

Although it is well known that the *B. tabaci* is already widely distributed and has other host species, modeling other hosts may have predictions that differ from our study, on the basis of specific host sensitivity to climatic changes. In this study, we did not take into account potential genetic progress as *B. tabaci* has shown high adaptability and numerous biotypes. Therefore, the results of these models can be used in other studies, including non-climatic factors such as differences of the existing biotypes, other pest-plant interactions, natural enemies, pest resistance, dispersal and adaptations.

Our study indicates that climate change may impact on the geographical distributions of the pest *B. tabaci* and the host *S. lycopersicum*. Our study provides important information on the risk of *B. tabaci* for open-field tomato crops using the MaxEnt model. Considering both species together (*B. tabaci* and *S. lycopersicum*), it seems large areas with optimal conditions for *S. lycopersicum* under current climate are already at medium and high risk of *B. tabaci,* areas with high risk of *B. tabaci* will increase and areas with medium risk will decrease in the future (2050 and 2070). The future projections in areas with optimal conditions for open field tomato shows that some regions (e.g. Brazil), where *B. tabaci* currently shows medium and high risk will become less favorable (risks will decrease) in the years 2050 and 2070. Conversely in some places such as China (from east to central areas), and Europe (e.g. France, Italy and Spain) projections show large increases in susceptibility to *B. tabaci* in regions with optimal climatic conditions for tomato crops in open field. The main reason for this is related to the predicted increase of temperature in the world, which may affect not only the pest, but also the host. Our results can be used in designing strategies to prevent the introduction and establishment of *B. tabaci* in areas still *B. tabaci* free, such as Finland, Sweden, Republic of Ireland and the UK, as well as implementing pest management programs in areas of current occurrence, particularly at sites under high risk.

AUTHOR CONTRIBUTIONS

RSR and MCP conceived and designed research. RSR acquired and analyzed the data. RSR wrote the manuscript. LK and FS made critical revisions (providing language help, and writing assistance). LK and MCP made critical revisions and approved final version. All authors reviewed and approved of the final manuscript.

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CONFLICT INTEREST

The authors declare that they have no conflict of interest.

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***Table A1.** Cross-correlation (Pearson correlation coefficient, r) among environmental variables. (Models: *B. tabaci* and *S. lycopersicum*).
*Supplementary material

	bio1	bio2	bio3	bio4	bio5	bio6	bio7	bio8	bio9	bio10	bio11	bio12	bio13	bio14	bio15	bio16	bio17	bio18	bio19
bio2	0.521																		
bio3	0.839	0.387																	
bio4	-0.833	-0.210	-0.891																
bio5	0.896	0.707	0.613	-0.513															
bio6	0.968	0.355	0.888	-0.936	0.764														
bio7	-0.730	0.015	-0.826	0.971	-0.358	-0.876													
bio8	0.812	0.533	0.638	-0.501	0.845	0.704	-0.387												
bio9	0.938	0.439	0.808	-0.861	0.792	0.949	-0.781	0.609											
bio10	0.935	0.621	0.660	-0.585	0.988	0.825	-0.455	0.865	0.831										
bio11	0.980	0.425	0.891	-0.926	0.795	0.996	-0.847	0.731	0.950	0.848									
bio12	0.378	-0.245	0.565	-0.554	0.119	0.486	-0.615	0.252	0.375	0.200	0.454								
bio13	0.455	-0.104	0.581	-0.567	0.233	0.527	-0.589	0.370	0.413	0.303	0.511	0.896							
bio14	0.055	-0.375	0.221	-0.245	-0.139	0.167	-0.346	-0.066	0.107	-0.075	0.123	0.709	0.392						
bio15	0.367	0.514	0.282	-0.190	0.429	0.269	-0.069	0.449	0.260	0.412	0.317	-0.173	0.138	-0.517					
bio16	0.445	-0.124	0.581	-0.569	0.215	0.522	-0.595	0.352	0.408	0.286	0.504	0.922	0.993	0.429	0.094				
bio17	0.083	-0.372	0.255	-0.275	-0.121	0.197	-0.375	-0.044	0.135	-0.054	0.153	0.744	0.429	0.994	-0.515	0.466			
bio18	0.224	-0.202	0.353	-0.337	0.026	0.282	-0.389	0.254	0.153	0.100	0.265	0.797	0.743	0.558	-0.104	0.761	0.581		
bio19	0.249	-0.242	0.431	-0.405	0.055	0.357	-0.475	0.074	0.307	0.112	0.316	0.754	0.584	0.671	-0.273	0.610	0.698	0.374	

Bold font indicates variables in the final model.

Table 1. Environmental variables considered in *B. tabaci* (Biotype B and Q) niche models, and average percent contribution of environmental variables in the *B. tabaci* (Biotype B and Q) distribution model; values were averaged across 10 replicate runs. General statistics were calculated using all occurrences (n = 627). (Min=minimum, Max=maximum, and SD = standard deviation).

Variable	Percent contribution	Permutation importance	Min.	Max.	Mean	SD
Annual mean temperature (bio1; °C)	75.1	65.4	8.0	28.7	23.8	3.8
Precipitation seasonality (CV) (bio15)	7.2	6.4	0	160	89.4	30.3
Mean annual precipitation (bio12; mm)	6.5	8.5	0	3516	667	588.8
Precipitation of driest month (bio14; mm)	6.1	3.6	0	113	9.7	17.4
Mean diurnal range in temperature (bio2; °C)	2.7	7.8	6.0	18.9	13	2.7
Temperature annual range (bio7; °C)	2.4	8.3	8.5	40.7	28.4	9.7
Isothermality (bio3)	-	-	24	91	49.4	14.5
Temperature seasonality (SD x 100) (bio4)	-	-	251	10871	5199	2761
Maximum temperature of warmest month (bio5; °C)	-	-	22.8	46.3	37.4	5.6
Minimum temperature of coldest month (bio6; °C)	-	-	-9.9	22.8	8.93	6.4
Mean temperature of wettest quarter (bio8; °C)	-	-	6.2	34.5	27.2	6.4
Mean temperature of driest quarter (bio9; °C)	-	-	-2.6	36.1	21.7	4.8
Mean temperature of warmest quarter (bio10; °C)	-	-	16	36.1	29.9	4.5
Mean temperature of coldest quarter (bio11; °C)	-	-	-2.6	36.1	16.7	5.4
Precipitation of wettest month (bio13; mm)	-	-	0	815	140	113.7
Precipitation of wettest quarter (bio16; mm)	-	-	0	1875	348	293
Precipitation of driest quarter (bio17; mm)	-	-	0	381	41	62.6
Precipitation of warmest quarter (bio18; mm)	-	-	0	1219	189	178
Precipitation of coldest quarter (bio19; mm)	-	-	0	1865	118	174.5

Bold font indicates variables in the final model. Source of data: WorldClim (http://www.worldclim.org/bioclim; Hijmans et al., 2005).

Table 2. Environmental variables considered in *S. lycopersicum* niche models, and average percent contribution of environmental variables in the *S. lycopersicum* distribution model; values were averaged across 10 replicate runs. General statistics were calculated using all occurrences (n = 627). (Min=minimum, Max=maximum, and SD = standard deviation).

Variable	Percent contribution	Permutation importance	Min.	Max.	Mean	SD
Annual mean temperature (bio1; °C)	58.5	57.4	8.6	28.8	20.1	4.3
Temperature annual range (bio7; °C)	25.9	25.1	9.7	37.7	20.1	6.6
Mean diurnal range in temperature (bio2; °C)	8.5	7.8	7.1	17.0	11.3	19.3
Mean annual precipitation (bio12; mm)	5.9	6.7	3	3200	1039.6	598.6
Precipitation seasonality (CV) (bio15)	0.7	1.9	11	145	65.7	29.4
Precipitation of driest month (bio14; mm)	0.5	1.0	0	120	22.8	26.8
Isothermality (bio3)	-	-	24	91	59.9	15.4
Temperature seasonality (SD x 100) (bio4)	-	-	163	9490	2907.9	2204.8
Maximum temperature of warmest month (bio5; °C)	-	-	18.7	41.2	30.2	3.7
Minimum temperature of coldest month (bio6; °C)	-	-	-8.9	22.9	10.1	6.5
Mean temperature of wettest quarter (bio8; °C)	-	-	5.6	29.1	20.5	5.6
Mean temperature of driest quarter (bio9; °C)	-	-	-3.2	31.5	19.9	5.4
Mean temperature of warmest quarter (bio10; °C)	-	-	13.3	32.7	23.7	3.5
Mean temperature of coldest quarter (bio11; °C)	-	-	-3.2	27.9	16.3	6.3
Precipitation of wettest month (bio13; mm)	-	-	1	727	180.5	112.6
Precipitation of wettest quarter (bio16; mm)	-	-	3	1806	471.6	286
Precipitation of driest quarter (bio17; mm)	-	-	0	447	85.4	93.2
Precipitation of warmest quarter (bio18; mm)	-	-	0	1388	282.6	208.8
Precipitation of coldest quarter (bio19; mm)	-	-	0	1097	201.3	217.6

Bold font indicates variables in the final model. Source of data: WorldClim (http://www.worldclim.org/bioclim; Hijmans et al., 2005).

Table 3. Summary of performance statistics of *B. tabaci* (Biotype B and Q) MaxEnt models. The best model is highlighted in bold.

Model Rank	**Variables**	**MaxEnt settings**		**Test AUC_{cv} (±SD)**	**OR**	
		Features	**RM**		**0%**	**10%**
1	**bio1,bio2,bio7, bio12, bio14, bio15**	**LQPH**	**1.0**	**0.900 ± 0.017**	**0.0071**	**0.1086**
2	Same as above	LQPTH	2.0	0.896 ± 0.017	0.0048	0.1108
3	Same as above	LQH	1.0	0.889 ± 0.017	0.0096	0.1108
4	Same as above	LQP	2.0	0.886 ± 0.017	0.0024	0.113
5	Same as above	LQP	1.0	0.886 ± 0.017	0.0048	0.1134
6	Same as above	LQPH	2.0	0.896 ± 0.017	0.0024	0.1155
7	Same as above	LQPH	1.5	0.897 ± 0.016	0.0048	0.1155
8	Same as above	LH	2.0	0.884 ± 0.017	0.0024	0.1158
9	Same as above	LQH	2.0	0.882 ± 0.017	0.0024	0.1204
10	Same as above	LH	1.0	0.892 ± 0.017	0.0024	0.1205
11	Same as above	LQPTH	1.5	0.896 ± 0.017	0.0048	0.1226
12	Same as above	LQH	1.5	0.884 ± 0.017	0.0048	0.1227

Note: Variables' full names (see table 1). L, Q, P, T and H are linear, quadratic, product, threshold and hinge features, respectively. RM is regularization multiplier, and SD is standard deviation. OR is test omission rate. Test AUC_{cv} is MaxEnt 10-fold cross-validation Area Under the ROC curve.

Table 4. Summary of performance statistics of *S. lycopersicum* MaxEnt models. The best model is highlighted in bold.

Model Rank	**Variables**	**MaxEnt settings**		**Test AUC$_{cv}$ (±SD)**	**OR**	
		Features	**RM**		**0%**	**10%**
1	**bio1,bio2,bio7, bio12, bio14, bio15**	**LH**	**1.0**	**0.904 ± 0.023**	**0.0059**	**0.1016**
2	Same as above	LQP	2.0	0.902 ± 0.024	0.0059	0.1033
3	Same as above	LQPT	2.0	0.904 ± 0.024	0.0059	0.1075
4	Same as above	LH	2.0	0.902 ± 0.024	0.0173	0.1078
5	Same as above	LQP	1.0	0.901 ± 0.024	0.0110	0.1127
6	Same as above	LQH	2.0	0.901 ± 0.025	0.0118	0.1127
7	Same as above	LQH	1.5	0.903 ± 0.024	0.0056	0.1131
8	Same as above	LQPH	1.5	0.903 ± 0.023	0.0059	0.1150
9	Same as above	LQPH	2.0	0.898 ± 0.024	0.0110	0.1196
10	Same as above	LQPTH	1.5	0.906 ± 0.024	0.0167	0.1199
11	Same as above	LH	1.5	0.904 ± 0.025	0.0114	0.1203
12	Same as above	LQP	1.5	0.899 ± 0.024	0.0056	0.1206

Note: Variables' full names (see table 1). L, Q, P, T and H are linear, quadratic, product, threshold and hinge features, respectively. RM is regularization multiplier, and SD is standard deviation. OR is test omission rate. Test AUC$_{cv}$ is MaxEnt 10-fold cross-validation Area Under the ROC curve.

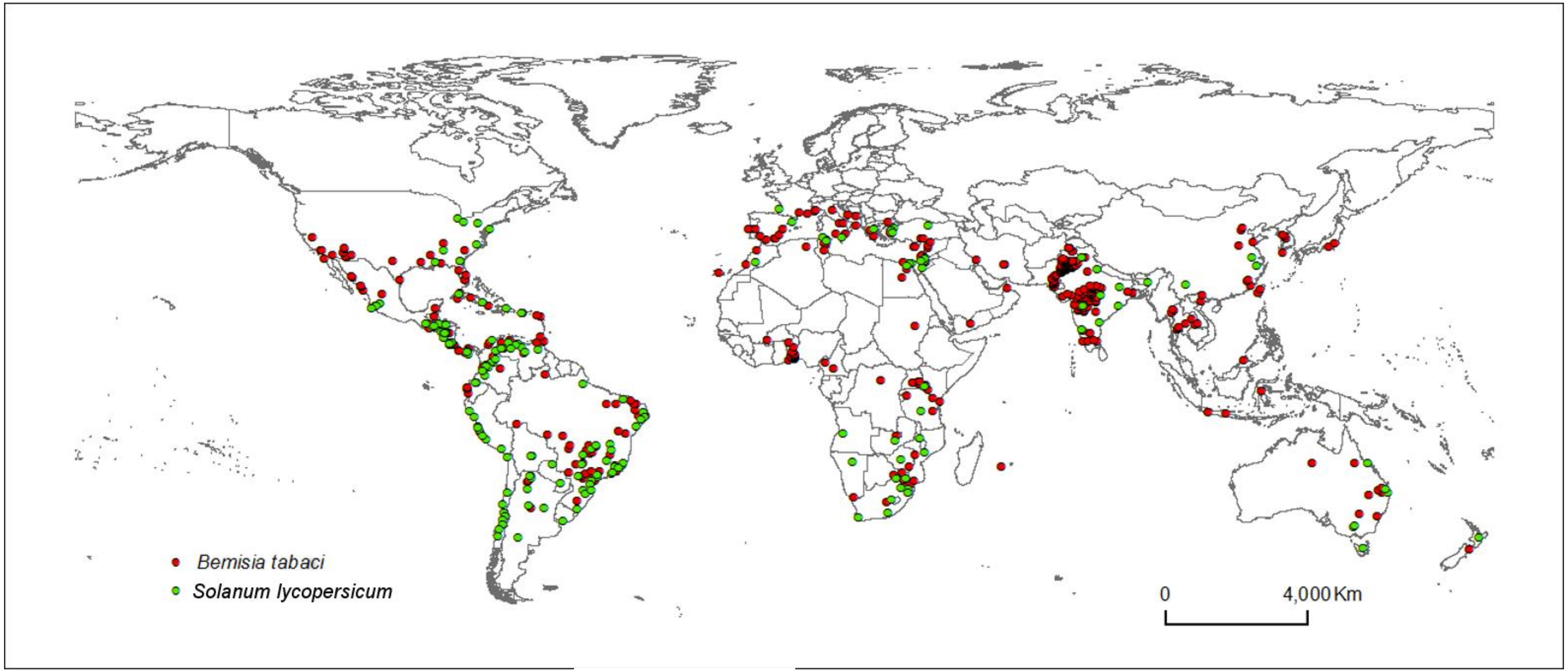
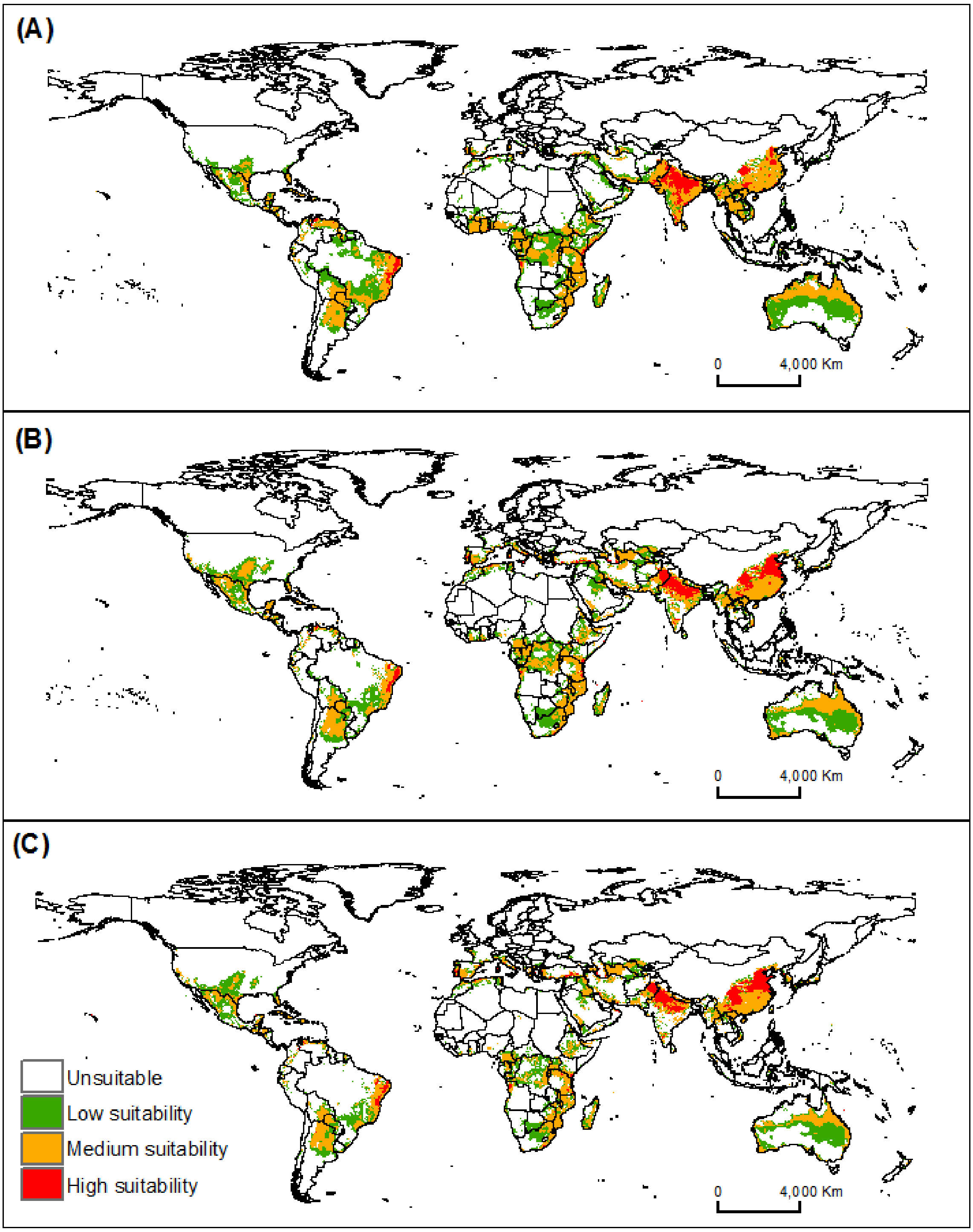


Figure1. Global known occurrences of *B. tabaci* (Biotype B and Q) in open field (red dots), and *S. lycopersicum* in open field (green dots).


(A)
0
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(C)
Unsuitable
Low suitability
Medium suitability
High suitability
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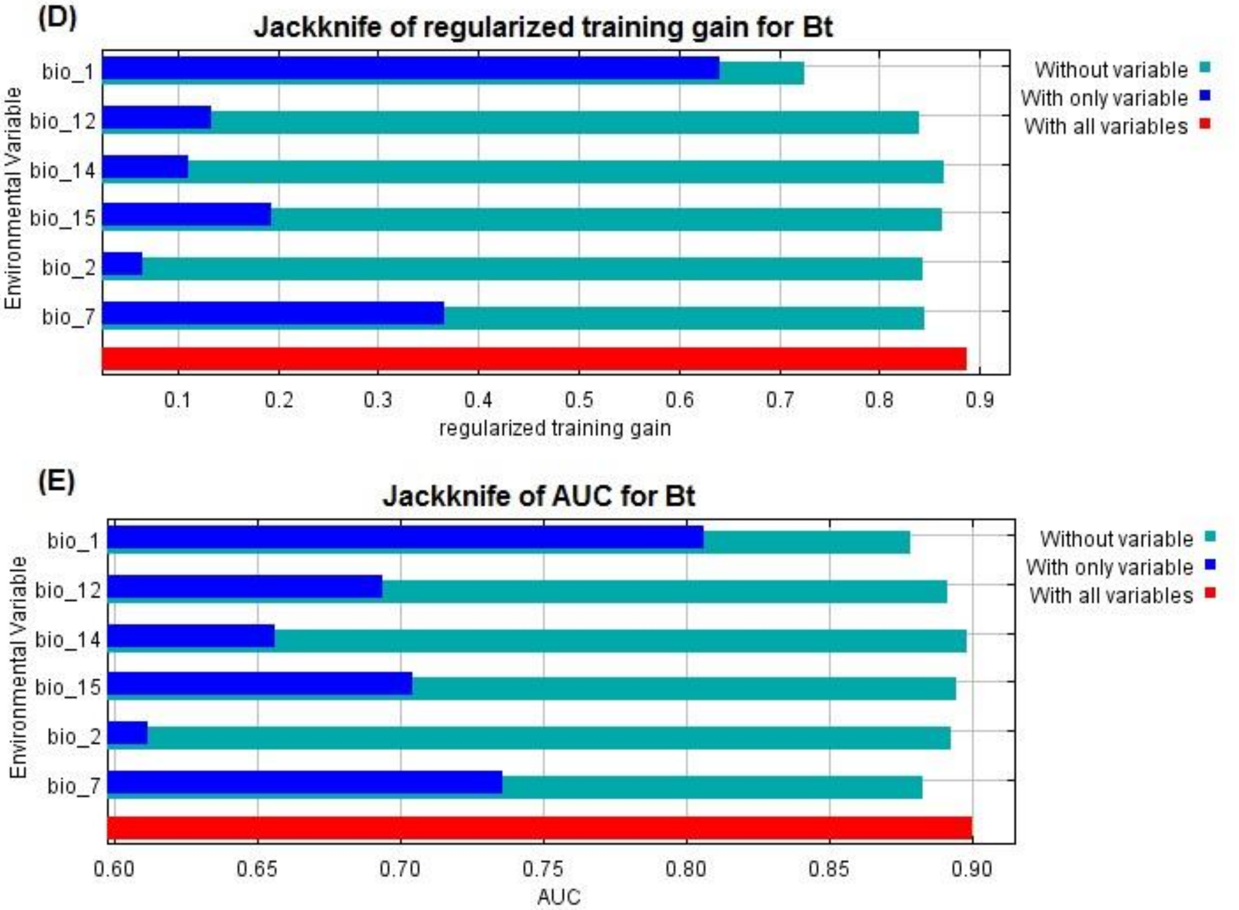
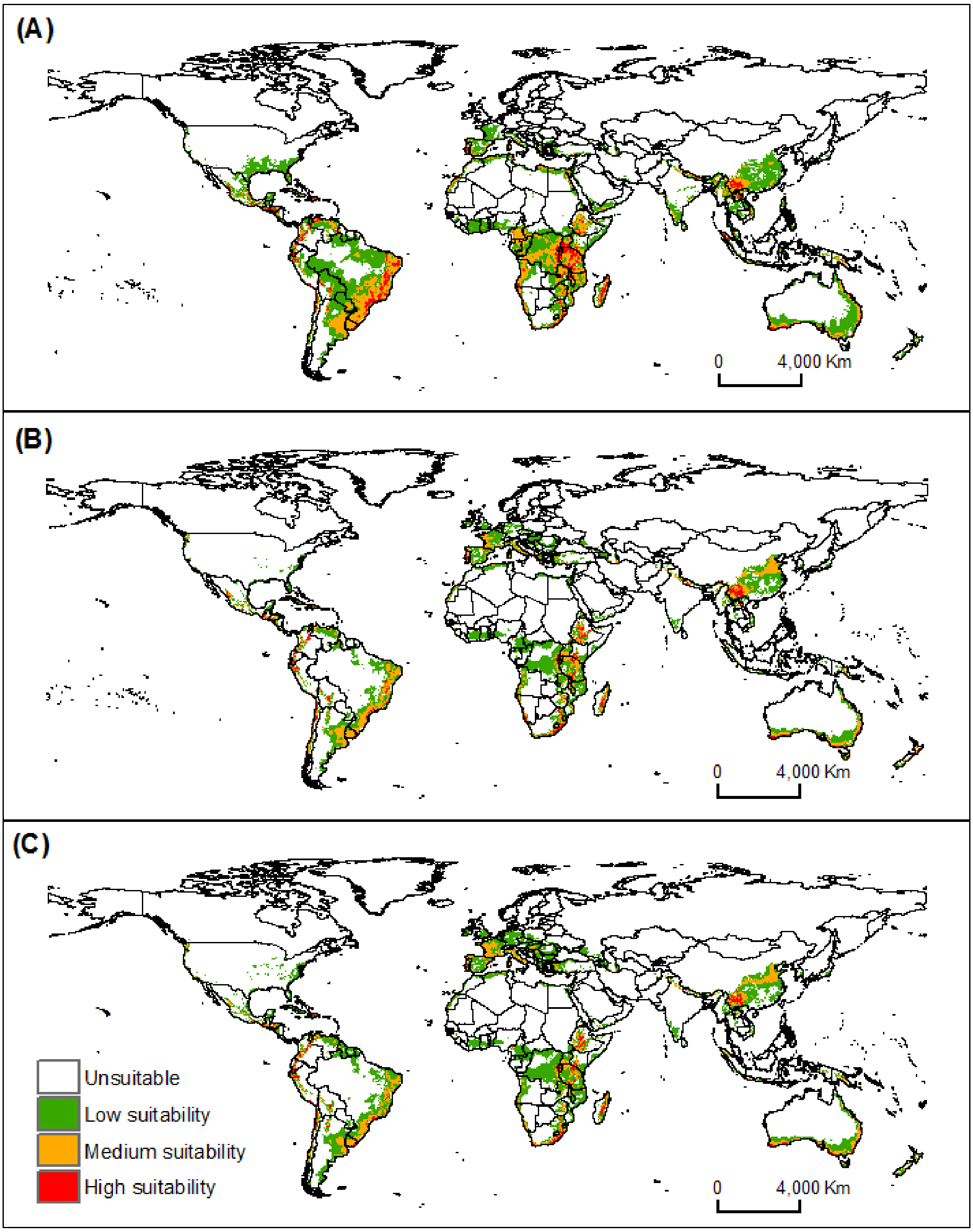


Figure 2. Habitat suitability under current and future climatic conditions of *B. tabaci* (Biotype B and Q). Maps (A) current global distribution using MaxEnt model, (B) 2050, (C) 2070. Relative importance of the environmental variables based on the JackKnife test (D) Regularized training gain and (E) AUC in *B. tabaci* model.


(A)
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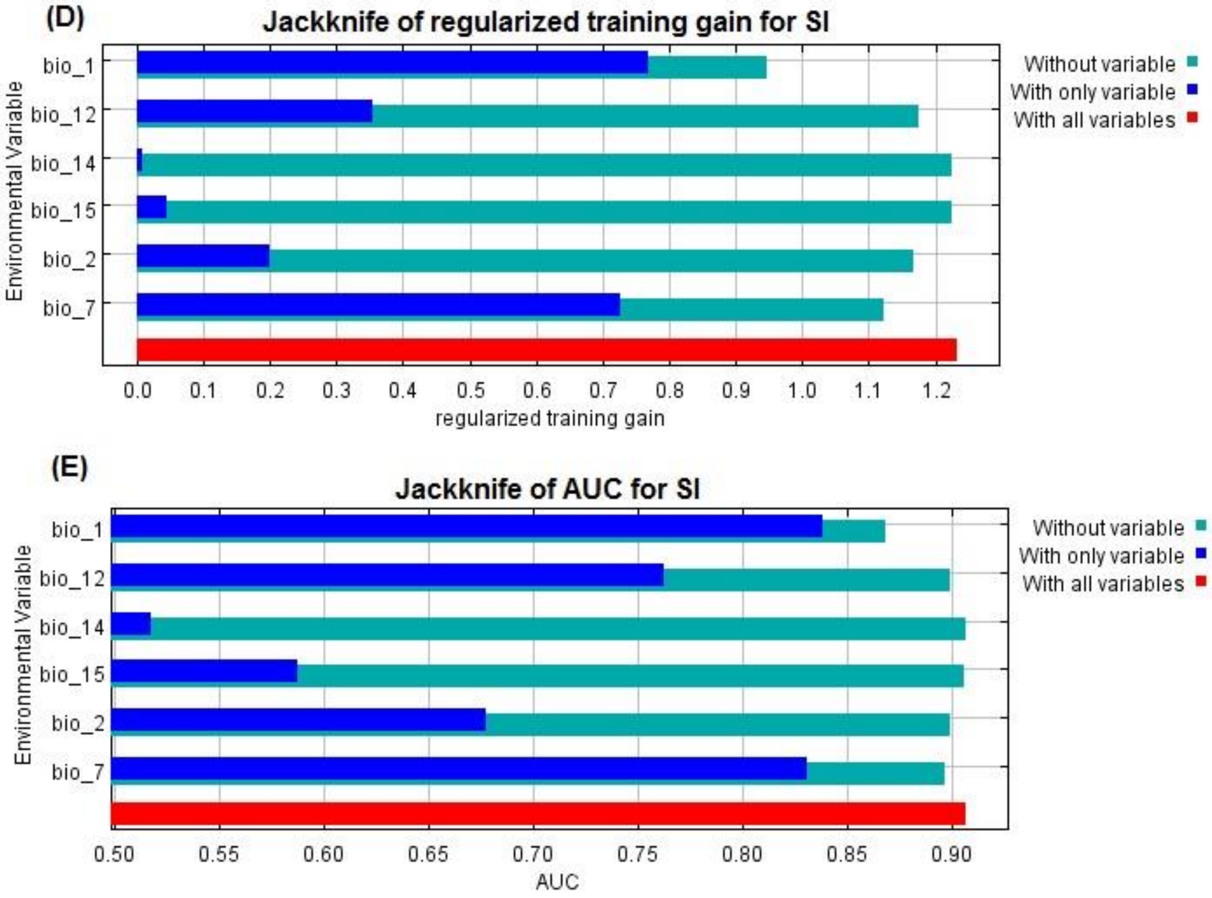

Figure 3. Habitat suitability under current and future climatic conditions of open-field *S. lycopersicum* cultivation. Maps (A) current global distribution using MaxEnt model, (B) 2050, and (C) 2070. Relative importance of the environmental variables based on the JackKnife test (D) Regularized training gain and (E) AUC in *S. lycopersicum* model.

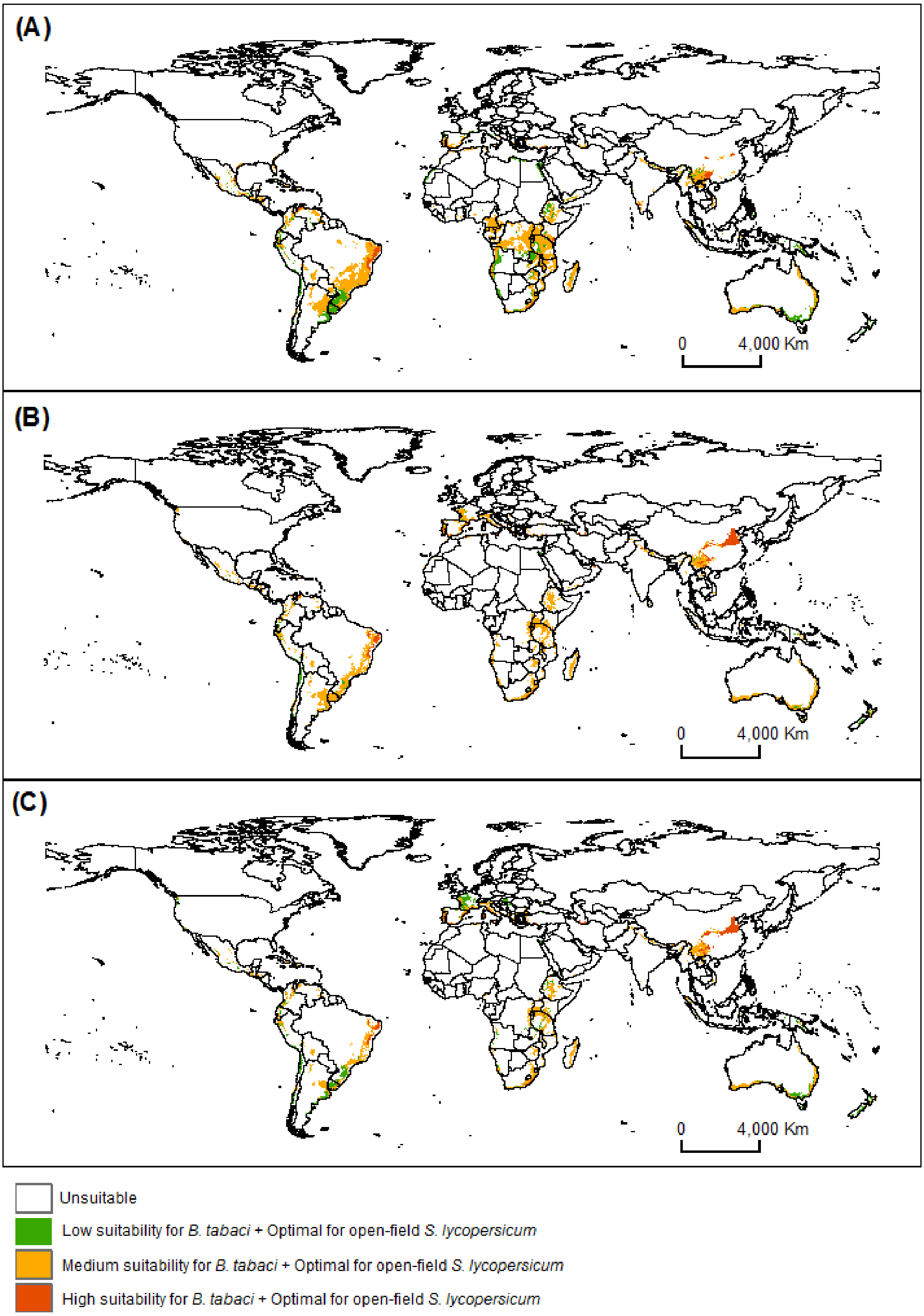

Figure 4. Habitat suitability under current and future climatic conditions in optimal areas for open-field *S. lycopersicum* cultivation with three suitability levels of *B. tabaci* (Biotype B and Q) using MaxEnt model. Maps (A) current time, (B) 2050, and (C) 2070.

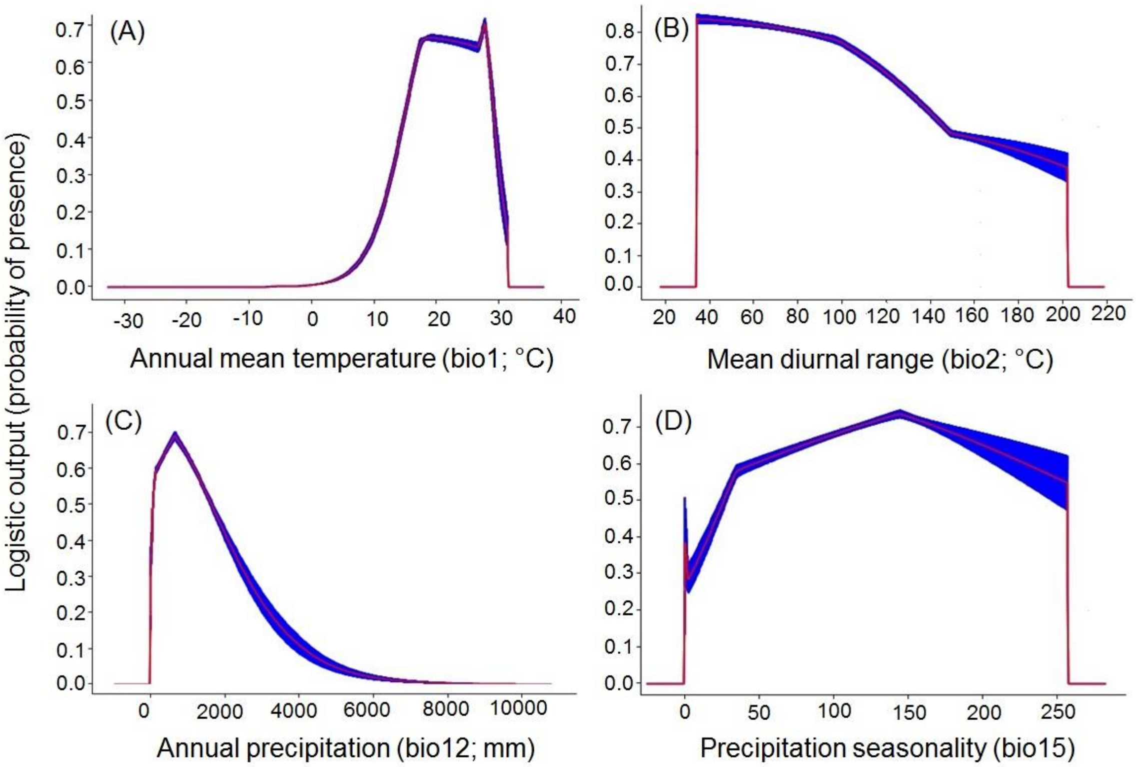

Figure 5. Response curves of the best predictors of *B. tabaci* (Biotype B and Q) in the best model. (A) Annual mean temperature (bio1; °C), (B) Mean diurnal range (Mean of monthly (max temp – min temp)) (bio2), (C) Annual precipitation (bio12; mm), and (D) Precipitation seasonality (Coefficient of variation, bio15).

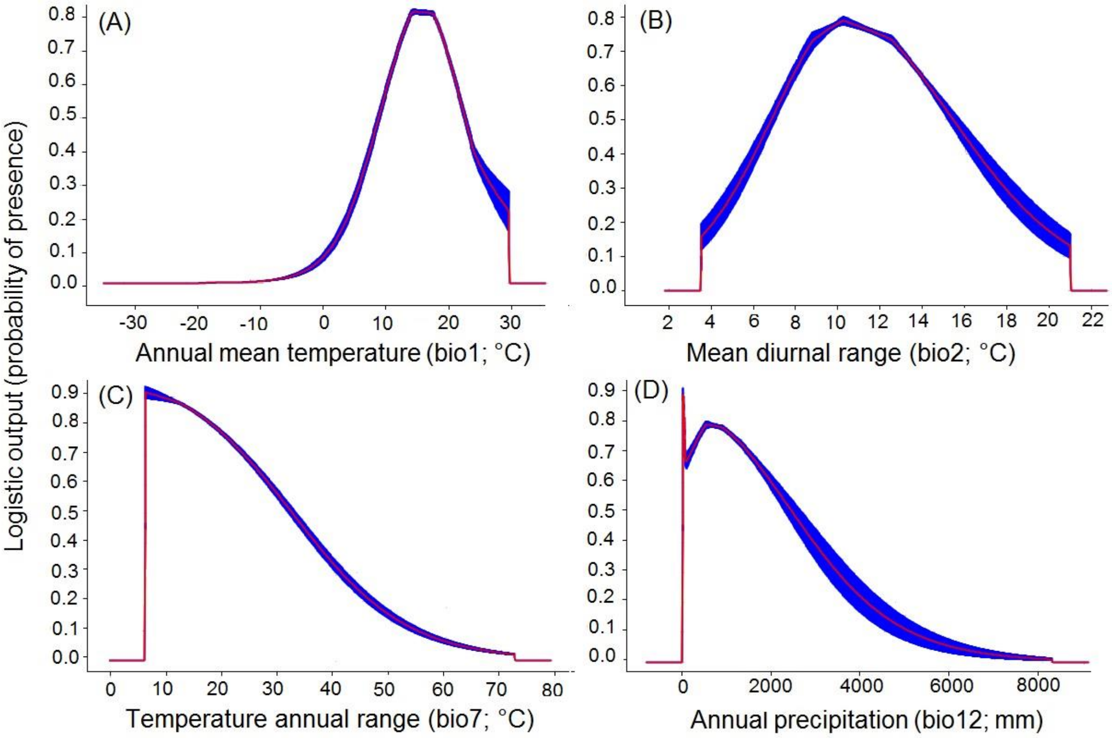

Figure 6. Response curves of the best predictors of *S. lycopersicum* in the best model. (A) Annual mean temperature (bio1; °C), (B) Mean diurnal range (Mean of monthly (max temp – min temp)) (bio2), (C) Temperature annual range (bio7; °C), and (D) Annual precipitation (bio12; mm).

CHAPTER 2: Risk of spread of tomato yellow leaf curl virus (*TYLCV*) in tomato crops under various climate change scenarios

ABSTRACT

Species distribution models (SDMs) are valuable for the information they provide for reducing potential negative effects of climatic factors on agricultural production systems. Such information may be used to prevent the entry and spread of invasive species in new areas, as well as for monitoring of regions with current occurrence. This is the first study of Tomato yellow leaf curl virus (*TYLCV*) global distribution, focusing on risk of this disease in areas projected to be suitable for open-field tomato and for whitefly. *TYLCV* (Begomovirus) is a devastating virus transmitted by *Bemisia tabaci* and poses a risk to *Solanum lycopersicum* cultivation worldwide. Despite the importance of *TYLCV*, the potential impact of climatic change on the global distribution of *TYLCV* in agricultural crops remains unstudied. The aim of this study was to identify risk levels for *TYLCV*, in areas optimally conducive for open field tomato cultivation and suitable for *B. tabaci*, under projected climate changes for the years 2050 and 2070, using MaxEnt and the Global Climate Model (HadGEM2_ES) under four scenarios (RCPs 2.6, 4.5, 6.0, 8.5). Our results show that large regions are projected to be suitable for *TYLCV* in areas of suitability for *B. tabaci* and optimal for open-field tomato cultivation. In the predictions, most areas with optimal conditions for *S. lycopersicum* and suitable for *B. tabaci* will be under medium suitability for *TYLCV*. This research may be useful in designing strategies to prevent the introduction and establishment of *TYLCV* where the occurrence has not yet been reported.

Keywords: MaxEnt, Climate change, Begomovirus, tomato, *Bemisia tabaci,* modelling.

1. INTRODUCTION

Tomato yellow leaf curl virus (*TYLCV*) (family Geminiviridae, genus *Begomovirus*) is globally one of the most devastating viruses affecting cultivated tomatoes (Czosnek and Laterrot 1997). *TYLCV* virus was first reported in Middle-Eastern Mediterranean areas and has spread to many tropical and subtropical regions around the world (Czosnek and Laterrot 1997; Kil et al. 2016; Lefeuvre et al. 2010; Ning et al. 2015; Zhang et al. 2009). Recently, *TYLCV* have been reported to be seed-transmissible (Kil et al., 2016a; Kil et al., 2018; Kil et al., 2017) but most transmitted by the vector *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae), one of the most invasive and devastating insect pests of vegetables and other crops worldwide, and can be spread solely by adult stages of whiteflies (Ning *et al.*, 2015; Pakkianathan *et al.*, 2015). The virus has the potential to cause large economic losses in crops, even annihilating a complete production cycle, depending on the phase of crop development at the time of infection (Pan et al. 2012), and is primarily known for its infestations of the tomato, *Solanum lycopersicum*, a vegetable crop of global economic importance, especially in tomato producing countries such as China, Italy, Egypt, Iran, Spain, India, the United States and Turkey ((FAOSTAT) 2017). After infection, tomato plants may show some symptoms such as severe stunting, marked reductions in leaf size, interveinal chlorosis, mottling, upward cupping, and abscission of flowers and fruit, which if produced at all, are small, dry and unsaleable (Inoue-Nagata et al. 2016; Lefeuvre et al. 2010; Papayiannis et al. 2010). The severity of infection is linked with the level of population of *B. tabaci*, the vector for *TYLCV* (Czosnek and Ghanim 2011). In this context, the best way to prevent losses due to *TYLCV* disease is to prevent its establishment in areas where tomato cultivation has importance. To achieve this, it is important to consider the use of genetic resistance in the plant host, to avoid the trade of infected host plants and seedlings, and to control *B. tabaci* in fields, greenhouses, seedling nurseries and surrounding vegetation (Hanssen et al. 2010).

Global warming can have direct and indirect impact on food production, with environmental conditions in many regions becoming inadequate for the growth and development of crops and even favoring invasions of pests and diseases. These negative effects of global warming on food production systems are potentially a major threat to global food security (Chakraborty and Newton 2011).

Climate is a major factor affecting the global distribution of a species (Elith and Leathwick 2009a; McDowell et al. 2014). Studies of climate effects on the future distribution of plant diseases have advanced and attained significant relevance in recent years (Galdino et al. 2016; Shabani and Kumar 2013). Climatic parameters, particularly temperature and precipitation, play a significant role in the development of diseases and in the interactions of vectors, crops, and diseases, since alterations of climate may alter the conditions for infectious disease organisms, plant hosts and vectors (Daugherty et al. 2017; Patz et al. 1996). *TYLCV* infection prefers high temperatures and is found to be most destructive in many tropical and subtropical regions at higher temperatures (Lapidot et al. 2006; Lapidot et al. 2000). The infection is also enhanced by the presence of whiteflies (*B. tabaci*), infected transplants and weedy fields with many alternative hosts. Further, the insect vector (*B. tabaci*) also prefers high temperatures (Morales and Jones 2004). Climate change will clearly affect the pathogen host interaction and altered conditions may contribute more favorably to the transportation/relocation, introduction, establishment, and then spread of a virus or its vector, in previously unfavorable regions.

The study of species distribution models (SDMs) provides the data on which to base decisions and plan strategically, in order to reduce the potential negative impact of changing climatic factors, such as temperature and precipitation, on agricultural production systems (Crespo-Pérez et al. 2015). This is particularly applicable in predicting the effects of global warming on economically important crops such as tomatoes, as well as the altered risk of insect and disease attacks (Jarošík et al. 2015). SDMs generate categories of climate suitability which may be used to prevent the introduction and establishment of invasive species in new areas, as well as adapting and tailoring such programs in regions with current occurrence (da Silva et al. 2016).

Climatic models are considered an important tool in determining the sensitivity of species such as plants, invasive insects, and diseases to climate alteration (Adams et al. 1990; Shabani and Kumar 2013). Modeling offers a technique for simulating future climates using different climate change scenarios (Kriticos et al. 2012) based on the species' tolerance limits under the current climate range. Studies based on modeling can predict potential distributions and abundance under future climate scenarios, which is vital in developing management strategies and highlighting interactions between environmental variables, such as temperature and precipitation, and species, as well as the principal abiotic factors that may affect the introduction and establishment of some species (Pearson and Dawson 2003; Soberon and Peterson 2005).

Despite the impact of *TYLCV* and the substantial body of research on the interaction of *B. tabaci* as an insect vector, tomato as its principal host and *TYLCV* as pathogen, there have been no studies on the potential impact of climate change on the global distribution of *TYLCV* in agricultural crops, particularly in tropical and subtropical regions. In light of this absence of research, we modeled the risk of *TYLCV* in areas suitable for open-field *S. lycopersicum* cultivation and for *B. tabaci* under climate change, using MaxEnt and a global climate model, HadGEM2_ES, under four future scenarios (RCP`s 2.6, 4.5, 6.0, 8.5). Note that model projections for *S. lycopersicum* and *B. tabaci* have been undertaken in the past (Ramos et al. 2018), but they [model projections] have only been made for RCP4.5. Here we extend the modelling for these two species to RCP 2.6, 6.0, 8.5 and also model future projections for *TYLCV* for all four RCP`s for 2050 and 2070. Thereafter, we overlaid these onto predicted future distributions of *S. lycopersicum* and *B. tabaci*, to ascertain areas optimally conducive for *S. lycopersicum* cultivation and suitable for *B. tabaci*, but at different risk levels of *TYLCV.* We also identified climatic factors associated with *TYLCV* distribution and describe the implications of these for both the present and future, in terms of successful tomato crop production and the design of more efficient strategies for controlling the spread of *TYLCV* in open-field tomato farming.

2. MATERIAL AND METHODS

2.1. Current distribution of *TYLCV*, *S. lycopersicum* and *B. tabaci*

The data for three species included in this research were collected from GBIF GBIF.org (2nd May 2017) (http://doi.org/10.15468/dl.mwb31), EPPO, Geminivirus database (http://geminivirus.org:8080/geminivirusdw/) (Silva et al. 2017), and other references (for *TYLCV:* 134 locations, for *S. lycopersicum:* 186 occurrences and *B. tabaci:* 962 occurrences). We crosschecked all countries worldwide and included only locations with open field tomato cultivation. Eventually, *TYLCV* records were reduced to 118, *S. lycopersicum* to 177 occurrences and *B. tabaci* to 421 occurrences after applying spatial filtering using spThin, an R package to reduce spatial autocorrelation (Aiello-Lammens et al. 2015). We selected this method, as it retains as many localities possible and is more effective than other methods in reducing spatial autocorrelation (Boria et al. 2014). Filtered occurrence data points were >5 km apart (Boria et al. 2014; Veloz 2009). This distance was selected to restrict each cell to only one occurrence point since we used ~5-km spatial resolution climatic data in the model.

2.2. Global Climate Models and Climate Change Scenarios

For modelling the potential distributions, for the years 2050 and 2070, of *TYLCV* as a pathogen, *S. lycopersicum* as host and *B. tabaci* as an insect vector, one Global Climate Model (GCM), namely HadGEM2_ES, was selected to run under four Special Report on Emissions Scenarios (SRES) scenarios, RCP2.6, RCP4.5, RCP6.0 and RCP8.5. The chosen model HadGEM2-ES is a product of Hadley Centre Global Environmental Model associated cycle of the fifth phase of the CMIP5 (http://www.ipcc.ch/report/ar5/wg1/) (Taylor et al. 2012). This model incorporates interactive land and ocean carbon cycles and dynamic vegetation, offering the option to prescribe either atmospheric CO_2 concentrations or anthropogenic CO_2 emissions with simulated CO_2 concentrations. With a CO_2 doubling rate of approximately 4.68°C, it ranks near the top of the CMIP5 range (Andrews et al. 2012; Dike et al. 2015).

Our study focuses on the future predictions under four different scenarios. The four RCPs represent “low” (RCP 2.6), “Medium” (RCP 4.5 and RCP 6.0) and “High” (RCP 8.5) scenarios featured by the radiative forcings of 2.6, 4.5, 6.0 and 8.5 W m^{-2} by 2100, respectively. The RCPs offer an extensive range of potential changes in future anthropogenic, greenhouse gas (GHG) emissions (2014). Across all RCPs, global mean temperature is projected to increase in the range by 0.3 to 4.8 °C by the late-21st century (IPCC 2014).

2.3. Environmental Data layers

Initially, we considered nineteen variables of temperature and precipitation (Table 1). These bioclimatic parameters were obtained from WorldClim dataset (http://www.worldclim.org/) (Hijmans et al. 2005). The data layers used had 2.5min spatial resolution (~5Km), a resolution of sufficient high quality to support climatic variables at global scale (Daly 2006; Elith and Leathwick 2009b). The average temperature and precipitation data covering 1960-1990 and other parameters (Table 1) were drawn from the seasonal variables and climatic extreme indices (Hijmans et al. 2005).

We used the SDMtools in ArcGIS software to remove variables with high correlation, and only one variable from a group with correlation was included, based on the Pearson correlation coefficient, r ≥|0.75| (Table S1). Also, these variables are considered biologically more meaningful than annual means of temperature and precipitation (Hijmans *et al.*, 2005). In this study, only six bioclimatic variables were selected, based on realistic biological relevance to the species (*TYLCV*, *S. lycopersicum* and *B. tabaci*) (Table 1; Table S1).

2.4. MaxEnt software - Model development and validation

MaxEnt, maximum entropy based model algorithm, version 3.3.3k (Phillips et al. 2006), was used for the potential global distributions of *TYLCV*, *S. lycopersicum* and *B. tabaci* (Ramos et al 2018).

MaxEnt was chosen because it uses species presence and background data (absence data are not needed) and it is appropriate for small sample sizes (Kumar and Stohlgren 2009; Pearson et al., 2007). MaxEnt is a machine learning method that predicts the potential distribution of species based on maximum entropy (Phillips et al. 2006). This method is less sensitive to small sample sizes (using small sampling and background data) (Kumar et al. 2014a; Kumar et al. 2014b; Kumar et al. 2009; Kumar and Stohlgren 2009). This program was most suited to our research based on the presence-only data available for pathogen and host (Phillips et al. 2006). MaxEnt generates a suitability index of the species ranging from 0 (for unsuitable) to 1 (for optimum suitability) per grid cell. A total of 50,000 background points were selected at random from locations of current occurrence for each species. A sampling bias was generated in that the data was collected from external sources, in which we had no control of the sampling process. SDMToolbox was employed to generate the bias surface using a kernel density estimate (Brown 2014). The bias surface will result in a raster where cells with lower values will represent places with lower bias (Galdino et al., 2016; Phillips et al., 2006). The bias surface was used to establish sampling intensity and potential sampling bias (Jarnevich et al. 2015).

We made adjustments to the MaxEnt default settings combining different feature types, and the regularization multiplier (RM) to find the best model for the species *TYLCV*, *S. lycopersicum* and *B. tabaci* (Jarnevich et al. 2015; Kumar et al. 2014b; Merow et al. 2013). We first combined different sets of MaxEnt features: linear [L], quadratic [Q], product [P], threshold [T], and hinge [H] (Table 2) with the RM. The RM was used to control the number of parameters and consequently the model complexity (Elith et al. 2011; Merow et al. 2013). We used three values of RM (1.0; 1.5 and 2.0) for the species (Table 2). Models are very restricted when RM is below 1 and is inappropriate for global predictions. An RM value greater than 1 generates models with a broader potential distribution (Phillips et al. 2006).

For elimination of extrapolations from the environmental range, we used the MaxEnt 'fade-by-clamping' (Owens et al. 2013). The 'jackknife' technique and percentage contribution were used to estimate the importance and the contribution of the environmental variables. Response curves were generated in MaxEnt and we used only those that represented relationships between probabilities of presence for the species, in terms of each environmental predictor. All response curves were evaluated in terms of making biological logic, and those failing this test were not considered for further evaluations.

To compare performance of the models, we selected test sensitivities of 0% and 10% training Omission Rates (OR) (Kumar et al. 2014a; Kumar et al. 2015; Liu et al. 2013) and the AUC_{cv} (area under the receiver operating characteristic [ROC] curve) (Peterson et al. 2008). For calculating AUC_{cv} and OR, a 10-fold cross-validation was run in MaxEnt. AUC_{cv} was also used for discriminating presence from background data. When the AUC_{cv} value is 0.5 it indicates that model predictions are no better than random; values below 0.5 are less than random; values between 0.5 and 0.7 indicate poor performance; values between 0.7 and 0.9 indicate moderate performance, and values greater than 0.9 indicate high performance (Peterson et al. 2011). In the case of OR, the expected value at 0% training is 0 and at 10% it is 0.10; models show poor performance when the value exceeds the expected omission rates (Boria et al. 2014). Model ranking was based on 10% training OR, 0% training OR, and AUC_{cv} (Kumar et al. 2014a; Liu et al. 2005; Merow et al. 2013). ArcGIS 10.3.1 software was used to extract the MaxEnt outputs, in order to project areas suitable for open field tomato cultivation under varying levels of risk of invasive *TYLCV* under future scenarios.

2.5. Determining *TYLCV* risk levels and combination of model outputs for *TYLCV*, *S. lycopersicum* and *B. tabaci*

Maximum Test Sensitivity Plus Specificity (MTSPS) threshold was chosen to extract from the projected future distributions of *TYLCV, B. tabaci* and *S. lycopersicum* which areas would be optimal for open field tomato crops and suitable for *B. tabaci* and would be at high, medium or low risk levels for *TYLCV*. This threshold was chosen since it is considered to be simple and effective to the average probability/suitability approach (Liu et al. 2005). For overlaying, “optimal conditions” were defined as areas of medium or high suitability for *S. lycopersicum*, in that these corresponded to areas that either are, or would be, of high suitability based on climate conditions for growing and development of tomato crops. For projections for the three species, as well as for the overlaying to determine risk levels of *TYLCV* in areas with optimal conditions for tomato crops and suitable for *B. tabaci,* we used four suitability classes (unsuitable, low, medium and high).

3. RESULTS

The annual mean temperature (bio1; °C), temperature annual range (bio7; °C), mean diurnal range in temperature (bio2; °C), precipitation seasonality (CV) (bio15), precipitation of driest month (bio14; mm) and mean annual precipitation (bio12; mm) were the climatic variables that most contributed to *TYLCV* distribution (Table 1). Accordingly, to the observed occurrences, *TYLCV* occurs in areas with mean annual temperature of 19.5°C, and annual precipitation range of 7-3146mm, with mean of 890.5mm (Table1).

All MaxEnt model performances were evaluated to determine where *TYLCV* potential distribution exceeded random, using test AUC_{cv} values higher than 0.5 (Table 2). Average AUC_{cv} values were based on 10-fold cross validation and ranged from 0.879 to 0.887 (Table 2). These models displayed low test omission rates, with values varying from 0.0083-0.0614 at 0% training omission rate, and from 0.1114-0.2091 at 10% (Table 2). The best model comprised three environmental variables, Linear, Quadratic, Product (LQP) features, regularization multiplier=1.0, with lowest omission rate, at 10% and 0% respectively (Table 2).

The Jackknife test of importance of variables indicated that mean annual temperature had more information than other variables. The highest probability for *TYLCV* presence was found in localities with mean annual temperature of 19-20°C. The probability of *TYLCV* infection was higher in areas with lower precipitation, decreasing with the increase in precipitation. The probability of *TYLCV* presence was also higher in areas of low mean diurnal temperature range (Response curves, Figure S6 – supplementary material).

Comparing the MaxEnt global climate suitability model with global distribution of *TYLCV* (Figure 1A), open field *S. lycopersicum* (as a host) (Figure 1B), and *B. tabaci* distribution (as an insect vector) (Figure 1C) show consistency with the current global distributions of their known occurrences. Climatic conditions suitable for *TYLCV* are projected for many regions globally. Although there are areas in South America, which are under risk for *TYLCV*, this virus strain has not yet been reported from those areas (Figure 1A, S2 and 3). The tomato model also displayed global agreement between known occurrences and projections (Figures 1B, S3 and 3). The current and projected climate results for *TYLCV* indicate low, medium and high suitability areas in Europe, Asia, North Central and South America, and Africa (Figure 1A, S2 and 2).

3.1. Projected result from the model for *TYLCV* under various climate change scenarios

According to projected scenarios for 2050 and 2070, many areas in the world, such as in South America (e.g. Argentine and some areas along coastlines of Brazil), North America (United States), Africa (along coastlines of the continent) and south of Europe, are projected by the HadGEM2_ES model to sustain suitability for *TYLCV* (Figure S2 and 2). The model further demonstrates that this suitability will increase for 2050 and 2070 in a northern direction in Europe (in countries such as Spain, Italy, France, Germany and Hungary), Asia (Northern China), North America (some sites in the United States), and decrease in Asia (India) and Africa. However, suitability will decrease in South and Central America, Africa, Asia (India) and Iran (Figures S2 and 2).

It should be noted that while there are not many differences among the scenario (RCP 2.6, RCP 4.5, RCP 6.0, RCP 8.5) projections, RCP8.5 shows larger areas under low suitability (e.g. the United States, Northern of Europe and Northern of China) compared to the other scenarios.

3.2. Projected result from the model for tomato crops under various climate change scenarios

According to projected scenarios for 2050 and 2070, many areas on all continents (Americas, Africa, Asia, Europe, and Oceania) are projected by the HadGEM2_ES model to decrease in suitability for tomato crops (Figures S3 and 3). However, the model demonstrates that suitability will increase in a northern direction in some European countries (e.g. Spain, Italy, France, Germany and Hungary), and will be maintained in other areas (e.g. along of coastlines of Brazil, south of Europe and western of Africa) for this host species for 2050 and 2070. Again, although there are not many differences between the scenarios (RCP 2.6, RCP 4.5, RCP 6.0, RCP 8.5), RCP 6.0 and RCP 8.5 show a larger decrease in areas (e.g. Africa, South America, Australia and China) suitable for open field tomato crops, above the general decline in suitability for 2050 and 2070 (Figure S3 and 3).

3.3. Projected result from the model for *B. tabaci* under various climate change scenarios

According to projected scenarios for 2050 and 2070, many areas on all continents (Americas, Africa, Asia, Europe, and Oceania) in the world are projected by the HadGEM2_ES model to maintain suitability for *B. tabaci* (Figures S4 and 4). However, this model demonstrates that suitability for this insect vector species will increase for 2050 and 2070 in European countries (Spain, Italy, France, Germany and Hungary), North America (United States), and decrease in parts of South America, India and Australia. While there are few differences between the scenarios (RCP 2.6, RCP 4.5, RCP 6.0, RCP 8.5) RCP 8.5 shows a greater decrease in some areas (e.g. Africa and India) of suitability for *B. tabaci*, but an increase in others (e.g. United States and Europe) (Figure S4 and 4).

3.4. Combining the results of the model outputs for *TYLCV*, open field tomato cultivation and *B. tabaci* under four climate change scenarios

Overlaying the results for the three species shows that some areas in China, Australia, Europe, Africa, and North and South America will be optimal for open field tomato and suitable for *B. tabaci* at low (38%), medium (52%) and high risk (10%) of *TYLCV* until 2070 (Figure S5).

According to the four projected scenarios for 2050 and 2070, the risk of (high suitability for *TYLCV* will increase by 111% compared to the current risk level, in many locations, such as the United States, northern and northeastern of China, southern Kazakhstan and in many European countries. Alternatively, the low and medium suitability risks decrease to 93% and 92%, respectively, compared to the current risk levels in areas of varying suitability in South America (e.g. Argentina and Brazil), Central America, Mexico, Africa, Saudi Arabia, India and Iran. Host, *S. lycopersicum*, indicates decreases in low, medium and high suitability categories compared to the present, at many sites in South and North America, Africa, and in countries such as Australia, India, Thailand and China. Increased areas are only evident in the low and medium suitability categories, only occurring in Europe. High suitability for *B. tabaci* shows increases compared to current levels in China and Europe, but decreases in low and medium suitability in South America, Africa, India and Australia.

Overlaying the results for *TYLCV*, *S. lycopersicum* and *B. tabaci* indicates that most of the countries projected to be optimally suitable *S. lycopersicum* as well as suitable for *B. tabaci* will be under medium suitability for *TYLCV*, with few sites (e.g. South America and Africa) at low risk. The future predictions for the four scenarios show large reductions in areas with *TYLCV* risk levels, most of them due to the reduction of climatic conditions suitable for the host (*S. lycopersicum*).

4. DISCUSSION

A comparison of the global climate suitability model with the current global distribution of *TYLCV* (Figure 1A) shows consistency. Climatic conditions suitable for *TYLCV* are projected for many places in the world with low, medium and high suitability areas in Europe, Asia, North Central and South America, and Africa. However, there are some projections in areas in South America, for example in Brazil, where the virus has not yet been reported. Although the climate conditions show medium and high suitability in those areas, the reason for that may be due to the fact that Brazil does not import tomato seedlings, or alternatively due to the extensive use of tomato resistance plants in many sites in the country (in case this virus had reached the country but couldn't establish). We highlight this point because there are so many places on the continent under high risk for *B. tabaci* (which is the insect vector) (Figure 1 C), and for that reason, those areas might be under risk from *TYLCV* since the insect vector is already present there. Further, in 2007 *TYLCV* was reported for the first time on the continent, at a location in Venezuela (Zambrano et al. 2007). *B. tabaci* is spread in America and once the insects have acquired the virus they are able to spread it everywhere else. The introduction *B. tabaci* in areas never previously reported, or *TYLCV* in areas where *B. tabaci* is already present, can lead to invasion, and severe virus outbreaks (Götz and Winter 2016).

To the best of our knowledge, this is the first study of *TYLCV* potential distribution on a global scale. *TYLCV* is distributed in all continents and induces severe yield losses in tomato production in the Mediterranean and many tropical and subtropical regions worldwide (Hanssen and Lapidot 2012; Lapidot and Friedmann 2002; Navas-Castillo et al. 2011) (Figure 1 A).

The models presented in this study show great degree of reliability. The *TYLCV* model produced an 88.7% agreement under AUC, with the current modeled global climate and test omission rate at 10% and 0% of 0.1 and 0.02, respectively. All models performed better than expected at random and show a high validation statistic. The high level of accordance with current *TYLCV* and *S. lycopersicum* distribution confirm the consistency of models (Figure 1 A, B).

TYLCV was observed occurring in a wider range of precipitation (7-3146mm) but most preferably in low rainfall sites, with mean of 890.5mm (Table 1). The virus may occur in low rainfall areas due to tomato crop irrigation, accounting for the development of the host and consequently for the viruses. We also observed that *TYLCV* is more likely to occur in areas with high temperatures (Ghandi et al. 2016). High temperatures have been observed to favor virus replication, while low temperatures delay infections and display only mild symptoms (Ghandi et al. 2016; Health 2014). This is confirmed by the results (response curves), in locations with high mean annual temperature (Figure S6).

TYLCV dynamics may be influenced negatively at high temperature, since the current *B tabaci* biotypes exhibit a lower fertility than at temperate climates. New emerging biotypes, much more resistant to heat, may be selected by increased temperatures. It is known that the biotypes of *B tabaci* are very dynamic and one may replace another within a few year (i.e. Biotype B replacing A in the USA, and Biotype Q replacing B in the middle and far east).

The climatic conditions for *TYLCV* found in this study match the ideal conditions for tomato open-field cultivation. Tomato crops have an optimum temperature range from 20 to 27°C, as well as poorer development in regions with high annual precipitation (> 1800mm) (FAO 2007). All climatic factors used in this study indicate that *TYLCV* has climatic requirements similar to the host, further confirming the quality of our model in predicting *TYLCV* occurrence in most locations where tomato is cultivated in open field conditions (Figure 1, Table S1). Climatic conditions such as suitable temperature may, therefore, contribute to the potential invasion of *TYLCV* in regions of open field tomato where the presence of the virus has not yet been reported, thus compromising the tomato productivity in many important tomato production regions.

Although *TYLCV* may establish across a wide thermal range, the virus is affected by global temperature changes (Figures S2 and 2). If the increase of the temperature predicted in the HadGEM2-ES model occurs, it may extend the limits for occurrence, as well as limiting growth and development of the host, and affecting the insect vector distribution. *TYLCV* virus requires the interaction of a susceptible host and the environment (it has to be favorable for disease development). This means that the virus is dependent on the survival of the host, *S. lycopersicum*, a species that shows great sensitivity to extreme environmental conditions, especially temperature. In this context, studies have reported that temperature (high or low) may affect the suitability of host (host resistance) and the interaction between host and virus (Anfoka et al. 2016; Canto et al. 2009). Our model results, for all scenarios in the future, indicated greater reductions in suitability for tomato crops are predicted, even more than for *TYLCV*. The virus can establish in an area even without the vector and spread there through seeds. However without the vector its establishment can be less sure if seeds are not taken from the produced plants but new crops are always started form new seeds coming from somewhere else. The presence of the vector ensures that the virus spreads between host plants and may also end up in weeds and be preserved in the field.

According to projected scenarios for 2050 and 2070 many global regions, such as in South America (e.g. Argentine and some areas along coastlines of Brazil), North America (United States), Africa (along coastlines of the continent) and south of Europe, are projected to maintain *TYLCV* suitability (Figures S2 and 2). Similarly, suitability will be maintained in many regions for tomato cultivation (e.g. along of coastlines of

Brazil, southern Europe and West Africa), as well as for *B. tabaci* (e.g. along of coastlines of southern, southeastern and northeastern Brazil and southern and eastern Australia (Figures S4 and 4). However, the model demonstrates that this suitability for *TYLCV* will increase for 2050 and 2070 in a northern direction in Europe (Spain, Italy, France, Germany and Hungary), Asia (Northern China) and North America (some sites in the United States). Tomato cultivation suitability will increase in a northern direction in European countries (Spain, Italy, France, Germany and Hungary), but decrease in Asia (India) and Africa. In general, suitability for *TYLCV* will decrease for 2050 and 2070 for South and Central America, Africa, Asia (India) and Iran (Figures 2 and 3) and for the host in all continents (America, Africa, Asia, Europe, and Oceania) (Figures S3 and 3). While the differences between the scenarios are few for all three species (virus, host and vector); RCP 8.5 shows larger areas under low suitability for *TYLCV* (e.g. the United States, Northern of Europe and Northern of China) compared to the others. The fact that RCP8.5 projects the greatest mean global temperature projected increase and is the only scenario assuming the continuation of greenhouse gas emission increases throughout the 21st century, may explain these larger areas (Meinshausen et al. 2011). For tomato open field cultivation, both RCP 6.0 and RCP 8.5 show larger decreases of suitable regions (e.g. Africa, South America, Australia and China) than the general decrease for 2050 and 2070 (Figures S3 and 3). For *B. tabaci* suitability, again RCP 8.5 indicates larger decreased areas (e.g. Africa and India), but an increase in some areas (e.g. United States and Europe), compared with the general maintaining of suitability for 2050 and 2070 (Figures 4S and 4).

Our models does not take into account the fact that most cultivars are now tolerant to *TYLCV*. This means that there is several orders of magnitude less virus in the plants than in susceptible cultivars. As a result, the whiteflies pick up much less virus and altogether the amount of infection decreases. It is possible that *TYLCV* will disappear on tomato in the future. The virus will still exist but on alternative host such as weeds. On the other hand, new variants may occur which will break tolerance.

Combining the results for the three species shows that some areas in China, Australia, Europe, Africa, and North and South America will be optimal for open field tomato, and suitable for *B. tabaci* with low, medium and high risk of *TYLCV* until 2070 (Figure S5). According to the four projected scenarios, the risk levels (low or high suitability) for *TYLCV* will increase when compared to the current levels in many regions, such as the United States, northern and northeastern China, southern Kazakhstan and northern European countries. However, a decrease in risk is shown in some areas with different suitability levels in South America (e.g. Argentina and Brazil), Central America, Mexico, Africa, Saudi Arabia, India and Iran. For *S. lycopersicum*, the suitable levels (low, medium and high suitability) will decrease when compared to the current levels for many regions in South and North America, Africa, and in countries such as Australia, India, Thailand and China; increasing (low and medium) suitability in Europe. The overlaying results for *TYLCV*, *S. lycopersicum* and *B. tabaci* indicate that most countries projected to be optimally conducive for *S. lycopersicum*, and suitable for *B. tabaci* will be under medium suitability for *TYLCV*, with few localities at low risk (Figures S5 and 5). The future predictions for the four scenarios show large reductions in areas of *TYLCV* risk levels. The main reason for the significant decrease in total area conducive for open field tomato is overall the reduction of suitable climatic conditions (Figures S5 and 5).

5. CONCLUSIONS

Our study shows that climate change may affect *TYLCV* global distribution, as well as that of its host, *S. lycopersicum*, and vector, *B. tabaci*. The methods utilized in this study have relevance and application for other agricultural crops and for the management of other viruses (i.e. Begomovirus). The results of the climate change for two different species, using HadGEM2-ES model under four different scenarios, provides an indication of potential global climatic changes and the impact of these on tomato production. Globally, there are areas at increased risk of *TYLCV*, some that will maintain current risk levels, and others in which the risk will decrease. Some regions are predicted to become optimally conductive for open field, *S. lycopersicum*, as well as suitable for *B. tabaci*, with different risk levels of *TYLCV*. For 2050 and 2070, most areas with optimal conditions for *S. lycopersicum*, and suitable for *B. tabaci* will be under medium suitability for *TYLCV*, with few localities at low risk. Future research could consider the impact of non-climatic factors under MaxEnt modeling, overlaying additional layers to refine the results in a more extensive range of environmental scenarios and locations. Since *TYLCV* may be transmitted for different ways, most by the vector but it is also seed-transmissible. In order to prevent the infection or spread of *TYLCV* is it very important to control the vector but also new strategies to avoid seed transmissions is needed. Our results may be useful in designing strategies to prevent the introduction and establishment of *TYLCV* in some countries in South America, where the occurrence of the virus has not yet been reported, as well as promote greater investment in pest management programs, especially in areas becoming more suitable for the host, but under medium and high risk for the virus.

AUTHOR CONTRIBUTIONS

RSR and MCP conceived and designed research. RSR acquired and analyzed the data. RSR wrote the manuscript. LK and FS made critical revisions (providing language help, and writing assistance). LK and MCP made critical revisions and approved final version. All authors reviewed and approved of the final manuscript.

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CONFLICT INTEREST

The authors declare that they have no conflict of interest.

Table 1. Environmental variables considered in *TYLCV* niche models, and average percent contribution of environmental variables in the *TYLCV* distribution model; values were averaged across 10 replicate runs. General statistics were calculated using all occurrences (n = 133). (Min=minimum, Max=maximum, and SD = standard deviation).

Variable	Percent contribution	Permutation importance	Min.	Max.	Mean	SD
Annual mean temperature (bio1; °C)	60.2	56.5	8.5	29.1	19.5	5.2
Temperature annual range (bio7; °C)	14.5	8.6	7.3	45.4	26.8	8.9
Mean diurnal range in temperature (bio2; °C)	14.1	16.3	5.2	18.4	10.9	2.7
Precipitation seasonality (CV) (bio15)	6.2	8.6	27	159	73.8	32.3
Precipitation of driest month (bio14; mm)	2.9	4.3	0	221	22.1	30.5
Mean annual precipitation (bio12; mm)	2.2	5.7	7	3146	890.5	710.2
Isothermality (bio3)	-	-	23	82	44.3	16.2
Temperature seasonality (SD x 100) (bio4)	-	-	533	12234	5597	2985
Maximum temperature of warmest month (bio5; °C)	-	-	16.1	46.0	32.8	4.3
Minimum temperature of coldest month (bio6; °C)	-	-	-16.3	21.9	6.0	8.8
Mean temperature of wettest quarter (bio8; °C)	-	-	7.3	31.4	21.3	6.3
Mean temperature of driest quarter (bio9; °C)	-	-	-8.2	35.4	17.9	10.6
Mean temperature of warmest quarter (bio10; °C)	-	-	11.5	35.4	26.5	3.5
Mean temperature of coldest quarter (bio11; °C)	-	-	-8.2	26.7	12.2	85.0
Precipitation of wettest month (bio13; mm)	-	-	2	666	165	119.8
Precipitation of wettest quarter (bio16; mm)	-	-	4	1878	419.7	318.3
Precipitation of driest quarter (bio17; mm)	-	-	0	736	79.2	101.6
Precipitation of warmest quarter (bio18; mm)	-	-	0	1454	307.4	147.1
Precipitation of coldest quarter (bio19; mm)	-	-	0	1210	147	171.2

Bold font indicates variables in the final model. Source of data: WorldClim (http://www.worldclim.org/bioclim; Hijmans et al., 2005).

Table 2. Summary of performance statistics of *TYLCV* MaxEnt models. The best model is highlighted in bold.

Model Rank	Variables	MaxEnt settings		Test AUC_{cv} (±SD)	OR	
		Features	RM		0%	10%
1	**bio1,bio2,bio7, bio12, bio14, bio15**	**LQP**	**1.0**	**0.887 ± 0.036**	**0.0258**	**0.1114**
2	Same as above	LQP	2.0	0.883 ± 0.038	0.0341	0.1189
3	Same as above	LQP	1.5	0.882 ± 0.040	0.0348	0.1277
4	Same as above	LQPTH	1.5	0.886 ± 0.036	0.0364	0.1310
5	Same as above	LQH	2.0	0.887 ± 0.035	0.0083	0.1364
6	Same as above	LQH	1.5	0.886 ± 0.033	0.0174	0.1379
7	Same as above	LH	2.0	0.886 ± 0.034	0.0167	0.1455
8	Same as above	LQPH	1.5	0.887 ± 0.035	0.0174	0.1477
9	Same as above	LQPT	1.5	0.884 ± 0.036	0.0265	0.1689
10	Same as above	LH	1.0	0.886 ± 0.034	0.0174	0.1735
11	Same as above	LQPH	1.0	0.880 ± 0.039	0.0523	0.1932
12	Same as above	LQPT	1.0	0.879 ± 0.033	0.0614	0.2091

Note: Variables' full names (see table 1). L, Q, P, T and H are linear, quadratic, product, threshold and hinge features, respectively. RM is regularization multiplier, and SD is standard deviation. OR is test omission rate. Test AUC_{cv} is MaxEnt 10-fold cross-validation Area Under the ROC curve.

*__Table S1.__ Cross-correlation (Pearson correlation coefficient, r) among environmental variables. (Model: *TYLCV, B. tabaci* and *S. lycopersicum*) – *Supplementary material

	bio1	bio2	bio3	bio4	bio5	bio6	bio7	bio8	bio9	bio10	bio11	bio12	bio13	bio14	bio15	bio16	bio17	bio18	bio19
bio2	0.521																		
bio3	0.839	0.387																	
bio4	-0.833	-0.210	-0.891																
bio5	0.896	0.707	0.613	-0.513															
bio6	0.968	0.355	0.888	-0.936	0.764														
bio7	-0.730	0.015	-0.826	0.971	-0.358	-0.876													
bio8	0.812	0.533	0.638	-0.501	0.845	0.704	-0.387												
bio9	0.938	0.439	0.808	-0.861	0.792	0.949	-0.781	0.609											
bio10	0.935	0.621	0.660	-0.585	0.988	0.825	-0.455	0.865	0.831										
bio11	0.980	0.425	0.891	-0.926	0.795	0.996	-0.847	0.731	0.950	0.848									
bio12	0.378	-0.245	0.565	-0.554	0.119	0.486	-0.615	0.252	0.375	0.200	0.454								
bio13	0.455	-0.104	0.581	-0.567	0.233	0.527	-0.589	0.370	0.413	0.303	0.511	0.896							
bio14	0.055	-0.375	0.221	-0.245	-0.139	0.167	-0.346	-0.066	0.107	-0.075	0.123	0.709	0.392						
bio15	0.367	0.514	0.282	-0.190	0.429	0.269	-0.069	0.449	0.260	0.412	0.317	-0.173	0.138	-0.517					
bio16	0.445	-0.124	0.581	-0.569	0.215	0.522	-0.595	0.352	0.408	0.286	0.504	0.922	0.993	0.429	0.094				
bio17	0.083	-0.372	0.255	-0.275	-0.121	0.197	-0.375	-0.044	0.135	-0.054	0.153	0.744	0.429	0.994	-0.515	0.466			
bio18	0.224	-0.202	0.353	-0.337	0.026	0.282	-0.389	0.254	0.153	0.100	0.265	0.797	0.743	0.558	-0.104	0.761	0.581		
bio19	0.249	-0.242	0.431	-0.405	0.055	0.357	-0.475	0.074	0.307	0.112	0.316	0.754	0.584	0.671	-0.273	0.610	0.698	0.374	

Bold font indicates variables in the final model.

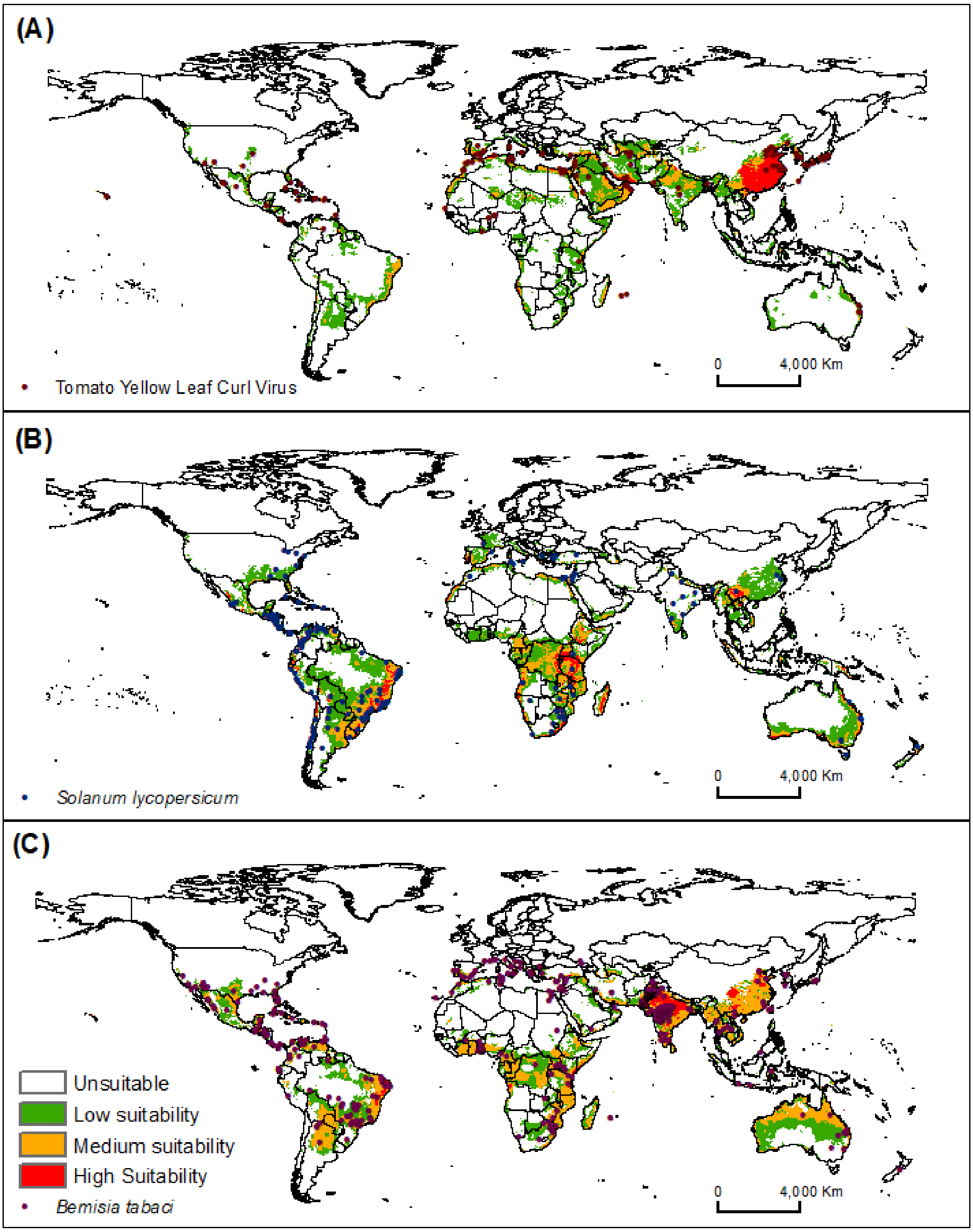

Figure 1. Habitat suitability under current climatic conditions using MaxEnt model, (A) *TYLCV*, (B) *S. lycopersicum* (Ramos et al. 2018*)* and (C) *B. tabaci* (Ramos et al. 2018). Global know occurrences of *TYLCV* in open field (brown dots), and *S. lycopersicum* in open field (blue dots).

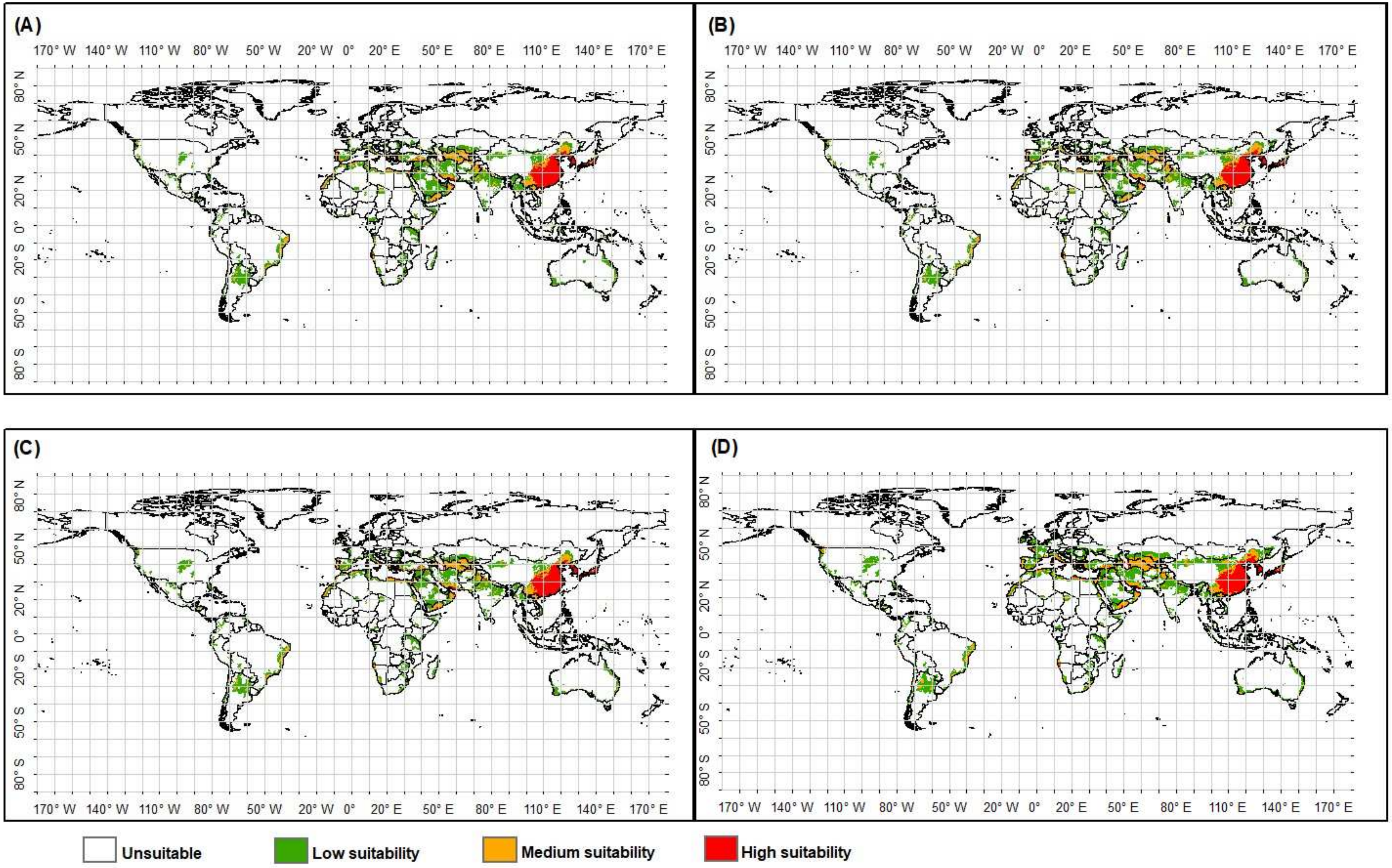

Figure S2. Habitat suitability under future climatic conditions (2050) for *TYLCV* using the MaxEnt model running four scenarios (A) RCP 2.6, (B) RCP 4.5, (C) RCP 6.0 and (D) RCP 8.5.

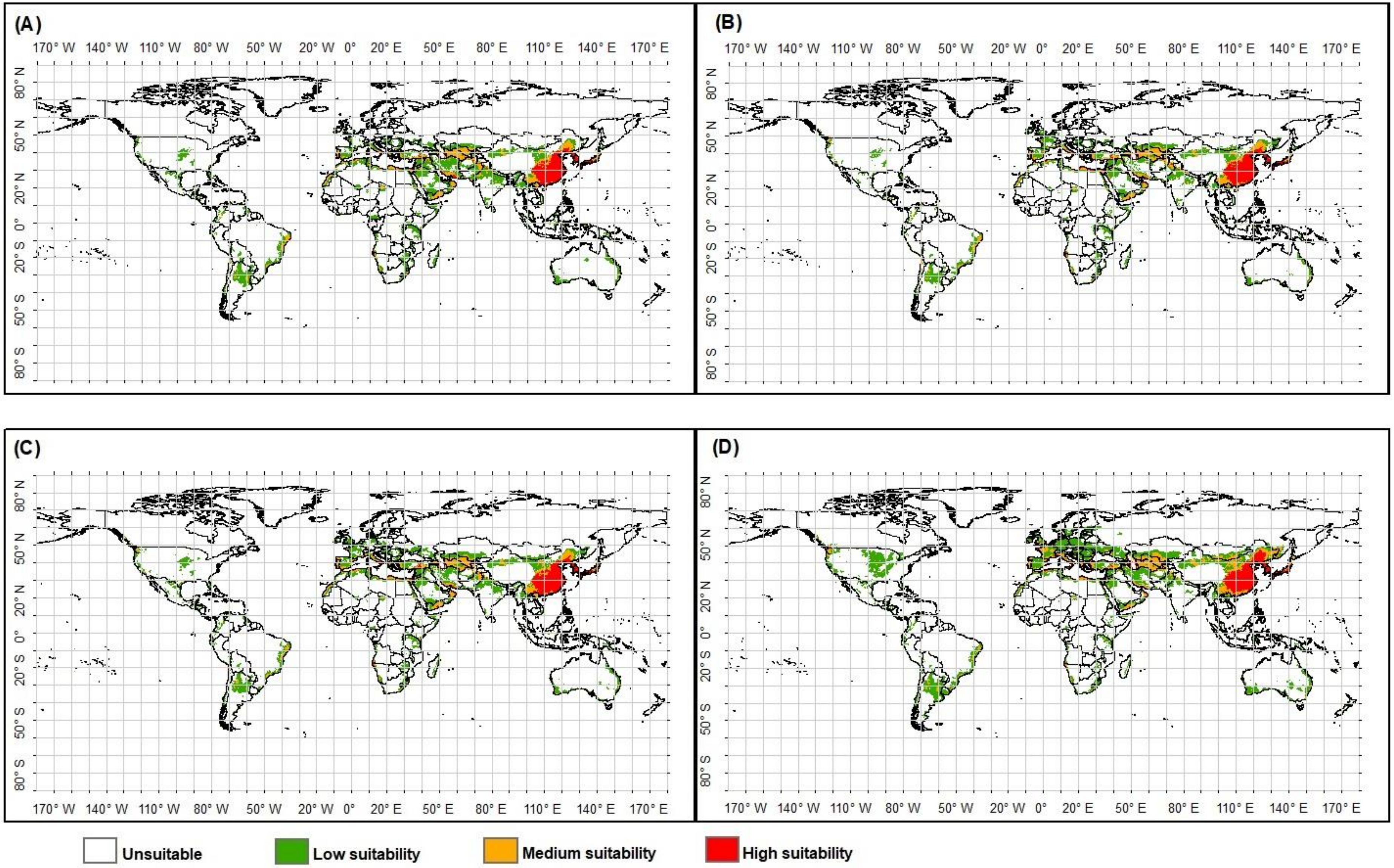

Figure 2. Habitat suitability under future climatic conditions (2070) for *TYLCV* using the MaxEnt model running four scenarios (A) RCP 2.6, (B) RCP 4.5, (C) RCP 6.0 and (D) RCP 8.5.

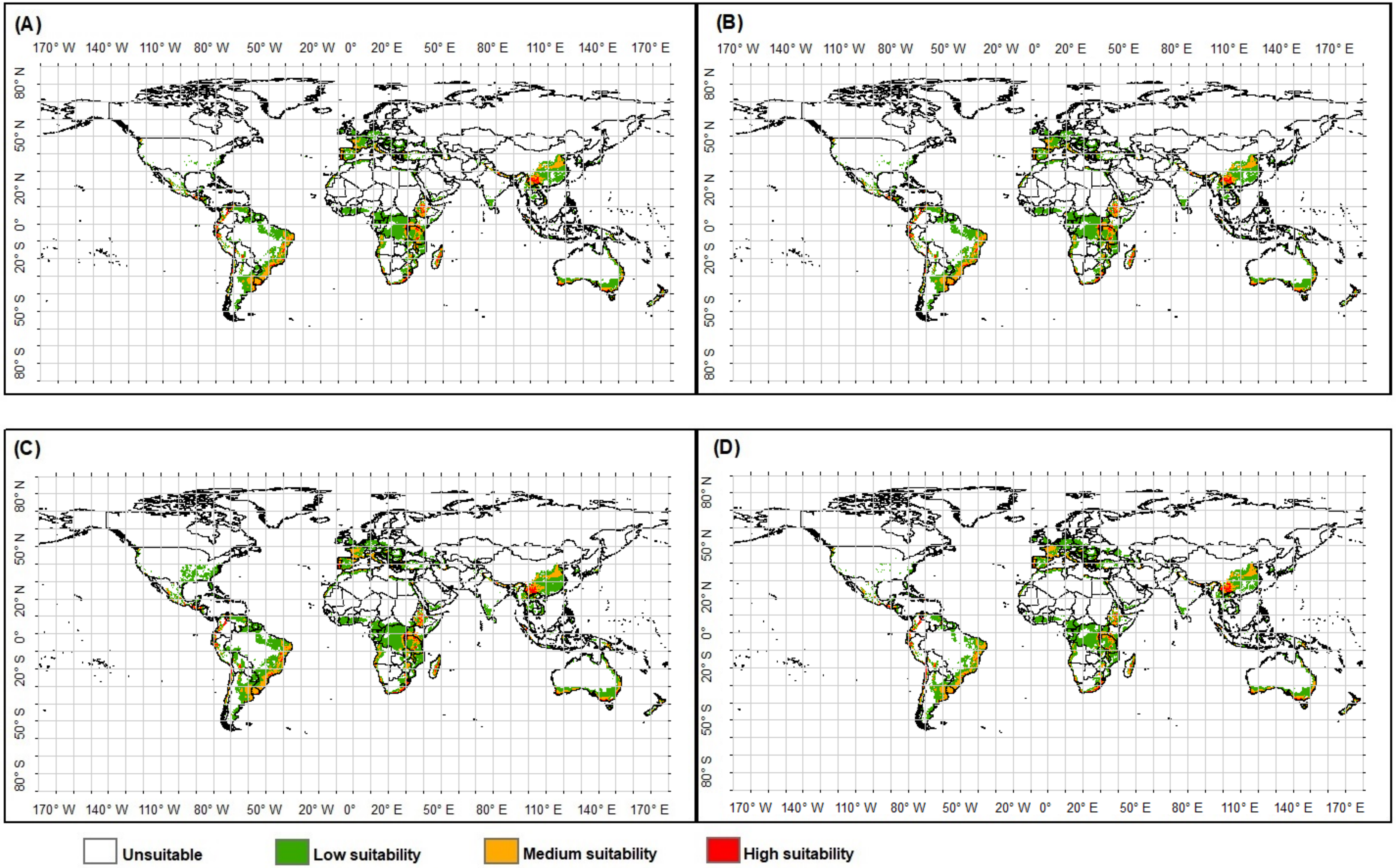

Figure S3. Habitat suitability under future climatic conditions (2050) for *S. lycopersicum* using the MaxEnt model running four scenarios (A) RCP 2.6, (B) RCP 4.5 (Ramos et al. 2018), (C) RCP 6.0 and (D) RCP 8.5.

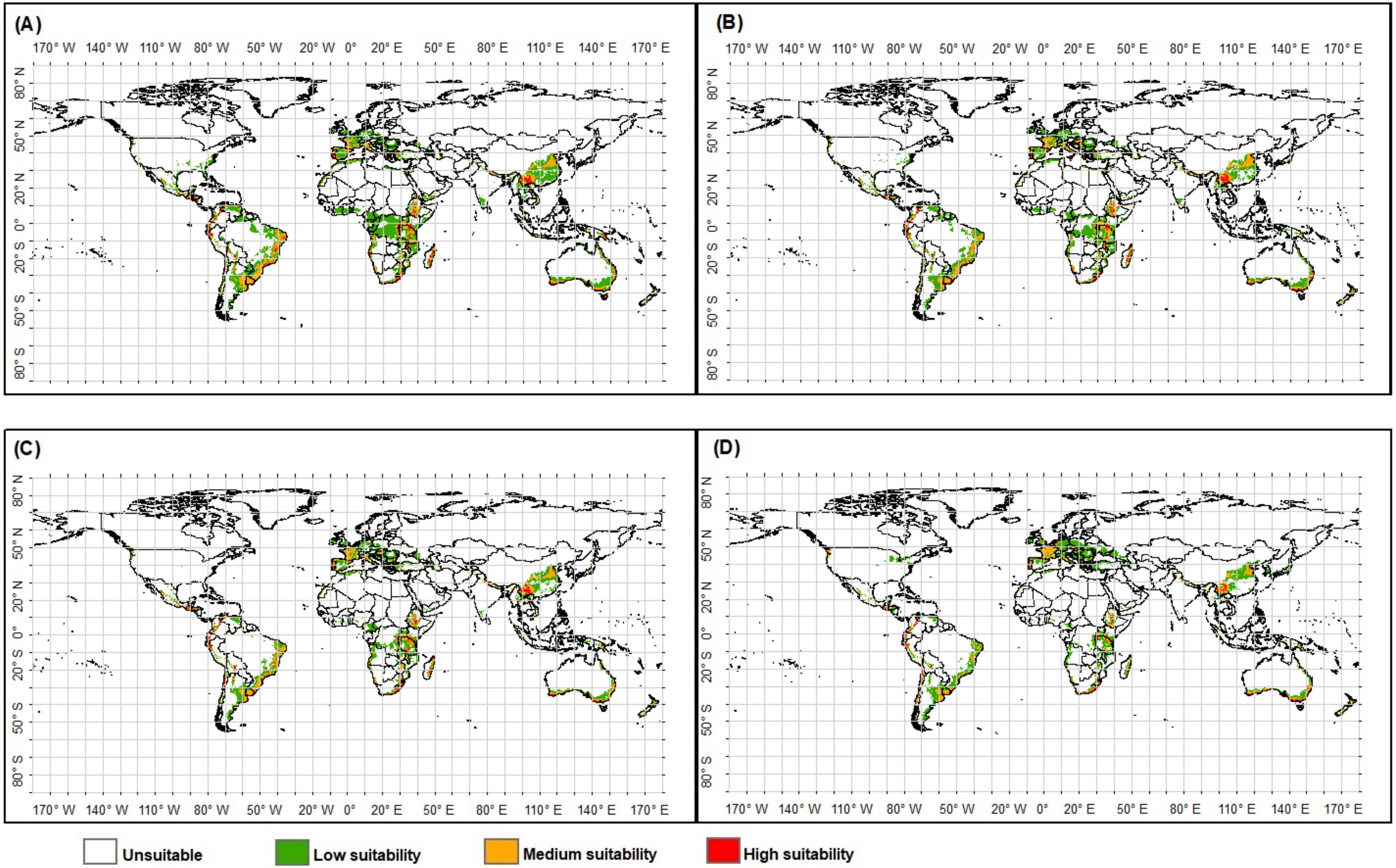

Figure 3. Habitat suitability under future climatic conditions (2070) for *S. lycopersicum* using the MaxEnt model running four scenarios (A) RCP 2.6, (B) RCP 4.5 (Ramos et al. 2018), (C) RCP 6.0 and (D) RCP 8.5.

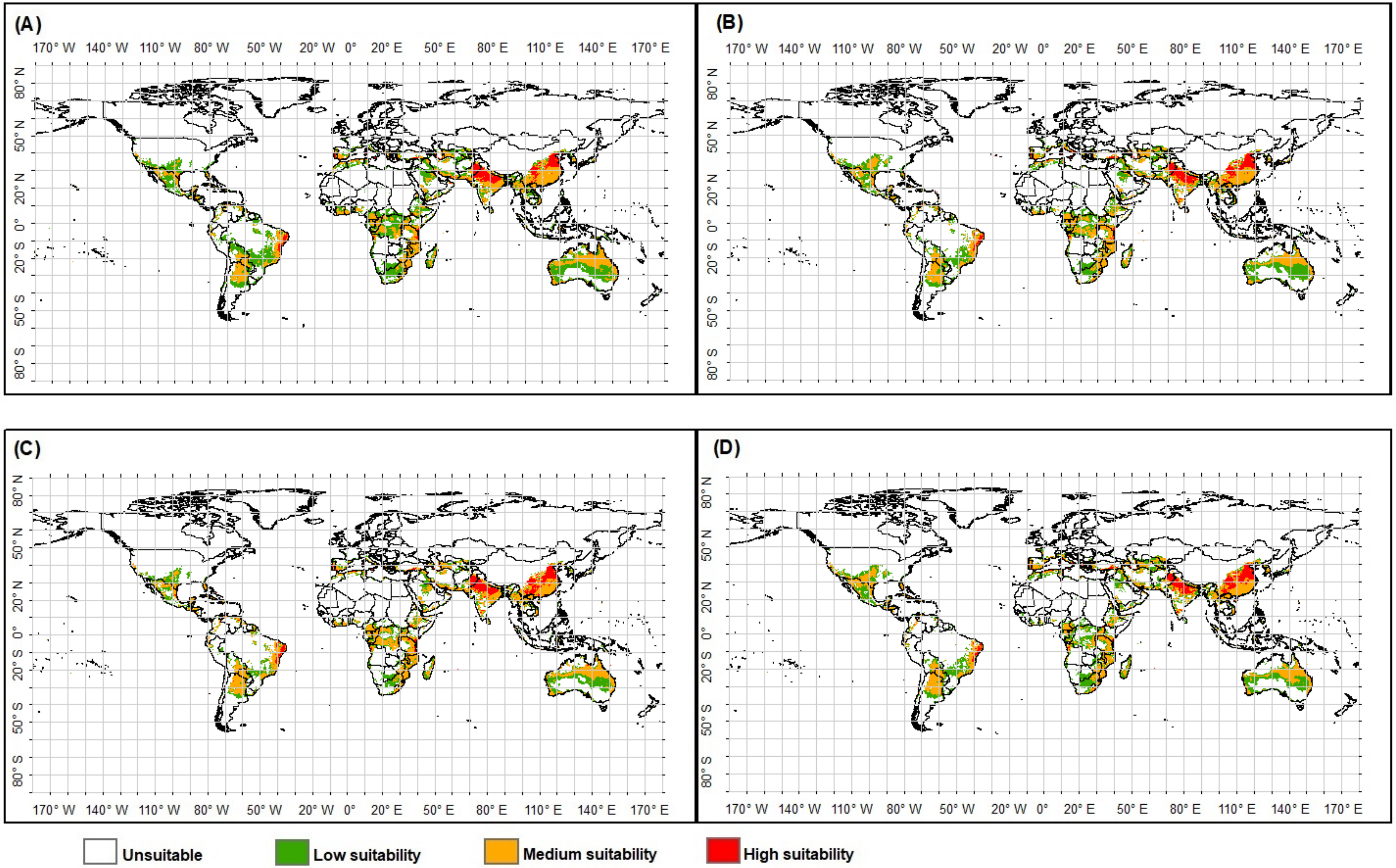

Figure S4. Habitat suitability under future climatic conditions (2050) for *B. tabaci* using the MaxEnt model running four scenarios (A) RCP 2.6, (B) RCP 4.5 (Ramos et al. 2018), (C) RCP 6.0 and (D) RCP 8.5.

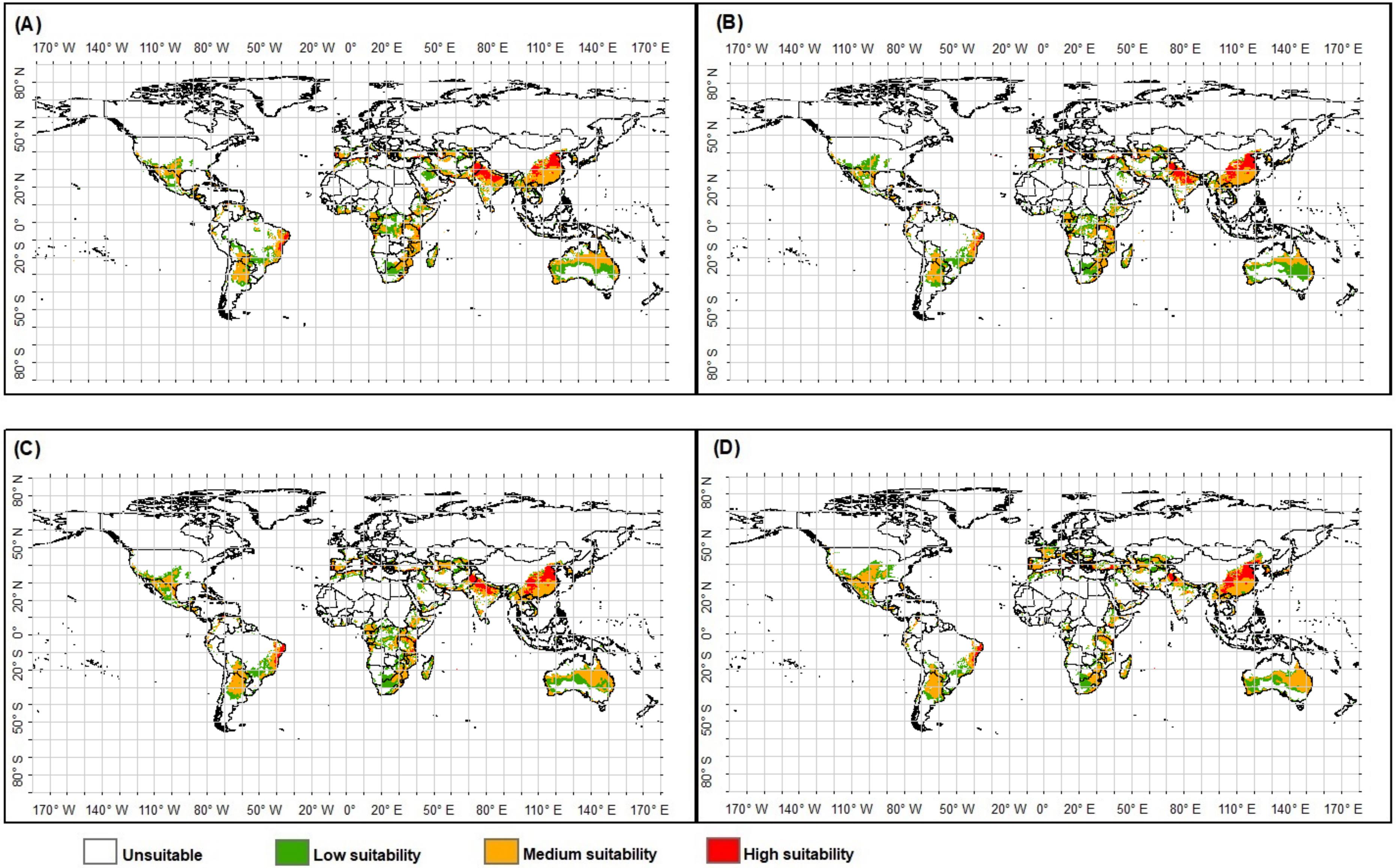

Figure 4. Habitat suitability under future climatic conditions (2070) for *B. tabaci* using the MaxEnt model running four scenarios (A) RCP 2.6, (B) RCP 4.5 (Ramos et al. 2018), (C) RCP 6.0 and (D) RCP 8.5.

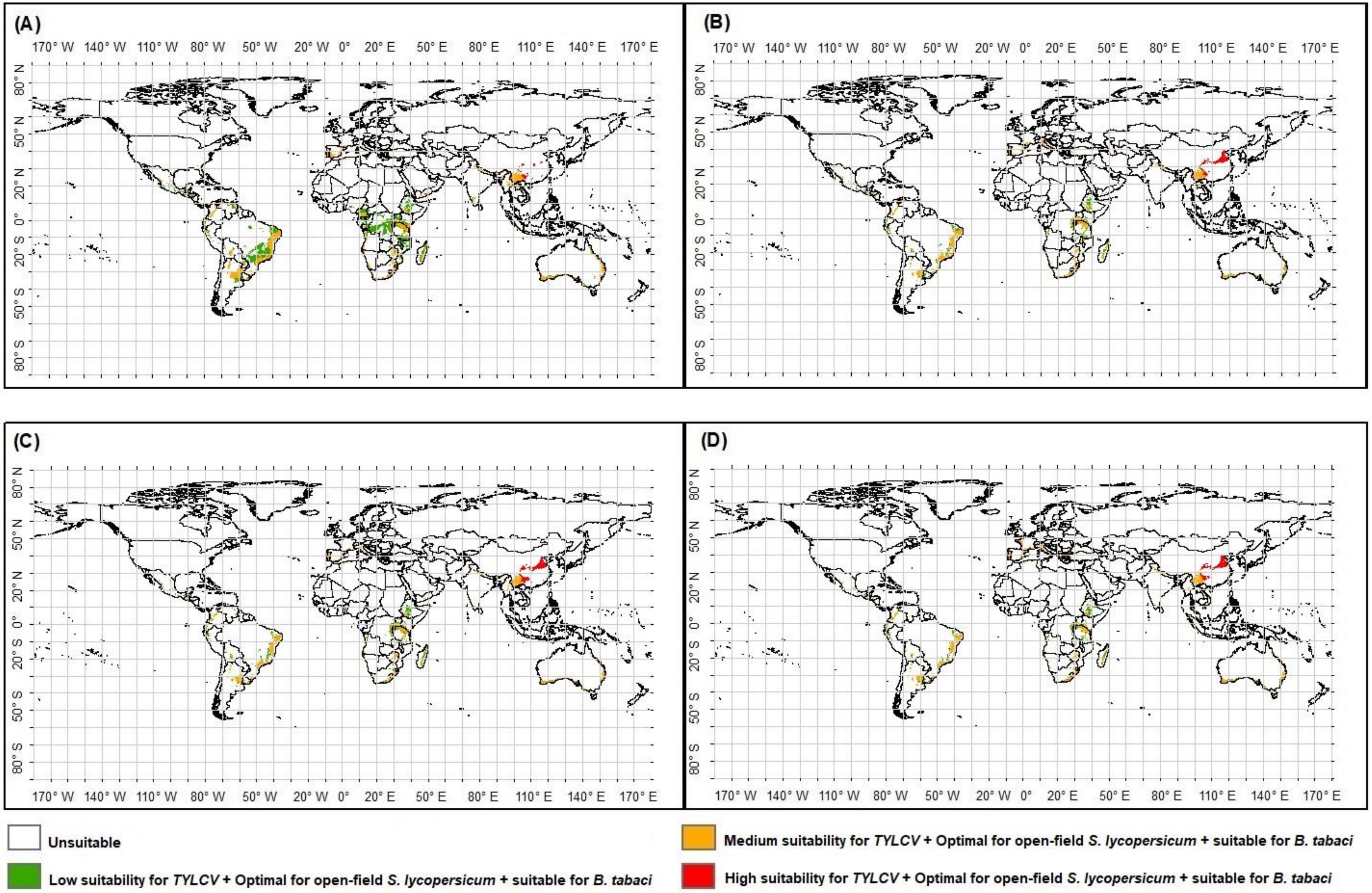

Figure S5. Agreement in the MaxEnt projection of suitable areas for *B. tabaci* and optimal for open-field *S. lycopersicum* with four risk levels of invasive *TYLCV* under HadGEM2_ES (GCM) running four different scenarios (A) RCP 2.6, (B) RCP 4.5, (C) RCP 6.0 and (D) RCP 8.5 for 2050 based on MTSPS threshold for the three species.

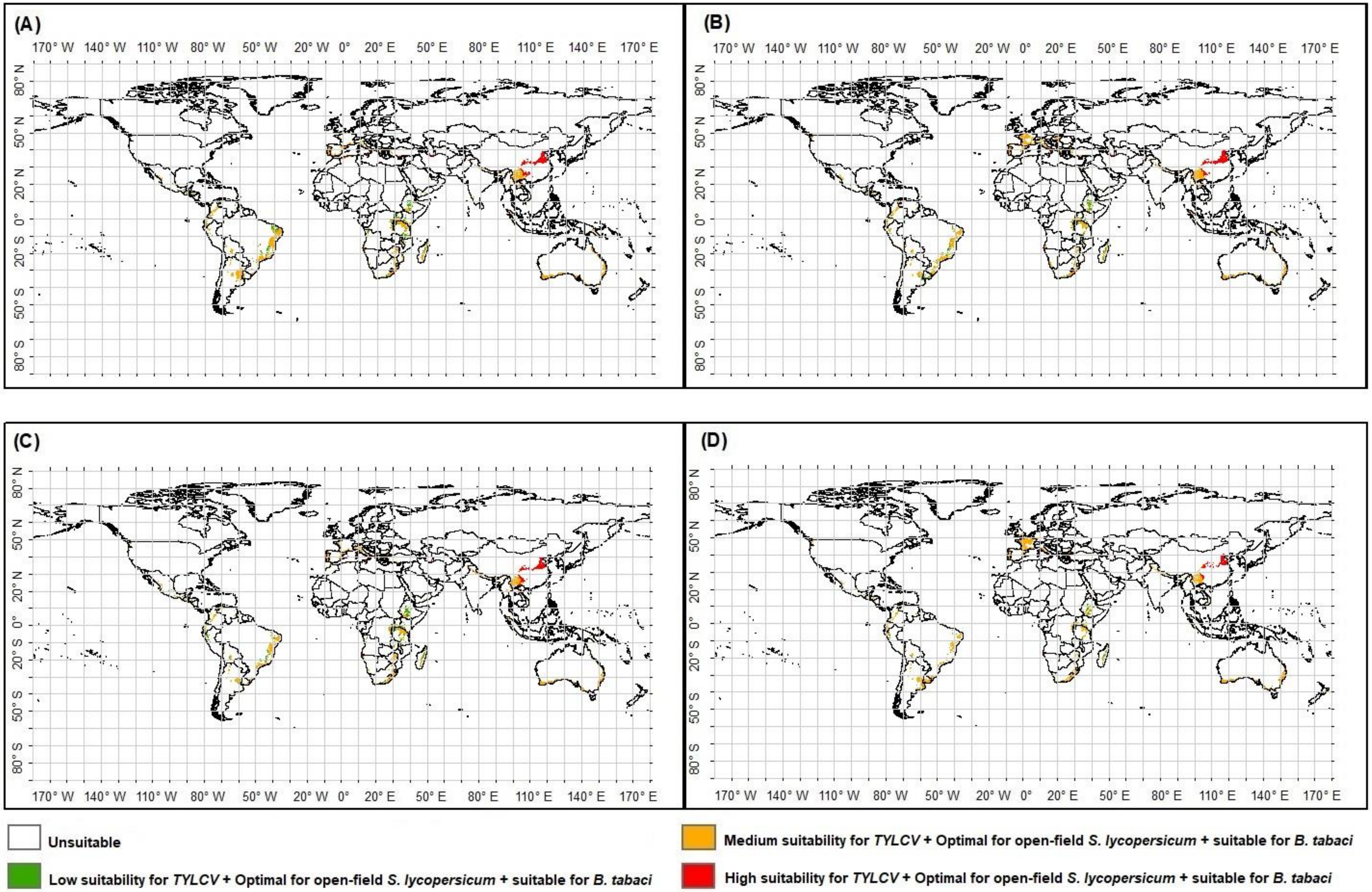

Figure 5. Agreement in the MaxEnt projection of of suitable areas for *B. tabaci* and optimal for *S. lycopersicum* with four risk levels of invasive *TYLCV* under HadGEM2_ES (GCM) running four different scenarios (A) RCP 2.6, (B) RCP 4.5, (C) RCP 6.0 and (D) RCP 8.5 for 2070 based on MTSPS threshold for the three species.

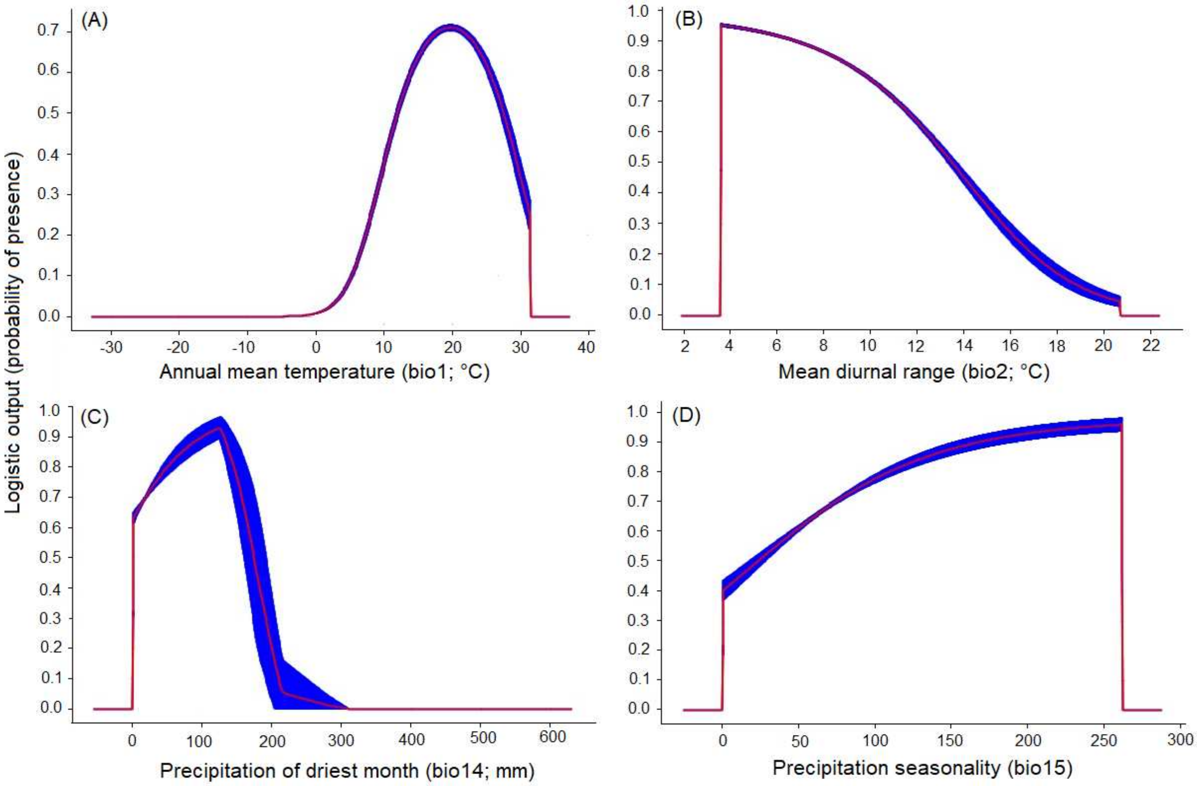

Figure S6. Response curves of the best predictors of *TYLCV* in the best model. (A) Annual mean temperature (bio1; °C), (B) Mean diurnal range (Mean of monthly (max temperature-min temperature)) bio2, (C) Precipitation of driest month (bio14; mm) and (D) Precipitation seasonality (Coefficient of variation; bio15).

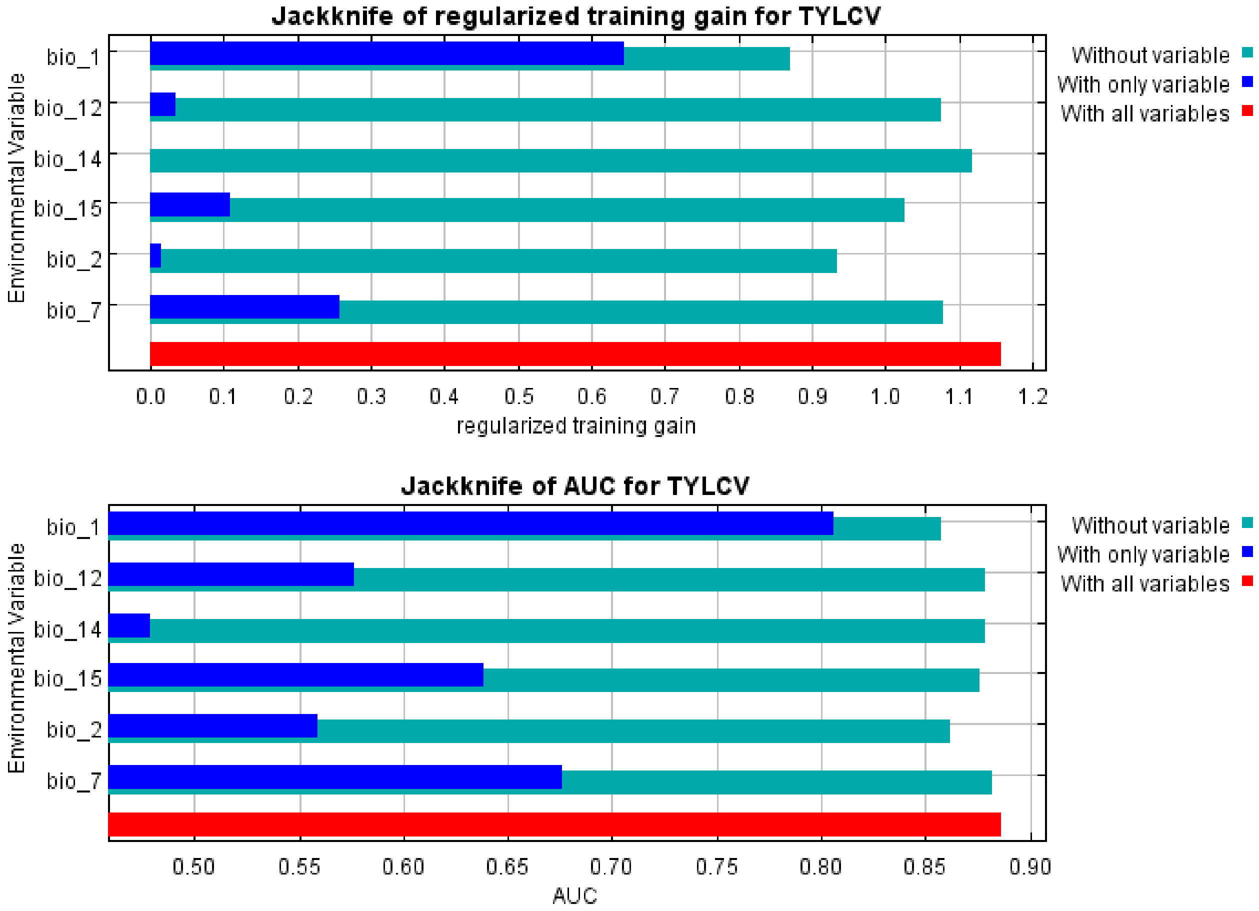

Figure S7. Relative importance of the environmental variables based on the Jackknife test. (A) Regularized training gain, and (B) AUC in *TYLCV* model.

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CHAPTER 3: Climate model for seasonal variation in *Bemisia tabaci* using CLIMEX in tomato crops

ABSTRACT

The whitefly, *Bemisia tabaci*, is considered one of the most important pests for tomato *Solanum lycopersicum*. The population density of this pest varies throughout the year in response to seasonal variation. Studies of seasonality are important to understand the ecological dynamics and insect population in crops and help to identify which seasons have the best climatic conditions for the growth and development of this insect species. In this research, we used CLIMEX to estimate the seasonal abundance of a species in relation to climate over time and species geographical distribution. Therefore, this research is designed to infer the mechanisms affecting population processes, rather than simply provide an empirical description of field observations based on matching patterns of meteorological data. In this research, we identified monthly suitability for *Bemisia tabaci,* with the climate models, for 12 commercial tomato crop locations through CLIMEX (Version 4.0). We observed that *B. tabaci* displays seasonality with increased abundance in tomato crops during March, April, May, June, October and November (first year), and March, April, May, September and October (second year) in all monitored areas. During this period, our model demonstrated strong agreement between *B. tabaci* density and CLIMEX weekly growth index (GIw), which indicates significant reliability of our model results. Our results may be useful to design sampling and control strategies, in periods and locations when there is high suitability for *B. tabaci*.

Keywords: Seasonality, Whiteflies, Modelling, CLIMEX

1. INTRODUCTION

The whitefly *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae) is an extremely polyphagous species, considered a key pest for many crops worldwide, including vegetables, ornamentals and field crops [1,2,3]. The damage caused by this pest may occur directly through phloem feeding or indirectly through the excretion of honeydew and consequent development of sooty molds on the leaves, leading to a reduction of photosynthesis, which may consequently lead to plant mortality, and production losses of up to 100% [4-7]. In Latin America, the tomato (*Solanum lycopersicum* L.) is one of the main crops attacked by *B. tabaci* [8,9]. Additionally, this insect pest transmits several plant viruses. In terms of area coverage, tomatoes suffer one of the greatest crop losses valued at US$ 3806/ha caused by insect pests [10].

Every year, many of papers are published investigating *B. tabaci* from different perspectives, such as chemical control [11], molecular design [12], plant-insect interaction[13], disease-insect interaction [14], virus transmission [15], transcriptome [16], symbiosis [17], resistance to insecticides [18], taxonomy [19] and others. However ecological studies using *B. tabaci* are frequently neglected due to requiring detailed field studies over a long period.

B. tabaci is highly sensitive to climate fluctuations due to its ectothermic physiology [20] and exhibits these fluctuations as a response to climate variations[21]. Seasonality is a key component to understand the ecology of insect populations in field crops, especially pests [22,23,24]. Ecological studies using insect pest monitoring over time in field crops and climate dynamics for insect species occurrence provide a useful method to better understand the spatio-temporal climate dynamics that determine seasonality patterns of insects in field crops.

One of the tools to determine spatio-temporal climate dynamics for species is using CLIMEX software. It has been considered an inferential modelling software, which enables the user to estimate the potential geographical distribution with great reliability [25]. This program simulates the mechanisms that limit species distribution based on ecophysiological parameters. Additionally, it is possible to describe the spatio-temporal dynamics in climate suitability [25]. Modelling using CLIMEX provides map sequences displaying the suitability changes in both space and time. Thus, it is now possible to increase our understanding of climatic influence on spatio-temporal species dynamics (e.g. *B. tabaci*) and produce robust models that can correlate with field monitoring data [26,27]. All this information is relevant to plan management strategies and ecological field studies during periods when suitability and/or insect pest density is higher.

A better understanding of the temporal dynamics of favourable conditions for *B. tabaci* considering climate dynamics is needed. Therefore, our aim in this study was to determine *B. tabaci* seasonal variability in a commercial tomato crop over two years and the influence of climate dynamics. To determine the monthly climatic variations suitable for *B. tabaci*, we used 12 different locations with tomato cultivation from two years (2015 and 2016) of monitoring, as well as the influence of monthly climate on the species, using CLIMEX modelling – CLIMEX (Version 4.0).

2. MATERIALS AND METHODS

2.1. *Bemisia tabaci* distribution

In our research, we collected ninety-four records of *Bemisia tabaci* from the published literature [28,29], GBIF (Global Biodiversity Information Facility) GBIF.org (2nd May 2017) (http://doi.org/10.15468/dl.mwb31) and confirmed these using the software PQR - EPPO Plant Quarantine Data Retrieval system (version 5.3.5, 2015).

All records (94 occurrences) used in this study from central and South America are shown in figure 1.

2.2. Field data collection

In this study, *B. tabaci* densities were assessed in tomato crops from 12 commercial farms located in Coimbra, Minas Gerais State, Brazil (20º 51' 24"S, 42º 48' 10" W; altitude 720 m). The tomato crops were established in areas ranging from 2.5 – 6 ha, with a spacing of 1.0 m between rows and 0.5 m between plants using local procedures [30,31].

B. tabaci population density was monitored weekly from the beginning of the transplanting of the seedlings until the last harvest for each evaluated tomato crop (12 crops total) over a two year period. Crop 1: from January (2015) to April (2015), Crop 2: from February (2015) to May (2015), Crop 3: from March (2015) to June (2015), Crop 4: from July (2015) to October (2015), Crop 5: from November (2015) to December (2015), Crop 6: from October (2015) to January (2016), Crop 7: December (2015) to February (2016), Crop 8: from February (2016) to March (2016), Crop 9: March (2016) to June (2016), Crop 10: July (2016) to October (2016), Crop 11: from August (2016) to November (2016) and Crop 12: October (2016) to December (2016). In each field, we evaluated *B. tabaci* density in 300 sampling units per location, per week. The sampling was performed in all locations, randomly monitored on a grid pattern to avoid bias in the choice of sampling location[32,33]. The sampling method applied for *B. tabaci* involved the direct counting of adults using plastic trays where a leaf from the apex of a plant was struck on a white background tray, and direct counting of nymphs on a leaf from the basal third of the tomato plant [34-37]. We counted the number of nymphs present in the basal part of the tomato canopy, and the number of adults present on the white plastic tray. Mean temperature, rainfall, and photoperiod were obtained daily from a local weather station.

2.3. Climex Model

To study the spatio-temporal dynamics of climate suitability we chose to use CLIMEX because this software provides a resource to compare Locations/Years and create maps of average conditions. This tool creates map sequences that allow us to visualize how suitability changes across both space and time [25]. The simulation of how climatic factors may simultaneously influence species range in space and time is considered a significant and powerful tool not available in other software [25].

CLIMEX software simulates the mechanisms that limit species' geographical distributions and determines their seasonal phenology, which may affect species abundance such as insects [25]. This software enables us to describe how species respond to climatic variables at different, specific times (e.g. daily or weekly) [25]. To set the biological parameters in CLIMEX we used biological information from the species and from the locations where their occurrence is reported. Additionally, this software helps to predict and map potential distributions [25]. The Growth and Stress Indices are combined into an Ecoclimatic Index (EI), which is considered an average yearly index; this index gives an overall measure of climatic suitability of a location for a target species. The EI values are scaled from 0 to 100.

EI values close to 0 means that the location is inadequate for the establishment of the species while an EI value higher than 30 indicates that there is suitability in terms of climatic conditions for the growth and development of a species [25]. We used CLIMEX version 4.0, which is software that can draw maps describing the spatial distribution of species over a given period of time using the weekly growth index (GIw) and describe suitable conditions for population growth on a scale from 0 to 1 [25]. GIw is maximized (GIw > 0) in appropriate seasons, when the weekly suitability of climate for species growth and development is present, and minimized during unfavorable seasons. To determine the GIw value, we used the temperature (TI) and moisture (MI) indices to include *B. tabaci* growth requirements. We used the stress indices in relation to the moisture index and temperature for species survival. These indices need to be considered because all of these abiotic indices contribute to a good species distribution result in relation to the adverse climatic conditions that occur at different times throughout the year [25].

2.4. Model Calibration and Validation

CLIMEX model for *B. tabaci* was adjusted using 60 occurrence records and biological data of the species, such as thermal requirements, moisture index, stress indices (cold, heat dry and wet stress). For model validation, data from Brazil was omitted, adjusting parameters only. For parameter adjustments, we used *B. tabaci* biological data from the literature and unpublished information from the Integrated Pest Management Lab at Universidade Federal de Viçosa, Minas Gerais, Brazil; where numerous studies with *B. tabaci* have been conducted in the laboratory and in the field. In our model, we used CliMond 10′ gridded climate data.

To represent historical climate (data from 1961 to 1990, 30 years, centered on 1975), we used the average maximum monthly temperature (Tmax), average minimum monthly temperature (Tmin), average monthly precipitation (Ptotal) and relative humidity at 09:00 h (RH09:00) and 15:00 h (RH15:00). All values were fitted to match to the location records for the pest with exactness of prediction by the CLIMEX generated model in different regions (Figure 1). Agreement between species distribution and the model for the seasonal phenology provided cross validation for our model [25].

2.5. Temperature index

Albergaria and Cividanes [38] have previously reported the thermal requirements for *B. tabaci*. They presented a lower temperature threshold of 8.3°C for life cycle (egg- adult) and an upper temperature threshold of 37 °C. Above this temperature, *B. tabaci* eggs became infertile. We established a lower temperature limit (DV0) of 8.3°C and an upper temperature limit (DV3) of 37 °C. We considered the range from 15 °C to 35 °C as most appropriate for *B. tabaci* survival, growth and development [38]. Regarding the lower (DV1) and upper (DV2) optimal temperatures, we established values of 15 °C and 35 °C, respectively. In this same research, Albergaria and Cividanes [38] indicated significant adult emergence after 413.2 degree-day. Thus, PDD was set to 472.6 °C days.

2.6. Moisture index

We used *B. tabaci* records for distribution in wet tropical regions with highest GI values. High *B. tabaci* incidence in tomato cultivation located in Coimbra, Minas Gerais State, Brazil, regularly occurs in seasons with mean rainfall of 90mm [39]. For the moisture index, we used 0.1 (denoting permanent wilting point) as a lower soil moisture threshold (SM0), 0.4 for lower optimum soil moisture (SM1), 0.7 for upper optimum soil moisture (SM2), and 1.5 for upper soil moisture threshold (SM3). These selections were used based on literature and to obtain better model results. All adjustments were made in terms of the *B. tabaci* location records and considering *B.tabaci* density within the monitored areas. In addition, these values provided the best fit for host distribution (for tomato crops).

2.7. Stress indices

Cold Stress

The cold stress temperature threshold defines a temperature below which cold stress begins to occur. As a poikilothermal species, *B. tabaci* may die when daily thermal accumulation is too low to maintain metabolism [25]. In another words, this occurs when a threshold number of degree-days above the developmental temperature threshold are not reached.

In this context, this parameter is considered an important parameter for *B. tabaci* because it affects species survival. Therefore, we determined a threshold number of degree-days in the model, which is defined by the developmental temperature threshold (DVCS). This parameter is expressed in cold stress degree-day threshold (DTCS), and is defined by degree-day units. In the present study, the DTCS used was 10 °C days and for the cold stress degree day, expressed in units per week (DHCS), it was 0 week^{-1}. We selected all these values based on the published literature which presented some similarities for *B. tabaci* distribution in Central and South America [39-42]. All values used to adjust the model are presented in table 1, and are matched for the locations where *B. tabaci* occurs.

Heat Stress

High temperatures may be excessive and have a negative impact on insect growth and development [33,43,44]. *B. tabaci* do not survive temperatures higher than 37 °C [38]. The heat stress parameter (TTHS) was set at 35 °C and its accumulation rate (THHS) was 0.0007week^{-1}. High temperatures may cause physiological disorders in insects and is in accordance to the nonoccurrence of the species in some regions in northern Brazil.

Dry Stress

The most significant, known *B. tabaci* distributions are recorded in tropical and subtropical regions with some humid areas [45,46,47]. Another important parameter that may cause stress for a species is when the soil moisture level is too low or too high [25]. For our model, the soil moisture threshold (SMDS) was set at 0.1 and stress accumulation rate (HDS) at −0.001 week^{-1}.

Wet Stress

Wet stress can affect insects in several ways, especially increasing mortality due to high precipitation [24,32,48]. The soil moisture threshold for wet stress (SMWS) was set at 2.0, and stress accumulation rate (HWS) was set at 0.002 week^{-1}. The parameter values presented an adequate match with known pest distributions, for example, the Brazilian Atlantic forest area [33,49].These values are presented in table 1.

2.8. Meteorological data

The monthly time–series was used to compare locations by loading the model with "CL – Grid Data" simulation file within a year in CLIMEX [25]. Climatic Research Unit (CRU) - CRU TS3.23, Norwich (http://www.cru.uea.ac.uk/cru/data/hrg.htm), Time-Series (TS) Version 3.23 with monthly climate variations was used. This version has the data for all parameters reformatted which is required when using this software. Variables such as monthly average daily maximum and minimum temperature, precipitation and vapor pressure [50] were included. Then, CLIMEX model (from January 2015 to December 2016) and maps for the same period during which *B. tabaci* was monitored, were generated.

2.9. Model validation

The *B. tabaci* nymph and adult densities observed over two years of collection in tomato plantations were compared with the monthly suitability maps generated for the same period. The model results were found to be consistent with real *B. tabaci* distribution and therefore demonstrated significant reliability. We used all occurrences registered in Central and South America (94 occurrences) to test the model. The percentage of the occurrence data which falls within the model projection was calculated and used to evaluate our model's reliability.

3. RESULTS

The model presented in this study showed a consistent match between the current distribution of *Bemisia tabaci* in central and south America and the EI from the CLIMEX (Figure 1). To validate our model, we checked the reports of occurrence for this species in all areas (Central and South America), and 99% of *Bemisia tabaci* occurrences were within favorable climate categories. This characteristic is important and we may confirm the reliability and confidence in the values selected for the parameters we used to generate our current model applying CliMond 10′ gridded climate data for modeling in CLIMEX.

The highest *B. tabaci* densities were found in crops 2, 3, 6 and 10. Of these, crops 3, 6 and 10 showed the highest density of adults and crop 2 the highest nymph density. The lowest density was observed in crops 1, 4, 8, 9, 11 and 12. Only crops 5 and 7 showed intermediate density in relation to the other crops evaluated in this study (Figure 2).

The highest nymph densities were observed between October and December in crop 6 in the first year, and between September and October in crop 10 in the second year. The peaks for *B. tabaci* adults occurred in June, and between November and December for the first year (for crops 3 and 6), and in October for the second year (for crop 10) (Figure 2).

B. tabaci occurrence in crops 1, 4, 8, 9, 11 and 12 (during January-March, and July until beginning of September), was low for *B. tabaci* nymphs and adults in both years evaluated. We noticed highest attack intensity for *B. tabaci* during October to December and lowest intensity during January to April and June to September in open field conditions. We observed spatio-temporal variation for climate suitability for *Bemisia tabaci* over the two years (Figure 3). October and November were the months with the highest climate suitability in Central and South America (e.g. countries such as, Brazil, Bolivia, Ecuador, Peru, Colombia and Andes Region) (Figures 4 and 5).

For the greater part of the year, we observed high suitability in coastal and southern Brazil, and also in countries such as Costa Rica, Guatemala, Honduras, Colombia, southern Chile and Venezuela. Climate suitability increased in June, October - December throughout the five Brazilian regions (North, Mid-west, Southeast, Northeast and South), and large regions of Bolivia, Peru and Argentina. June, July and August present a change to climatically unfavorable conditions for *B. tabaci* in the Mid-west and some regions of southeastern Brazil also. Additionally, a decrease was observed in January- April in the north, mid-west and in some parts of southeastern Brazil, as well as in other countries such as Peru and Ecuador (Figures 4 and 5).

When we performed a zoom into an area, we noticed climatic variability for *B. tabaci* that includes the monitored fields (where the evaluated crops were planted) (Figure 6). Increased climatic suitability for *B. tabaci* was observed between the months of April – May and October- November in the first year, and March-April and September- October in the second year. The highest growth index was observed during the months May/April and October/November for the first year; and in the second year, during April and October. On the other hand, a reduction was observed between June and September, and between November and January. There was almost zero climate suitability for *B. tabaci* in January and August in both years. By February, climate suitability returns with progressive increases until May/June and September until November (Figure 6).

4. DISCUSSION

We noticed that significant intensity of *B. tabaci* attacks occurred during October to December and lowest intensity occurred during January to April and June to September in open field tomato crops. The main reason for this may be related to the environmental conditions of this season. October to December proved to be significant for growth and development of the species in open field conditions because the precipitation rate is not too high and temperature during this period is within the highest range for the growth and development of this species. However, this pest species presents great adaptability to different climatic conditions [51]. Additionally, it is common to find a high number and diversity of host plants in the field during this season, which contributes to the successes of any invasive species.

The environment directly and indirectly affects the seasonality of *B. tabaci* in the field [39,52,53]. Variability of insect density may be directly influenced by seasonality due to the impact of climate factors (i.e. rain, wind and temperature) and indirectly due to food availability. For *B. tabaci,* food availability does not appear to be a main factor when defining *B. tabaci* seasonality in the field because it is a polyphagous species that can be hosted by numerous plant species.

When we see our model results, it is clear that climate suitability for *B. tabaci* presented variability in several areas throughout the months of the year (Figures 4 and 5). The direct influence of climatic factors on seasonality for *B. tabaci* seems to be greater than the indirect influence of host plant availability, since host plants (such as tomato crops) were available in the field for *B. tabaci* throughout the whole evaluation period. This can be observed in figures 2 and 5, where *B. tabaci* density varied over time, coinciding with the highest and lowest growth index, respectively.

B. tabaci density was highest between September to December, while its lowest densities were observed during January - February and June – August. When we observe the data for *B. tabaci* density in the field and the CLIMEX model GIw for these periods, we notice significant agreement between them, which reinforces confidence in the model's results. Further, the rapid decrease and increase observed during the evaluation period in the field matched the period of time (increase and decrease of *B. tabaci* densities with the growth index of CLIMEX model) which reinforces the validity, highlighting the robustness of the model presented.

In the second year of evaluation, *B. tabaci* densities in tomato crops were low from February to May but our model showed a progressive increase in the growth index for the area monitored. One of the possible reasons that might explain this fact is related to the effectiveness of the pest control method applied by the farmers in these crops, which contributes to the low *B. tabaci* density. Additionally, this was a period where rainfall was very low, which affected the planting of many vegetable crops (including tomato cultivation) in the region. Most of the host crops require a significant volume of water for growth and development, in cases of adverse conditions this implies a low number and diversity of hosts (low food availability). Consequently, the population of this pest in the field over the colonization period was very low. This is just one example of how climate conditions are important and may indirectly affect species fluctuations. In the present case, this may have affected the environment and consequently *B. tabaci* density. In addition, the climate may affect natural enemy populations, leading to low density which implies a low rate of natural biological control. Therefore, it is important to intensify the monitoring at this time of the year since the climate conditions show themselves to be favorable.

The combination of a high number of host plants (tomato plantations), favorable climate, *B. tabaci* presence and inadequate control methods in the field led to increased *B. tabaci* numbers in the monitored area over 5-6 months of the year.

In March, from the first year, we observed initial colonization by nymphs in the monitored areas (Figure 2). Even though this period was favorable for *B. tabaci*, no increase in the number of adults was observed. This might be explained by the efficient control applied during that stage, which contributed to decreased nymph numbers thereby reducing the number of individuals that reached adult stage.

In October (in the first year) and September (in the second year), colonization by *B. tabaci* started in the monitored areas and a population increase (nymphs and adults) on crops was observed over time. This occurred because no efficient control method was applied and all conditions (favorable climate, food availability and pest presence) were significant during this period.

This seasonal variation matches our spatio-temporal climate dynamics model. These results provide a significant contribution for management and further study of *B. tabaci* in field crops, since the model results determine seasons with favorable climate conditions for occurrence and the best moment to encounter *B. tabaci*. Our results indicate periods when risk of *B. tabaci* is highest and may help farmers to focus on specific times of the year for *B. tabaci* control. Additionally, further research could be conducted to determine other important factors (e.g natural enemies) that influence the seasonal variations of *B. tabaci* and its interactions with spatio-temporal climate dynamics in terms of ecological studies.

5. CONCLUSION

Our study shows that seasonal variation may affect *B. tabaci* in favourable locations. The methods utilized in this study have relevance and application for other agricultural crops and for the management of this species. We have provided information of favourable periods for *B. tabaci*, such as October and November, in both Central and South America, with great incidence of *B. tabaci* in tomato crop, which matches with our data from the field 100% of the time. The results of the climate change for *B. tabaci* is useful for planning strategies to minimize the economic impacts in favourable seasons with greater abundance of *B. tabaci*. Future research could consider the impact of non-climatic factors, such as natural enemies (natural biological control), density and quality of plants (number of host plants) or other factor that may influence the seasonal variations of *B. tabaci*. Seasonal variations have influence the density of *B. tabaci* in commercial tomato crops, with the highest incidence of nymphs and adults during the October to December and lowest incidence of *B. tabaci* in the January-March, and July until beginning of September. Our results may be useful in designing sampling strategies and control, in times when there are high degree of suitability for this pest.

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Table 1. CLIMEX parameter values used for *Bemisia tabaci* modelling.

Index	Parameter	Values	Unit	References
Temperature	DV0 = lower threshold	8.3	°C	Albergaria and Cividanes 2002
	DV1 = lower optimum temperature	15	°C	Albergaria and Cividanes 2002
	DV2 = upper optimum temperature	35	°C	Albergaria and Cividanes 2002
	DV3 = upper threshold	37	°C	Albergaria and Cividanes 2002
Moisture	SM0 = lower soil moisture threshold	0.1	[a]	Leite et al. 2006
	SM1 = lower optimum soil moisture	0.4	[a]	Leite et al. 2006
	SM2 = upper optimum soil moisture	0.7	[a]	Leite et al. 2006
	SM3 = upper soil moisture threshold	1.5	[a]	Leite et al. 2006
Cold stress	TTCS = temperature threshold	8.3	°C	Albergaria and Cividanes 2002
	THCS = stress accumulation rate	-0.001	week^{-1}	Tomar and Malik 2017; Gusmão et al. 2006
	DTCS = degree day threshold	10	°C days	Tomar and Malik 2017; Gusmão et al. 2006
	DHCS = stress accumulation rate	-	week^{-1}	Tomar and Malik 2017; Gusmão et al. 2006
Heat stress	TTHS = temperature threshold	35	°C	Albergaria and Cividanes 2002
	THHS = stress accumulation rate	0.0007	week^{-1}	Moraes and Foerster 2015
Dry stress	SMDS = soil moisture threshold	0. 1		Jafarbeigi 2014
	HDS = stress accumulation rate	-0.001	week^{-1}	
Wet Stress	SMWS = soil moisture threshold	2	[a]	
	HWS = stress accumulation rate	0.002	week^{-1}	
Hot-Wet Stress	TTHW = hot-wet temperature threshold	32	°C	Albergaria and Cividanes 2002
	MTHW = hot-wet moisture threshold	0.2	SMC	
	PHW = hot-wet stress rate	0.03	week^{-1}	
Degree Days	PDD= degree days per generation	472.6	°C days	Albergaria and Cividanes 2002

[a] Values without units are dimensionless indices of soil moisture (0 = over dry, 1 = field capacity).

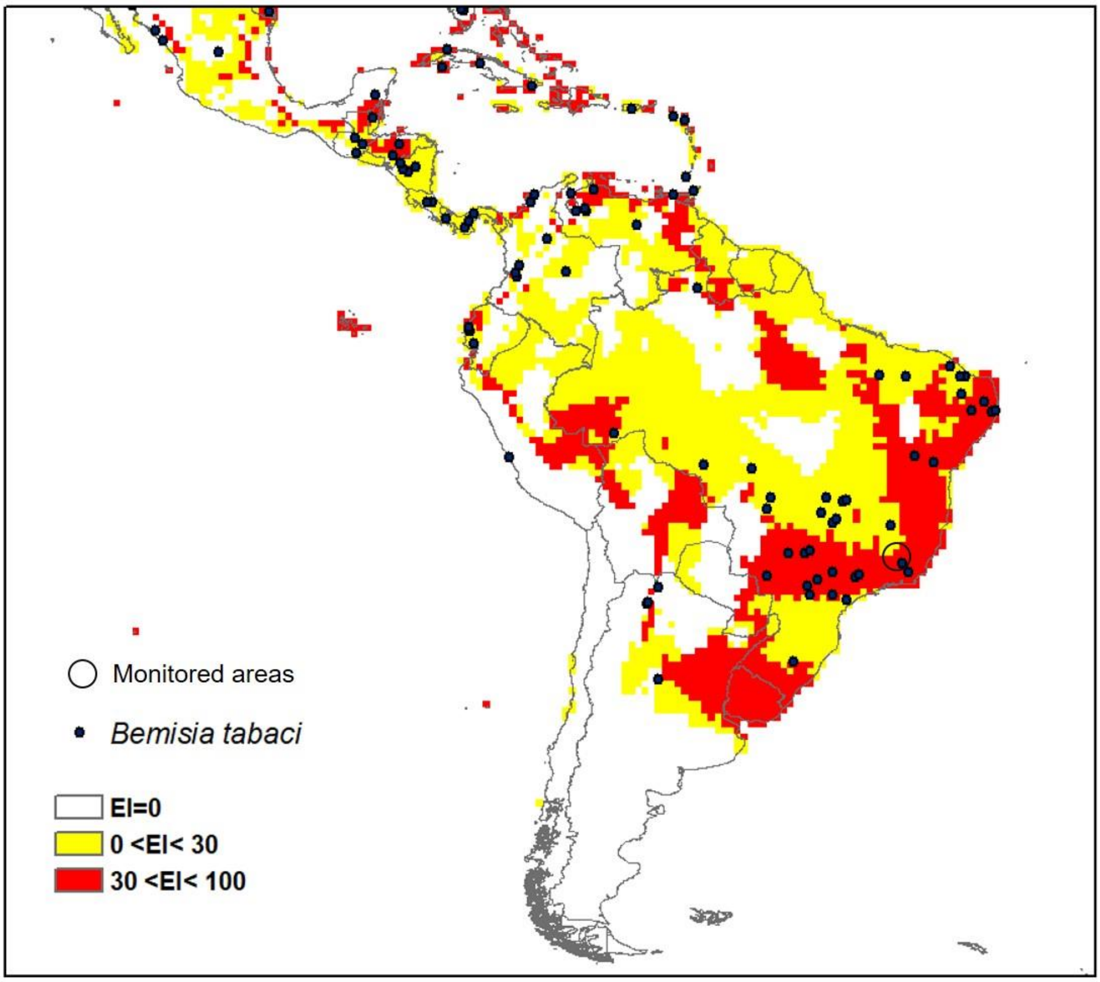


Fig 1. Records of *B. tabaci* in Central and South America and current distribution of *B. tabaci* in validation region based on EI index. The areas in white (EI = 0), yellow (0 < EI < 30) and red (30 < EI < 100) indicate unfavourable, less favourable and highly favourable climate areas for *B. tabaci*, respectively. The circle is indicating the monitored areas (12 different tomato field crops).

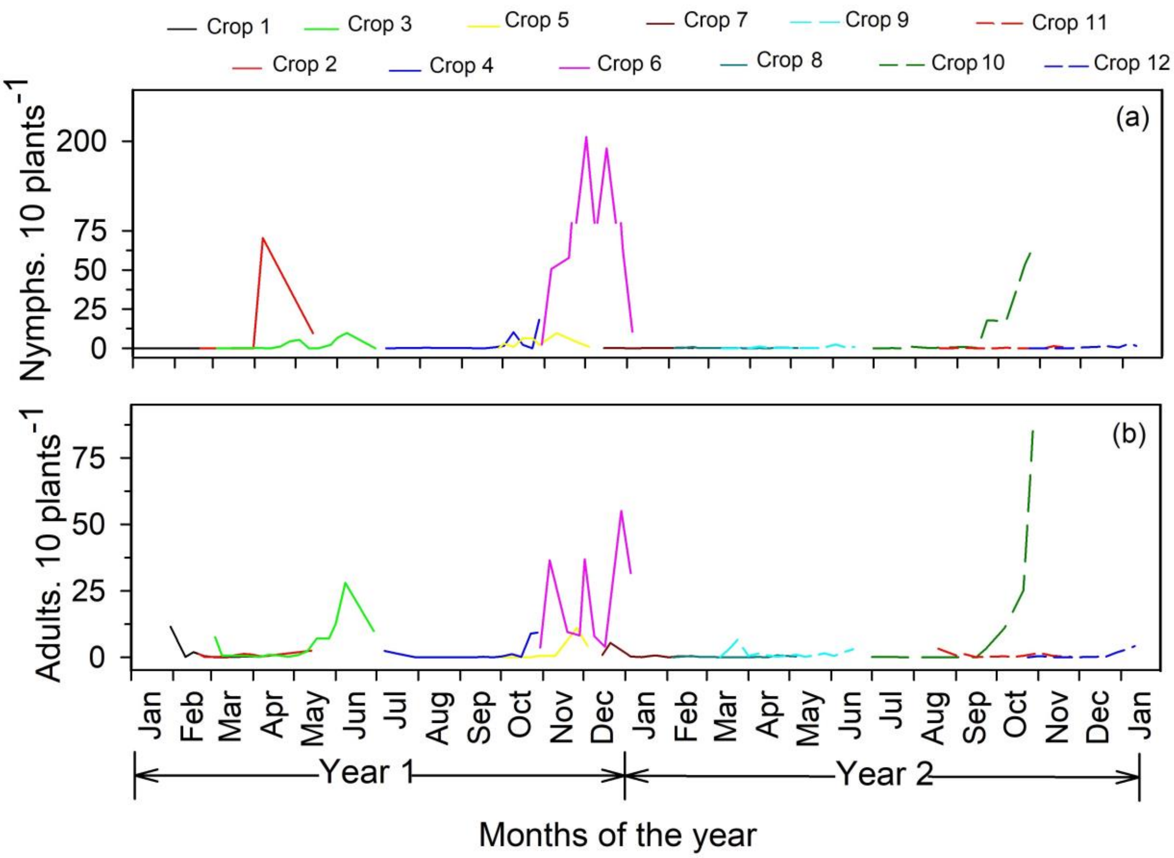


Fig 2. Density of nymphs and adults of *B. tabaci* in commercial tomato crops at Coimbra, Minas Gerais, Brazil in 2015 and 2016.

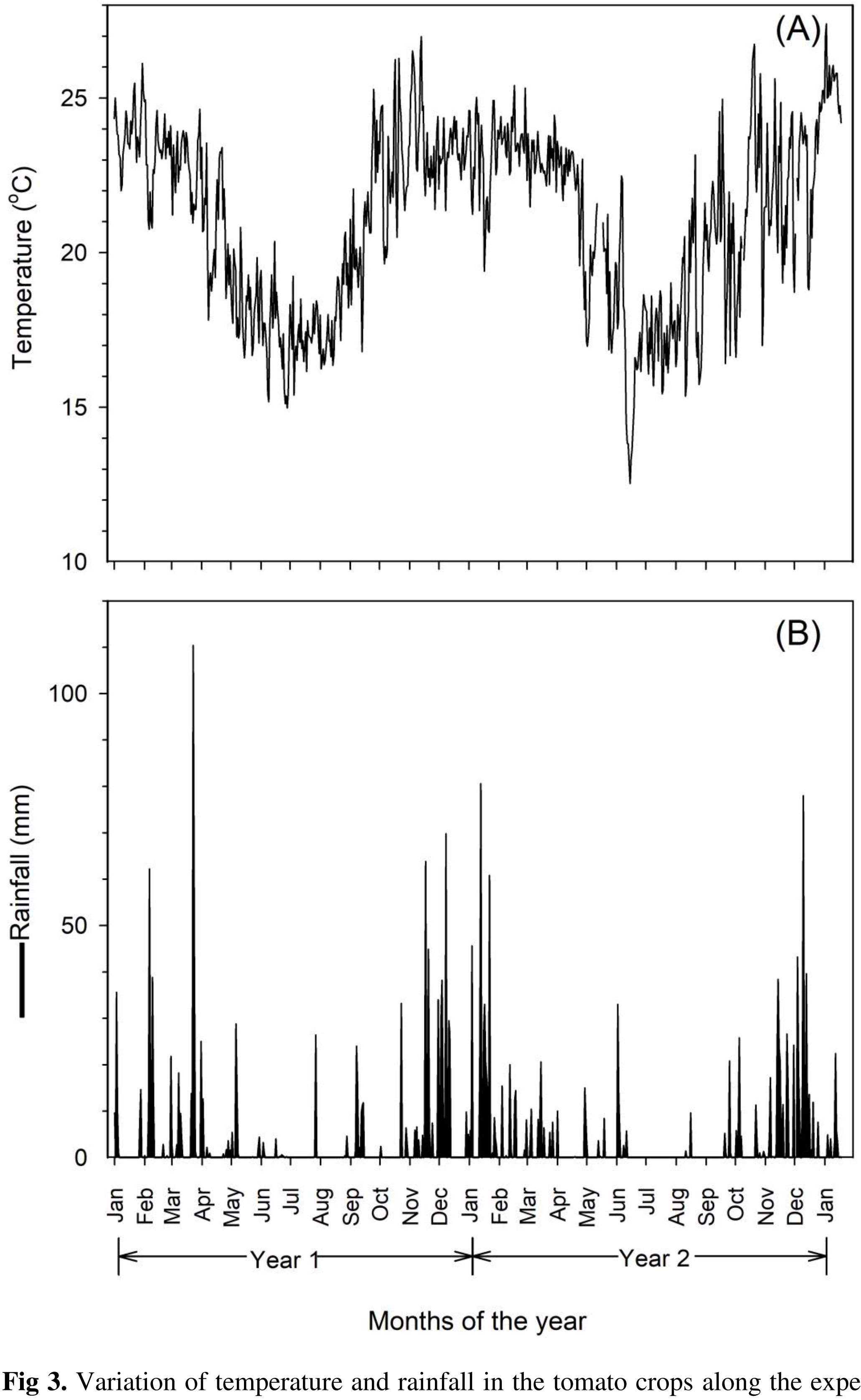
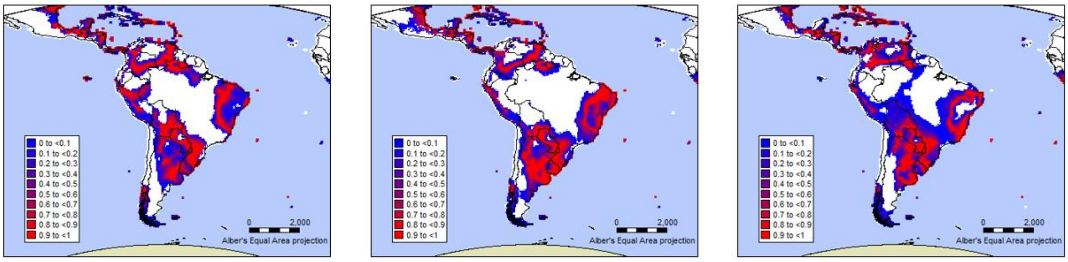
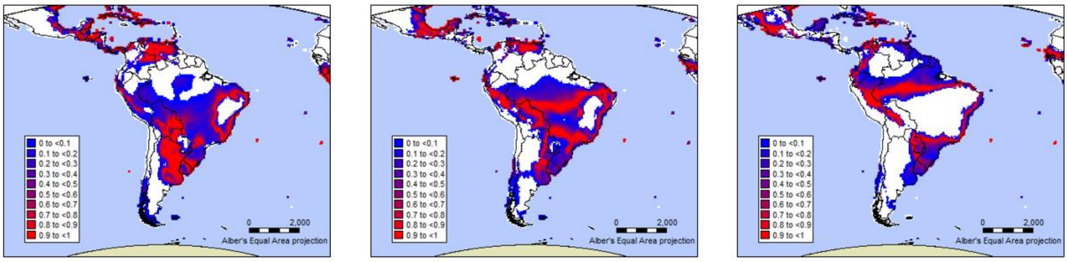


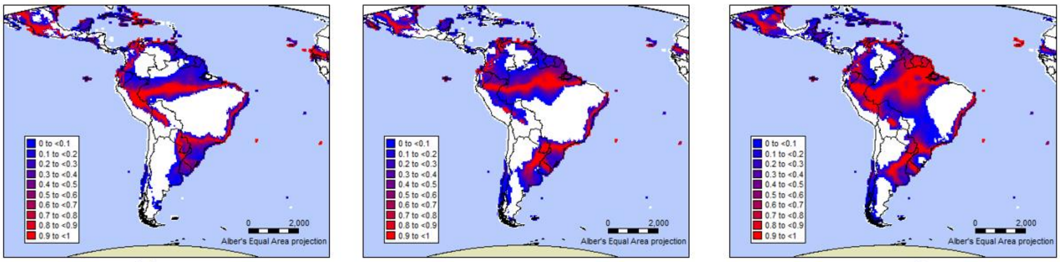
Fig 3. Variation of temperature and rainfall in the tomato crops along the experimental period.



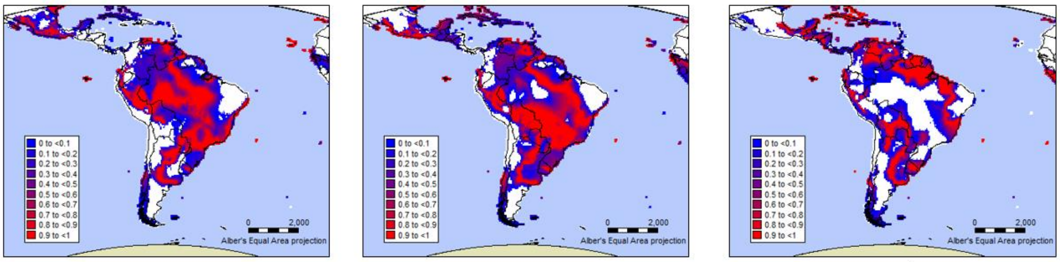
January February March



April May June

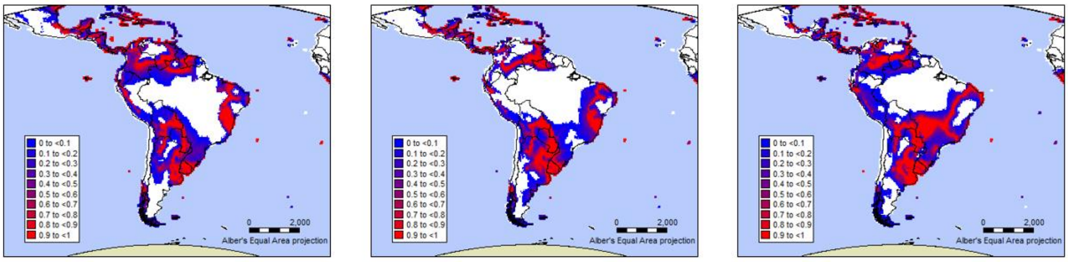


July August September



October November December

Fig 4. Climate variability by month based on growth index (0 to 1) for *B. tabaci* for the Central and South America for the year 1.



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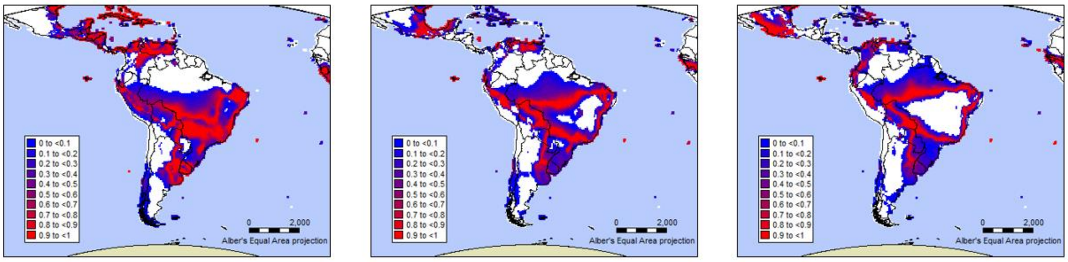
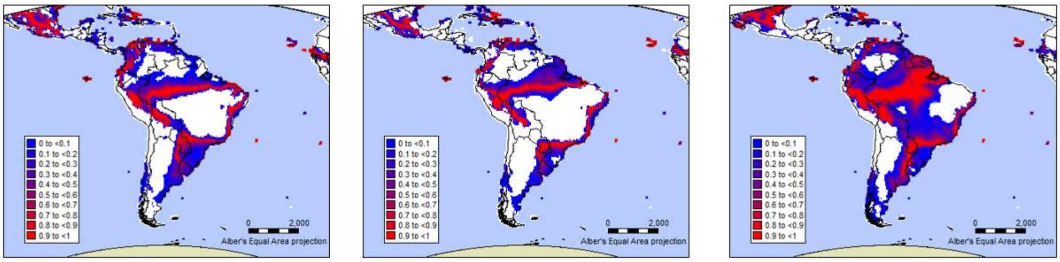
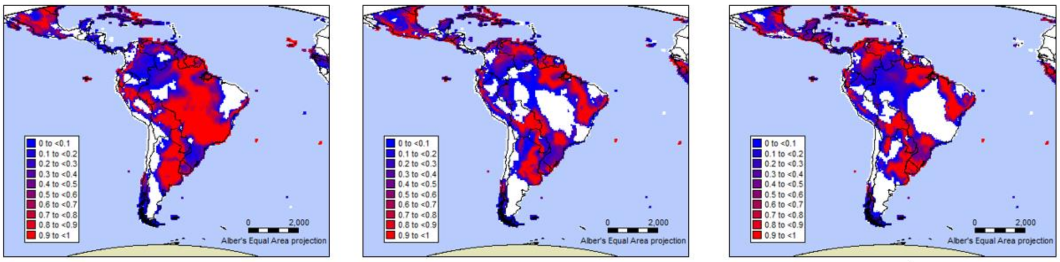


April May June



July August September



October November December

Fig 5. Climate variability by month based on growth index (0 to 1) for *B. tabaci* for the Central and South America for the year 2.

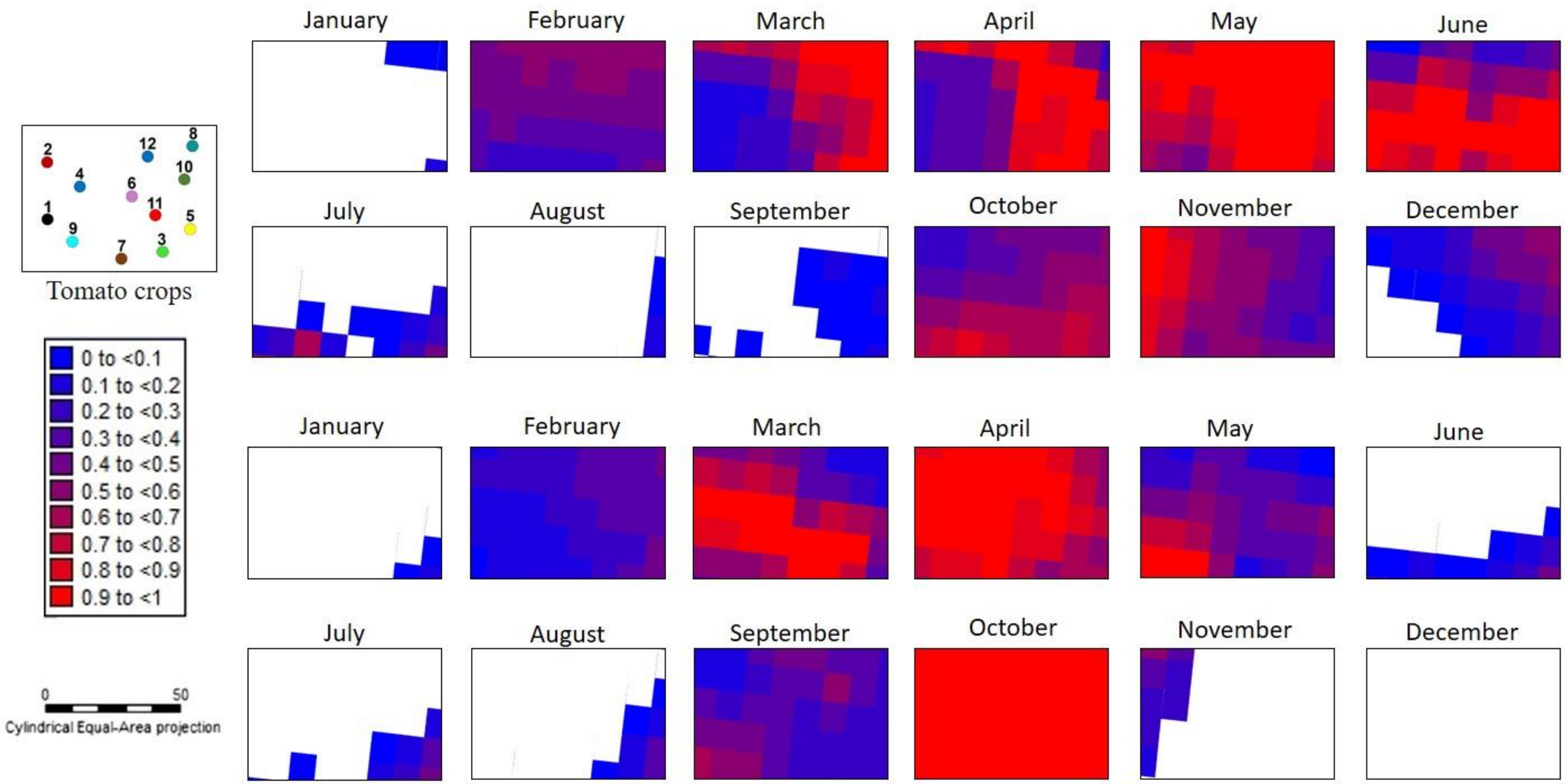


Fig 6. Climate variability by month based on growth index (0 to 1) for *B. tabaci*, displaying an area and the location of the 12 monitored tomato crops.

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CONCLUSÕES GERAIS

Este estudo mostra que as mudanças climáticas pode afetar a distribuição geográfica do inseto vetor *B. tabaci*, da virose *TYLCV* e do hospedeiro *S. lycopersicum*. Os modelos usando o MaxEnt que foram aqui selecionados, apresentam um alto grau de confiabilidade. Observamos que a mosca branca atualmente ocorre no campo em locais com temperatura média anual entre 8.0°C e 28.8°C, já a virose entre 8.5°C e 29.1°C. A temperatura média anual foi o fator que mais contribuem para a probabilidade de ocorrência da mosca branca (75,1%), do vírus (60,2%) e do hospedeiro (58,5%) em um determinado local.

As projeções futuras em áreas ótimas para cultivo de tomate em campo aberto mostram que algumas regiões do Brasil que estão atualmente em médio e alto risco para *B. tabaci* poderão ficar menos favorável nos anos de 2050 e 2070. Já em outras regiões da China, França, Itália e Espanha as projeções mostram grandes aumentos de susceptibilidade para *B. tabaci* em regiões ótimas para o cultivo do tomateiro. A principal razão é devido ao aumento da temperatura previsto no planeta, que irá afetar não somente a distribuição da mosca branca mas também do vírus e do hospedeiro.

O modelo realizado no CLIMEX mostra que a variação sazonal do clima afeta a densidade populacional de *B. tabaci* ao longo do ano em diferentes localidades. Sendo os meses de Outubro e Novembro os meses com maior incidência da praga na América do Sul. Os modelos apresentam elevada confiabilidade e coincidem nas previsões com 100% dos dados coletados de campo durante dois anos de monitoramento. Os resultados são uteis no manejo da praga, pois aponta as épocas de elevada adequabilidade para *B. tabaci* e identificar as épocas que se deve ter maior atenção no monitoramento e controle.

Os resultados desse trabalho são importantes para o manejo da mosca branca bem como a virose (Begomovirus), essas informações permitem que os órgãos responsáveis de cada país possam desenvolver estratégias para evitar a entrada e o estabelecimento da mosca branca (em países como Inglaterra, Suécia e Irlanda), e do vírus (*TYLCV*) (em países da América do sul, como por exemplo, o Brasil). Além disso, os modelos de previsões futuras indicam os locais com maiores riscos para a *B. tabaci* e *TYLCV* em condições ótimas de cultivo do tomateiro em campo aberto, o que poderá ajudar o processo de implementação dos programas de manejo de pragas principalmente em áreas sob médio e alto risco para a *B. tabaci* e *TYLCV*.