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Assessing the impact of climate change on the worldwide distribution of *Dalbulus maidis* (DeLong) using MaxEnt

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ABSTRACT

BACKGROUND: For the first time, a model was applied at the global scale in order to investigate the effects of climate change on *Dalbulus maidis*. *D. maidis* is the main vector of three plant pathogens of maize crops and has been reported as one of the most important maize pests in Latin America. We modeled the effects of climate change on this pest using three Global Climate Models under two Representative Concentration Pathways (RCPs) using the MaxEnt software. **RESULTS:** Overall, climate change will lead to a decrease in the suitable areas for *D. maidis*. In South America, climate change will decrease the areas that are suitable for the pest, especially in Brazil. However, Argentina, Chile, Colombia, Ecuador, Peru, and Venezuela will have small areas that are highly suitable for the corn leafhopper. Outside of the pest's range, Ethiopia, Kenya, Rwanda, Burundi, and South Africa also should be concerned about the risk of corn leafhopper invasions in the future since they are projected to have highly suitable conditions for this insect in some areas. **CONCLUSION:** This study will allow the relevant countries to increase their quarantine measures and guide researchers to develop new *Z. mays* varieties that are resistant or tolerant to *D. maidis*. In addition, the maize-stunting pathogens for the areas are highlighted in this modeling.

Keywords: MaxEnt; ecosystem modeling; corn leafhopper; ecological niche model; climate change; *Zea mays*.

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INTRODUCTION

Maize (*Zea mays* L.) is the most widely grown and produced cereal worldwide [1]. In 2017, the global production of maize reached more than 1.07 billion metric tons, which is an increase in production of 210% compared with 1975 [1]. The high production of maize is related to the economic importance of this crop in many sectors of industry, such as food components, rubber, plastics, fuel, clothing and many others [2,3]. Due to its versatile uses, the worldwide maize industry is worth 170.3 billion dollars annually [1].

Many factors contributed to the increase in maize productivity, such as its efficient use in fertilizers, improvements in agronomic practices, and advances in plant breeding. The adoption of genetically engineered maize was itself responsible for a significant 25% increase in the grain yield [4]. Since the first genetically engineered plant was commercially introduced in 1996 [4,5], maize has become the crop with more genetically modified registered varieties, and it represents almost US$ 8 billion dollars' worth of business [4].

Insect-resistant maize varieties, which are capable of synthesizing the *cry* toxin, is one of the many genetically engineered varieties, and it has yielded several benefits, especially decreasing the use of pesticides to control insect pests [6,7]. The *Bt* (*Bacillus thuringiensis*) varieties are widely used to control pests of the Lepidoptera and Coleoptera orders [8]; however, the adoption of this technology has led to the increase in damages associated with other nontarget species [9], including the corn leafhopper *Dalbulus maidis* (DeLong) (Hemiptera: Cicadellidae) [9,10], especially due to the decreasing number of insecticide applications that are needed in these crops. In 2010, a study found that the *D. maidis*

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population was higher in the *Bt* crop than in the conventional maize in South America, but the reasons for this have still not been completely determined [10].

Dalbulus maidis is the main vector of three plant pathogens of maize crops, including the corn stunt spiroplasma (*Spiroplasma kunkelii*), the maize bushy stunt phytoplasma (MBS) and the maize rayado fino virus (MRFV). The transmission of these pathogens occurs in a persistent and propagative manner, which can result in high infestation rates [11]. In Central America, Peru, Brazil, and Argentina, infestations by these pathogens can affect 100% of the plants in some areas [12], which translates into yield losses of up to 90% [13,14]. Therefore, the direct (i.e., sap sucking) and indirect (i.e., pathogens transmission) damages caused by this pest have been an ever-increasing concern.

Due to its increasing importance, many types of research have focused on *D. maidis*, but none of these studies have assessed the effects of climate change using modeling tools for different climate change scenarios and considering the host plant. It is expected that anthropogenic greenhouse gases emissions will result in alterations in the earth surface temperature and precipitation in the future [15]. These alterations can lead to improvement or deterioration of the climatic suitability for corn leafhoppers in some areas, which can result in changes in the corn leafhopper's habitats. In this context, alteration in pests' suitable habitats can jeopardize food security due to the negative impacts on agriculture. Therefore, studies on the effects of climate change are essential in order to establish a reliable decision-making process, to design quarantine measures and to guide plant breeding research that can select the genetic materials that are best suited for certain areas.

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The effects of climate change have been assessed mainly through ecological niche models [16-18]. The effects of climate change can be grouped as correlative models or mechanistic models [18-20]. Correlative models correlate environmental variables and occurrence data in order to make projections of the potentially suitable areas for species [18]. Examples of correlative models are the Generalized Linear Model, the MaxEnt, the Random Forest, the Boosted Regression Tree, and the Bioclim [18]. On the other hand, mechanistic models (e.g., CLIMEX) use the combination of environmental variables with information about the species' environment tolerances in order to make their projections [18].

Among these models, one tool that is frequently used to assess the potential distribution of species is the correlative maximum entropy-based model or MaxEnt [18-20]. The MaxEnt model correlates the species' occurrence and the background data points from spatial environmental variables in order to make projections for the suitable areas for the species [21]. In addition, it has also been widely recognized to perform robust projections for species with restricted distributions and small sample sizes, which is advantageous compared to other algorithms such as the CLIMEX [20-22].

Within this framework, this study aims to investigate the suitable areas for *D. maidis* at the global scale and predicts the effects of climate change in 2050 and 2070 under two distinct climate change scenarios. For this, we built two spatial distribution models (pest and host plant). It is envisaged that this study will provide a comprehensive understanding of the effects of climate change on the corn leafhopper and identify those areas that are at the greatest risk from *D. maidis* due to highly favorable conditions for both the pest and its host plant.

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MATERIALS AND METHODS

Species Occurrence Data

In order to identify the highly suitable areas and the effects of climate change on the distribution of *D. maidis*, we developed two spatial distribution models (pest and host plant). For this purpose, the open-field occurrence records of *D. maidis* were cataloged and confirmed from sources including field surveys and the published literature (Table S1). The occurrences of *Z. mays* L. were gathered from the Global Biodiversity Information Facility (GBIF.org (05 February 2018) GBIF Occurrence Download https://doi.org/10.15468/dl.lr9vsp) and literature resources [23,24]. The presence of *D. maidis* was confirmed at a total of 344 sites, and the pests were only on the American continent (Fig. 1a). Therefore, there are no occurrences of *D. maidis* outside this continent (Fig. 1a). For *Z. mays*, 754 records were confirmed to be distributed worldwide (Fig. 1c).

First, the records of both the *D. maidis* and *Z. mays* species were cleaned by removing duplicate records, evaluating the coordinate records when possible, and removing spurious locations outside the species' known geographic ranges. Then, the *D. maidis* and *Z. mays* records were reduced to 334 and 614, respectively, after applying the spatial filtering tool using the spThin package that is available in the R software (version 3.2.2) [25,26]. This procedure was performed to achieve the spatial independence of the data, and the occurrence data were kept at least 10 km apart from each other [27,28]. This method performs a better spatial autocorrelation reduction than other available methods and allows us to keep as many

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of the records as possible [27]. Therefore, when building the models, the species' filtered data that were related to the open-field were used.

Environmental Data

Nineteen variables were considered in this study. Eleven variables were derived from the monthly temperature and eight from the monthly precipitation (Table 1). The variable layers were obtained from the Worldclim dataset (http://www.worldclim.org) [29] at the 2.5 min resolution (~5 km), which is sufficient for supporting climatic variables at the global scale [30]. The Worldclim variables were derived from the monthly temperature and precipitation, seasonal variation, and climatic extreme indices covering a period of time from 1950 to 2001 [29]. According to Jarnevich, *et al.* [31], the predictors that directly influence the species' distributions, such as those selected in this study, are more transferable than indirect predictors (i.e., elevation, land use, etc.), especially for studies that aim to project the potential current and future areas that are at risk of pest invasions. For this reason, this study only used environmental variables when making its projections.

The environmental variables were examined for any cross-correlation in order to avoid multicollinearity [32]. This procedure was undertaken using the SDMtoolbox and only one variable that was derived from each set of the highly correlated predictors (Pearson correlation coefficient, $r = |0.75|$) was included in the model (Table S2) [18]. Thus, only six environmental variables were selected and considered sufficiently biologically relevant to be included in the models (Tables 1 and 3).

Model Development and Validation

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The correlative maximum entropy-based model or MaxEnt (version 3.3.3k) [21] was chosen to assess the suitable areas and the impacts of climate change on the *D. maidis* distribution. MaxEnt correlates the background data points from the spatial environmental variables representing different environmental gradients and species' occurrence data in order to make projections of the potential suitable areas for the species [21]. MaxEnt classifies the areas from 0 to 1, where 0 represents unsuitable areas for the species' development, and 1 represents highly suitable areas. MaxEnt is also recognized to perform good projections with small samples sizes [20,22]. To build the model, a total of 50,000 background points were randomly selected from the areas where the insect is currently found [31,33], which is recommended in studies that are carried out on a global scale. Additionally, a sampling bias surface was developed using the kernel density estimate that is available in the SDMToolbox. Considering that the collected data were from external sources and we were not able to control the sampling process, the development of the bias surface is recommended [33].

To select the best model, different settings were adjusted in MaxEnt [18,31,34]. Thus, different combinations of the regularization multiplier (RM) and feature types were set in order to generate different models. Through the RM, MaxEnt selects the features that contribute the most to the model, thus reducing the model's overfitting [34]. It is recommended that researchers explore a range of RM coefficient values and choose the value that maximizes a measure of fit for a cross-validation data set [34]. Thus, the RM values that were used in this study were 1.0 and 1.5. Different sets of MaxEnt features (e.g., linear [L], quadratic [Q], product [P], threshold [T], and hinge [H]) and RM combinations were performed in order to obtain the best model for each species (Tables 1 and 3). The 'fade-by-

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clamping' option was selected in the software in order to avoid extrapolations that are outside the species' environmental range [35]. Species 'response curves' were also generated by employing the 'Jackknife' feature, the percent contribution, and the permutation importance in MaxEnt (Figs. S1 and S2) [21].

The 'response curves' allow us to assess the relationships between the predicted probabilities for the species and each environmental predictor [18,21]. Therefore, all curves were evaluated and were kept for further evaluations only for the models that presented biologically coherent curves (Fig. S1, S2). The 'Jackknife' feature evaluates the relative influence of different environmental predictors on the insects' distributions (Fig. S3). The percentage contribution estimates the contribution of a certain variable to the model, and the permutation importance indicates the dependence of the model on that variable [21].

To select the best model for *D. maidis*, a 10-fold cross-validation was performed in MaxEnt in order to calculate the AUC_{cv} (area under the receiver operating characteristic [ROC] curve) [36] and the test sensitivity at 0 and 10% training omission rates (OR) [19,37]. The AUC_{cv} is a measurement of the model's ability to discriminate presence from background. Based on the AUC_{cv}, the models can be classified into models in which predictions are worse than random ($AUC_{cv} < 0.5$), models in which predictions are not better than random ($AUC_{cv} = 0.5$), models with poor performance ($AUC_{cv} < 0.7$), models with reasonable or moderate performance (0.7 d AUC_{cv} < 0.9), and models with high performance (AUC_{cv} e 0.9) [38]. The OR represents the percentage (0 and 10%) of the training presence locations for the model that fall outside the predicted suitable area. Therefore, with respect to the test sensitivity at 0

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and 10%, the training OR threshold is expected to be 0 and 0.10, respectively. Values higher than the expected values indicate poor model performance [27].

Future Projections and Model Combinations

For the future projections for 2050 and 2070, the Global Climate Models (GCMs) MIROC5, HadGEM2-AO and HadGEM2-ES under the Representative Concentration Pathways (RCP) RCP4.5 and RCP8.5 were used for both species. Theses GCMs have been widely used to assess the spatial distributions of many species based on climate change, ecosystems, and other long timescale components of the Earth, including the simulations of the currently available RCPs [39-41]. These models were three of the models that were used in the Intergovernmental Panel on Climate Change (IPCC) Fifth Assessment Report (AR5) and the associated cycle of the fifth phase of the CMIP5 (http://www.ipcc.ch/report/ar5/wg1/) [42]. These models take into account various factors, which includes greenhouse gas emissions, aerosols, solar irradiance, ozone, and others [43]. Here, only the projections that performed under the MIROC5 (GCM) are presented, while the HadGEM2-AO and HadGEM2-ES projections are included in the electronic supporting information.

Anthropogenic greenhouse gas (GHG) emissions are widely known to increase the global mean surface temperature, and these emissions are related to the population size, economic activity, lifestyles, energy use, land use patterns, and so forth [15]. Based on these factors, the Representative Concentration Pathways (RCPs) are used in order to make projections of the effects of climate change [15]. The RCPs are divided into four categories: RCP2.6, which predicts a severe mitigation scenario; RCPs 4.5 and 6.0, which predict intermediate scenarios; and RCP8.5, which predicts very high GHG emissions. In this study,

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we selected the RCP4.5 and RCP8.5 scenarios in order to project the effects of climate change on *D. maidis.* We selected these two scenarios since they allow us to investigate the effects of climate change on these species under both reasonable and extreme climate change scenarios. RCP4.5 projects an increase in the global surface temperature from 1.1 to 2.6 ºC by the end of the 21st century, while RCP8.5 projects an increase from 2.6 °C to 4.8 °C by the end of the same period [15]. Changes in the global precipitation patterns are also predicted to occur.

For the combined models, the Prevalence Threshold Approach was selected. This approach was chosen in order to highlight the areas that will be highly suitable for maize with marginal and high suitability for the corn leafhopper in 2070 for both scenarios. This threshold approach was selected based on its recognized simplicity and efficiency in defining habitats and nonhabitats [37]. We merged the marginal and highly suitable areas for *D. maidis* because this insect is the vector of maize-stunting pathogens, and, even in low-density populations, it can lead to large losses due to its negative effects, as mentioned above.

RESULTS

Prediction variables for *Dalbulus maidis*

According to the current distribution of the corn leafhopper on the American Continent, *D. maidis* occurs mainly in areas with a mean annual temperature of 22.6 ºC and annual precipitation of 1260.5 mm (Table 1). The minimum temperature of the coldest month (61.5%), the mean annual precipitation (12%) and the precipitation of driest month (10.2%) were the variables that most contributed to the *D. maidis* projections (percent contributions in

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parentheses) (Table 1). Therefore, *D. maidis* favors areas where there are higher winter temperatures, moderate to low annual precipitation and characteristic wet and dry seasons. The minimum temperature of the coldest month (58.9%) was the variable that individually contributed the most to the *D. maidis* model, and this variable was followed by the annual mean temperature (11.4%) and the mean diurnal temperature variation (10.2%).

Dalbulus maidis model assessment

Twelve combinations of regularization multipliers (RMs) and feature types were tested in this study in order to select the best model for *D. maidis* (Table 2). All tested models performed very well in their projections; they had low omission rates at 0 and 10% and excellent AUC_{cv} values. The lowest ORs at 0 and 10% were 0.01 and 0.11, respectively, while the highest AUC_{cv} was 0.97 (Table 2). Therefore, the best model for *D. maidis* includes six environmental variables, linear [L] and quadratic [Q] features, and RM = 1.5. It resulted in the lowest tested ORs at 10 and 0%, respectively (Table 2).

Predicted distribution of _D. maidis_

The current distribution of *D. maidis* and the MaxEnt projections were very well matched (Figs. 1a and b). Most of the areas that are infected by the corn leafhopper on the American continent were projected to be highly suitable for *D. maidis.* It is worth mentioning that the areas that are projected as highly suitable for *D. maidis* include sites where it is very abundant (e.g., northwest of Argentina, central and mid-west of Brazil and the Jalisco region in Mexico). Outside the pest's range, large areas in Africa, Asia and Australia were projected as lowly or highly suitable for this insect. On the other hand, most areas in Europe were considered to be unsuitable for the corn leafhopper (Figs. 1a and b).

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In general, all three models under both the RCP4.5 and RCP8.5 scenarios will result in a decrease in the suitability for *D. maidis* (Figs. 2 and 3, Supplementary material). Under the RCP4.5 scenario, the areas in South America, especially in the northern and central regions of Brazil, are projected to have decreased suitability for the corn leafhopper. Similar results are expected to occur in Central Africa and Asia. In North America, climate change will lead to a slight decrease in the suitability of Mexico (Figs. 2a and b, Supplementary material). The same patterns are projected to occur under the RCP8.5 scenario (Figs. 3a and b, Supplementary material). The difference is that, under the RCP8.5 scenario, the changes in suitability will be slightly accentuated (Figs. 3a and b, Supplementary material).

Predictor variables for *Zea mays* L.

Based on the current distribution of *Z. mays,* this crop is mostly cultivated in areas with a mean annual temperature of 16.7 ºC and precipitation of 929 mm (Table 3). The predictor variables that most influenced the *Z. mays* projections were the minimum temperature of the coldest month (72.2%), the mean annual temperature (9.6%) and the mean annual precipitation (9%) (Table 3). These results highlight the role of low temperatures in limiting maize cultivation. The susceptibly of maize to frost is well known, especially with temperatures below 6 ºC [44], which supports the fact that the temperature of the coldest month significantly influences the *Z. mays* projections.

***Zea mays* model assessment**

For *Z. mays,* eight combinations of regularization multipliers (RMs) and feature types were tested in order to select the best model (Table 4). It included six environmental

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variables; linear [L], quadratic [Q] and product [P] features; and RM = 1.0. It resulted in the lowest test ORs at 10% = 0.11 and 0% = 0.002, respectively (Table 4).

Predicted distribution of *Z. mays*

The MaxEnt projections also very well matched the current distribution of *Z. mays* (Figs. 1c and d). In both scenarios, the suitability for *Z. mays* will decrease in South America, some areas in Central Africa and Oceania, and Asia (Figs. 2 and 3, Supplementary material). The difference between the RCPs is that under the RCP8.5 scenario, the changes in the suitability will be slightly accentuated (Figs. 3c and d, Supplementary material).

Agreement of *D. maidis* and *Z. mays* projections

Through the combination of the *D. maidis* and *Z. mays* projections for 2070 under both scenarios, it is possible to highlight some areas that will be highly suitable for pest infestations (Fig. 4). These areas correspond to areas in South America, Africa, and small areas in Asia and Oceania (Fig. 4). In South America, countries such as Argentina, Bolivia, Chile, Colombia, Ecuador, Peru, and Venezuela have few optimal areas for *Z. mays* and highly suitable areas for *D. maidis.* In North America, Mexico has areas that are highly suitable for pest infestations (Fig. 4). In Africa, these areas correspond to small parts of Ethiopia, Kenya, Rwanda, Angola, South Africa and Tanzania (Fig. 4).

DISCUSSION

For several years, *D. maidis* has been reported as one of the most important maize pests in Latin America [45]. In Brazil, *D. maidis* is responsible for 10 to 100% of the plants with symptoms of the maize-stunting pathogens, which can lead to complete production

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losses [45,46]. Therefore, understanding the interactions between this pest and its host crop under changing climate is vital for its future control and planning. This study is the first that has been undertaken to assess the suitable areas for the corn leafhopper and the impact of climate change on this pest worldwide. The consistency of the validation statistic for the pest and host plant projections demonstrates the models' robustness. Therefore, the results of overlaying these models (pest and host plant) allow us to make very reliable assumptions about the highly suitable areas for the pest's development.

In the model that was proposed in this study, the bioclimatic variable related to temperature had an important role in the spatial distribution projections of the corn leafhopper. Together, the temperature related variables determined 86.1% of the *D. maidis* model (permutation importance) (Table 1). In another research, Van Nieuwenhove, *et al.* [12] reported the effects of the temperature on several life-history parameters of *D. maidis* under laboratory conditions. The temperature affected the egg-laying and hatchability, development, and pre-imaginal survival of *D. maidis*. According to their study, the optimum temperature range for the corn leafhopper is between 20 to 30 ºC [12]. Therefore, the fact that the mean annual temperature that was found in the occurrence data on the American continent was between the temperature ranges that were previously proposed reinforces the consistency of the projections of our study.

The results of this research highlight some areas that are not infested by the corn leafhopper. These areas correspond to countries in Central Africa and some areas in Asia (Fig. 1b). Most of the research that has been performed to assess the effects of climate change on pests projects increasing invasion risks; however, in the case of *D. maidis*, we found that

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climate change will lead to a decrease in the suitability of most of these areas (Figs. 2 and 3). This is important information for countries in South America, especially for Brazil, which is the third largest producer of maize in the world [3], and where this insect is a critical pest [10,12,47]. Large areas of this country will become less suitable for the corn leafhopper. Based on our projections, most of the areas that are currently highly suitable for the corn leafhopper will experience increased temperatures of approximately 5 °C until 2070. This increase will raise the mean annual temperature of these regions from 22.6 to 27.6 °C, which is very close to the upper thermal requirement threshold for *D. maidis*, as was previously mentioned (30 °C). Thus, the decreasing suitability for the corn leafhopper is probably due to the increased temperatures in these areas.

According to the overlay of the pest and host plant future projections, some countries on the American Continent such as Argentina, Chile, Peru, Ecuador, Mexico, and Uruguay will still have areas that are highly suitable for the pest. Since the corn leafhopper is reported in these countries, these countries should be aware of the potential future increases in the damages that are associated with *D. maidis*. Other countries such as Ethiopia, Kenya, Rwanda, Burundi, and South Africa should also be concerned about the potential future invasion of the corn leafhopper since these countries also have large areas that are highly suitable for this insect. Therefore, in these countries, vigilance and quarantine measures should be implemented in order to avoid *D. maidis* invasions.

In this study, two different climate change scenarios (RCPs) were selected in order to assess the impacts of climate change on *D. maidis*: RCP4.5, which predicts a more reasonable mitigation scenario of GHG emissions; and RCP8.5, which predicts very high CHG

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emissions. Although the selected RCPs are very different from each other, the projection results are only slightly different. RCP8.5 projects a slightly higher loss of areas that are suitable for the corn leafhopper. However, it is seen that the differences in the projections of the temperature increases between the two RCP scenarios will not significantly affect the distribution of the areas that are suitable for *D. maidis*.

Limitations of modeling approach

Many factors can affect the distribution of a species, such as the ability to reach and develop at a potential site and to compete with others occupying the same habitat [48]. It is important to note that, in this study, we considered only the climatic suitability; therefore, there are other factors that might limit the distribution of the corn leafhopper, such as geographic barriers and natural enemies. In addition, spatial distribution studies have some uncertainties, and they might be associated with future GHG emissions levels, the magnitude of the climate change projections, the model's parameterization, and the currently broad-scale climate data that are available [31,49,50].

For example, the future GHG emissions levels will alter the temperature and precipitation, which, in turn, will alter plant phenology. This alteration might influence the synchronization between herbivores and their hosts, thereby altering the herbivores and their natural enemies' abundance. In general, there is consistency among the climate change projections of the different models. However, the magnitude of climate change strongly depends on the mitigation policies that may be applied in the future [15,51]. The model's parameterization has to be performed in order to obtain results that are consistent with the

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known distribution of the species and its habitat requirements [31]. Therefore, the knowledge and experience of the modeler about the species are essential.

Another important aspect of this study is that the evolutionary and adaptation processes that insects are likely to experience were not considered in this modeling [49,50]. The projection of the effects of climate change on insects normally assumes that the thermal requirements for a certain species are static and cannot evolve [49]. However, these physiological requirements are flexible and, through acclimation and diapause/quiescence, they might respond differently during the evolutionary process [49].

Conclusion

This is the first study that has been undertaken to assess the predicted effects of climatic change in 2050 and 2070 on an important pest of maize, the corn leafhopper *D. maidis*. Our models were proven to be very reliable based on the current distribution of the studied insect. According to the proposed model, temperature was one of the predictors that most affected the distribution of this insect. Overall, climate change will decrease the areas that are suitable for *D. maidis*. In South America, climate change will decrease the areas that are suitable for the pest, especially in Brazil. Argentina, Chile, Colombia, Ecuador, Peru, and Venezuela will have small areas that are highly suitable for the corn leafhopper. Outside the pest's range, Ethiopia, Kenya, Rwanda, Angola, South Africa and Tanzania also should be concerned about the risk of corn leafhopper invasions in the future since these countries have highly suitable projections for this insect in some areas. The results that were generated in this research will be useful for the relevant countries that are at risk of *D. maidis* invasions. This study provides a warning call for the vulnerable areas to implement quarantine strategies

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and to develop new *Z. mays* varieties that are resistant or tolerant to *D. maidis* and the maize-stunting pathogens that this insect transmits.

AUTHOR CONTRIBUTION STATEMENT

PASJ, LK, RSDS, and MCP conceived and designed the research. PASJ built the models. JLP and AGLS carried out the field trials. PASJ wrote the manuscript. LK, RSDS, JLP, and MCP made critical revisions and approved the final version. All authors reviewed and approved the final manuscript.

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COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interest: The authors declare that they have no conflicts of interest.

Ethical approval: This article does not contain any studies with human participants or animals that were performed by any of the authors.

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Table 1: The environmental variables that were considered in the *D. maidis* niche models, and the average percent contributions of the environmental variables in the *D. maidis* distribution model. The values were averaged across 10 replicate runs. The general statistics were calculated using all occurrences (n = 150). (Min=minimum, Max=maximum, and SD = standard deviation).

Variable	Percent contribution	Permutation importance	Min.	Max.	Mean	SD
Minimum temperature of coldest month (bio6; °C)	**61.5**	**64.5**	**4.8**	**17.0**	**12.1**	**3.1**
Mean annual precipitation (bio12; mm)	**12.0**	**3.8**	**588**	**1886**	**1260.5**	**317.5**
Precipitation of driest month (bio14; mm)	**10.2**	**0.1**	**0**	**25**	**9.06**	**6.8**
Mean diurnal range in temperature (bio2; °C)	**6.0**	**10.2**	**11.3**	**16.3**	**12.9**	**1.1**
Annual mean temperature (bio1; °C)	**5.9**	**11.4**	**17.6**	**24.9**	**22.6**	**1.5**
Precipitation seasonality (CV) (bio15)	**4.5**	**9.9**	**59**	**111**	**78.7**	**11.5**
Isothermality (bio3)	-	-	49	75	67.3	7.0
Temperature seasonality (SD x 100) (bio4)	-	-	691	4578	1717.7	1104.8
Maximum temperature of warmest month (bio5; °C)	-	-	28.6	35.2	31.5	1.3
Temperature annual range (bio7; °C)	-	-	15.2	27.2	19.4	3.5
Mean temperature of wettest quarter (bio8; °C)	-	-	19.5	27.6	23.9	1.3
Mean temperature of driest quarter (bio9; °C)	-	-	13.6	24.1	21.0	2.5
Mean temperature of warmest quarter (bio10; °C)	-	-	19.9	27.6	24.4	1.4
Mean temperature of coldest quarter (bio11; °C)	-	-	13.5	23.7	20.1	2.7
Precipitation of wettest month (bio13; mm)	-	-	109	335	235.2	49.2
Precipitation of wettest quarter (bio16; mm)	-	-	306	963	626.4	136.1
Precipitation of driest quarter (bio17; mm)	-	-	1	86	34.9	23.4

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Precipitation of warmest quarter (bio18; mm)	-	-	129	561	364.4	115.1
Precipitation of coldest quarter (bio19; mm)	-	-	10	187	64.3	42.7

Bold font indicates the variables in the final model. Source of data: WorldClim (http://www.worldclim.org/bioclim) [29].

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Table 2: Summary of the performance statistics of the *D. maidis* MaxEnt models. The best model is highlighted in bold.

Model Rank	Variables	MaxEnt settings		OR		Test AUC_{cv} (±SD)
		Features	RM	10%	0%	
1	**bio1,bio2,bio6, bio12, bio14, bio15**	**LQ**	**1.5**	**0.11**	**0.01**	**0.973 ± 0.005**
2	Same as above	LH	1.5	0.11	0.01	0.987 ± 0.001
3	Same as above	LQ	1.0	0.12	0.01	0.977 ± 0.005
4	Same as above	LQP	1.0	0.12	0.01	0.977 ± 0.003
5	Same as above	LH	1.0	0.14	0.01	0.988 ± 0.002
6	Same as above	LQH	1.0	0.14	0.01	0.987 ± 0.002
7	Same as above	LQPT	1.0	0.16	0.01	0.987 ± 0.002
8	Same as above	LQT	1.0	0.16	0.01	0.987 ± 0.003
9	Same as above	LQPTH	1.0	0.17	0.01	0.988 ± 0.001
10	Same as above	LQPT	1.5	0.17	0.01	0.987 ± 0.003
11	Same as above	LT	1.0	0.19	0.01	0.986 ± 0.005

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

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Table 3: The environmental variables that considered in the *Z. mays* L. niche models, and the average percent contributions of the environmental variables in the *Z. mays* L. distribution model. The values were averaged across 10 replicate runs. The general statistics were calculated using all occurrences (n = 61). (Min=minimum, Max=maximum, and SD = standard deviation).

Variable	Percent contribution	Permutation importance	Min.	Max.	Mean	SD
Minimum temperature of coldest month (bio6; °C)	**72.2**	**17**	**-26.2**	**22.3**	**3.9**	**9.4**
Annual mean temperature (bio1; °C)	**9.6**	**58.5**	**1.3**	**28.6**	**16.7**	**6.1**
Mean annual precipitation (bio12; mm)	**9.0**	**10.7**	**2.0**	**3860.0**	**929.0**	**496.4**
Mean diurnal range in temperature (bio2; °C)	**5.9**	**5.2**	**5.7**	**18.0**	**11.8**	**2.5**
Precipitation seasonality (CV) (bio15)	**2.7**	**5.9**	**8.0**	**150.0**	**54.2**	**31.9**
Precipitation of driest month (bio14; mm)	**0.6**	**2.7**	**0.0**	**141.0**	**27.3**	**28.8**
Isothermality (bio3)	-	-	20.0	92.0	50.6	18.6
Temperature seasonality (SD x 100) (bio4)	-	-	0.0	141.0	27.3	28.8
Maximum temperature of warmest month (bio5; °C)	-	-	18.0	46.1	29.5	4.3
Temperature annual range (bio7; °C)	-	-	10.1	53.7	25.6	8.4
Mean temperature of wettest quarter (bio8; °C)	-	-	2.4	32.3	19.4	5.9
Mean temperature of driest quarter (bio9; °C)	-	-	-17.8	35.8	13.9	10.0
Mean temperature of warmest quarter (bio10; °C)	-	-	11.3	35.8	22.5	4.0
Mean temperature of coldest quarter (bio11; °C)	-	-	-17.8	27.4	10.5	9.8
Precipitation of wettest month (bio13; mm)	-	-	1.0	1062.0	149.9	92.0
Precipitation of wettest quarter (bio16; mm)	-	-	2.0	2741.0	394.6	240.8
Precipitation of driest quarter (bio17; mm)	-	-	0.0	466.0	98.1	97.7

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Precipitation of warmest quarter (bio18; mm)	-	-	0.0	1235.0	278.1	169.4
Precipitation of coldest quarter (bio19; mm)	-	-	0.0	1005.0	160.0	157.2

Bold font indicates the variables in the final model. Source of data: WorldClim (http://www.worldclim.org/bioclim) [29].

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Table 4: Summary of the performance statistics of the *Z. mays* L. MaxEnt models. The best model is highlighted in bold.

Model Rank	Variables	MaxEnt settings		OR		Test AUC_{cv} (±SD)
		Features	RM	10%	0%	
1	**bio1,bio2,bio6, bio12, bio14, bio15**	**LQP**	**1.0**	**0.11**	**0.002**	**0.848 ± 0.016**
2	Same as above	LQ	1.0	0.11	0.002	0.836 ± 0.024
3	Same as above	LQPTH	1.5	0.11	0.002	0.873 ± 0.010
4	Same as above	LQPTH	1.0	0.12	0.002	0.876 ± 0.014
5	Same as above	LQH	1.0	0.12	0.007	0.873 ± 0.017
6	Same as above	LPH	1.0	0.13	0.002	0.873 ± 0.019
7	Same as above	LQPT	1.0	0.16	0.003	0.873 ± 0.014
8	Same as above	LQT	1.0	0.16	0.003	0.871 ± 0.023

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

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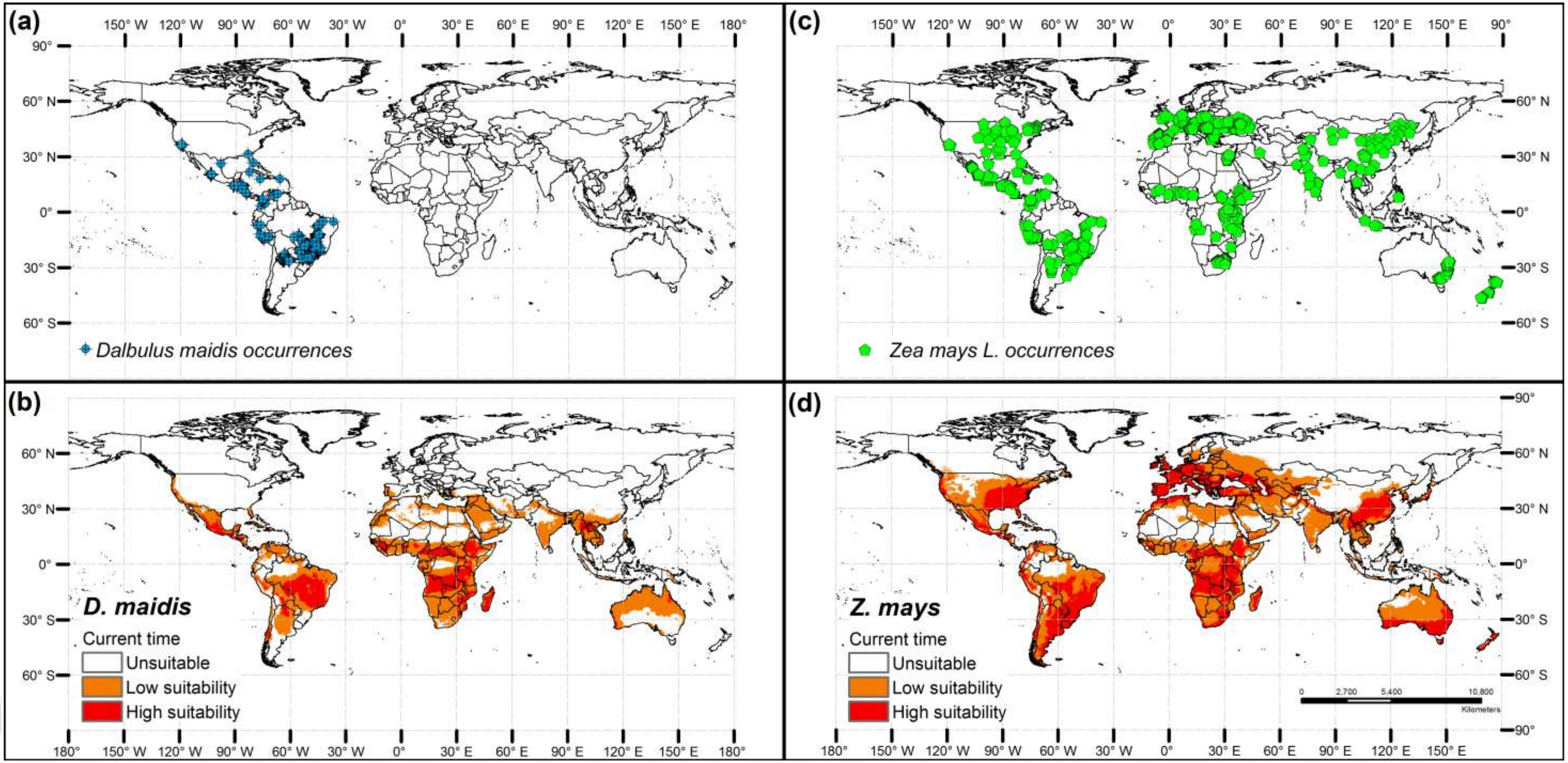

Figure 1: Current global distribution of *D. maidis* in open field (a), its potential distribution at the current time (b), the current global distribution of *Z. mays* L. in open field (c) and the potential suitable areas for this crop in the current time (d) using the MaxEnt model.

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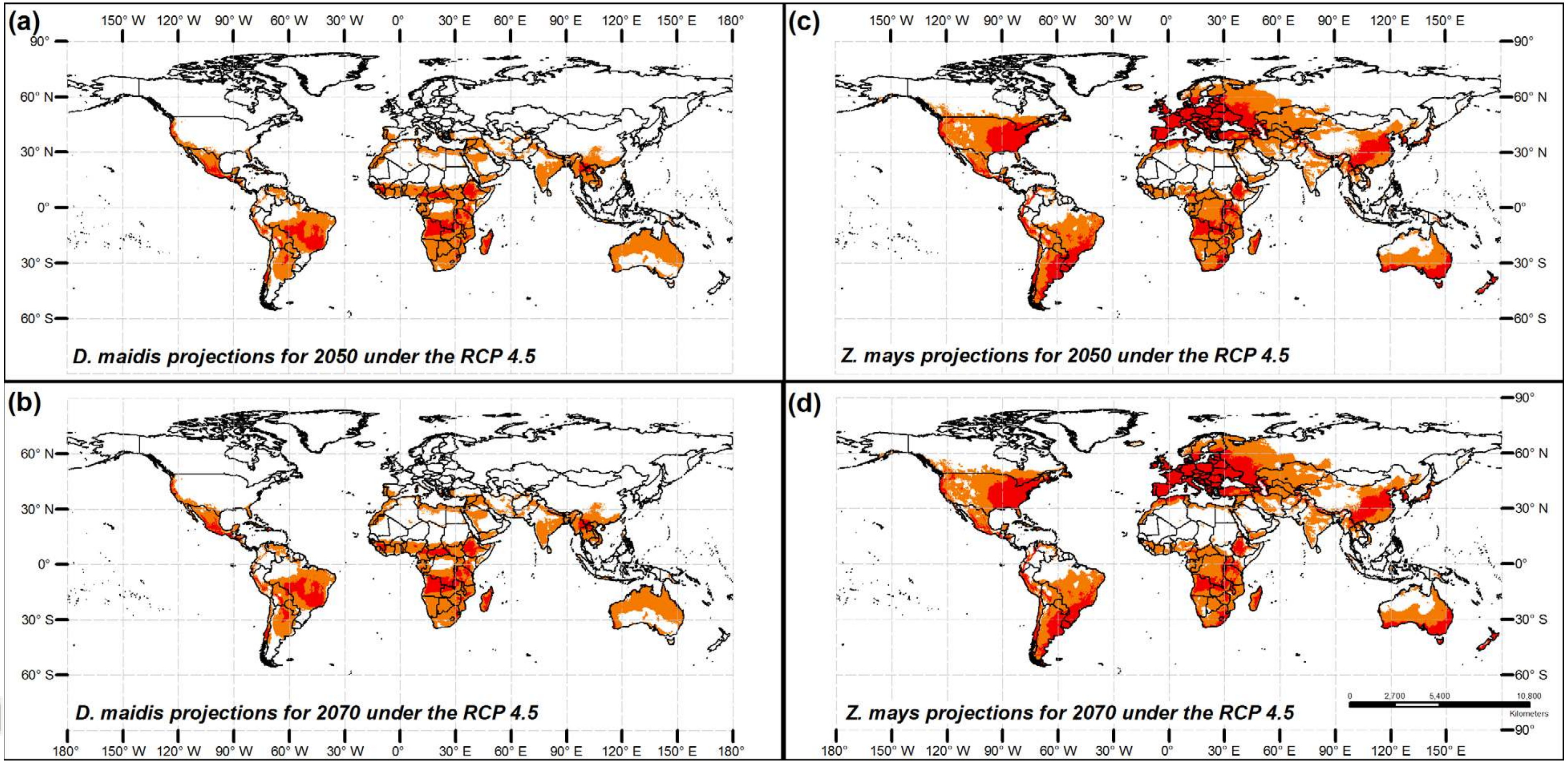

Figure 2: Future projections for 2050 and 2070 for *D. maidis* (a, b) and *Z. mays* L. (c, d) using the MaxEnt model running the MIROC5 (GCM) under the RCP 4.5 scenario.

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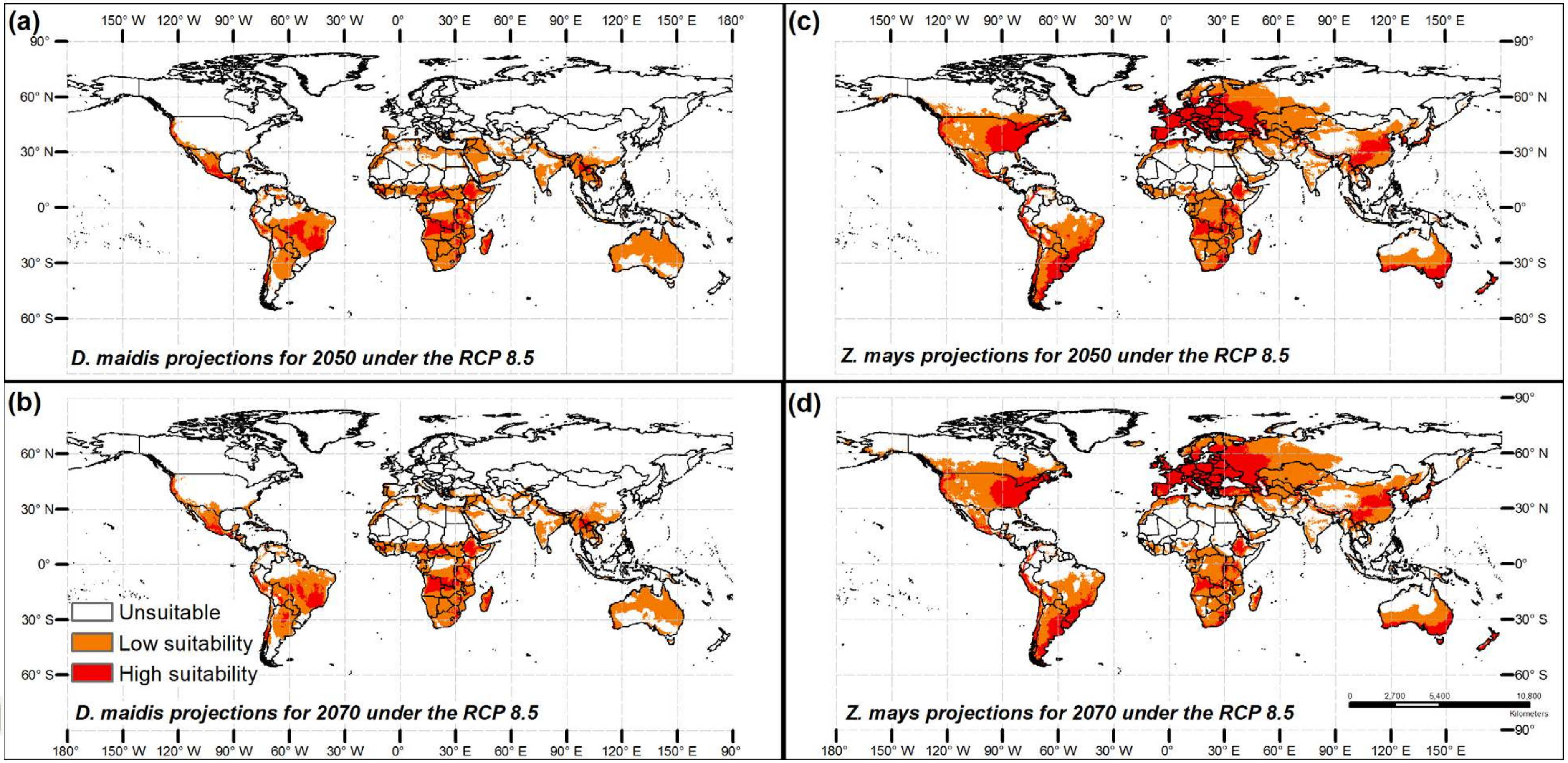

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Figure 3: Future projections for 2050 and 2070 for *D. maidis* (a, b) and *Z. mays* L. (c, d) using the MaxEnt model running the MIROC5 (GCM) under the RCP 8.5 scenario.

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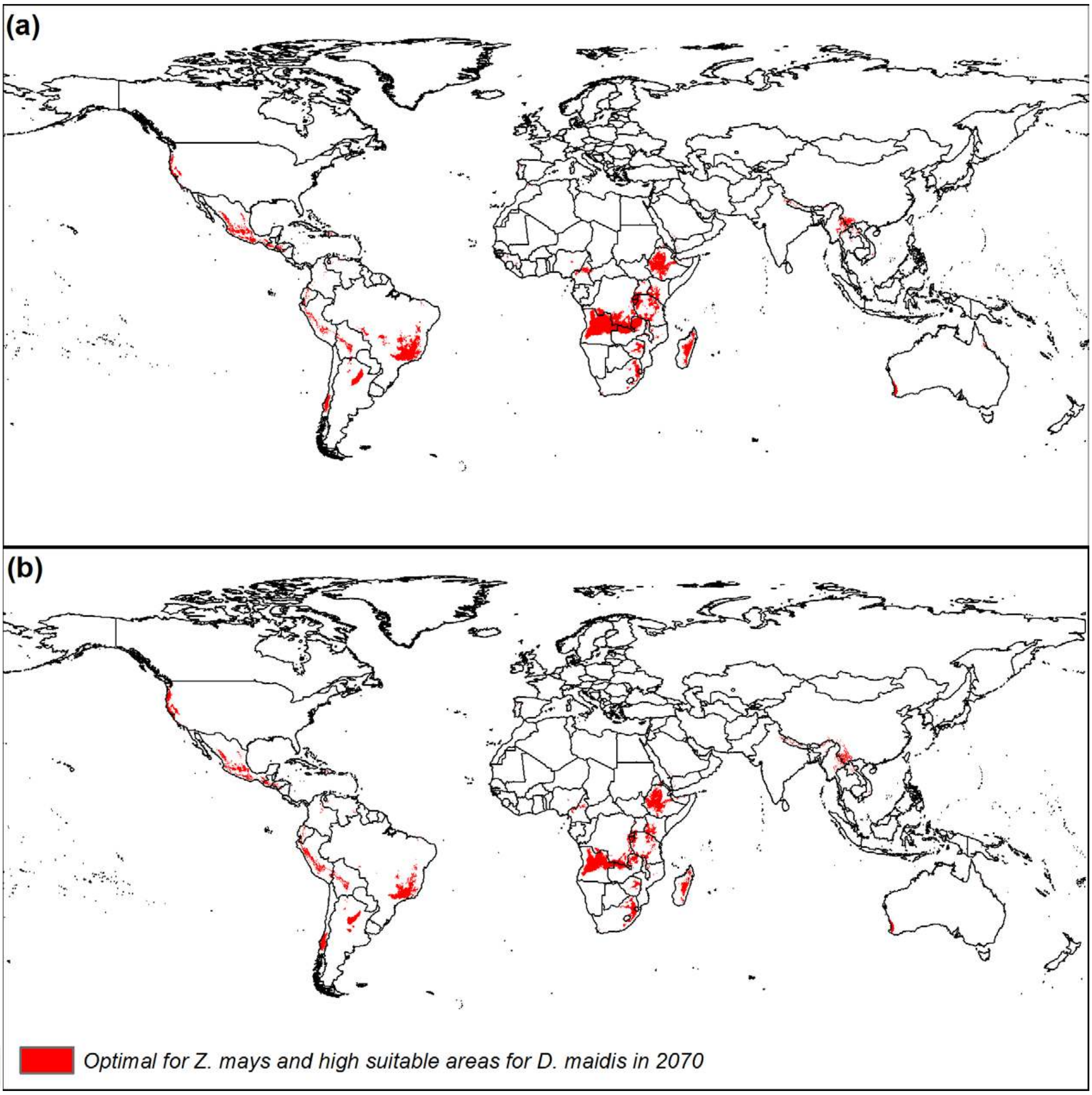

Figure 4: Agreement in the MaxEnt projection of optimal areas for *Z. mays* L. and high for *D. maidis* under MIROC5 (GCM) running the RCPs 4.5 (a) and 8.5 (b) for 2070.

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