



Habitat suitability and distribution potential of *Liberibacter* species (“*Candidatus Liberibacter asiaticus*” and “*Candidatus Liberibacter africanus*”) associated with citrus greening disease

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Abstract

Aim: To quantify current and predict future distribution of the citrus greening pathogens “*Candidatus Liberibacter asiaticus*” (Las) in Africa and “*Candidatus Liberibacter africanus*” (Laf) globally.

Location: Africa.

Methods: Three species distribution models (MaxEnt, BIOCLIM and Boosted Regression Trees) were used to predict the current and future potential distribution of Las in Africa, and the potential global distribution of Laf, using long-term bioclimatic variables. Two climate change scenarios (moderate and extreme) were employed to determine how future climate alterations may affect the potential distribution of Las in Africa. Presence data from global reports of Las, as well as the new positional points obtained in this survey, were used to predict the habitat suitability of the pathogen in Africa, while the presence data points of Laf were used to predict the global habitat suitability. Testing data comprised 25% of the presence only points.

Results: Consensus of the three models predicted a potential distribution of Las in large areas of Western, Eastern and sub-Saharan Africa. North Africa was mostly unsuitable for Las, except for the northern fringes. The potential distribution of Laf included South and Central America, Asia and Australia. In Europe, the United Kingdom and the Iberian Peninsula showed marginal suitability for Laf. The projections under the future climate change scenarios showed an increase in the Laf habitat suitability hotspots under the extreme scenario.

Main conclusions: This study highlights the potential establishment and distribution in Africa of Las-associated Huanglongbing and globally for Laf-associated with African citrus greening disease. The ensemble modelling approach for the distribution of plant pathogens is a valuable tool for the development of strategies for crop protection. These results constitute an early alert for citrus-producing regions that

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should inform strategies for surveillance and preventive management against the invasion and spread of this destructive disease.

KEYWORDS

African citrus greening, *Candidatus Liberibacter africanus*, *Candidatus Liberibacter asiaticus*, climate change, habitat suitability, Huanglongbing, species distribution

1 | INTRODUCTION

Citrus is an economically important crop with annual production estimates standing at over 122 million tons of fruits from the top producing countries (Brazil, USA and China) (Mendonça, Zambolim, & Badel, 2017). A large portion of economic losses in citrus production in Africa, Asia and the American continent is attributed to Huanglongbing (HLB) (Krishna, 2015). HLB is associated with the phloem-limited bacterium "*Candidatus Liberibacter asiaticus*" (Las) (Gottwald, 2010) occurring in Asia and the Americas and recently reported in Africa (Saponari et al., 2010). In addition to the Las-HLB association, there are two other citrus-infecting *Liberibacter* species: *Candidatus Liberibacter americanus* (Lam) and "*Candidatus Liberibacter africanus*" (Laf). Laf, which causes African citrus greening disease (ACG) is widespread in Africa, where a number of new lineages of the species have been reported recently including "*Candidatus Liberibacter africanus* subsp. *clausenae*" (LafCl), "*Candidatus Liberibacter africanus* subsp. *capensis*" (LafC), "*Candidatus Liberibacter africanus* subsp. *tecleae*" (LafT), "*Candidatus Liberibacter africanus* subsp. *vepridis*" (LafV) and "*Candidatus Liberibacter africanus* subsp. *zanthoxyli*" (LafZ) (Roberts, Steenkamp, & Pietersen, 2015). Laf is transmitted by the African citrus psyllid *Trioza erytreae* (del Guercio) and usually occurs in cool highland regions, mostly above 900 meters above sea level (m.a.s.l.) (Narouei-Khandan, Halbert, Worner, & VanBruggen, 2015). In contrast, Las is transmitted by the Asian citrus psyllid *Diaphorina citri* Kuwayama and is more heat-tolerant and can withstand temperatures of 30 to 35°C (da Graça & Korsten, 2004). All citrus species and cultivars have been reported to be susceptible to infection by Las, which also infects some related plant genera such as *Murraya* and *Clausena* (Halbert, Manjunath, Ramadugu, & Lee, 2012; Manjunath, Halbert, Ramadugu, Webb, & Lee, 2008). Dispersal takes place by movement of adult psyllids and transportation of infected nursery citrus stock (Gottwald, 2010; Lopes & Frare, 2007), with the latter being the most important factor in the long-distance dispersal of HLB and its vector (Halbert et al., 2010, 2012; Narouei-Khandan et al., 2015). Trees infected with the *Liberibacter* pathogens show mild-to-severe yellowing on the shoots and subsequently progressive yellowing of the entire tree (Batoool et al. 2007). Leaves may also become thicker, leathery and midribs, and lateral veins are sometimes enlarged, swollen and corky (Batoool et al. 2007). Mottling and chlorosis are the main characteristic leaf symptoms. The fruits are often underdeveloped, lopsided, show colour inversion and can have a sour or

bitter taste (Akhtar & Ahmad, 1999; ANR, 2010; Garnier & Bové, 1983; Jepson, 2009). Ultimately, the infected tree dies as there is currently no treatment for infected trees, and all commonly grown citrus varieties are susceptible to the disease (Li et al., 2019). This will lead to a decline in the production and subsequent collapse of the citrus industry in the region.

Presently, Huanglongbing has been reported in 44 countries in the Americas and Asia (CABI/EPPO, 2017). The first report of HLB on the African mainland was in Ethiopia (Saponari et al., 2010). African citrus greening disease, on the other hand, has been reported only in 19 countries within Africa since the 1920s (Buitendag & von Broembsen, 1993; CABI/EPPO, 1998; EPPO, 2014; Massonié, Garnier, & Bové, 1976; McClean & Oberholzer, 1965; Rasowo et al., 2019; Roberts et al., 2017).

Currently, the habitat suitability for *Liberibacter* infection in Africa is poorly known. As a consequence, the design of spatially explicit management strategies to minimize losses in the citrus industry is challenging. Africa is an ecologically diverse continent with great diversity of agro-ecological zones varying in natural resources and land use patterns, which could lead to differences in the habitat suitability of *Liberibacter* in the continent. Generally, the distribution of species is significantly affected by climate change (Kerr, 2001), but no studies have assessed the role of climate change in the current and future suitability and distribution of *Liberibacter* in Africa.

Few risk assessment models are available currently for predicting the potential establishment of HLB (Gutierrez & Ponti, 2013), despite a call for predictive global mapping of the disease fifteen years ago (da Graça & Korsten, 2004). Most available models on the potential spread of HLB are based on suitable climate conditions for the psyllid vector *D. citri* (Aurambout, Finlay, Luck, & Beattie, 2009; Gutierrez & Ponti, 2013; Torres-Pacheco et al., 2013). However, the risk of the establishment of HLB is not based solely on the distribution of the vector, because other factors such as environmental requirements may differ between the psyllid and the bacterial pathogen (Gottwald, 2010; Narouei-Khandan et al., 2015).

Species distribution models are important tools for investigating the potential impacts of climate change on the distribution of species (Wiens, Stralberg, Jongsomjit, Howell, & Snyder, 2009). These models are employed to project potential future changes in the geographic ranges of species (Barrows, Rotenberry, & Allen, 2010; Gritti, Smith, & Sykes, 2006), estimate rates of extinction (Thomas et al., 2004; Williams, Bolitho, & Fox, 2003), examine the efficacy of existing reserve systems (Araujo, Cabeza, Thuiller, Hannah, &

Williams, 2004; Tellez-Valdes & Davila-Aranda, 2003) and help to prioritize biodiversity conservation efforts (Pyke, Anelman, & Midgley, 2005). Emissions scenarios represent probable futures and are used in species distribution predictions (Porfirio et al., 2014; Rosentrater, 2010; Weaver et al., 2013). They comprise of representative concentration pathways (RCPs) which are scenarios that describe alternate trajectories for carbon dioxide emissions and the resulting atmospheric concentration from the year 2000 to 2,100. Four representative concentration pathway scenarios (rcp2.6, rcp4.5, rcp6 and rcp8.5) have been selected for climate modelling. The moderate scenario (rcp4.5) is a stabilization scenario where total radiative forcing is stabilized shortly after the year 2,100, without overshooting the long-run radiative forcing target level (Clarke et al., 2007; Wise et al., 2009). The extreme scenario (rcp8.5) is characterized by continuous rapid increase in concentrations of atmospheric carbon dioxide reaching 950 ppm by the year 2,100 and continued increase for another 100 years (Riahi, Grübler, & Nakicenovic, 2007). Representative concentration pathways are useful in species distribution modelling, as they aid in clarifying future climate scenarios and their impact on distribution range and the suitable habitat of species based on possible future greenhouse gas emission trajectories (Chhetri, Badola, & Barat, 2018). The use of the moderate and extreme scenarios in this study seeks to establish a wide prediction range on the effects of change in climate on species distribution while being realistic on the current global climatic trends. The use of the moderate and extreme scenarios in this study seeks to establish a wide range for predicting the effects of change in climate on species distribution while being realistic about the current global climate trends.

As a vector-borne plant pathogen, the *Candidatus Liberibacter* species resides mainly in the plant tissue. Therefore, the presence of the host plant under a particular bioclimatic condition will almost certainly mean the probable survivability of the *Liberibacter* species. Furthermore, the habitat suitability of certain bacterial species has been shown to be influenced by bioclimatic conditions for example; Stream ecosystem specificities related to the climatic and biogeochemical context can influence the microbial colonization (Sabater et al., 2008). The hydrological regime, nutrient content, temperature conditions and biological interactions depend on the climate (Sabater et al., 2008). Bioclimatic conditions have also been shown to influence the abundance of the bacterial microbiome in amphibian microbiome (Kueneman et al., 2019). Thus, our approach seeks to provide an alternative method for surveillance purposes in addition to vector surveillance since non-vector transmission (human-mediated) is also a factor in the spread of the pathogen.

This study aimed to quantify the current and predict the future habitat suitability and distribution of Las in Africa under different climate change scenarios and to identify hotspots of habitat suitability of Las using consensus models. We also aimed to quantify the current and predict the future global habitat suitability of Laf to establish the potential worldwide distribution and risk of spread of African citrus greening disease.

2 | METHODS

2.1 | Species data

Historical global presence points from previous reports of Las and Laf were obtained from the Centre for Agriculture and Bioscience International (CABI) Invasive Species Compendium (CABI, 2018) and European Plant Protection Organization (EPPO) Global Database (EPPO, 2018) (Figure S1-S2, Table S1-S2).

New presence points in Ethiopia, Kenya, Tanzania and Uganda were obtained between March 2017 and December 2018, during surveys on the incidence of HLB and African citrus greening carried out on citrus orchards located in various regions to determine the extent of the spread of the disease in the sampled areas (Table S3). Assessment of affected trees was made by visual inspection of foliage on site, and symptomatic tissue was tested for the presence of Las and Laf by PCR, and identities were confirmed by Sanger sequencing (Ajene et al., 2019; Rasowo et al., 2019). The presence data were cleaned by removing duplicate coordinates from the final dataset before running the models.

2.2 | Models

Three species distribution models were selected to study the potential distribution of Huanglongbing in Africa and African citrus greening disease in other parts of the world: (a) The classic climate-envelope-model BIOCLIM (Booth, Nix, Busby & Hutchinson, 2014), which employs only occurrence data to define a multidimensional environmental space in which a species can occur. The model predicts suitable conditions in a "bioclimatic envelope," consisting of a rectilinear region in environmental space representing the range (or some percentage thereof) of observed presence values in each environmental dimension (Phillips, Anderson, & Schapire, 2006). To avoid the overpredictive effect of outliers, the resulting envelope can be reduced at specified percentiles or standard deviations (Araujo & Petersen 2012).

(b) Maximum Entropy (MaxEnt) (Phillips et al., 2006), which is a general-purpose method for making predictions from incomplete information (Phillips et al., 2006). It requires only presence data, together with environmental data of the study area, employs both continuous and categorical data, can incorporate interactions between different variables and can converge to the optimal probability distribution as a result of deterministic algorithms which have been developed within the model (Phillips et al., 2006).

(c) Boosted Regression Trees (BRT) (Friedman, 2001), which is one of several techniques that enhance the accuracy of a single model by using two algorithms: regression trees and boosting. Boosting improves the model accuracy (Schapire, 2003). It is a forward, stagewise procedure. In boosting, models are fitted in a stepwise manner to the training data; subsequently, appropriate methods are employed to gradually increase emphasis on poorly modelled observations by the existing collection of trees (Friedman, 2001).

These models were selected to represent a spectrum of model complexity as well as make up for the limitations of each individual model via the consensus approach.

2.3 | Selection of bioclimatic variables

Environmental predictors included 19 bioclimatic variables (Table 1) of 2.5 km spatial resolution for the current scenario using the baseline average [1950–2000] (Fick & Hijmans, 2017) and for each future scenario using the Coupled Model Intercomparison Project, Phase 5 (CMIP) 2055 average [2041–2070] (Taylor, Stouffer, & Meeh, 2012). To assess the effect of climate change in the potential distribution of Las, we used two RCPs: CMIP5 rcp4.5 (moderate scenario) and CMIP5 rcp8.5 (extreme scenario). The environmental variables were obtained from the WorldClim database (<http://www.worldclim.org/>).

Expected multicollinearity among all the predictor bioclimatic variables were tested using the Pearson correlation test. The highly correlated variables were eliminated using the “findCorrelation” function in the “Caret” package (Kuhn et al., 2016) in R v3.5.1 environment via R-Studio (R development Core Team, 2008). The

TABLE 1 Predictor bioclimatic variables used for modelling the ecological niche for “*Candidatus Liberibacter asiaticus*” and “*Candidatus Liberibacter africanus*.” Variables selected through a multicollinearity test using the “Find correlation” function in the caret package in the R software are shown in bold. Data were sourced from the WorldClim database accessed on November 2018

Variable	Code	Units
Annual mean temperature	Bio 1	°C
Mean diurnal range	Bio 2	°C
Isothermality	Bio 3	°C
Temperature seasonality	Bio 4	°C
Max temperature of warmest month	Bio 5	°C
Min temperature of coldest month quarter	Bio 6	°C
Temperature annual range	Bio 7	°C
Mean temperature of wettest quarter	Bio 8	°C
Mean temperature of driest quarter	Bio 9	°C
Mean temperature of warmest quarter	Bio 10	°C
Mean temperature of coldest quarter	Bio 11	°C
Annual precipitation	Bio 12	mm
Precipitation of wettest month	Bio 13	mm
Precipitation of driest month	Bio 14	mm
Precipitation seasonality (coefficient of variation)	Bio 15	mm
Precipitation of wettest quarter	Bio 16	mm
Precipitation of driest quarter	Bio 17	mm
Precipitation of warmest quarter	Bio 18	mm
Precipitation of coldest quarter	Bio 19	mm

correlation coefficient of $|r| > 0.7$ was set as a collinearity indicator for variables that would affect the models (Dormann et al., 2012). Variables within this range were eliminated from the analysis, and only the uncorrelated predictor variables were used in the models. A Jackknife test for variable importance was run on the selected variables in MaxEnt to determine the percentage contribution of each selected variable to the model.

2.4 | Model evaluations

Model accuracy was assessed using the area under receiver operating characteristic curve (ROC curve) (Thuiller, Araujo, & Lavorel, 2003). The ROC curve is a graphical technique that represents the relation between the false-positive fraction (1–specificity) and the sensitivity for a number of thresholds (Fielding & Bell, 1997; Phillips et al., 2006). A curve that maximizes sensitivity for low values of (1–specificity) infers good model performance. The classification of the accuracy of a diagnostic test is the traditional academic point system (Swets, 1988): 0.90–1.00 = excellent; 0.80–0.90 = good; 0.70–0.80 = fair; 0.60–0.70 = poor; and 0.50–0.60 = fail. The difference between the areas under ROC curves generated by two or more models provides a measure of comparative discrimination ability of these models when applied to independent evaluation data. All models were run in R v3.5.1 environment via R-Studio, and the data were exported as ASCII files for enhanced visualization with QGIS software v2.18.15 (QGIS Development Team, 2016).

2.5 | Model calibration

2.5.1 | MaxEnt

Presence locations for Las and Laf (occurrence data) were compared against all the pseudo-absence points that are available in the study area to avoid model overfitting of spatially clustered presence points and inability to predict spatially independent data. Pseudo-absence points are randomly sampled points from a given geographic area and treated like locations where the species of interest is absent. Pseudo-absence points were generated automatically in MaxEnt by random selection from all points within the studied area excluding available presence points (Barbet-Massin, Jiguet, Albert, & Thuiller, 2012) (Figure S4). The model was trained using 75% of the presence data and validated using 25%. The model was run with 5,000 iterations and > 10,000 background points for both current and future climate scenarios.

2.5.2 | BIOCLIM

The mean and standard deviation for each environmental variable were used individually to compute bioclimatic envelopes. The level

of fitness between the environmental values on a point and the respective envelopes classifies each point as Suitable, Marginal or Unsuitable for presence. The categorical output is mapped to probabilities of 1.0, 0.5 and 0.0, respectively. The presence points were used to find the bioclimatic envelope during model creation, and the occurrence data were compared versus 10,000 background points generated by random selection of points from all points outside of the suitable area estimated by a rectilinear surface envelope from the presence sample (Barbet-Massin et al., 2012; Thuiller, Lafourcade, Engler, & Araujo, 2009).

2.6 | Boosted Regression Trees

The model was calibrated using the gradient boosting function “gbm.step” in the “dismo” package (Hijmans, Phillips, Leathwick, & Elith, 2017) in R. The data and settings were as follows: the data frame containing the trained data, the predictor variables— $\text{gbm.x} = 2.20$, the response variable— $\text{gbm.y} = 1$, the nature of the error structure (family = “bernoulli”), the tree complexity (5), the learning rate (0.01), and the bag fraction (0.5). All other parameters not named in the call were set at as default.

2.6.1 | Model consensus

Consensus models have been shown to have higher predictive capacity than any of the single SDMs alone (Forester, Dechaine, & Bunn, 2013). Furthermore, they have been shown to outperform individual models thereby providing more robust projections of habitat distributions (Grenouillet, Buisson, Casajus, & Lek, 2011; Marmion, Parviainen, Luoto, Heikkinen, & Thuiller, 2009). Additionally, the use of several algorithms to project species distributions is important because models with the highest accuracy on current climate data may not be optimal in projecting onto new areas or climate conditions (Heikkinen, Marmion, & Luoto, 2012). We employed an ensemble modelling method of obtaining a consensus of the three models, weighted by their AUC scores. Averaging several models have shown that the “output” of interest is isolated from the “noise” associated with individual model errors and uncertainties. When combining forecasts for consensus, one can produce weighted and unweighted averages (Araújo & New, 2007). To obtain a three-model consensus, we first rescaled the raster outputs from the individual models to uniform values between 0 and 1. We combined the individual models weighted by their AUC scores, subtracted 0.5 and squared the results to give further weight to the higher AUC values, thus obtaining the weighted average. Finally, we made a Raster Stack of our individual model predictions and computed the average. Habitat suitability hotspots were identified by points on the final raster with a probability of occurrence of > 0.05 .

The final output of level of fitness on the consensus models which ranged between 0 and 1 was classified based on the estimated

value cut of the full extent in QGIS as follows: $> 0.2 = \text{optimal}$, $0.2 - 0.01 = \text{highly suitable}$, $0.01 - 0 = \text{marginal}$ and $0 = \text{unsuitable}$.

2.7 | Effect of climate change

The impact of climate change on the future distribution of HLB was determined using the raster calculator in QGIS to resolve the differences between the outputs of the two scenarios assessed. The effect of climate change was calculated by subtracting the raster outputs. The potential distribution due to a change from the extreme emission scenario to the moderate emission scenario was calculated as $\text{CMIP5 rcp 4.5} - \text{CMIP5 rcp 8.5} = \text{change}$. The potential distribution due to a change from the moderate emission scenario to the extreme emission scenario was calculated as $\text{CMIP5 rcp 8.5} - \text{CMIP5 rcp 4.5} = \text{change}$. The final output was streamlined to project only the optimum habitat suitability for better visualization of the change in the distribution of the hotspots.

3 | RESULTS

3.1 | Environmental variables affecting the model

Expected multicollinearity among all the predictor bioclimatic variables tested using the “findCorrelation” function showed high correlation between 10 of the 19 bioclimatic variables, while nine bioclimatic variables were uncorrelated (Figure S3). To account for biological plausibility of the model, precipitation-dependent variables which were correlated were included in the model because precipitation has been known to have a greater effect on the spread of plant pathogens (Velásquez, Castroverde, & He, 2018). The uncorrelated predictor variables, as well as the biologically relevant precipitation-dependent variables (Table 1), were used in the models. The jackknife test for variable importance showed that the precipitation of the wettest month, and the annual mean temperature had the highest percentage contribution and permutation importance to the model, respectively. Precipitation of the driest month had the least percentage contribution, while the mean temperature of the warmest quarter had the least permutation importance (Table 2).

3.2 | Predicted current distribution of Huanglongbing in Africa

The predicted current distribution of HLB, as obtained from the three-model consensus, showed all countries of Central, Eastern, Southern and Western Africa having marginal to optimal habitat suitability for Las (Figure 1a). In contrast, large areas of North Africa were predicted to have habitat unsuitable for Las, but the northern fringes of Morocco, Algeria, Tunisia and Egypt showed marginal habitat suitability.

Variable	Percentage contribution	Permutation importance
Precipitation of wettest month	35.6	25.6
Annual mean temperature	21.5	25.7
Precipitation of warmest quarter	20.6	4.4
Precipitation of coldest quarter	8.5	17.1
Temperature annual range	6	10.5
Mean temperature of warmest quarter	2.9	1.7
Precipitation seasonality	2.5	3.9
Mean diurnal range	1.5	8
Precipitation of driest month	1	3.1
Precipitation of driest quarter	0.5	2.9
Annual precipitation	0.1	0
Precipitation of wettest quarter	0	0

TABLE 2 Percentage contribution and permutation importance of predictor variables as obtained from Jackknife test, used for modelling the ecological niche for “*Candidatus Liberibacter asiaticus*” (Las) and “*Candidatus Liberibacter africanus*” (Laf)

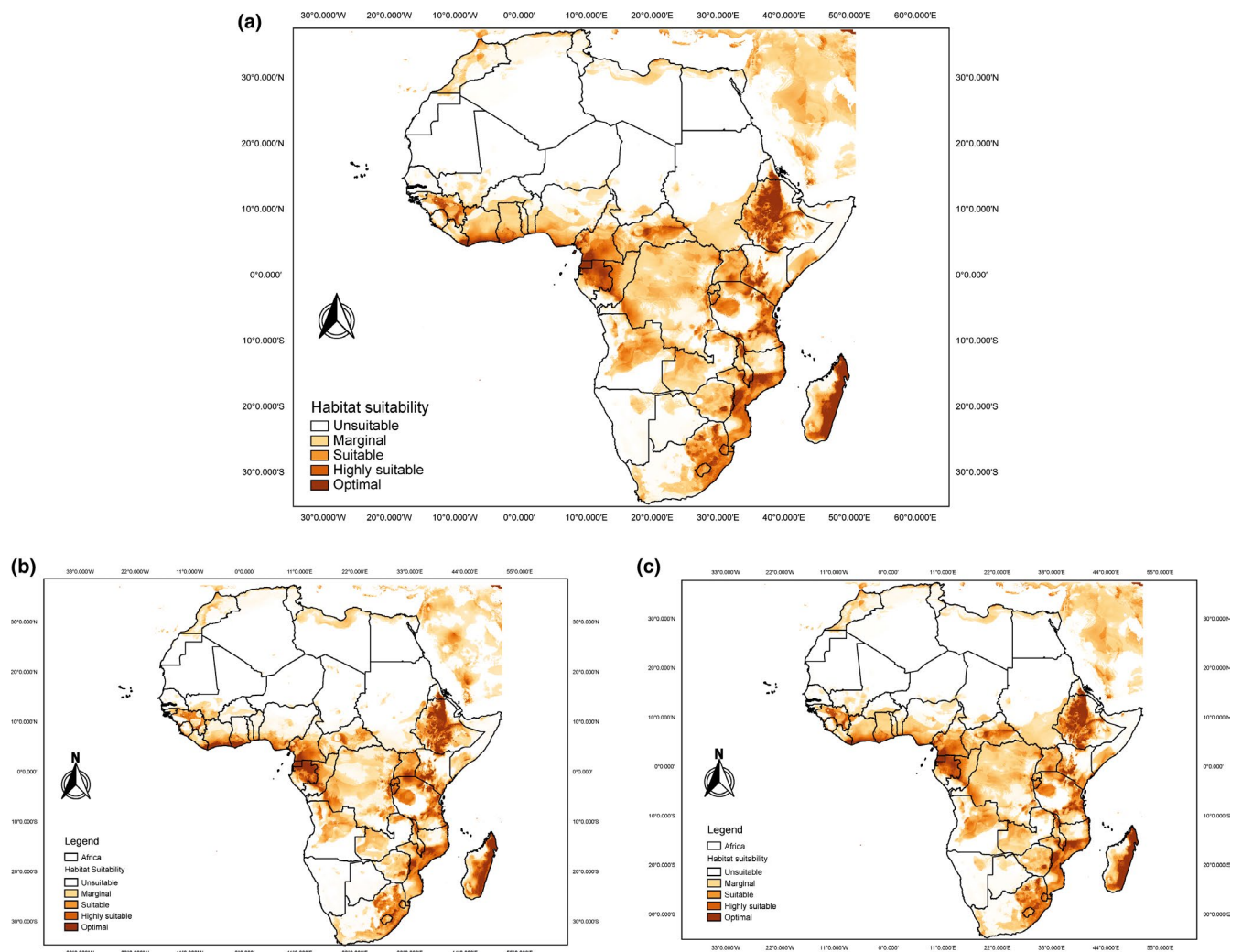


FIGURE 1 Potential distribution of Huanglongbing in Africa, as predicted by three-model consensus (BIOCLIM, MaxEnt and Boosted Regression Trees) showing (a) potential current distribution of Huanglongbing in Africa, (b) future (2055) potential distribution of Huanglongbing (HLB) in Africa under extreme scenario (Representative Concentration Pathway 8.5) and (c) future (2055) potential distribution of Huanglongbing (HLB) in Africa under moderate scenario (Representative Concentration Pathway 4.5). The maps were generated using the World Geodetic System 1984 (WGS84) projection

3.3 | Predicted future (2050) distribution of Huanglongbing in Africa

The future distribution of HLB in Africa predicted using the three-model consensus also showed a wide distribution under the moderate (CMIP5 rcp4.5) climate scenario and the extreme (CMIP5 rcp8.5) climate change scenarios. All countries of Central, Eastern, Southern and Western Africa showed marginal to optimal habitat suitability for Las (Figure 1). The extreme scenario (Figure 1b) showed increased areas of habitat suitability compared to the moderate scenario (Figure 1c). A shift in the distribution of HLB was shown by the difference in the hotspots between the current and the future scenarios showed. Under the extreme scenario, the areas of optimum habitat suitability absent in the current distribution and present in the future distribution were predominantly in Western, Central and Eastern Africa (Figure 2a), whereas under the moderate scenario, these areas were predominantly in Southern Africa (Figure 2b).

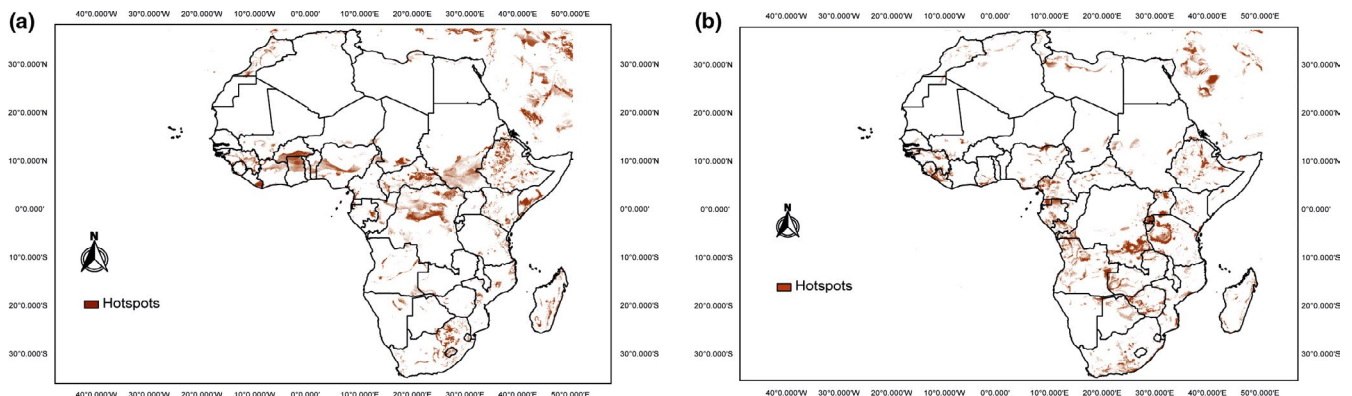


FIGURE 2 Difference in Las habitat suitability hotspots between the current distribution and future distribution under (a) extreme scenario (Representative Concentration Pathway 8.5) and (b) moderate scenario (Representative Concentration Pathway 4.5). The maps were generated using the World Geodetic System 1984 (WGS84) projection

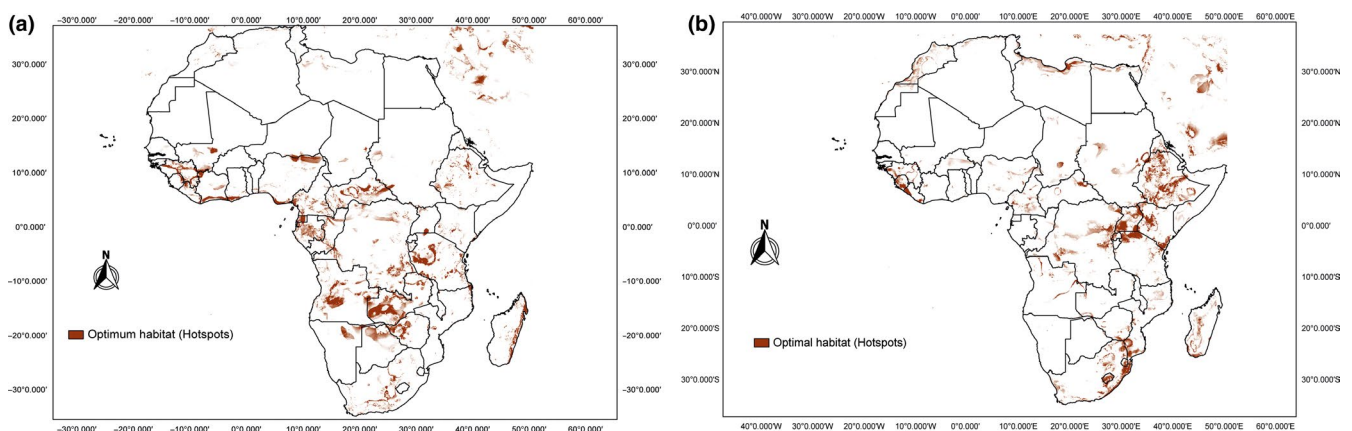


FIGURE 3 Predicted effect of climate change on Las habitat suitability hotspots areas: (a) Hotspot areas present under the moderate scenario (Representative Concentration Pathway 4.5) and absent under the extreme scenario (Representative Concentration Pathway 8.5) and (b) Hotspot areas present under the extreme and absent under the moderate scenario. The maps were generated using the World Geodetic System 1984 (WGS84) projection

3.4 | Predicted effect of climate change on habitat suitability of Huanglongbing in Africa

Assessment of predicted habitat suitability showed that there are more areas of optimal habitat suitability for Las under the extreme scenario (CMIP5 rcp8.5) than in the moderate scenario (CMIP5 rcp4.5) (Figure 3a). The major citrus exporting countries in Africa (Egypt, Ethiopia and South Africa) showed fewer hotspots in the moderate scenario than in the extreme scenario (Figure 3b).

3.5 | Predicted current distribution of African citrus greening globally

The predicted current global distribution of ACG obtained from the three-model consensus showed a marked distribution in large areas of Africa, South and Central America, Asia and Australia. Countries of South and Central America showed marginal to optimal suitability

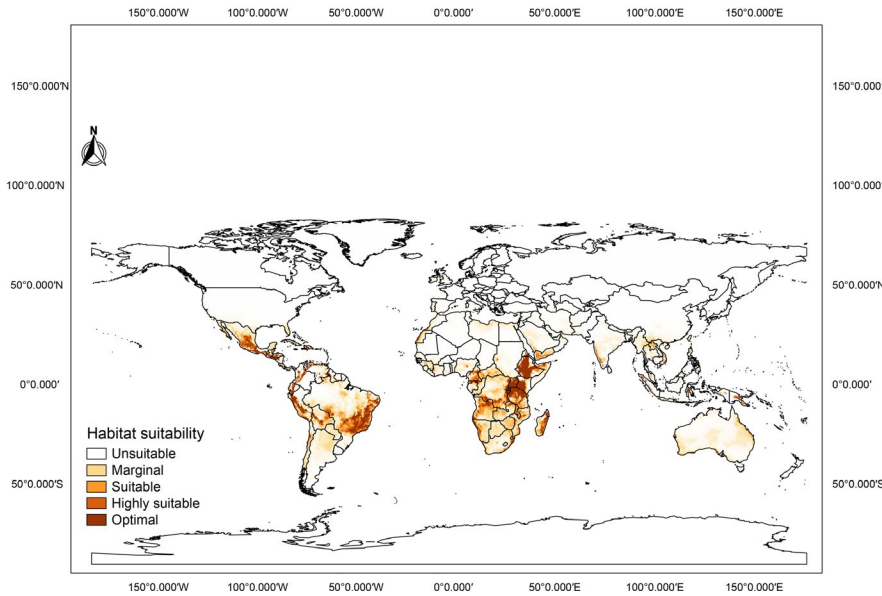


FIGURE 4 Three-model consensus (BIOCLIM, MaxEnt and Boosted Regression Trees) of global potential current distribution of African citrus greening disease. The map was generated using the World Geodetic System 1984 (WGS84) projection

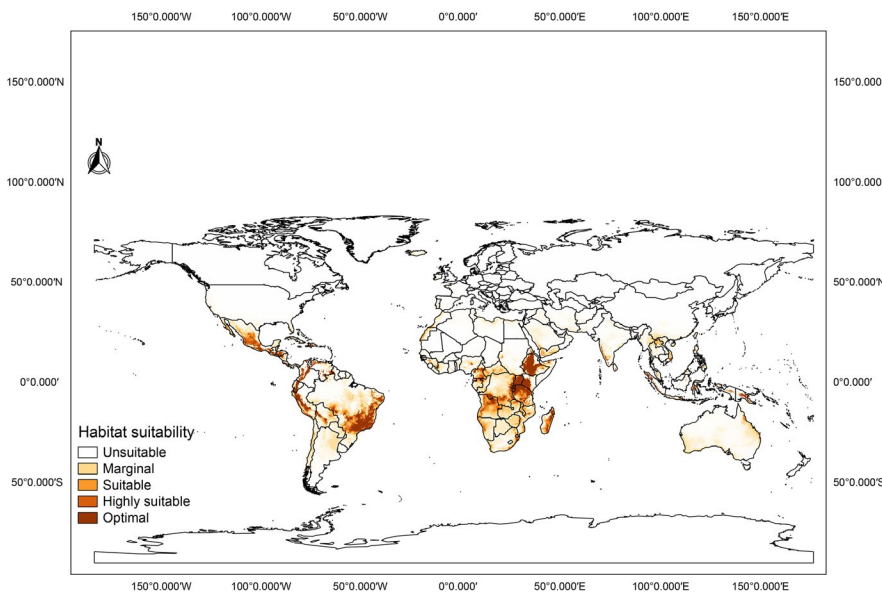


FIGURE 5 Three-model consensus (BIOCLIM, MaxEnt and Boosted Regression Trees) of global potential future (2055) distribution of African citrus greening disease under Representative Concentration Pathway 8.5 (extreme scenario). The map was generated using the World Geodetic System 1984 (WGS84) projection

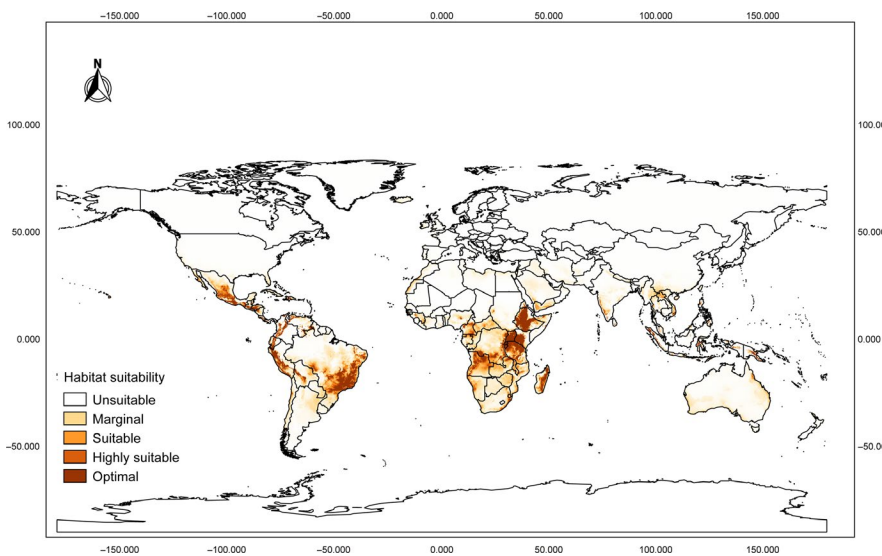


FIGURE 6 Three-model consensus (BIOCLIM, MaxEnt and Boosted Regression Trees) of global potential future (2055) distribution of African citrus greening disease under Representative Concentration Pathway 4.5 (moderate scenario). The map was generated using the World Geodetic System 1984 (WGS84) projection

for the pathogen, while the southern fringe of North America, especially Florida, showed marginal suitability. Most Asian countries, as well as Australia, showed marginal suitability for Laf, while Indonesia, Papua New Guinea, Singapore and the Philippines were highly suitable. The United Kingdom, Spain and Portugal showed areas of marginal suitability (Figure 4).

3.6 | Predicted future (2050) distribution of African citrus greening globally

The predicted future distribution of ACG globally under the extreme scenario (CMIP5 rcp8.5) showed an increase in the areas of habitat suitability from the current distribution from the current scenario (Figure 5). Specifically, few areas showed a slight alteration: Papua New Guinea showed a slight increase, while Australia showed a decrease. The predicted future distribution of ACG globally under the moderate scenario (CMIP5 rcp4.5) showed a decrease in the areas of habitat suitability from the current distribution from the current scenario (Figure 6).

4 | DISCUSSION

Huanglongbing caused by Las is a destructive disease of citrus worldwide and has recently been reported on the African continent (Ajene et al., 2019; Saponari et al., 2010), while Laf-associated African citrus greening disease has been reported in Africa since the 1920s (Buitendag & von Broembsen, 1993; Massoné et al., 1976; McClean & Oberholzer, 1965; Rasowo et al., 2019; Roberts et al., 2017). Vector-based modelling has been the norm for predicting the distribution of HLB because modelling ecological niches for plant pathogens can be a problematic endeavour considering the different variables involved. However, environmental and climate data, including monthly temperature and rain, are assumed to reflect the climate suitability for the growth and development of different organisms, including plant pathogens (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). Ecological factors such as temperature, light and water availability, soil fertility, methane and CO₂ concentration can have positive, neutral or negative effects on disease development, as pathogens show varying responses to these factors (Velásquez et al., 2018). Furthermore, increased industrialization of developing countries leads to has a direct effect on the CO₂ emissions and hence an effect on the distribution of plant pathogens (Anderson, 2010). Studies have shown CO₂ levels affect the photosynthetic rate and crop yield of C₃ plants such as soybean, cotton, oranges and lemon. The increase in CO₂ concentrations has also been shown to increase disease severity in some plants such as rice and wheat (Kobayashi et al., 2006; Váry, Mullins, McElwain, & Doohan, 2015). Precipitation and soil moisture have a crucial effect on plant disease establishment, because most plant diseases are favoured by conditions of rain, high air humidity and high soil moisture (Velásquez et al., 2018). For instance, fungal pathogens such as *Magnaporthe oryzae* require

a minimum of five hours of leaf wetness for disease establishment (Magarey, Sutton, & Thayer, 2015). Temperature also plays a vital role in plant–pathogen interaction. Disease development in plants generally have an optimal range; for example, *Xanthomonas oryzae* has been shown to have an optimal daytime temperature of 35°C and night time temperature of 27°C for the infection of rice (Horino, Mew, & Yamada, 1982), while a temperature range between 26°C and 31°C are optimal for papaya ringspot virus to colonize papaya (Mangrauthia, Singh Shakya, Jain, & Praveen, 2009). Temperature is a crucial factor in the development of plant diseases, as the projected increase in the global temperature may change the areas where crops are susceptible to a particular pathogen (Velásquez et al., 2018). Furthermore, certain diseases with the potential to cause epidemics may never do so due to transient shifts in temperature (Velásquez et al., 2018). Temperature also has a significant effect on vectorborne pathogens such as Las transmitted by *Diaphorina citri*, Laf transmitted by *Trioza erytrae* and Banana bunchy top virus (BBTV) transmitted by *Pentalonia nigronervosa* (Robson, Wright, & Almeida, 2007) and influences the incidence and severity by affecting the vector (Robson et al., 2007). Temperatures favourable for the *D. citri* and *T. erytrae* could explain epidemics in Las and Laf even if the conditions are suboptimal for the bacterial replication.

HLB is known to be most severe in warm and wet climates (Bové, 2014), which are common in the areas that showed optimal habitat suitability in this study. We found that the environmental variables which had the highest contribution to the models were the temperature and temperature-dependent precipitation variables. Specifically, the precipitation of the wettest month had the highest contribution to the habitat suitability of Liberibacter, while the annual mean temperature was the most important variable when considered in combination with other variables. These results are in agreement with a previous study that showed that optimal and limiting temperature conditions for HLB depend on rainfall (Shimwela et al., 2016). Also, the vector *D. citri* is heat-tolerant and survives in tropical and subtropical climates.

The ensemble approach to plant pathogen predictive modelling carried out in this study corroborates previous vector-based approaches to HLB prediction. Our results highlight the potential distribution of Las in Africa and show that large areas of Central Africa, Eastern Africa, Southern Africa and some parts of Western Africa are highly suitable for HLB establishment. This is in agreement with a global study on the potential spread of HLB that used two correlative modelling approaches to predict the potential distribution of Las based on the distribution of the insect vector (Narouei-Khandan, Halbert, Worner, & VanBruggen, 2015). The authors also pointed to central and south-eastern parts of Africa as highly suitable for HLB. Our results concur with a previous study highlighting areas in West Africa as highly suitable for HLB, also based on habitat suitability of the vector, as obtained from a multimodel framework (Shimwela et al., 2016). The differences in the predictions between the current and future distributions showed clear variations between the distributions under the moderate and extreme scenarios, and overall, the extreme scenario

showed an increased distribution of the disease. The inclusion of the presence points of Las in Ethiopia from previous studies to the background points validated the accuracy of the ensemble approach to plant pathogen predictive modelling. The predicted optimal areas for the establishment of Las were the same areas where the pathogen was found in previous studies (Ajene et al., 2019; Saponari et al., 2010). In 2016, the presence of Las was reported in Uganda (Kalyebi et al., 2016). However, the presence points from Uganda were not included in the models as the report was shown to be a misidentification of LafCI (Roberts et al., (2017). In Uganda, large areas of marginal suitability and a few areas of high suitability for Las were predicted but no areas of optimal suitability for the pathogen were observed.

Citrus cultivation in most parts of Africa is a key source of livelihood for small holder farmers as production ranges from small to medium scale (Aidoo et al., 2019). In Kenya and Tanzania, ACG has had the greatest impact on citrus production in the cooler highland regions, causing yield losses of 25%–100% (Pole, Ndung'u, Kimani, & Kagunu, 2010). The small-scale production is mostly in backyard gardens with minimal pest control measures applied; this is usually problematic as it serves as reservoirs for plant diseases and their vectors. This is key in the distribution of Las and Laf because these backyard gardens may become a constant source of infestation by the vectors of Las and Laf to the large-scale commercial orchards which are constantly surveyed, and pest control measures applied.

African citrus greening, the disease caused by the pathogen Laf, has only been reported in Africa thus far. However, our study highlighted the potential areas of suitability for Laf in other parts of the world. Our predictive maps showed large areas of the Americas, Asia and Australia included in the potential distributional range of ACG in the world. In Europe, only the Iberian Peninsula showed suitability for the disease, although marginal. However, the recent introduction of *T. erytrae*, the native African vector of Laf, to Spain and Portugal (Cocuzza et al., 2017; Siverio et al., 2019) highlights increased potential for spread of ACG outside Africa. Thus, the prediction of potential habitat suitability of the bacteria in other areas of the world provides valuable information required for monitoring and implementation of preventive measures.

Vector-based modelling has shown that it took more than seven years after documented individual insect-based infections for the entire grove to become fully symptomatic (Kobori, Takasu, & Ohto, 2012). In the context of invasive pathogens such as Las, this approach could prove fatal as infected saplings from seemingly uninfected orchards can be unintentionally transferred to new groves, thereby facilitating non-vector dissemination of the disease. Infection of trees due to the presence of *D. citri* can occur such that, within 1–2 years, the entire grove can be asymptotically infected (Lee et al., 2015). HLB surveillance has been problematic because infected citrus groves may not show symptoms of the disease until up to 5 years after infection (Manjunath et al., 2008). Therefore, surveillance has

relied on the detection of the pathogen within insects because the infection can be detected in the vector months before the plants develop symptoms (Manjunath et al., 2008; Shen et al., 2013). Our projection of the distribution of Las will inform; closer vector monitoring in citrus-producing areas with high suitability for HLB establishment, as well as periodic testing of asymptomatic citrus plants in these high-risk areas.

Liberibacter presence points obtained from detection in citrus plants and used in the models show that the habitat suitability for citrus production has an implicit impact on the potential distribution of HLB, ACG and their vectors *D. citri* and *T. erytrae* (Narouei-Khandan et al., 2015). Our study showed variations between the current predicted habitat suitability of Las and the future predictions under different climate change scenarios. This suggests that extreme changes in climate influence the potential establishment of the disease in areas suitable for citrus production. The change in the distribution of HLB in climate change scenarios showed a dramatic shift from a sparing distribution in Western, Central and Southern Africa under a moderate scenario to a higher distribution concentrated in Northern, Eastern and Southern Africa under the extreme scenario. This prediction alerts to the possibility that the top citrus exporting countries in Africa may be greatly affected, as rising temperatures and rainfall patterns will affect the distribution of HLB and its vector.

We demonstrated the potential of an ensemble approach using bioclimatic variables to model the distribution of plant pathogens and predict future habitat suitability of Liberibacter species. These results constitute an early alert for citrus-producing regions where HLB and ACG are not yet present. Plant protection strategies based on future habitat suitability of plant pathogens would be an important inclusion in the integrated pest management systems for citrus production.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Raster layers of the models are available to managers and the scientific community upon request.

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BIOSKETCHES

The project “Strengthening Citrus Production Systems through the Introduction of Integrated Pest Management Measures for Pests and Diseases in Kenya and Tanzania” focused on the different aspects of pests and diseases of citrus in East Africa. The specific aim of the research team is to assess the current status of the citrus industry in Africa, pest and diseases of the crop, greening disease in Africa, resolve the identities of *Candidatus Liberibacter* species associated with citrus greening disease and identify potential management strategies against the disease to protect the citrus industry on the continent. **Inusa Jacob Ajene** is a lecturer and PhD student under DAAD scholarship programme with a background in molecular plant pathology and epidemics.

Author contributions: I.J.A., F.K., S.E. and S.M conceived the ideas; I.J.A. and B.A.R. collected the data; I.J.A analysed the data; and I.J.A., B.V.A, F.K. and G.P. led the writing.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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