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# Landscape-scale biogeographic distribution analysis of the whitefly, *Bemisia tabaci* (Gennadius, 1889) in Kenya

Bester Tawona Mudereri<sup>1,2</sup> · Emily Kimathi<sup>1</sup> · Tavengwa Chitata<sup>2,3</sup> · Moleseng Claude Moshobane<sup>4,5</sup> · Elfatih M. Abdel-Rahman<sup>1,6</sup>

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## Abstract

Understanding the drivers of habitat use and the suitability of landscape patches by invasive insect species is crucial in their control and management. This simplifies the comprehension of the processes driving invasive insect population dynamics, their functioning, and potential disturbance within their introduced ecosystems. The whitefly, *Bemisia tabaci* (Gennadius, 1889), is ranked among the world's 100 most invasive insect pests and is a major threat to many important cash and staple food crops. In this study, we identified levels and areas at risk of the invasive *B. tabaci* at a landscape scale in Kenya using elevation, land surface temperature, land cover, rainfall, and temperature of the present and future (the year 2050 of the community climate system model version 4 (CCSM4)), and using a maximum entropy (MaxEnt) model. Our results show that ~14% of Kenya's land area is currently at risk of *B. tabaci* invasion. This area is likely to increase to 15% and 16% because of climate change using the representative concentration pathways (RCP) i.e. RCP 2.6 and RCP 8.5 of the year 2050, respectively. Land cover, particularly croplands, provided the highest permutation importance together with precipitation variables in determining the occurrence of the pest. A wide preference range within elevation, precipitation, temperature, and plant hosts was observed suggesting a great potential for *B. tabaci* to establish in many areas in Kenya and potentially in other countries with similar conditions in Africa. However, the predicted increases in global temperature could reduce the pest's preferred environment, but this also imposes limitations on the productivity of many of its host crops. Therefore, our results can be used in adaptive management to control the pest and to prevent the introduction and spread of *B. tabaci* in areas where it is yet to establish.

**Keywords** Biogeography · Climate change · Ecological niche · Entomology · Invasive species

## Introduction

The Whitefly, *Bemisia tabaci* (Gennadius, 1889) (Hemiptera: Aleyrodidae) is an insect pest of global importance that occurs widely in many countries, including Kenya (CABI 2020). Many studies have established that *B. tabaci* can survive on more than 600 different plant species making it one of the most invasive and devastating insect pests of field and horticultural crops (Kumar et al. 2019; Parry et al. 2020). Early research has also shown that the pest has the potential to attack its host and transmit several plant viruses that cause diseases to some of the most important staple and ornamental crops (Stansly et al. 2010; Bradshaw et al. 2019; Kanakala and Ghanim 2019; CABI 2020; Kriticos et al. 2020). In Africa, the insect is known to cause crop (e.g. cassava, cotton, sweet potato, tobacco, watermelon) losses of up to 100%, threatening livelihoods of more than 2 million households in sub-Saharan Africa (SSA: Gangwar and Charu 2018).

✉ Bester Tawona Mudereri  
bmudereri@icipe.org

- <sup>1</sup> International Centre of Insect Physiology and Ecology (ICIPE), P.O. Box 30772, Nairobi 00100, Kenya
- <sup>2</sup> Department of Animal and Wildlife Science, Midlands State University, P. Bag, 9055 Gweru, Zimbabwe
- <sup>3</sup> Department of Geography, The University of Sheffield, Western Bank, Sheffield S10 2TN, UK
- <sup>4</sup> South African National Biodiversity Institute, Pretoria National Botanical Garden, 2 Cussonia Avenue, Brummeria, Pretoria, South Africa
- <sup>5</sup> Department of Biology, Sefako Makgatho Health Sciences University, Ga-Rankuwa, South Africa
- <sup>6</sup> Department of Agronomy, Faculty of Agriculture, University of Khartoum, 13314 Khartoum North, Sudan

The pest status of *B. tabaci* insects is complex because the assessment of the mitochondrial cytochrome oxidase 1 (mtCO1) gene shows that *B. tabaci* is a complex of 11 genetic groups (CABI 2020). These genetic groups are composed of at least 34 morphologically indistinguishable species (De Barro et al. 2011; Tay et al. 2012; Boykin and De Barro 2014). This creates daunting complexities to tailor-make mechanisms using the most common pest control methods such as the use of integrated pest management tools (Kanakala and Ghanim 2019; Parry et al. 2020). The challenges and complexity of *B. tabaci* control are further enhanced by its high breeding and dispersion rate, polyphagy, and excessive resistance to insecticide (Kumar et al. 2019; CABI 2020). Thus, on-farm scale control technologies are needed to constrain the spread of the pest to new areas. However, these on-farm approaches require spatial explicit locational information on farms experiencing *B. tabaci* occurrence and potential farms at risk for coordinated localized intervention. This information affords precise and accurate intervention mechanisms and allows for the prescription of site-specific and befitting control approaches (Mudereri et al. 2020a). Unfortunately, the landscape scale requisite baseline information of this devastating pest occurrence, spatial configuration, infestation extent, and intensity remains rudimentary in SSA, including Kenya (Labou et al. 2017; Macfadyen et al. 2018; Ramos et al. 2018).

The global geographic expansion of many crop insect pests has increased in the last decade, because of the increased agriculture exports across continents and the exchange of seeds (McCullough et al. 2006; Tay et al. 2012; Moshobane et al. 2019). Thereafter, the ability of a pest to establish and become invasive in a new area relies on many factors that determine the availability of the hosts and ensure the successful completion of their development cycles (Azrag et al. 2018; Tonnang et al. 2020). Among others, precipitation and temperature have been reported by earlier studies as key environmental factors that affect the ability of insect pests to adapt to an area and ultimately their distribution (Labou et al. 2017; Azrag et al. 2018; Otieno et al. 2019b). These variables are however highly correlated with elevation, land surface temperature (LST), and frequently influence the land use and land cover (LULC) regimes (Labou et al. 2017; Saghafipour et al. 2020). Although the LULC (availability of the host plants) parameter is highly dynamic, insects such as *B. tabaci* are often associated with specific LULC classes such as croplands (Gangwar and Charu 2018). Therefore, if the conditions are suitable in the introduced area, the pest species becomes invasive and establishes itself, causing severe negative impacts on the local ecosystem and economy (Ramos et al. 2018; Saghafipour et al. 2020). Therefore, as the climate factors are the anchors of the other variables, they stand out as the key elements impacting the abundance and distribution of most arthropod species including *B. tabaci* (Saghafipour et al. 2020). Thus,

there is a need for an immediate understanding of the potential risks that will be brought by climate change and crop insect pests such as *B. tabaci*.

It is predicted that climate change will have a great impact on most hosts of insect pests such as maize (Midega et al. 2018), wheat and cotton (Kumar et al. 2019), rice (Rodenburg et al. 2010), and other crops (Abd-Rabou and Simmons 2015; Ramos et al. 2018; Sokame et al. 2020), within the natural and agroecosystems (Sango and Godwell 2015; Mudereri et al. 2019). As the atmospheric CO<sub>2</sub> and temperature increase or decrease, they will likely result in warmer, colder, wetter, or dryer conditions (Kriticos et al. 2020). Thus, these conditions may become suitable for specific pests or hosts (Macfadyen et al. 2018). For instance, Africa climate projections indicate temperature increases of between 3 °C to 6 °C compared with those at the end of the twentieth century, particularly in the in-land sub-tropics (Serdeczny et al. 2016). These temperature increases are likely to cause frequent and severe heat incidents, an upsurge in aridity, and variations in precipitation across Africa particularly the arid and semi-arid regions like North Africa, western South Africa, Botswana, Namibia, and parts of Kenya (Kotir 2010; Niang et al. 2014; Serdeczny et al. 2016). Thus, a mean temperature increase will likely speed up the maturing period of numerous insect species, subsequently altering their known life cycles, reproductive success, and mobility (Ramos et al. 2018). Therefore, the distribution of many species will likely depend on the prevailing climate conditions, which generally define most of the geographical distribution observed in many species distribution modeling outputs (Otieno et al. 2019b). Despite the impact of *B. tabaci* and the large body of research on the species, the potential impact of climatic change on the geographical distribution of *B. tabaci* at a landscape scale remains understudied in SSA regions like Kenya.

Species distribution models (SDMs) are tools widely used in understanding the habitat suitability of an organism (Ramos et al. 2019; Ajene et al. 2020a, b). Furthermore, SDMs are one of the most important tools that are currently available to assess the potential impacts of climate change on the habitat suitability and distribution of a species. They are commonly used to project potential future changes in the geographic ranges of species to inform planning and developing control mechanisms especially for pests such as *B. tabaci*. Although this species is already widely distributed globally, there is a great need to access and project its future distribution at scale mainly targeting the data deficient areas such as in SSA countries. Earlier studies have already demonstrated the distribution of *B. tabaci* globally (Ramos et al. 2018), in Europe (Gilioli et al. 2014), in South America (Ramos et al. 2018, 2019), the Middle East, and Asia (Kriticos et al. 2020), but very little has been done in SSA.

Predicting the possible species distribution using SDMs involves combining current occurrence data of a species with appropriate environment variables (Ajene et al. 2020a;

Mudereri et al. 2020b). SDMs have been used widely for many purposes in conservation biology, biogeography, and ecology (Muposhi et al. 2016; Masocha and Dube 2017; Shekede et al. 2018). Examples of the frequently used SDMs include the ecological niche factor analysis (ENFA), genetic algorithm for ruleset prediction (GARP), random forest (RF), and maximum entropy (MaxEnt). All these models are designed to predict species distribution using multiple environmental variables under current and potential future climate change (Biber-freudenberger et al. 2016). Nevertheless, contrasted with other models, MaxEnt is reliably better in its predictive performance, versatility, and usefulness, as evidenced by over 1000 ecological applications published since 2006 (Merow et al. 2013).

Thus, in this study, we used the MaxEnt to model the biogeography associated with the risk of *B. tabaci* at a landscape scale using the present and future (the year 2050) climate scenarios and Kenya as a study site. Predicting geographical distributions of *B. tabaci*, at a localized scale provides essential local guidance and solutions to the control and management efforts in regions with a higher risk of invasion or establishment. Despite the global modeling of the distribution of *B. tabaci*, the species remains understudied within localized contexts such as in Kenya (Ramos et al. 2018). Moreover, predicting areas that require control and intervention with high precision, is essential to safeguard the success of producing viable and sustainable cropping systems that are designed for the control of *B. tabaci*. Thus, this study contributes to the understanding of the Kenyan trend in *B. tabaci* occurrence and feeds into the broad body of knowledge that aids the understanding of the connectivity of the global ecosystems for *B. tabaci* establishment and control. The specific objectives of the study were to: (1) predict and understand the determining factors of the suitability of *B. tabaci* habitat at a localized scale in Kenya and (2) estimate the suitable areas using the future scenarios i.e. the lowest representative concentration pathways (RCP 2.6 and highest RCP 8.5) predicted CO<sub>2</sub> emissions in the year 2050.

## Study area

The study was conducted in Kenya, which is subdivided into 47 very diverse counties covering a total area of 582,650 km<sup>2</sup>. Kenya is bound by latitudes 4° 45' S and 5° 25' N and longitudes 33° 55' E and 41° 55' E, bordering South Sudan to the northwest, Uganda to the west, Somalia to the east, Tanzania to the south, and Ethiopia to the north (Fig. 1). It has a coastline with the Indian Ocean on the southeast, which contains swamps of East African mangroves. The central and western Kenya is characterized by the Kenyan Rift Valley and home to the highest mountain, Mount Kenya, and Mount Elgon on the border between Kenya and Uganda.

Approximately 80% of Kenya, lies in the semi-arid to very arid agroclimatic zones, which are predominantly inhabited by pastoralists and agro-pastoralists with an average rainfall of between 200 mm/yr and 600 mm/yr and mean annual temperature range of 23 °C–34 °C. These regions support about seven million people and more than 50% of the country's livestock population. The Central and Western regions exhibit cooler (14 °C–28 °C) and wetter climatic conditions (950 mm/yr–3000 mm/yr) which are particularly favorable for crop production and thus the occurrence of most crop pests. The two regions experience a bimodal rainfall distribution with the major crops grown in these regions being maize, tomato, vegetables, and beans, which are in most cases interspersed with a variety of fruit trees, tea, and coffee. In the low-lying coastal region with higher temperatures and higher humidity levels, farmers cultivate a wide range of food crops as well as tree crops like coconut palms, mango, citrus, and pawpaw. The Eastern region is in the hot and dry semi-arid savannah biome and has similar cropping patterns as the coastal region.

## Methodology

### *B. tabaci* occurrence data collection

The reference distribution data of *B. tabaci* in Kenya ( $n = 201$ ) that were used in the analysis were obtained from the Global Biodiversity Information Facility (GBIF: (GBIF 2020). The GBIF (<https://www.gbif.org>) is the largest global online database for occurrence data of over a billion biological records collated from field observed data contributed by accredited institutions across the world. The data were filtered to eliminate duplicate samples and samples without detailed location information. Further, to reduce sampling bias, only one sample was kept for each 1 km × 1 km grid to match the resolution of the environmental variables as suggested by Phillips et al. (2009). The latitude and longitude of the retained samples ( $n = 83$ ) with detailed location information were validated using the Google Earth platform (<https://www.google.com/earth/>). The retained independent occurrence points of the *B. tabaci* were used as the occurrence data in the MaxEnt modeling and for the generation of the bias file.

### Predictor variables

The predictor variables that were used in this study were derived from, bioclimatic, elevation, land cover, and LST. Variable spatial and temporal resolutions are a key notion in determining a dataset's fitness for a given usage as they influence the pattern that can be observed during the analysis (Degbelo and Kuhn 2018). However, Csillag et al. (1992) indicated that when combining environmental variables of

varying resolutions there is no absolute best resolution since this depends on the objective of the study. In our case, we had variables ranging in a pixel size of  $5.6 \text{ km} \times 5.6 \text{ km}$  to approximately  $20 \text{ m} \times 20 \text{ m}$  spatial resolution. This variation influences the integration of multiresolution variables within models particularly MaxEnt. We, therefore, counteracted the variation by resampling all the datasets to the  $1 \text{ km} \times 1 \text{ km}$  pixel size to match the bioclimatic variables. All variables used in this study were clipped to the Kenyan administrative boundary and saved in the .asc file format for input in the MaxEnt model. The ‘raster’ package (Hijmans 2020) in R (R Core Team 2020) was used for all these processes.

### Bioclimatic variables

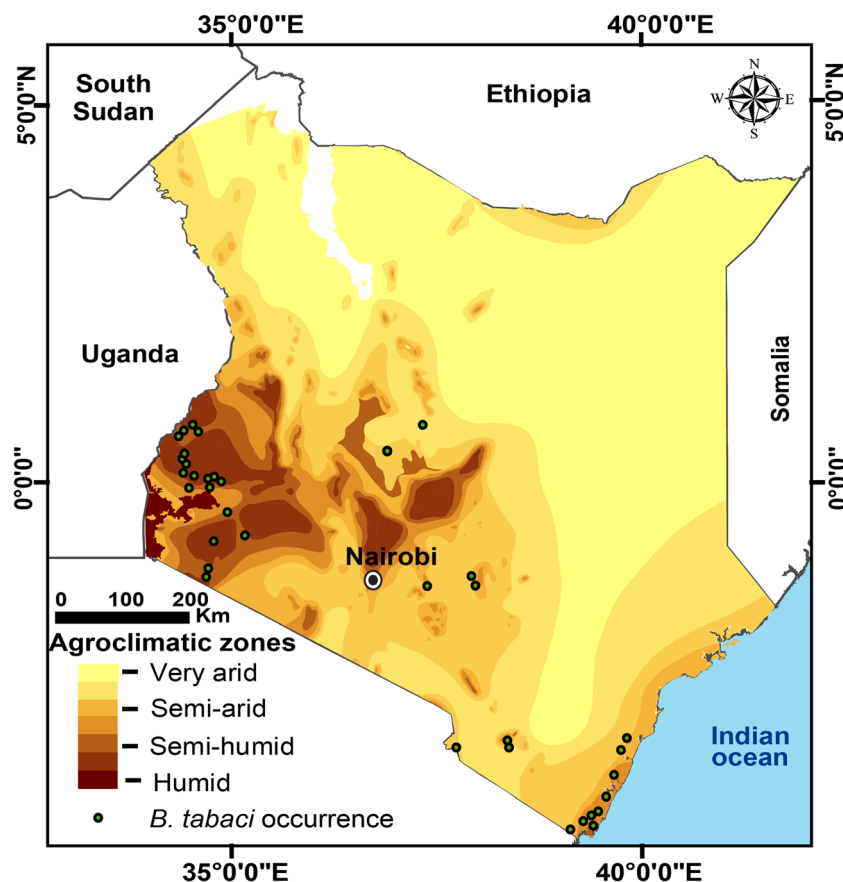
We initially considered 19 bioclimatic variables that were downloaded from the WorldClim platform ([www.worldclim.org](http://www.worldclim.org)) at approximately  $1 \text{ km} \times 1 \text{ km}$  spatial resolution (Fick and Hijmans 2017; Booth 2018). These data are interpolated from data obtained from weather stations globally using the thin-plate smoothing spline algorithm implemented in ANUSPLIN (Fick and Hijmans 2017). For the future climatic scenarios, global climatic data from two of the four RCPs set by the intergovernmental panel on climate change (IPCC) using the

total radioactive forcing of values 2.6, 4.5, 6, and  $8.5 \text{ watts/m}^2$  (IPCC 2014) were used as the future climatic scenarios. Specifically, the current long-term bioclimatic data (1950–2000) and a fourth version of the community climate system model (CCSM4) derived from a one-time step i.e. 2050 (average of predictions for 2041–2060) of the future climate data on the minimum (based on the Paris Agreement targets) and maximum (worst case) emission i.e. RCP2.6 and RCP8.5, respectively, were used to capture the whole range of future climate possibilities. Bioclimatic variables encompass both precipitation and temperature variables that have been reported in literature to influence the occurrence and distribution of most insects including *B. tabaci* (Azrag et al. 2018; Pathania et al. 2020).

### Land surface temperature

The ‘daytime’ land surface temperature climate modeling grid (LST\_Day\_CMG) was downloaded from <https://lpdaac.usgs.gov/products/mod11c2v006/> (Wan et al. 2015). Specifically, we used the long-term ‘multi-day’ MOD11C2 LST product of  $5.6 \text{ km} \times 5.6 \text{ km}$  spatial resolution available from the year 2000 to the present. We hypothesized that surface fluxes measured by the temperature at the land surface would influence

**Fig. 1** Location of Kenya relative to its neighboring countries in Africa, the agroclimatic zones of Kenya, and the *B. tabaci* occurrence points obtained from the Global Biodiversity Information Facility (GBIF). The map was developed using QGIS software (<https://www.qgis.org/en/site/>)



the general occurrence, and reproduction of *B. tabaci* and thus habitat suitability (Saghafipour et al. 2020).

### Elevation

Elevation was simulated from the shuttle radar topographic mission (SRTM) data which is available at approximately 90 m pixel size digital elevation model (DEM) with a vertical error of less than 16 m (CGIAR-CSI 2019). The elevation was anticipated to influence the occurrence and propagation of *B. tabaci* by altering precipitation, temperature, vegetation including crops, and the angle, direction, and intensity of the sun on the earth's surface (Azrag et al. 2018; Ramos et al. 2018; Bradshaw et al. 2019).

### Land cover data

We used the 20 m spatial resolution European Space Agency Sentinel-2 prototype land cover data for Africa which is freely downloadable from <http://2016africallandcover20m.esrin.esa.int/download.php>. The data are based on one year of Sentinel-2A observations from December 2015 to December 2016 classified using the random forest algorithm (ESA 2020). The legend includes 10 generic classes that appropriately describe the land surface at 20 m i.e. 'trees cover areas', 'shrubs cover areas', 'grassland', 'cropland', 'vegetation aquatic or regularly flooded', 'lichen and mosses / sparse vegetation', 'bare areas', 'built-up areas', 'snow and/or ice' and 'open water'. A total of nine classes were used in this study i.e. all the European Space Agency Sentinel-2 prototype land cover classes except for the 'snow and/or ice'. Studies have shown huge relevance and importance of land cover patterns on modeling insect pests' spatial distribution and association of *B. tabaci* with host crops such as tomato (Ramos et al. 2019), cassava (MacFadyen et al. 2018), cabbage (Labou et al. 2017) among other many crops (Gilioli et al. 2014; Abd-Rabou and Simmons 2015). This categorical data was formatted and resampled to the same standards of the other variables for input in the MaxEnt model.

### Collinearity test of predictor variables used in the MaxEnt model

To model the potential risk imposed by *B. tabaci*, there was a need for a set of explanatory variables that were independent of one another but of relevant ecological significance to the occurrence of the pest species (Makori et al. 2017). Thus, it was essential to reduce the expected collinearity among the 22 variables considered in this study i.e. the 19 bioclimatic and the three environmental variables. This procedure was conducted to avoid overfitting of the model and variable inflation (Dormann et al. 2013). We used 2-stage variable elimination criteria using the cluster analysis of the bioclimatic variables

and the variance inflation factor (VIF: Table 1). The bioclimatic variables provided by WorldClim (Fick and Hijmans 2017), are all derived from the same data, hence are highly correlated since they are mainly based on temperature and precipitation (Gaudreau et al. 2018). In the first step, we used the 'virtual species' package (Leroy et al. 2016) in R-software (R Core Team 2020) to initially explore the clusters of the spatial correlation of the 19 bioclimatic variables using the Pearson's correlation coefficient and the cluster tree (Fig. 2a). Five bioclimatic variables; namely Bio4, Bio5, Bio7, Bio13, and Bio19 (Table 1) were selected from this analysis using a cutoff of  $|r| = 0.7$ . These five bioclimatic variables were also chosen because of their ecological significance in predicting most crop insect pests suitable habitats (Azrag et al. 2018). In the second step, the bioclimatic variables that were selected from the cluster analysis were further analyzed together with the other three environmental variables using the VIF approach. A correlation matrix was then used to assess the correlation among the selected bioclimatic and the three other variables for inclusion in the final model (Fig. 2b).

VIF detects multicollinearity by taking each predictor and regressing it against the other variables in a multiple linear regression analysis (Plant 2012). The "usdm" package available in R and the "vifcor" function that iteratively selects pairs of variables with high linear correlation, then eliminates the one with the highest VIF were used for this analysis (Naimi et al. 2014). Similarly, we set the threshold at  $th = 0.7$ , which represents a Pearson's correlation coefficient ( $r \geq 0.7$ ). In principle, a VIF value greater than ten is evidence of the collinearity problem within a model (Dormann et al. 2013; Mudereri et al. 2020a). Therefore, 14 of the 22 variables that had VIFs greater than ten were eliminated leaving only eight suitable variables for the analysis.

### MaxEnt model and accuracy assessment

In our present study, we used the MaxEnt machine learning algorithm (version 3.4.1) (Phillips et al. 2006). MaxEnt was chosen for use in this study since it has been widely used to predict species distribution in many studies worldwide (Muposhi et al. 2016; Mpakairi et al. 2019). MaxEnt is statistically robust, adaptable to various environments, requires a relatively small sample size, and presence-only data (Marchioro and Krechmer 2018). We derived the optimum tuning and parameter settings for MaxEnt with presence-only *B. tabaci* observations from the "ENMevaluate" function in the package "ENMeval" (Muscarella et al. 2014) available in R-software (R Core Team 2020). This approach calculates multiple metrics to aid in selecting optimum model settings that balance goodness-of-fit and model complexity (Muscarella et al. 2014). Thus, the approach has been used by many studies because it allows a comparison of several configuration settings and to rank the resultant models

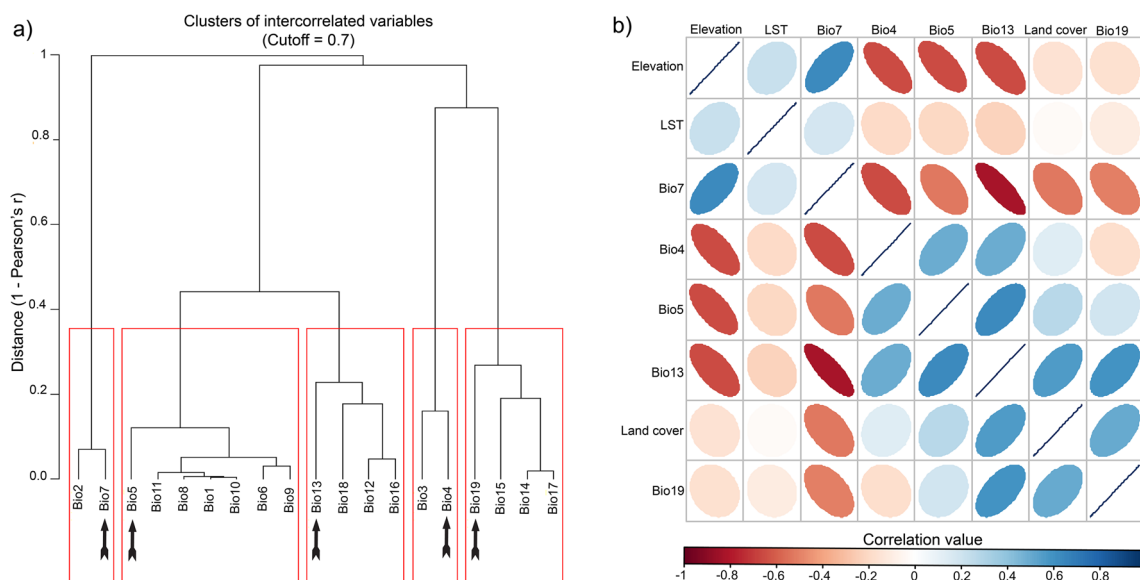
**Table 1** Environmental variables considered in the predictive modeling of the invasion risk by *B. tabaci* in Kenya

Variable name	Variable description	Unit	Variance inflation factor
<i>Bioclimatic variables</i>			
Bio4	Temperature seasonality (standard deviation ×100)		3.8
Bio5	Maximum temperature of the warmest month	°C	2.1
Bio7	Temperature annual range	°C	2.0
Bio13	Precipitation of the wettest month	mm	1.5
Bio19	Precipitation of the coldest quarter	mm	3.2
<i>Other variables</i>			
Elevation	Ground height above sea level	m	3.2
LST	Land surface temperature	K	1.4
Land cover	Land cover	Categorical	1.9

according to different metrics (Marchioro and Krechmer 2018; Arthur et al. 2019; Mudereri et al. 2020b). We used the following model parameters from the models with the lowest change in the Akaike information criterion ( $\Delta AIC_c = 0$ ) to perform the *B. tabaci* invasion risk assessment modeling in Kenya: linear/quadratic/product: 0.233, categorical: 0.250, threshold: 1.640, hinge: 0.500, beta-multiplier: 5.0, multivariate environmental similarity surface (MESS) analysis, clamping, extrapolate and fade with clamping. The MESS analysis in MaxEnt quantifies the measure of projection uncertainty by calculating the similarity of each point in the projected region to a set of reference points (Mesgaran et al. 2014), in our case into the future scenarios where occurrence reference data are unavailable.

Furthermore, we corrected for sampling bias using the eight variables used in this study (i.e. the five selected

bioclimatic variables, and elevation, LST as well as LULC:  $n = 8$ ) and the filtered *B. tabaci* points ( $n = 83$ ) as inputs. The kernel density estimator i.e. “kde2d” function of the “MASS” package (Venables and Ripley 2002) using the “block” sampling approach in R (R Core Team 2020) was used for this experiment. The “kde2d” function affords the performance of a two-dimensional kernel density estimate that is based on the spatial ‘X’ and ‘Y’ coordinates of the occurrence points to generate a raster bias file (Venables and Ripley 2002). It is important to correct for sampling bias particularly where data such as from GBIF is used since the collection of the data may be biased towards settlement areas, roads, or easily accessible areas (Phillips et al. 2009; Kramer-Schadt et al. 2013; Merow et al. 2013; Beck et al. 2014). MaxEnt modeling approach allows the inclusion of bias files in the model which facilitates the choice of background data within similar bias as the



**Fig. 2** a Cluster tree of the intercorrelated bioclimatic variables. The arrows show the selected variables based on their correlation distance from the other variables. b The correlation matrix of the eight selected

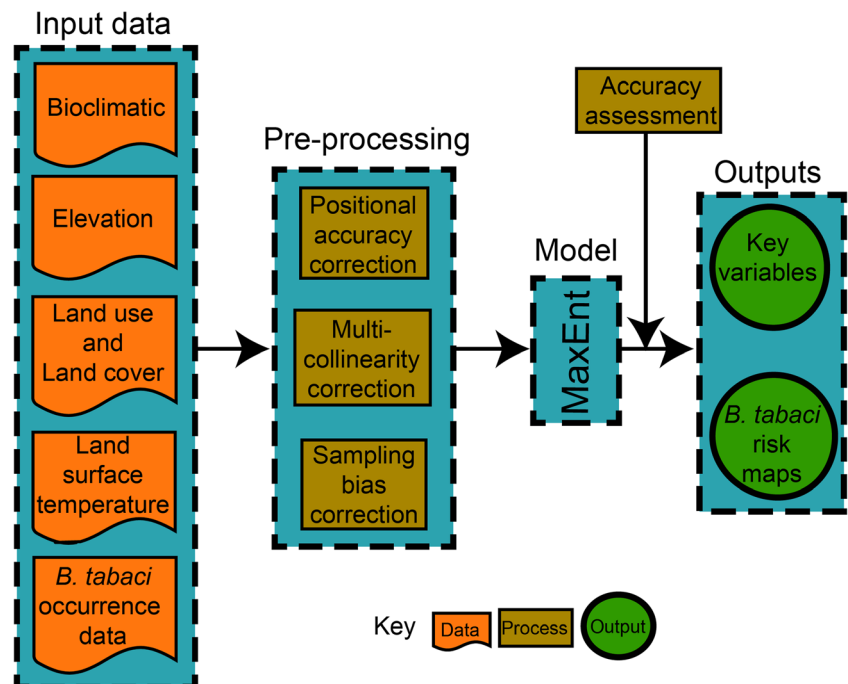
variables. Darker shades of blue and red show relatively high positive and negative correlation values, respectively, while lighter shades of blue and red show low positive and negative correlation values, respectively

occurrence data (Phillips et al. 2009). Our generated bias file was used for both the current and future projection models.

Furthermore, using the above-mentioned setting parameters, we replicated our model three times using the sub-sample method and averaged the three probability outputs to determine the optimum invasion risk and performance of the models. We used 70% ( $n = 58$ ) of the *B. tabaci* occurrence points for training, while 30% ( $n = 25$ ) were retained for testing the model performance. The comparative relevance of each environmental predictor for the models of *B. tabaci* was evaluated using the overall percentage contribution, permutation importance of each variable, the area under the curve (AUC) of receiver operating characteristic curves, and the Jackknife test (Phillips et al. 2006). The Jackknife test analysis has been reported to be the best comparative index for small sample sizes (Qin et al. 2017). Herein, we reported the AUC of the current climate scenario, since there are no future occurrence points to validate our future predictions. However, we assumed that if the model performs well with the currently available data, it would replicate the same strength when used to project predictions into the future.

Graphic outputs of the MaxEnt includes maps, highlighting the probabilities of invasion risk or habitat suitability of *B. tabaci* with values ranging from 0 (unsuitable) to 1 (optimum). We grouped the invasion risk probabilities into five categories as follows: very low (0–0.1), low (0.2–0.3), moderate (0.4–0.5), high (0.6–0.8), and very high (0.9–1). We used these five categories to estimate and intercompare the percentages of the suitability area predicted within the different climate scenarios. The summarized workflow followed in this study is shown in Fig. 3.

**Fig. 3** Flowchart of the process used in the predictive modeling of the invasion risk by *B. tabaci* in Kenya



## Results

### Maxent model evaluation

The models (both the test and training datasets) of the *B. tabaci* invasion risk in Kenya using the current and future (RCP2.6: 2050; RCP8.5: 2050) climatic variables showed a balance between goodness-of-fit and complexity (AUC > 0.90). This demonstrates that our models showed good predictive performance (Fig. 4).

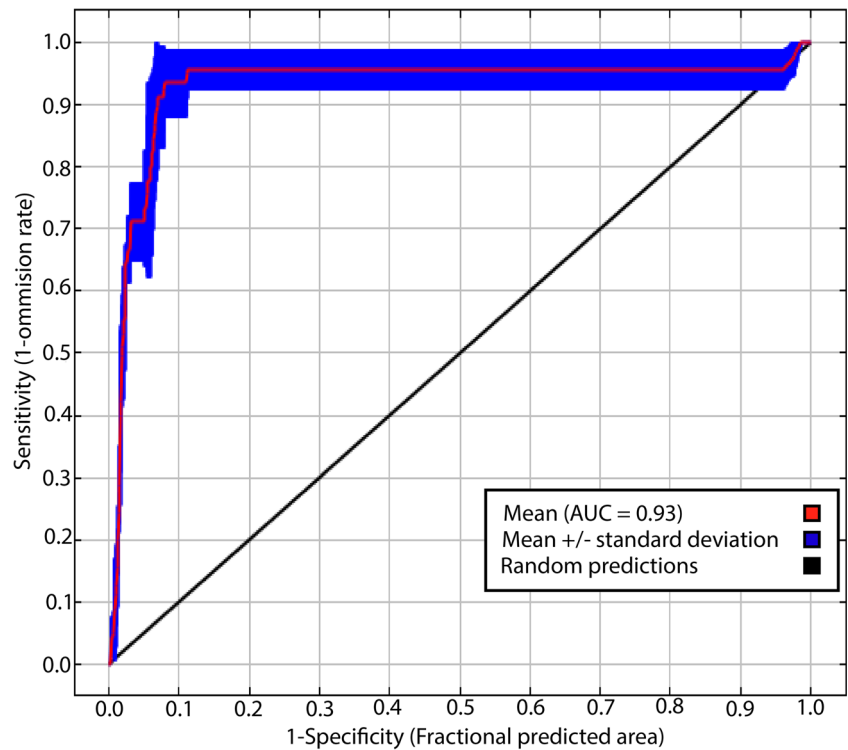
### Variable importance and response

In this study, precipitation-based variables were the most relevant predictors compared to temperature. Precipitation of the wettest month (Bio13) and landcover variables contributed the most as pointed by all the measures used in our analysis (i.e. Jackknife AUC, overall percentage contribution, and permutation importance). Based on the Jackknife results, Bio13 recorded the highest gain when used in isolation for the three tested climate scenarios and therefore, appears to provide the most useful information individually (Fig. 5).

The relative contributions of predictor variables to the MaxEnt models showed that only four of these variables accounted for more than 92% contribution in each model (Table 2). The four most significant variables affecting the distribution of *B. tabaci* in Kenya were land cover, precipitation of the wettest month (Bio13), precipitation of the coldest quarter (Bio19), and annual temperature range (Bio 7) (Table 2). Additionally, the land cover had the highest percentage contribution and permutation importance, having



**Fig. 4** Performance of the replicated MaxEnt models evaluated using the area under the curve (AUC). The red line presents the mean plot of the replicated models while the blue shade shows the standard deviation of the replicated models and the black line shows the predictions performed at random

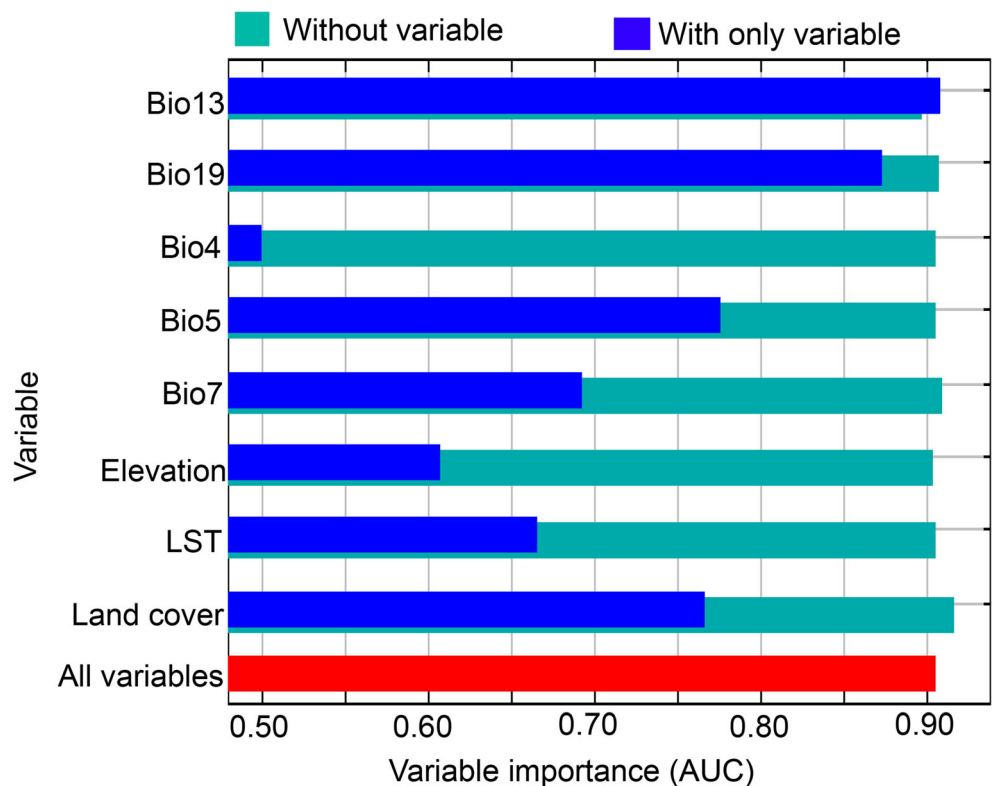


14% and 30.5%, respectively above the second-best contributor i.e. Bio13.

The curves in Fig. 6 show the marginal effect of varying one variable and how each variable affects the MaxEnt model.

In other words, the curves show how the *B. tabaci* predicted probability of presence changes as each variable is varied, keeping all the other variables at their average sample value. We show the response of the top five variable contributors to

**Fig. 5** Relative importance of the predictor variables for predicting the spatial distribution of *B. tabaci* based on the Jackknife test



**Table 2** The average percentage contribution and permutation importance of the predictor variables used for predicting *B. tabaci* invasion risk areas in Kenya

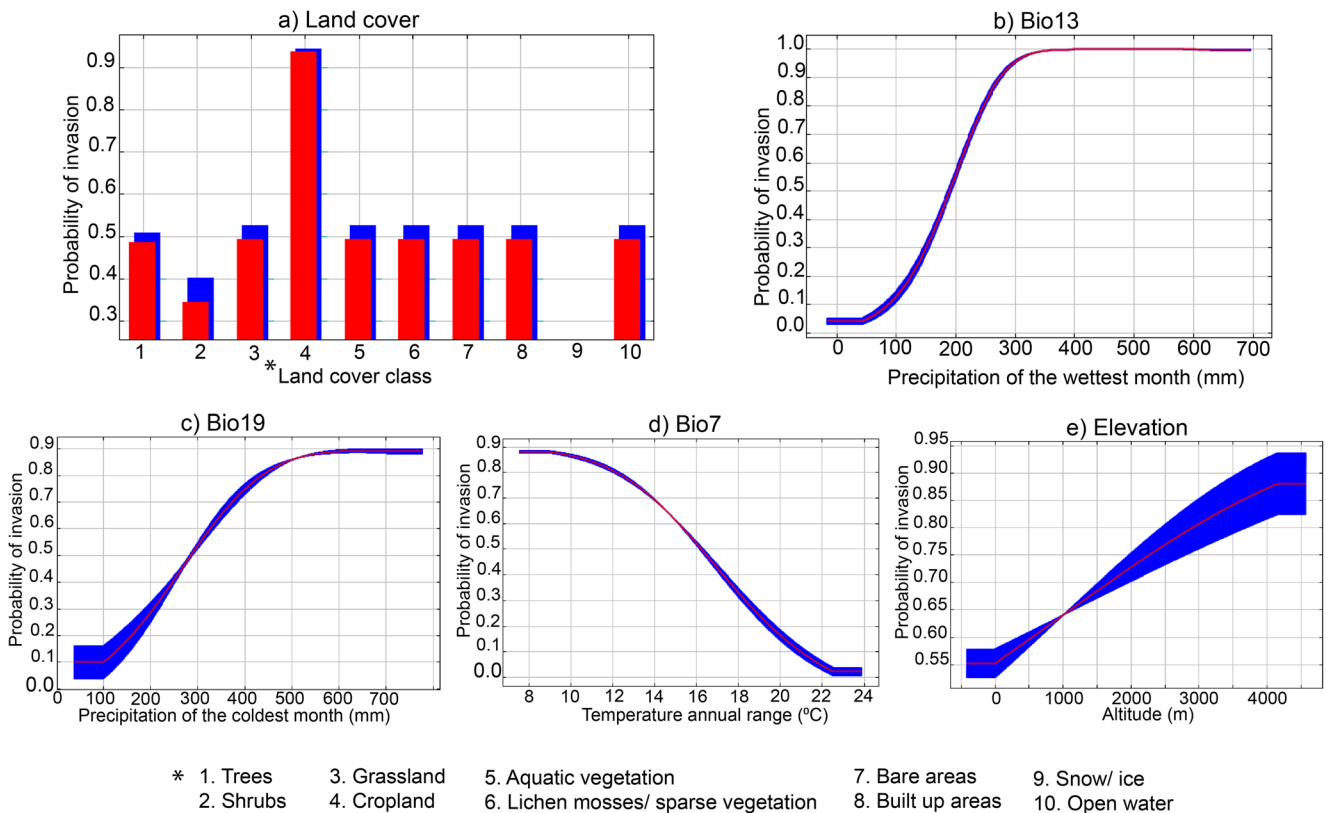
Variable	Percentage contribution	Permutation importance
Land cover	35.9	50.9
Bio13	21.6	20.4
Bio19	18.7	14.5
Bio7	18.6	5
Elevation	5.1	8.8
Land surface temperature	0	0.2
Bio5	0	0.2
Bio4	0	0

the model i.e. Landcover, Bio13, Bio19, Bio7, and Elevation. The response of the occurrence of the *B. tabaci* to the land cover variable showed that cropland (class number 4) is the most important class determining the potential *B. tabaci* occurrence (Fig. 6). Further, the results showed that precipitation and temperature are critical for *B. tabaci*. However, the range is very wide with species occurring within rainfall ranges as low as 200 mm and as high as >600 mm/year. The response obtained from Bio7 shows that *B. tabaci* performed better in

areas that do not possess a huge mean annual temperature range i.e. differences between the mean temperature of the hottest month and mean temperature of the coldest month ( $\pm 12^\circ\text{C}$ ). Similarly, a wide range of altitudes was observed to be suitable for the pest, but the probability of occurrence generally increases with an increase in altitude. Thus, the model indicates that wide ranges of temperature, rainfall, and elevation are suitable for the *B. tabaci* pest.

***B. tabaci* potential invasion risk areas under current and future climate conditions**

Approximately 40 of the 47 counties in Kenya were predicted to be at the risk of invasion by *B.tabaci*. Western counties showed the highest invasion risk potential compared to all the other counties with ~100% of the area being suitable for *B. tabaci* invasion. Also, the coastal counties i.e. Lamu, Kilifi, Kwale, and Mombasa showed high potential for *B. tabaci* invasion, particularly towards the coastline (Fig. 7). Notably, most of the sites and suitable habitat were in the humid to semi-humid agroclimatic zones, where most of the crop agriculture is conducted. Again, the northern and northeastern regions, where the climate is arid to very arid, exhibited the lowest potential of invasion by *B. tabaci*. Although the locations and patterns of the future potential risk areas are like the



**Fig. 6** Response curves derived from the MaxEnt model showing the influence of the predictor variables: **a** land cover **b** Bio13; **c** Bio19; **d** Bio7; and **e** elevation on the probability of occurrence of the *B. tabaci* in

Kenya. The red color (curves and bars) in all graphs (a–e) show the mean of the replicates while the blue color shows the variance in the replication

current potential distribution, our models' results suggest that the geographic extent and risk magnitude would generally increase under the tested scenarios of climate change. This holds, particularly for the central region counties such as Kitui, Makueni, and Machakos and the southeastern counties i.e. Garissa, Taita Taveta, and Turkana county in the north of Kenya (Fig. 7).

Table 3 shows the relative changes in area and area percentage in suitability for *B. tabaci* invasion in comparison to the total area of Kenya. Results show that there will be an increase in the total area, that is likely to be invaded by the pest, with the highest area predicted under the worst-case scenario (RCP8.5). Although there is a slight decrease in the area under 'very high' risk from the current (17,963 km<sup>2</sup>) to RCP 8.5 (16,842 km<sup>2</sup>) their respective percentages did not change (3%). Further, we observed that a large area that has a very low probability under the current scenario would become more susceptible to invasion under climate change. An area of approximately 41,170 km<sup>2</sup> will increase in invasion risk from very low suitability or become of moderate suitability.

## Discussion

The models produced in this study demonstrated a high level of reliability with AUC > 90%. Results suggested that all models performed better than at random with a high agreement statistic with the data. The high proportion of agreement with the potential invasion risk underscores the dependability of these models. Thus, the model outputs obtained from this study may be considered reliable as a foundation for research on *B. tabaci* occurrence and risk in Kenya. In this study, MaxEnt provided compelling results despite the integral uncertainty provided by niche modeling caused by the quality of occurrence data and sampling bias, selection of spatial data

layers and their resolution, species ecological characteristics (including environmental adaptation), and spatial autocorrelation (Phillips et al. 2006; Merow et al. 2013; Støa et al. 2018). Also, the results obtained from this study were robust since MaxEnt software has a user interface that can facilitate for correction of sampling bias and offers parameter adjustments which can enhance the quality of specific models (Kramer-Schadt et al. 2013). In this study, we adjusted the selection of feature types, the value of regularization multipliers, the selection of background points, and the extent to obtain model results adhering to the current occurrence of the species. The success of our models is supported by the biological validity of the attained response curves and robust validation results. Thus, our study provides critical information on the risk of *B. tabaci* for open-field agriculture in Kenya.

*B. tabaci* has been reported by many studies to occur in wide-ranging climatic envelopes and environments across all continents (Labou et al. 2017; Ramos et al. 2018; Bradshaw et al. 2019). However, our results suggest that in Kenya, it occurs in tropical to subtropical climatic zones that have high mean annual temperatures and possess broad differences in daily temperatures and a wider range in precipitation (Ramos et al. 2018). These generic characteristics substantiate the great potential for the *B. tabaci* invasion in several areas in other African countries (Labou et al. 2017; Kriticos et al. 2020). Although *B. tabaci* can occur across a wide elevation, land cover, precipitation, and temperature range as established by our study, the species can be affected by extreme weather conditions. Like other insect species, extreme temperatures or precipitation (either high or low) can change the development of the species (Janzen and Hallwachs 2019). Also, most vegetables that are typically the hosts of *B. tabaci* exhibit great sensitivity to extreme climatic conditions thereby reducing the conducive environment for the pest to proliferate (Ramos et al. 2018).

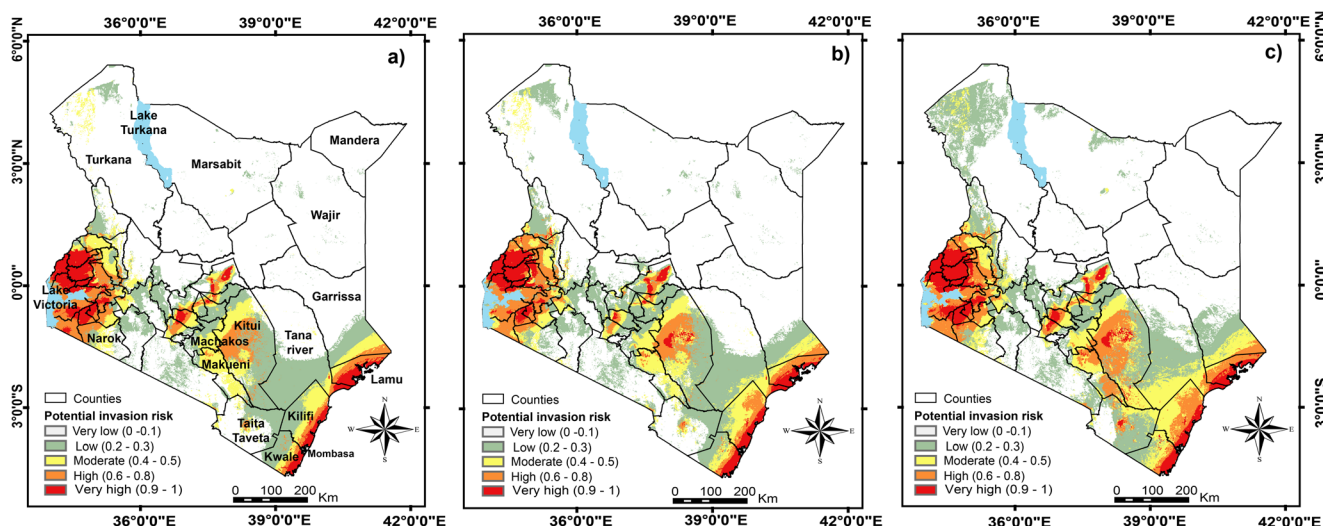


Fig. 7 Potential invasion risk of *B. tabaci* in the 47 counties of Kenya using the (a) current, b RCP2.5 of 2050, and c RCP 8.5 of 2050 climate scenarios

High precipitation levels generally promote vegetative growth and the establishment of diverse plant communities (Landmann et al. 2020). It is the availability of abundant host plants in areas of high precipitation that indirectly result in *B. tabaci* population build-up. If there are abundant host plants, *B. tabaci* remain active throughout the season. Furthermore, the polyphagous behavior of this pest means that the insect can utilize different types of plants, including wild host plants that are available within a production landscape to support population growth (Azrag et al. 2018). Earlier studies have forecasted a greater probability of the presence of *B. tabaci* in temperatures around 23 °C–24 °C (Labou et al. 2017; Macfadyen et al. 2018; Kumar et al. 2019). This could be the main explanation as to why *B. tabaci* occurrence was high in areas with a mean temperature close to the prime requirement for its growth in most areas in Kenya. However, a mixture of climate factors with other variables, such as a higher number of hosts, might be related to the success of the *B. tabaci* distributions in the western counties and most of the central counties that perform horticultural activities such as cassava and tomato production (Kyalo et al. 2017; Jozani et al. 2020). As established in this study, the cropland was the most relevant land cover class that defines the potential risk of *B. tabaci* invasion by providing the relevant host crops for the pest. This directly determines *B. tabaci* carry-over sequence from crop to crop with different biotypes preferring plants belonging to contrasting plant families, further enhancing the success and propagation of the *B. tabaci* species. Contrastingly, the decreased *B. tabaci* risk levels in the few areas observed in our study may be due to a decline in optimum climatic conditions and other suitability factors for the species or the unavailability of hosts.

Climate change has been predicted by many studies to increase the occurrence and spread of invasive insect species (Lebouvier et al. 2011; Otieno et al. 2019a; Ajene et al. 2020b; Mtengwana et al. 2020). Our current study established a similar pattern of the relative increase in the potential invasion area by *B. tabaci*, more so in open-field agriculture in the coastal and northern counties in Kenya. The main reason is related to the predicted increase in atmospheric CO<sub>2</sub> and

temperature coupled with erratic rainfall which will mainly affect both the pest and the host (Kinznier et al. 2019). Thus, our study employed a country level landscape approach, which provided a more robust result for Kenya or any other country with similar suitable conditions.

Our study focused on the holistic prediction of all potential *B. tabaci* biotypes in Kenya, which provides an overview of its occurrence in the country. However, the extensive biotypic variations described within whitefly species also account for their differential fitness within the environment. Therefore, their biological parameters are best explained by parameters such as host plants, temperature, and biotypes (Delatte et al. 2009). Biotype Q, for instance, can adapt to new environments in comparison to biotype B (Mahadav et al. 2009), hence has a greater survival chance under both low and high temperatures as evidenced by its presence in both tropical and temperate climates (Yu et al. 2012). While other studies have also shown that temperatures ranging from 17 °C to 35 °C allow for a linear relationship between development time and temperature (Bonato et al. 2007; Delatte et al. 2009), similar work using some temperature-dependent models have also established 10.2 °C (Bonato et al. 2007), 10.3 °C (Delatte et al. 2009) and 12.5 °C (Teng et al. 2010) as the lower temperature threshold for *B. tabaci* nymph development. This makes the understanding of the relevant climate envelope necessary for the pest to establish more complex particularly in the face of climate change.

Efforts to improve and develop new crop cultivars that adapt to the impending climatic conditions offer a new lifeline to most farmers and provides an opportunity to grow many crops in areas where temperatures are quite high or dry (Tonnang et al. 2020). However, there will always be the drawback of providing and allowing adaptation of insect pests such as *B. tabaci*. Hence, it is also prudent to develop and improve cultivars that are more resistant to pest invasion. Furthermore, integrated pest management controls can be used to enhance the control of these pests such as *B. tabaci*.

Currently, it is most preferred to conduct intensive horticulture cropping in greenhouses, net houses, or closed glasshouses, although these constitute negligible acreage based on the study's scale. In all these cases, appropriate aeration can

**Table 3** The relative predicted area (km<sup>2</sup>) and percentage of the potential invasion risk (%) of the *B. tabaci* in Kenya, using the current and future i.e. RCP2.6 and RCP8.5 for the year 2050 climate scenarios

Invasion risk	Current (km <sup>2</sup> )	RCP2.6 (km <sup>2</sup> )	RCP8.5 (km <sup>2</sup> )	Current (%)	RCP2.6 (%)	RCP8.5 (%)
Very low	398,264	388,450	357,088	69	67	61
Low	100,678	102,939	133,325	17	18	23
Moderate	36,435	38,774	45,172	6	7	8
High	29,310	36,168	30,224	5	5	5
Very high	17,963	16,319	16,842	3	3	3
Total	582,650	582,650	582,650	100	100	100

control the interior temperatures providing conducive environments for the propagation of *B. tabaci* (Bradshaw et al. 2019). Consequently, modeling studies such as presented in this current study cannot consider this phenomenon into account. For this reason, *B. tabaci* in sheltered environments may have been present in some other locations in Kenya but were not highlighted by our model.

## Conclusions

The generic characteristics required by *B. tabaci* to propagate, show the great potential for the pest to invade several other areas in other African countries with similar environmental conditions. Our study indicates that climate change will likely increase the geographical distribution range currently occupied by *B. tabaci* in Kenya particularly in response to the increase in temperature. Our results contribute as an empirical warning to agricultural authorities in the respective counties of Kenya to employ adaptive strategies to avoid a reduction in viability for open-field agriculture due to the invasion by this pest. Thus, preventive measures must be taken to combat the spread of viruses associated with *B. tabaci* into areas where they have not yet been reported. Phytosanitary strategies, cultural and biological control measures are necessary for locations that are at very high, high, and moderate risk of *B. tabaci*, to reduce the risk and economic losses to smallholder farmers in Kenya. The results of our study can also be used in future studies and other modeling approaches to establish the influence of differences of the existing and new biotypes, other pest-plant interactions, natural enemies, pest resistance, dispersal, and adaptations within the already identified and potentially susceptible areas to *B. tabaci* invasion.

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## Compliance with ethical standards

**Conflict of interest** The authors declare no conflict of interest.

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