Predicting the potential invasion suitability of regions to cassava lacebug pests (Heteroptera: Tingidae: *Vatiga* spp.)

S.I. Montemayor[1,2]*, P.M. Dellapé[1,2] and M.C. Melo[1,2]

[1]División Entomología, Museo de La Plata, Universidad Nacional de La Plata, Paseo del Bosque s/n, B1900FWA, La Plata, Argentina: [2]Consejo Nacional de Investigaciones Científicas y Técnicas, Buenos Aires, Argentina (CONICET)

Abstract

Cassava (*Manihot esculenta* Crantz) is one of the most important staple crops for small farmers in the tropics, feeding about 800 million people worldwide. It is currently cultivated in South and Central America, Africa and Asia. The genus *Vatiga* is widespread throughout the Neotropical region. Its species are sympatric and feed exclusively on cassava. The main objectives of this paper are: (1) to assess the potential distribution of *Vatiga*, one of the most relevant pests of cassava; (2) to project the resulting models onto the world; (3) to recognize areas with suitable and optimal climates (and thus, high probability) for future colonization, and (4) to compare this model with the harvested area of cassava analyzing the climatic variables required by both the host and the pest species. Species distribution models were built using Maxent (v3.3.3k) with bioclimatic variables from the WorldClim database in 2.5 arc min resolution across the globe. Our model shows that *Vatiga* has the potential to expand its current distribution into other suitable areas, and could invade other regions where cassava is already cultivated, e.g., Central Africa and Asia. Considering the results and the high host specificity of *Vatiga*, its recent appearance in Réunion Island (Africa) poses a serious threat, as nearby areas are potentially suitable for invasion and could serve as dispersal routes enabling *Vatiga* to reach the continent. The present work may help prevention or early detection of *Vatiga* spp. in areas where cassava is grown.

Introduction

Cassava (*Manihot esculenta* Crantz) is one of the most important staple crops for small farmers in the tropics. Recent estimates suggest that 800 million people worldwide consume cassava on a regular basis (FAO, 2013). Originally from Amazonia, it is currently grown in South and Central America, Africa and Asia (Monfreda *et al.*, 2008; Léotard *et al.*, 2009). Although it was long considered as unsuitable

for intensification, since the year 2000, the world's annual cassava production has increased by an estimated 100 million tons (FAO, 2013). According to this report, cassava will see a shift to monocropping, higher-yielding genotypes and greater use of irrigation and agrochemicals. But intensification carries great risks, such as the outbreak of pests and plant disease (FAO, 2013).

Several arthropods are pests of cassava, including lace bugs (Heteroptera: Tingidae), with *Vatiga* species being the most relevant (Froeschner, 1993; Neal & Schaefer, 2000). *Vatiga* is a Neotropical genus that is widespread throughout the tropical and subtropical areas of the region. Its five species are sympatric and feed exclusively on cassava (Froeschner, 1993). The species most frequently recorded as cassava pests

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*Author for correspondence
Phone: 54 221 4257744
E-mail: smontemay@fcnym.unlp.edu.ar

are *Vatiga illudens* (Drake) and *Vatiga manihotae* (Drake), which are exhaustively mentioned in the literature (Oliveira *et al.*, 2001; Moreira *et al.*, 2006; De Paula-Moraes *et al.*, 2007; Fialho *et al.*, 2009; Halbert, 2010; Alves *et al.*, 2012; Bellon *et al.*, 2012; Streito *et al.*, 2012). However, misidentifications are frequent because of the intraspecific variability within the genus (Froeschner, 1993), so that the number of species involved could be different.

The symptoms of *Vatiga* spp. infestation are evident. Leaves have yellowish stains, which later become reddishbrown. Sucking of the sap by the bugs weakens the plant and reduces its photosynthetic capacity, favoring the premature fall of basal leaves (Oliveira *et al.*, 2001; Moreira *et al.*, 2006). Few studies have evaluated the consequences of *Vatiga* spp. infestations, indicating a yield loss of 21% (Fialho *et al.*, 1994), 39% (Bellotti *et al.*, 1999), 35% (Moreira *et al.*, 2006) and 48–55% (Fialho *et al.*, 2009). Even though other arthropods (e.g., whiteflies, mealybugs and mites) are considered to be the main pests of cassava crops, there has been increasing incidence of *Vatiga* spp., which has become a serious concern to cassava farmers (Bellon *et al.*, 2012).

Recently, well-established populations of *V. illudens* have been reported outside their native range, i.e., in Florida, USA (Halbert, 2010) and in the Réunion Island, Africa (Streito *et al.*, 2012). In both cases, the most plausible means of entry is by accidental human action. The spread of *Vatiga* spp. outside its native range suggests its invasive nature. Streito *et al.* (2012) have warned that in the absence of phytosanitary control measures, it will quickly spread to the whole area of cassava crops.

The main objectives of this paper are: (1) to assess the potential distribution of *Vatiga* spp. through a species distributional model (SDM); (2) to project the resulting models to the world; (3) to recognize areas with suitable and optimal climates (and thus a high probability) for future colonization; and (4) to compare this model to the area where cassava is harvested, analyzing the climatic variables required by both the host and the pest species. This information may help prevention or early detection of *Vatiga* spp. in areas where cassava is grown.

Material and methods

Occurrence data

An occurrence database for the *Vatiga* species was compiled from the literature and from material studied from Museum collections (California Academy of Sciences, USA (CAS); the Instituto Oswaldo Cruz, Rio de Janeiro, Brazil (IOC); the Institut Royal des Sciences Naturelles de Belgique, Belgium (IRSNB); the Museo de La Plata, Argentina (MLP); the Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires, Argentina (MACN); and the National Museum of Natural History, USA (USNM)). This database comprises 92 localities: 82 from the Neotropics (native range), 1 from the Nearctic (Florida, USA), and 9 from the Ethiopian Region (Réunion Island).

One of the main problems of most SDMs is the failure to account for spatial dependence of occurrence data (Gelfand *et al.*, 2006; Bahn & McGill, 2007; Dormann, 2007; Elith *et al.*, 2010; Record *et al.*, 2013). Spatial autocorrelation arises in ecological data because the nearby points tend to be more similar in physical characteristics and/or species occurrences or abundances than are pairs of locations that are farther apart
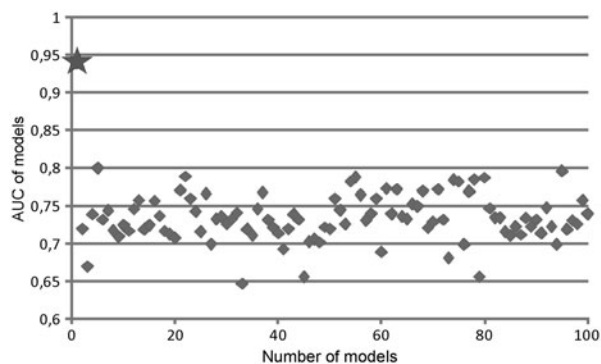

Fig. 1. Model performance is measured as the AUC of receiver operating characteristic (ROC) of model testing. Star, average AUC of real model; squares, AUC of null models.

(Legendre, 1993). In order to avoid spatial autocorrelation, a model with the 82 records from the native area was developed, and the spatial autocorrelation was measured among pseudo-residuals (1 − probability of occurrence generated by model) by calculating Moran's I at multiple distance classes using SAM v4.0 (Rangel *et al.*, 2010). Significance was determined using permutation tests. A minimum distance of 352-km was detected so a grid of cell of those dimensions was created and the occurrence point closest to the centroid of each cell was selected. As a result, the dataset was reduced from 82 to 44 occurrence points from the native range, which we used for model calibration.

Selection of variables

Climate match, although it has limitations, has been associated with the successful establishment of a range of non-indigenous organisms, and can be a useful predictor of risk (Floerl *et al.*, 2013). Moreover, climate sensitivity has been recognized as the main characteristic that is significantly associated with invasive species across biological groups (Hayes & Barry, 2008; Bomford *et al.*, 2009; Elith *et al.*, 2010). To train the model, data from WorldClim database were used in 2.5 arc min resolution across the globe (Hijmans *et al.*, 2005). To exclude correlated variables used for modeling, Pearson's correlation coefficient (r) was calculated between each pair of the 19 WorldClim variables for the 44 points from the native range. For each comparison with $r \geq 0.90$, one variable was selected for modeling. The discarded variables were those correlated with more than one variable, or if the pair of variables corresponded to monthly or quarterly information, the one corresponding to monthly information was discarded.

SDM and model evaluation

SDMs were built using Maxent v3.3.3k (Phillips *et al.*, 2006), which was developed to model species distributions using only presence data. Default settings were used to run the models, which were built through cross-validation. We excluded 10% of the occurrence data and then tested the accuracy of the model to predict the excluded data points. This was repeated 10 times for each model, and the mean output was used to determine distribution probabilities and overall model performance. The accuracy of each model was
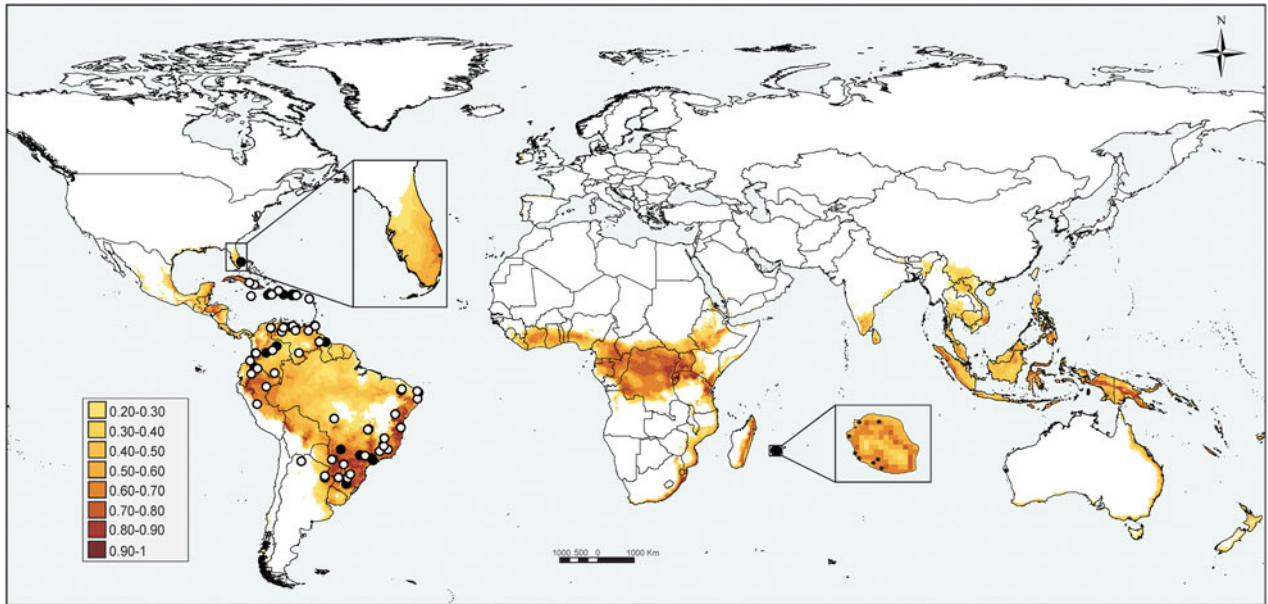
Fig. 2. Suitability map from a SDM for *Vatiga* spp. based on 44 presence records (empty circles) and 12 bioclimatic variables projected worldwide using Maxent. Filled circles represent all presence records of *Vatiga* spp.
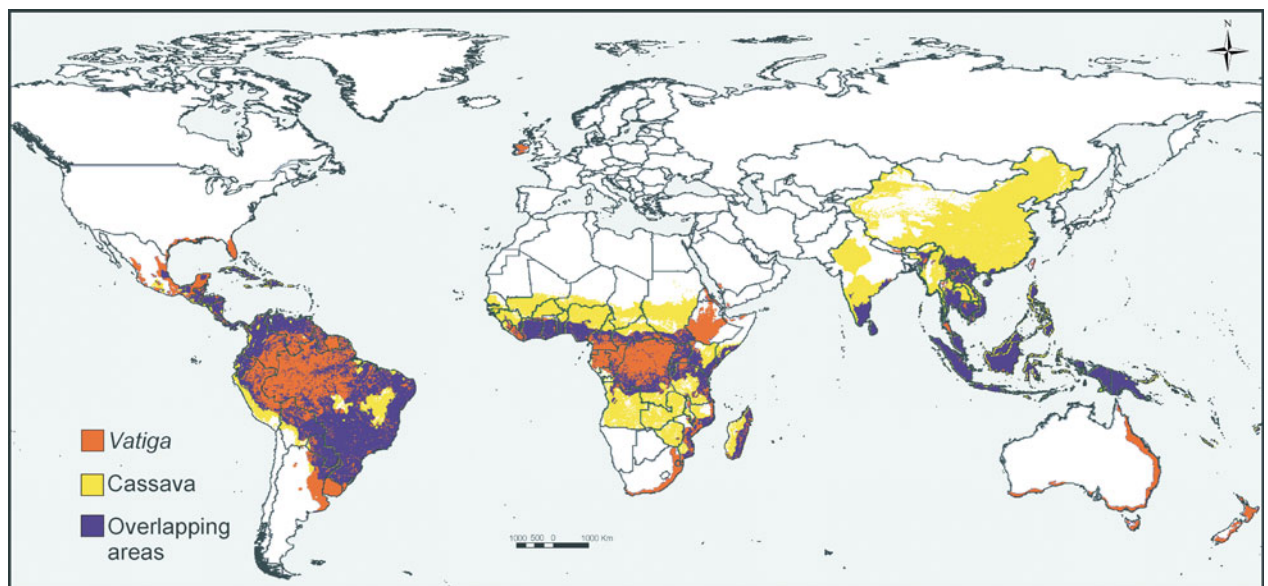

Fig. 3. Suitable area for *Vatiga* spp. based on the 'minimum training presence logistic threshold' provided by Maxent, and superimposed with the harvested area of cassava.

determined using the area under the curve (AUC). The null model approach was used to test whether the resulting models provide a better fit than chance. Ninety-nine null models were built by drawing occurrence points at random without replacement. Each null model was based on an equal number of occurrence points as the real model and modeled under the same conditions. The AUCs of the null models were used to test the significance of the real model. If the AUC of the real model fell in or above the highest 5% of the null models'

AUCs, the real model was considered statistically significantly better than random Raes & Ter Steege (2007).

Recognition of susceptible areas to infestation

In order to recognize areas susceptible to infestation, the Maxent logistic output was converted to two binary presence/absence climate suitability maps, one with suitable and the other with optimal climatic conditions. These maps were
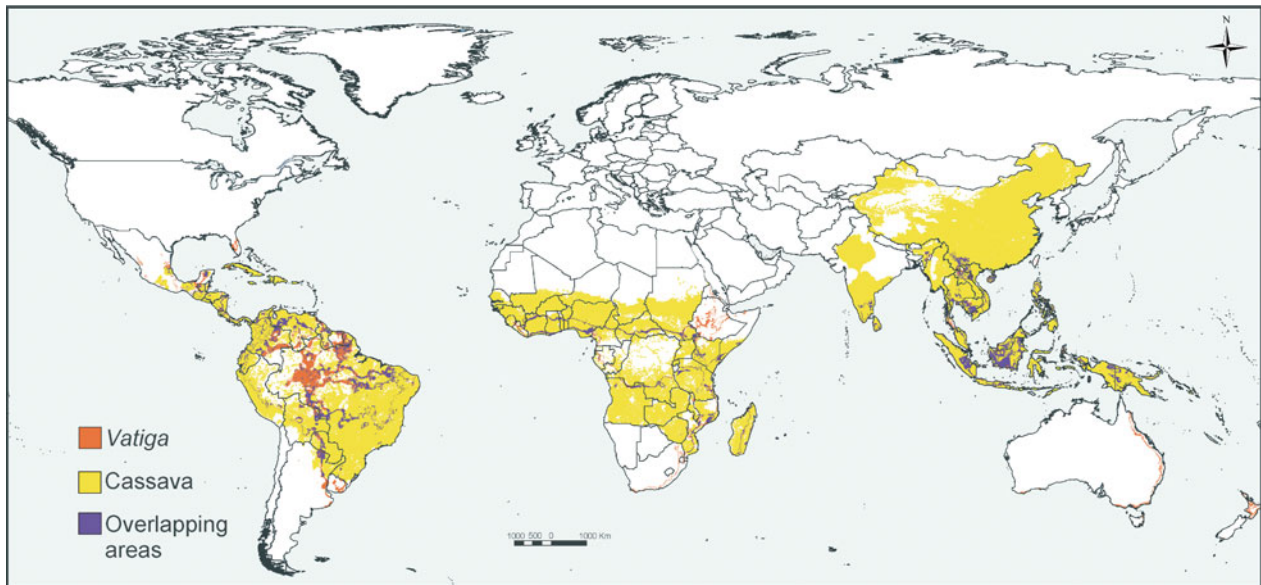
Fig. 4. Optimal area for *Vatiga* spp. based on the 'maximum test sensitivity plus specificity logistic threshold' provided by Maxent, and superimposed with the harvested area of cassava.

based on two thresholds provided by Maxent, the 'minimum training presence logistic threshold' that indicates values above which the climatic conditions are suitable, and the 'maximum test sensitivity plus specificity logistic threshold' that indicates values above which the climatic conditions are optimal (Kebede *et al.*, 2014). Both binary maps were superimposed with a map of the actual harvested regions of cassava downloaded from Monfreda *et al.* (2008).

Bioclimatic profiles

With the goal of comparing the climatic variables from the harvested area of cassava and the area modeled with suitable climatic conditions for *Vatiga* spp., we created box plots. We used the Maxent logistic output converted to binary presence/absence data (values above the 'minimum training presence logistic threshold') and the raw environmental data from the crop-layer of cassava (Monfreda *et al.*, 2008). The cassava and *Vatiga* spp. rasters were converted to point shapefiles using ArcGIS 10 and the values of the environmental data at each point were extracted using DIVA-GIS (Hijmans *et al.*, 2005). With this information, box plots were built for each of the variables used to construct the model.

In order to determine whether there is a niche shift when *Vatiga* spp. invades new areas and which variables it involves, we explored the bioclimatic profiles of *Vatiga* spp. in native and invaded areas using DIVA-GIS. The bioclimatic profiles were built considering all the distributional information for *Vatiga* spp. and all WorldClim bioclimatic variables. Values of the bioclimatic variables were extracted from the recorded localities of *Vatiga* spp. and arranged in a cumulative frequency distribution where native and invasive records were identified.

Results

Pearson results

The exploratory analysis of the climatic variables (Supplementary material S1) led to a combination of 12

minimally correlated variables. From the 19 climatic variables considered, we recorded the following: mean monthly temperature range (Bio2), isothermality (Bio3) [(BIO2/BIO7) (*100)], temperature annual range (Bio7), mean temperature of wettest quarter (Bio8), mean temperature of driest quarter (Bio9), mean temperature of warmest quarter (Bio10), annual precipitation (Bio12), precipitation seasonality (Bio15), precipitation of wettest quarter (Bio16), precipitation of driest quarter (Bio17), precipitation of warmest quarter (Bio18) and precipitation of coldest quarter (Bio19).

Predicted range of suitable climates for Vatiga *spp.*

Our model provides a significantly better fit than expected by chance alone (fig. 1), with high predictive performance. The average AUC of the 99 null models was 0.733, standard deviation was 0.029, and the AUC range was 0.647–0.800, in contrast to our model, for which average AUC was 0.940, standard deviation was 0.026 and the AUC range was 0.903–0.984. The pixels with highest probabilities are concentrated around the Equator; and the predicted climatically suitable range is between approximately 25°S and 25°N (fig. 2).

In America, we found suitable climatic conditions in almost all north-central South America, not extending west of the Andes. Suitable conditions are observed throughout continental Central America, in addition to the known distribution in the Caribbean Islands. In North America, conditions are suitable on the eastern coast of Mexico and a narrow strip along the west coast of USA. In Africa, conditions are favorable in lowland Central, southern West and coastal East Africa, and in Madagascar and neighboring islands. We observed the most suitable conditions (>50%) mainly around the Equator. In Asia, we found suitable climatic conditions in the southeast, with most favorable conditions (>50%) around the Equator between 10°S and 10°N. We also found suitable conditions (>30%) in Oceania, mainly on the southern and eastern coast of Australia, north West of New Zealand and almost all the territories of Papua, New Guinea and the Pacific Islands.
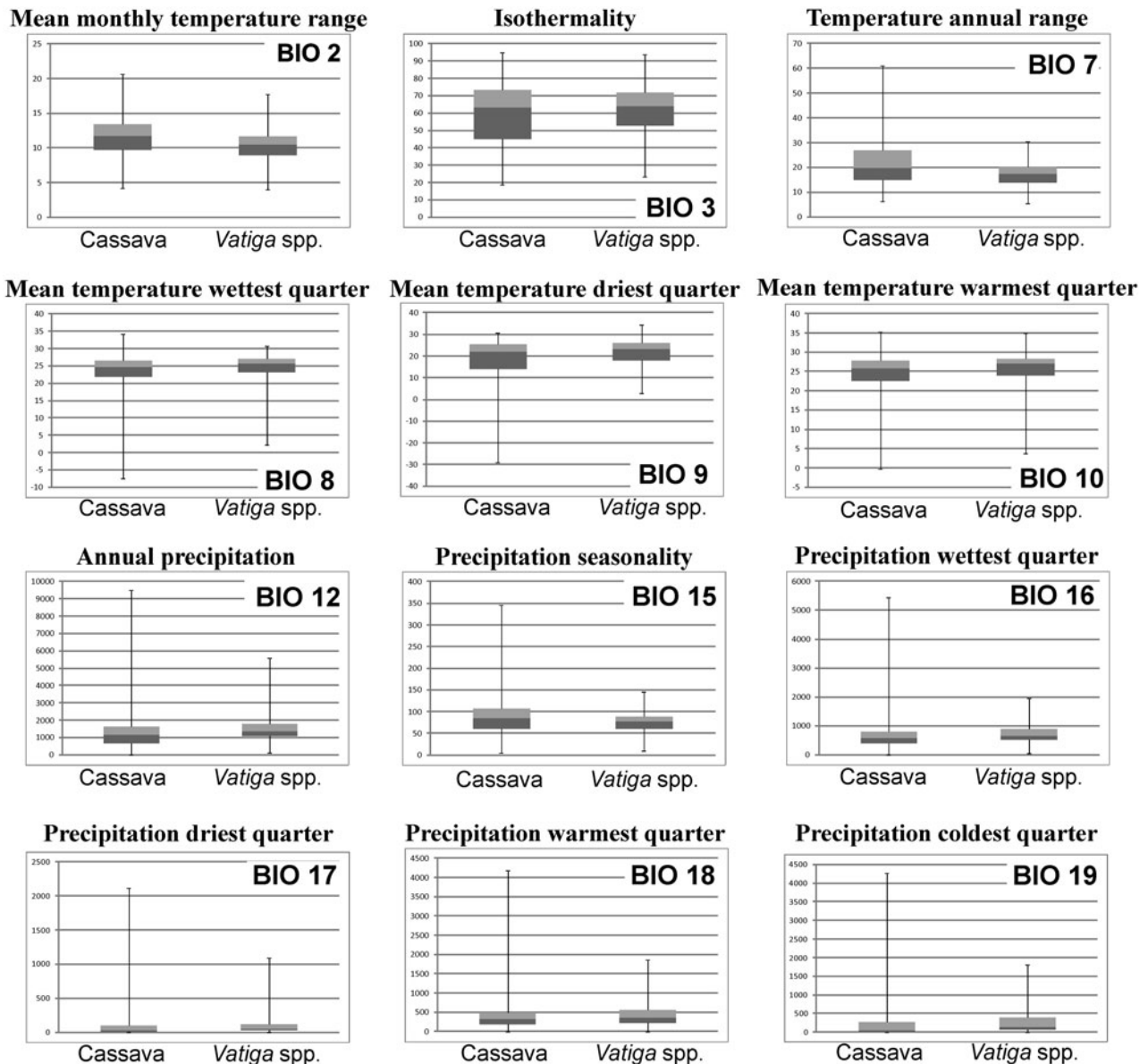
Fig. 5. Direct comparison of cassava harvested records and *Vatiga* spp. records extracted from the cassava harvested area and the Maxent logistic output at a threshold value above the 'minimum training presence logistic threshold'.

The main areas with highly favorable climatic conditions (>50%) correspond to Papua, New Guinea and the Pacific Islands.

Comparison with the actual area of cassava cultivation

The overlapping of the suitable climatic map with the harvested area of cassava (fig. 3), shows the areas where *Vatiga* spp. could actually be found, as they feed exclusively on this crop. According to our results, areas close to the Equator are the most susceptible of being invaded. The same pattern is observed in the optimal climatic map but the area covered is much smaller, forming small interconnected patches (fig. 4).

Bioclimatic conditions and profiles of Vatiga spp. and cassava

Climatic variable scores for the cassava harvested area and the potential distribution above the 'minimum training presence logistic threshold' of *Vatiga* spp. are shown as boxplots in fig. 5. The visual comparison of the boxplots of the 12 variables shows that the ranges of almost all the variables of cassava exceed those observed for *Vatiga* spp. Hence, the climatic niche of *Vatiga* spp. is, as expected, clearly narrower than that of cassava. The presence of cassava in areas where there is a remarkable difference in the ranges of the same variables, such as Bio7, Bio12, Bio15, Bio16, Bio17, Bio18 and Bio19, suggests that these variables could constrain the distribution of *Vatiga* spp. Importantly, all of these (except for Bio7) are related to precipitations.
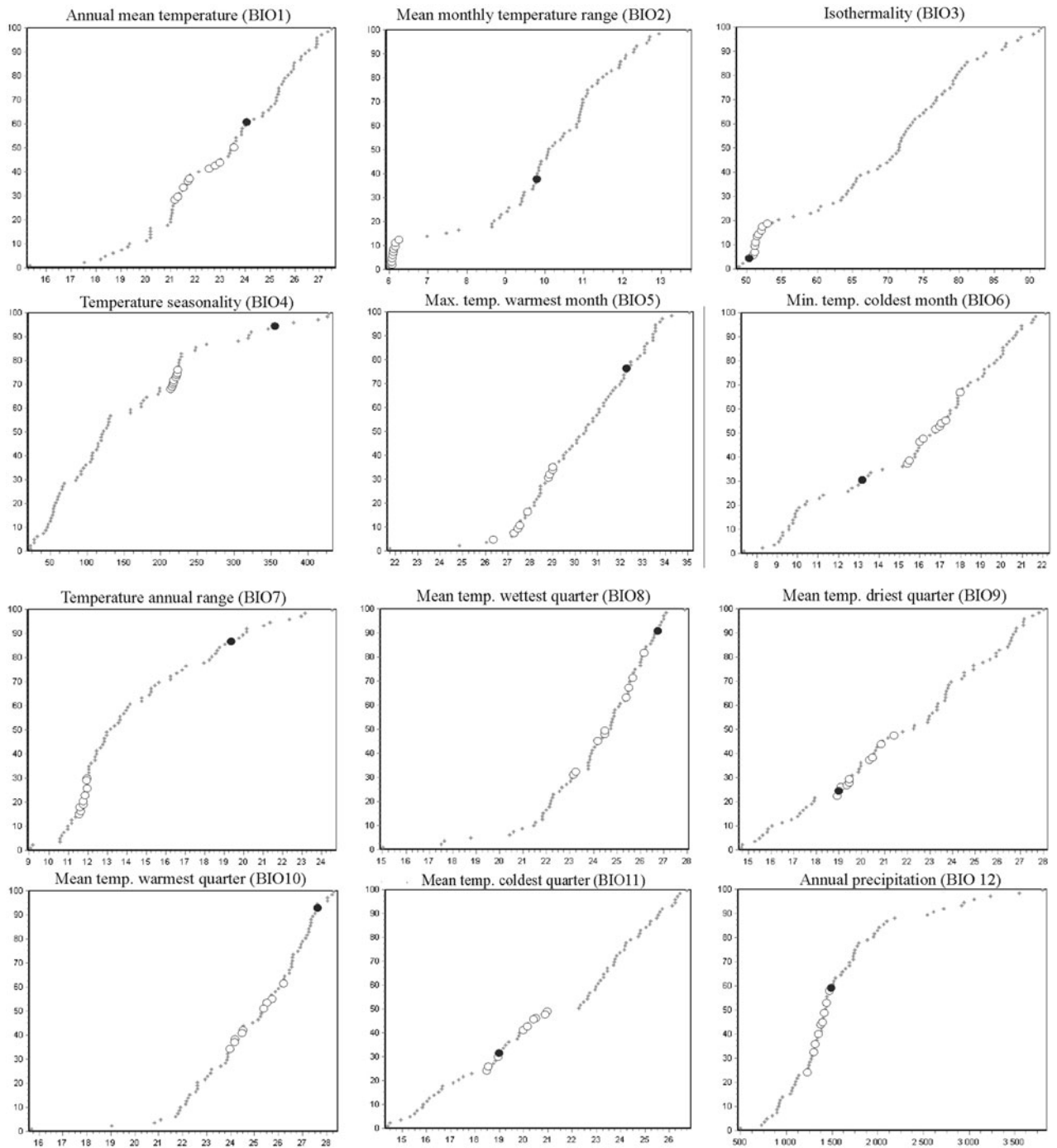
Fig. 6. Bioclimatic profile of *Vatiga* spp. using the climatic variables (Bio1–Bio12); cumulative relative frequencies (0–100) are displayed for the full data set. Smaller diamonds indicate native records; white circles represent African records from the Réunion Island and the black circle represents the Nearctic record from Florida.

The only variable whose upper range is wider in *Vatiga* pp. than in cassava is Bio9 (mean temperature in driest quarter), which indicates that there could be populations of *Vatiga* spp. in areas where the values of Bio9 are higher than in those where cassava is cultivated. A possible explanation could be that these higher values correspond to areas with

populations of *Vatiga* spp. that feed on wild varieties of cassava adapted to this kind of climatic conditions.

The bioclimatic profiles of *Vatiga* spp. (figs 6 and 7) invasive records are all within the ranges of the native records so no niche shift was observed, though the case of three variables related to temperature (mean monthly temperature range
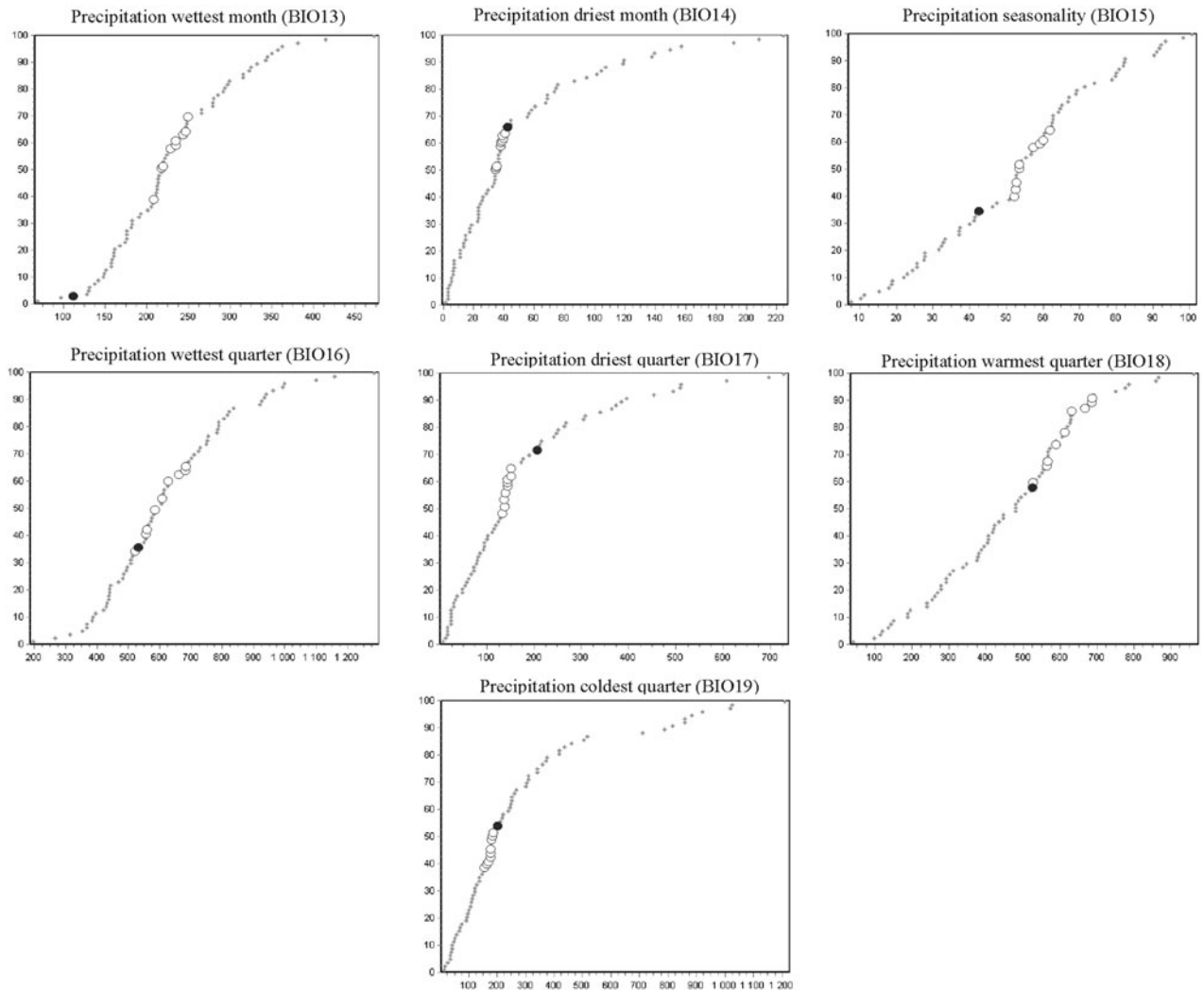
Fig. 7. Bioclimatic profile of *Vatiga* spp. using the climatic variables (Bio13–Bio19); cumulative relative frequencies (0–100) are displayed for the full data set. Smaller diamonds indicate native records; white circles represent African records from the Réunion Island and the black circle represents the Nearctic record from Florida.

(Bio2), isothermality (Bio3), and maximum temperature of warmest month (Bio5)) the invasive records are among the lowest values of the range. This situation is observed in the isothermality for the African and Nearctic records, and in the mean monthly temperature range and the maximum temperature of warmest months for the African records.

Discussion

Climatic model predictions are an important tool and a valuable first approach to the potential magnitude and distributional pattern of future impact of species, but they should be interpreted carefully as they do not consider important factors other than climate, such as biotic interactions (Montemayor *et al.*, 2014). Thus, an area predicted as suitable does not mean that populations of the species will necessarily become successfully established there, but it is useful information for identifying areas of potential invasion and spread. Models can also underestimate areas of potential invasion as

it has been suggested that a shift in the species' climate niche during a comparatively short time frame is possible during biological invasions (Broennimann *et al.*, 2007; Fitzpatrick *et al.*, 2007; Steiner *et al.*, 2008; Alexander & Edwards, 2010). Niches may even be conserved along some environmental axes but not along others (Fitzpatrick *et al.*, 2008).

Our model shows that the most suitable conditions in Africa include many countries in central Africa, for most of which cassava is among the three most important crops in terms of production for the year 2012 (FAO, 2013). Considering the results obtained and the invasive nature and high host specificity of *Vatiga* spp., its recent appearance in Réunion Island represents a serious threat, as nearby areas are potentially suitable for invasion and could serve as dispersal routes throughout the continent. The optimal climatic map shows that even though areas with suitable climatic conditions for *Vatiga* spp. are not large, there exists a connection between them forming potential pathways for invasion. This is valid not only for Africa but also for South America, Asia and Oceania.

As weak fliers, the dispersal of *Vatiga* spp. is limited and their entry into new environments depends on human actions. As a result of superimposing the optimal areas of *Vatiga* spp. with the harvested area of cassava we have been able to identify where it is important to take phytosanitary control measures, and in the case that species of *Vatiga* are detected in any of these areas, which of the neighboring areas are also at risk as the potential pathways for invasion have also being identified (fig. 4).

It must be considered that to analyze the potential distribution ranges of *Vatiga* spp., we assumed that the known range is in equilibrium with environmental parameters (Araújo & Pearson, 2005), and that the niche is conservative across space and time (Wiens & Graham, 2005). There are three variables (mean monthly temperature range, isothermality and maximum temperature of warmest month) where the invasive records are among the extreme lowest values of the range (figs 6 and 7) showing a tendency towards a climatic shift. However, because of lack of information regarding *Vatiga* spp. outside their native range any conclusion is speculative.

A further important step for future research would be to place more emphasis on the evaluation of the ecological and physiological characteristics of *Vatiga* spp. to identify other important environmental parameters, to evaluate if climatic shift should be expected in *Vatiga* spp. and how climatic change could affect its distribution. Similar approaches to the one used here may be of general application to other pests of crops for which maps of the cultivated areas are available. As noted by Neal & Schaefer (2000), it is likely that in absence of phytosanitary control measures, the economic importance of lace bugs will increase. It is to be expected that the range of the various *Vatiga* species will expand, following the wider cultivation and increasing importance of cassava to feed a growing world population.

Supplementary Material

The supplementary material for this article can be found at http://www.journals.cambridge.org/BER

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