Research Article

Horizon scanning to assess the bioclimatic potential for the alien species *Spodoptera eridania* and its parasitoids after pest detection in West and Central Africa

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Abstract

BACKGROUND: The southern armyworm (SAW) *Spodoptera eridania* (Stoll) (Lepidoptera: Noctuidae) is native to the tropical Americas where the pest can feed on more than 100 plant species. SAW was recently detected in West and Central Africa, feeding on various crops including cassava, cotton, amaranth and tomato. The current work was carried out to predict the potential spatial distribution of SAW and four of its co-evolved parasitoids at a global scale using the maximum entropy (Maxent) algorithm.

RESULTS: SAW may not be a huge problem outside its native range (the Americas) for the time being, but may compromise crop yields in specific hotspots in coming years. The analysis of its potential distribution anticipates that the pest might easily migrate east and south from Cameroon and Gabon.

CONCLUSION: The models used generally demonstrate that all the parasitoids considered are good candidates for the biological control of SAW globally, except they will not be able to establish in specific climates. The current paper discusses the potential role of biological control using parasitoids as a crucial component of a durable climate-smart integrated management of SAW to support decision making in Africa and in other regions of bioclimatic suitability.
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Keywords: southern armyworm; climate change; biological control; foresight analysis; decision support

1 INTRODUCTION

Invasive alien species (IAS) have negative ecological and economic consequences worldwide and the severity of these impacts is growing.[1,2] IAS have become major threats to global agriculture because of their rapid spread across the globe facilitated by increased trade and transport.[3,4] As an example, the increasing spread of pests into Africa has caused critical crop losses estimated to be several billions US dollars *per annum*.[5,6] The southern armyworm (SAW) *Spodoptera eridania* (Stoll) (Lepidoptera: Noctuidae) is one of these invaders. Shortly after the fall armyworm *Spodoptera frugiperda* (JE Smith) (Lepidoptera: Noctuidae) outbreaks were reported in West Africa[7] the southern armyworm *S. eridania* was also detected in December 2016 and in 2017 in West (Benin and Nigeria) and Central (Cameroon and Gabon) Africa.[8] SAW was observed for the first time in these countries feeding on various crops, including cassava, cotton, amaranth and tomato. Native to the Americas,[9] *S. eridania* is a voracious polyphagous defoliator known to damage major agricultural crops.[10,11] The most recent report on its host plants range comprises 106 plants species belonging to 33 plant families.[12,13]

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Neonate caterpillars are usually found on the lower surface of the leaves and only feed on the cuticle, while later larval stages (second to fifth instars) consume the entire leaves, leading to skeletonized plants. Control of the pest is possible through application of foliar pesticides on immature stages. However, the growing concern about insecticide resistance, and human and environmental health concerns suggests the need for sustainable approaches like biological control.

Insects pests and their associated parasitoids are poikilothermic organisms, their development being affected by temperature variations.[14,15] Outbreaks of major pests are frequently related to natural events such as drought, temperature increase, hurricane and flood.[14,16,17] These climate changes will affect, positively or negatively, the suitability of certain regions for insect pests and their natural enemies.[18–20] In extensive inventories in the Americas, dozens of parasitoids were found to be associated with SAW.[21] Among these, *Telenomus remus* (Nixon) (Hymenoptera: Platygastridae) and *Trichogramma pretiosum* (Riley) (Hymenoptera: Trichogrammatidae) were discovered to be the most important naturally occurring egg parasitoids.[22,23] In addition to the egg parasitoids, the egg-larval and larval parasitoids *Chelonus insularis* (Cresson) and *Cotesia marginiventris* (Cresson) (both Hymenoptera: Braconidae) emerged among the most frequent natural enemies and have also proven to be efficient against SAW.[24] These parasitoid species co-evolved with SAW and may be potentially relevant for long-term management of the pest in areas of invasion or locations with risks of spread.

The present work aimed to model the global current and future risks of southern armyworm distribution and habitat suitability of the four co-evolved SAW parasitoids, namely *Chelonus insularis* Cresson (Hymenoptera: Braconidae), *Cotesia marginiventris* (Cresson) (Hymenoptera: Braconidae), *Trichogramma pretiosum* Riley (Hymenoptera: Trichogrammatidae) and *Telenomus remus* Nixon (Hymenoptera: Platygastridae), through the maximum entropy (Maxent) algorithm. The result of this horizon scanning effort will support decision making in the newly invaded continent (Africa) and provide global assessments of SAW establishment, focusing on the potential role of biological control using parasitoids as a crucial component of durable climate-smart integrated management of SAW.

2 MATERIALS AND METHODS

2.1 Climate suitability modelling
The horizon scanning and bioclimatic potential assessment of the pest and parasitoids were performed using a combination of climate suitability modelling (HSM) and spatial analysis. HSM combines the observed presence records for each species (pest or parasitoid) with environmental data at the observed locations to generate (i) a prediction map for the suitable current climate for the target species and (ii) potential future distribution maps based on projections of selected global climate models (GCMs).

2.1.1 Species records and environmental data
Geographic coordinates (longitude and latitude) of observed locations of the pest (*S. eridania*) in West and Central Africa were mainly sourced from International Institute of Tropical Agriculture (IITA) records. Additional presence points and occurrences of the four modelled parasitoids (*Chelonus insularis*, *Cotesia marginiventris*, *Trichogramma pretiosum* and *Telenomus remus*) were obtained from the Global Biodiversity Information Facility (www.gbif.org) and from published papers. Before the modelling process, all the records were quality checked and exact duplicated records detected were removed for each species using the R package Environmental Niche Modeling (ENMTools)[25] (Table 1).

We used 19 bioclimatic variables from WorldClim version 1.4 for both present and future climatic conditions. The variables were downloaded from the worldclim (www.worldclim.org) database at spatial resolution of 2.5 arc minutes, ~4.64 km at equator. Distribution models were calculated for current climatic conditions and for two future climate models' representative concentration pathways (RCP), RCP8.5 'a high emissions/business as usual scenario' and RCP6.0 'a moderate reduced emissions scenario'.[26,27] Two global climate models (GCMs) from ensemble models were selected (Table 2) for our modelling experiments. The first GCM used is one of the warmer CMIP5 models for almost all locations: HadGEM2-ES (4.6 °C climate sensitivity). It was coupled with a relatively cool model over much of the land area, GISS-E2-R.[27,28]

Table 1. Number and sources of species records used for modelling

Species' name	Species' type	Total number of records after data clearing	Source of records	Number of records per source
Spodoptera eridania	Pest	238	IITA	63
			GBIF	146
			Published papers	29
Chelonus insularis	Parasitoid	116	IITA	35
			GBIF	05
			Published papers	76
Cotesia marginiventris	Parasitoid	74	IITA	48
			GBIF	12
			Published papers	14
Telenomus remus	Parasitoid	79	IITA	25
			GBIF	09
			Published papers	45
Trichogramma pretiosum	Parasitoid	82	IITA	59
			GBIF	23
			Published papers	00

Table 2. Outline of the two coupled model intercomparison project phase 5 (CMIP5) general circulation models (GCM) tested

GCM	Institution	Horizontal resolution	2x [CO2] Equilibrium climate sensitivity (°C)
GISS-E2-R*	National Aeronautics and Space Association Goddard Institute for Space Studies (NASA GISS)	2° × 2.5°	2.1
HadGEM2-ES*	UK Meteorological Office - Hadley Centre	1.25° × 1.875°	4.6

*HadGEM2-ES (4.6 °C climate sensitivity) is among the warmer CMIP5 models for almost all locations, while *GISS-E2-R (2.1 °C) inclines to be relatively cool over much of the land area.[27]

2.1.2 Modelling technique

The maximum entropy (Maxent) algorithm was used to predict the global environmental suitability of *S. eridania* and its four parasitoids, namely *C. insularis*, *C. marginiventris*, *T. pretiosum* and *T. remus*. Maxent has been demonstrated to perform well in the context of developing models using presence data only as input.[29] Its predictions rely on the ability to estimate a distribution of probability based on the physics science principle of 'maximum entropy' that satisfies a set of checks from environmental variables. The output of Maxent is the level of environmental suitability also considered as potential species ecological niche. Maxent is a machine learning approach. It estimates the most uniform distribution (maximum entropy) of sampling points compared to background locations given the constraints derived from the data.[30] Recent developments of the Maxent approach show that the same maximum likelihood estimates from the Gibbs distribution (an exponential family distribution) used by Maxent can be obtained from an inhomogeneous Poisson process (IPP) model.[31]

2.1.3 Variables selection and models calibration and validation for the pest and its parasitoids

To reduce correlations among predictor variables, climatic variables selection was performed using ENMTools to avoid redundancy, which could affect the accuracy of the model output, especially for future climate projections.[32,33] The least correlated variables selected for model calibration had correlation coefficients $\rho < 0.8$.[32] A jack-knife test was also performed on the selected bioclimatic variables to determine those which contribute best to the models. All models were run and validated by applying the cross-validation method with five replicates (i.e. 5-fold cross-validation). The method of cross-validation consists of splitting the occurrence records into five sets where one set is used to evaluate the model and the four other sets for calibration. The process was iterated five times. Average outputs were used for the pest and its parasitoid habitat suitability maps. In addition, average results from individual parasitoid species were combined through a prioritization process in Zonation for identifying combined suitability areas for all parasitoids together. Zonation develops a priority ranking. It iteratively ranks sites, at each step removing the spatial unit that leads to the smallest suitability. In this process, the least suitable climates received the lowest ranks (close to 0) and the most suitable received the highest ranks (close to 1).[34] Future predictions were also averaged over the two selected GCMs for each species and each climatic scenario before priority area analysis in Zonation.

We assessed model accuracy using the area under the receiver operating characteristic (ROC) curve (area under curve, AUC) and the true skill statistic (TSS). The AUC provides the probability that the predictive power of a model is better than random prediction (AUC = 0.5). A model with an AUC value close to unity ($0.75 \leq AUC \leq 1$) is considered to have a good fit. The TSS is an evaluation method of the model's power to detect true presence (sensitivity) and true absence (specificity). It is expressed as the sensitivity plus specificity minus one. A TSS > 0.5 indicates good predictive power.[35]

2.2 Determination of the ensemble model for the parasitoids

Based on the climate suitability layers obtained for each species of parasitoid, we implemented a spatial prioritization using the current distribution on one hand and the projected future potential distributions on the other hand using Zonation (a decision support system for spatial planning and described in section 1.3 above). Using climate suitability layers of parasitoids as features, Zonation produces a hierarchical priority ranking across all grid cells in the study area based on occurrence levels of each species in each grid cell, while it balances the output simultaneously for all species used in the analysis.[34] Core area zonation (CAZ) was applied to rank areas that have high occurrence levels for a single parasitoid species as potentially suitable climates for biocontrol considering the four modelled species.[36]

2.3 Mapping and biorisk analysis

2.3.1 Thresholding and habitat suitability mapping

The present-day and future layers for the pest and the ensemble layers for the parasitoids were imported in ArcMap to map the climate suitability. We converted the continuous predictions of habitat suitability into binary suitability based on a threshold using the SDMtoolbox in ArcGIS.[37] The probability of occurrence below the threshold is considered as unsuitable for the species, while those with probability greater than the threshold are considered suitable. For the pest species we analyzed habitat suitability based on two threshold levels: the minimum training presence (MTP) and the tenth percentile training presence (P10). Applying the MTP, we assumed that the least suitable habitat at which the species is known to occur (based on records used to train the model) is the minimum suitability value for the pest species. Using the P10 threshold, we considered that the least suitable climate from the continuous prediction containing 10% of the occurrence records was not representative for pest habitat suitability. Therefore, the MTP extends the habitat suitability of the pest while the P10 threshold minimizes it.

For the parasitoids, we applied only the P10 threshold option for the ensemble map using the average of the mean (over the five replicates) threshold value across the four parasitoid species.

2.3.2 Spatial analysis of SAW bioclimatic potential

We analyzed the global bioclimatic potential of *Spodoptera eridania* with a focus on the African continent based on each pest suitability index defined by the two selected thresholds (MTP and P10). To

Table 3. AUC and TSS values for the pest and parasitoids models

Species	AUC		TSS	
	Mean	Standard error	Mean	Standard error
Spodoptera eridania	0.955	(0.009)	0.7851	(0.0340)
Chelonus insularis	0.934	(0.026)	0.7399	(0.0459)
Cotesia marginiventris	0.905	(0.042)	0.6185	(0.0381)
Telenomus remus	0.921	(0.026)	0.6593	(0.0348)
Trichogramma pretiosum	0.833	(0.041)	0.5155	(0.0456)
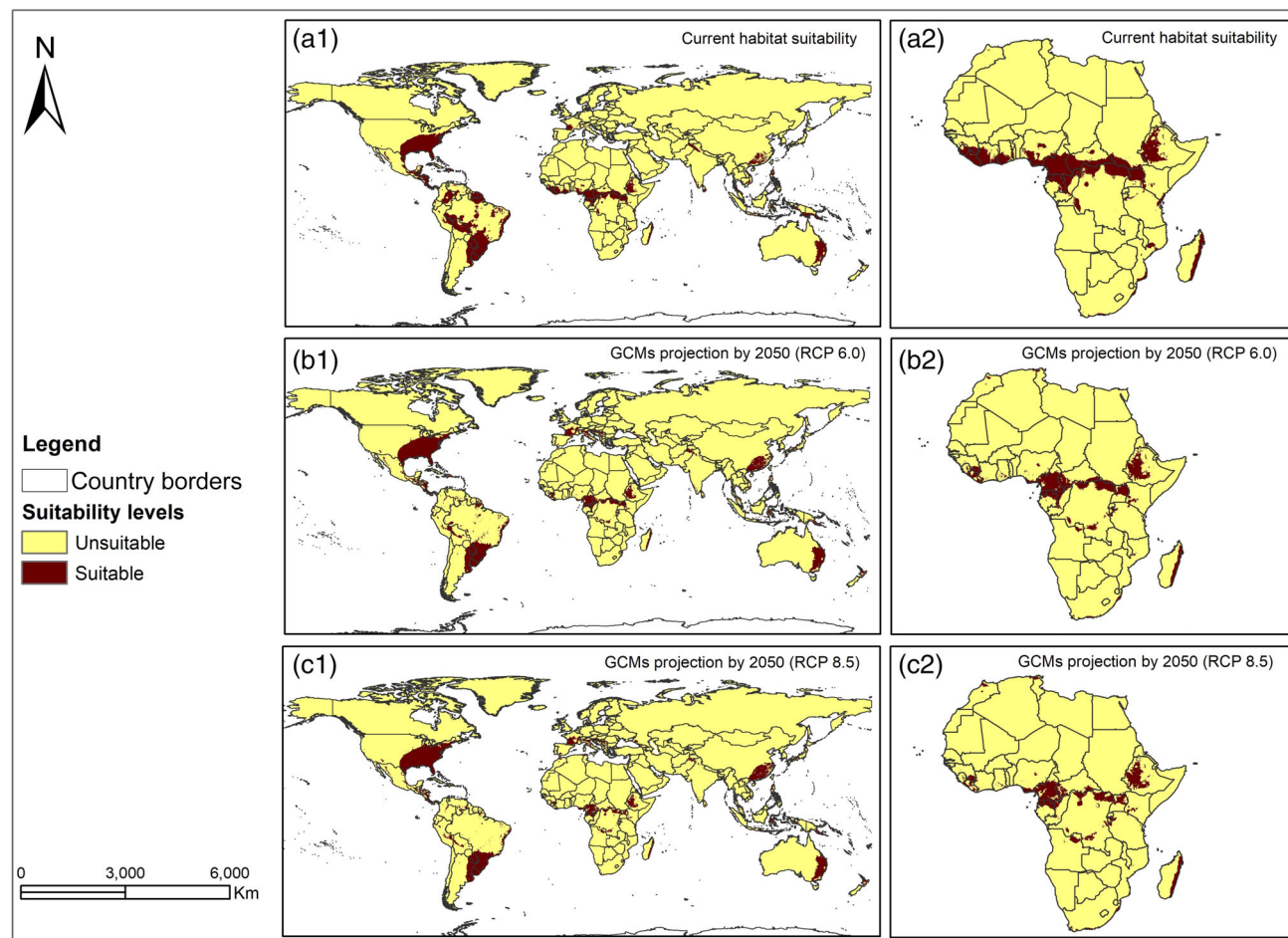
Figure 1. Predicted P10 current and future habitat suitability for *Spodoptera eridania*: (a) current suitable habitats, (b) and (c) future suitable habitats; 1, global; 2, Africa. Future predictions are based on two climate change scenarios for 2050: (b) RCP6.0 and (c) RCP8.5.

achieve this, we subtracted the binary suitability map of the pest from the binary suitability map of the parasitoids using raster calculation from spatial analysis tools of ArcGIS 10.1. Doing this, we obtained for each threshold option for the pest a map with three classes: 0 (pest with parasitoids), 1 (parasitoids without pest) and −1 (pest without parasitoids), where the areas of the study region classified as −1 represent those with high risk of *S. eridania* impact.

3 RESULTS

3.1 Model performance
The performance metrics (AUC and TSS) resulting from the models suggested that Maxent models for both SAW and its parasitoids performed better than random and showed a good predictive power (Table 3). The best predictive model was that of SAW, followed by *C. insularis*, *T. remus* and *C. marginiventris*.

Predictor variables were species-specific (Table S1) and derived from an initial selection of 11 uncorrelated bioclimatic variables: annual mean temperature (Bio1), mean diurnal range (Bio2), isothermality (Bio3), temperature seasonality (Bio4), minimum temperature of coldest month (Bio6), mean temperature of warmest quarter (Bio10), annual precipitation (Bio12), precipitation of driest month (Bio14), precipitation of wettest quarter (Bio16), precipitation of driest quarter (Bio17) and precipitation of coldest quarter (Bio19).
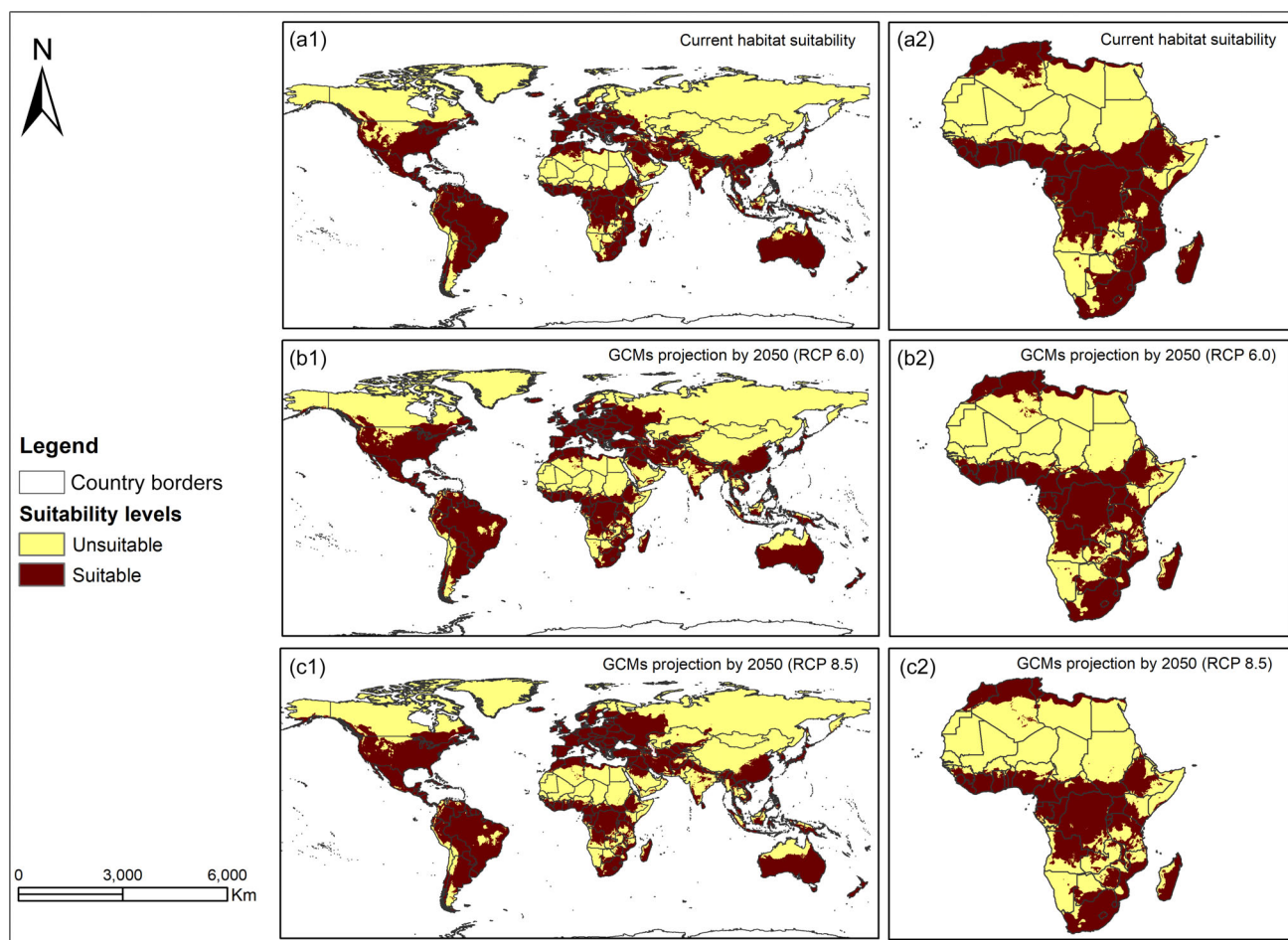
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Figure 2. Predicted MTP current and future habitat suitability for *Spodoptera eridania*: (a) current suitable habitats, (b) and (c) future suitable habitats; 1, global; 2, Africa. Future predictions are based on two climate change scenarios for 2050: (b) RCP6.0 and (c) RCP8.5.

3.2 SAW habitat suitability

The P10 models support that the pest can establish in coastal ecosystems of West African regions, including Guinea and Sierra Leone in current climates (Fig. 1). The models predict the southernmost parts of Central African Republic and Sudan, and the west of Ethiopia and Kenya as suitable for SAW establishment. Portions of northern Congo and Uganda, and the southern Democratic Republic of Congo can be suitable ecoregions. Likewise, eastern parts of Madagascar and northern states of Nigeria from Niger to Bauchi offer bioclimatic conditions for the establishment of *S. eridania*. The Benin Republic is totally unsuitable independent of climate conditions (current, RCP6.0 and 8.5). The whole of West Africa will become unsuitable in the event of climate change (RCP6.0 and 8.5) except parts of Guinea, Liberia and Sierra Leone. Small portions of southern and western Europe, southeastern China and Australia will become suitable in the event of climate change (RCP6.0 and 8.5).

MTP models predict larger habitat suitability of SAW globally with greater parts of southern and western Europe, southern, eastern and southeastern Asia, and Australia being particularly suitable for the pest independent of climate scenario (Fig. 2). West Africa except Sahelian countries can sustain *S. eridania*. The establishment potential in northernmost parts of Africa, such as portions of Algeria, Morocco and Tunisia, and Egypt and Libya northerly is higher with the MTP's models. The Congo basin, Madagascar, most of East Africa except Somalia and easternmost parts of southern Africa might be prone to the establishment of SAW (Fig. 2).

3.3 Parasitoid habitat suitability

Many parts of west, central and east Africa, including a large land area of Madagascar and eastern coasts of Southern Africa, are suitable for the egg parasitoids *T. remus* and *T. pretiosum* (Figs S1 and S2). Similarly, southern, eastern and southeastern Asia are suitable regions for both egg parasitoids. Our models suggest that *T. remus* and *T. pretiosum* can establish in northern and eastern coasts of Australia. Southern and western Europe can be particularly suitable for *T. pretiosum*. The suitability status of all these regions will not change despite global warming (RCP6.0 and 8.5), except for additional portions of Australia becoming suitable for *T. pretiosum*. The models predict that the egg-larval and larval parasitoids *C. insularis* and *C. marginiventris* have reduced suitability coverage compared to the two egg parasitoids (Figs S3 and S4). In west Africa, only small areas of Liberia, Guinea and Sierra Leone will be suitable. *C. marginiventris* can well establish in the Congo basin and Asia compared to *C. insularis*. Almost all of Madagascar is suitable for the egg-larval parasitoid *C. insularis*. It can also establish in northeastern Australia whereas
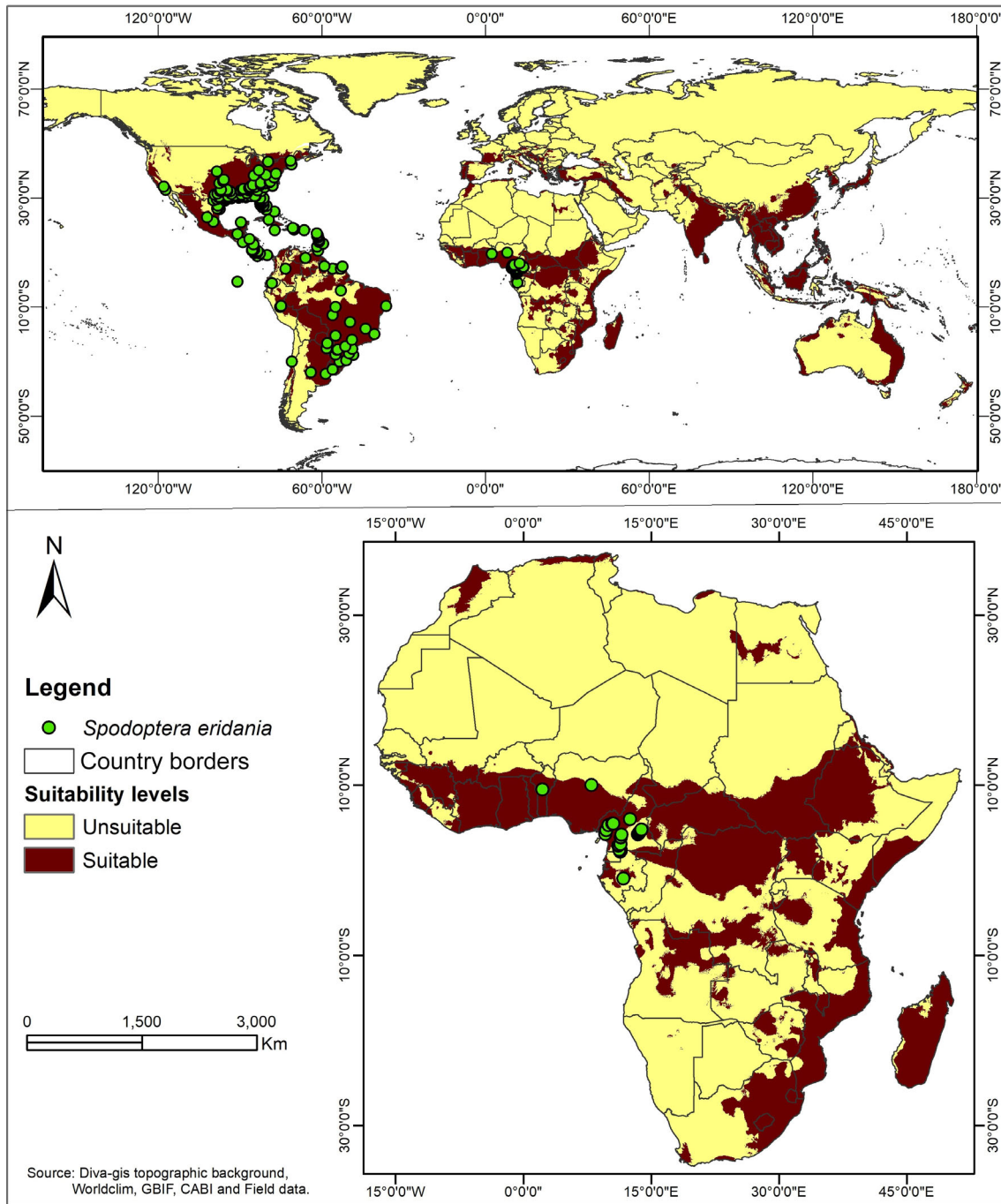
Figure 3. Georeferenced records for *Spodoptera eridania* and combined predicted current habitat suitability for its parasitoids *Telenomus remus*, *Trichogramma pretiosum*, *Chelonus insularis* and *Cotesia marginiventris*.

the eastern parts of the country are suitable for *C. marginiventris*. Our models indicate that Europe is totally unsuitable for *C. insularis* while southern Europe can sustain *C. marginiventris*, particularly in climate change situations (RCP6.0 and 8.5). Considered all together, the parasitoid suitability niche can decrease with global warming, particularly in the Congo basin and Southern Asia (Fig. S5). Conversely, the northern parts of Latin America will become more suitable in climate change conditions. P10 models show that the bioclimatic suitability of the parasitoids

matches perfectly that of SAW (Figs 1, 3, 4 and S1–S5) but not those of MTP (Figs 2 and S6).

4 DISCUSSION

4.1 Model performance
Our models demonstrated good results based on a bioclimatic analysis approach. However, a range of factors determine species distributions and distribution change dynamics, including biotic
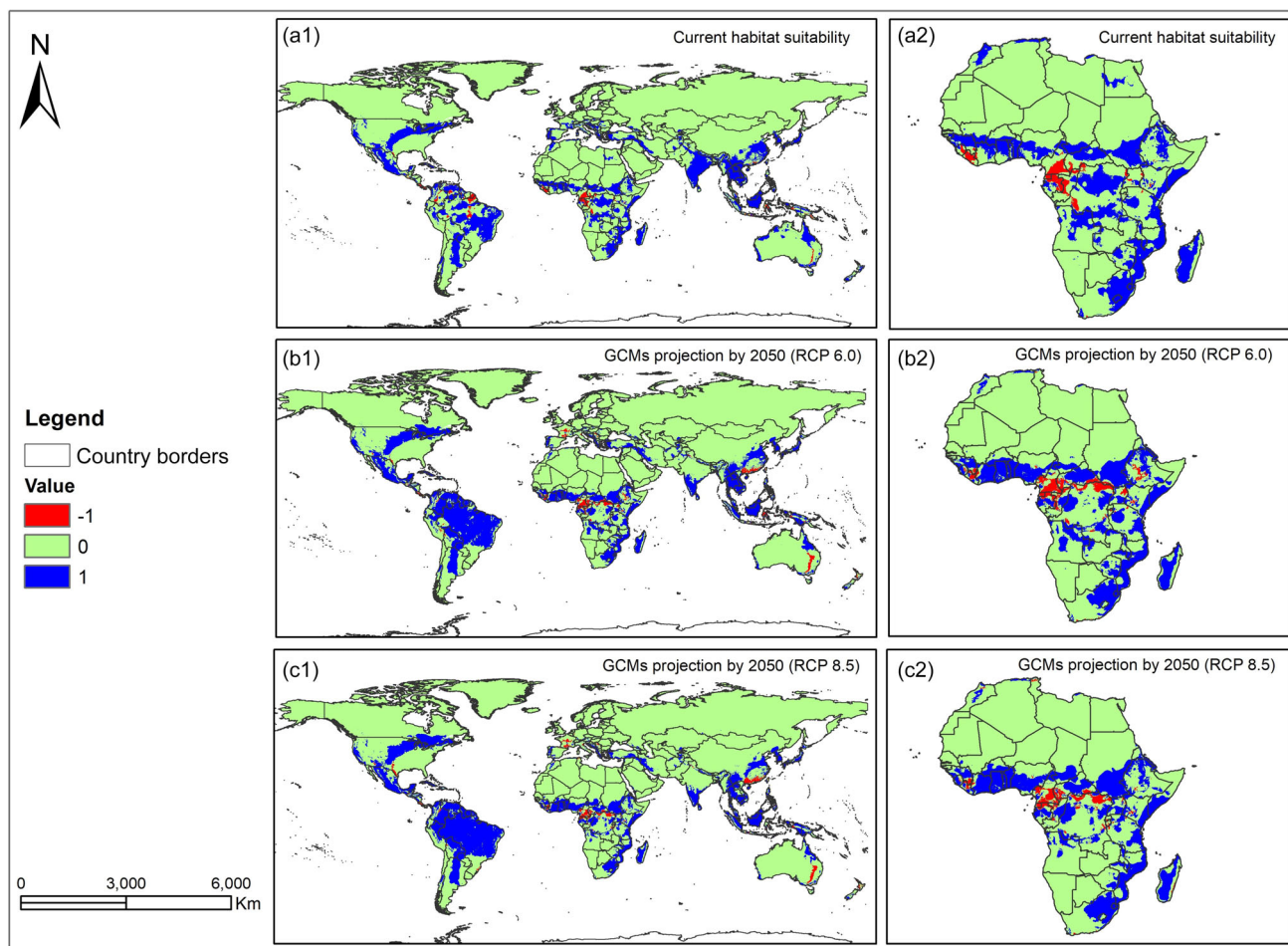
Figure 4. Subtracted P10 binary suitability map of *Spodoptera eridania* from that of its parasitoids *Telenomus remus*, *Trichogramma pretiosum*, *Chelonus insularis* and *Cotesia marginiventris*: (a) current suitable habitats, (b) and (c) future suitable habitats; 1, global; 2, Africa. Red gridcells show bioclimatic potential for the establishment of the pest and in the event of parasitoids absence.

interactions (such as host plant or host/prey availability), evolutionary change and dispersal ability.[38] Future climates together with landscape management may also influence the regulation of pests by natural enemies.[39] Another pitfall of the method used in this study is the integration in the models of factors such as irrigation. A significant effect of all these predictors might lead to a mismatch between host plants, pests and natural enemies in space and time, therefore decreasing the establishment likelihood of biocontrol agents.[40] Nevertheless, it is widely agreed that bioclimatic analysis can provide useful first estimates and guide decision making for medium- and long-term pest management.[41,42]

4.2 SAW habitat suitability

For the moment *S. eridania* has been reported in two countries in West Africa (Benin and Nigeria) and two in Central Africa (Cameroon and Gabon).[8] Our models demonstrate that the pest can establish in tropical moist and rain forests in Madagascar, and west and central Africa. We anticipate that the dispersal of the pest east and south from Cameroon and Gabon to suitable areas is likely to happen particularly in cool ecologies. The tropical mountain system in eastern Africa and subtropical humid forests in the Americas, eastern Asia and Australia are also shown to be suitable for SAW. These findings are supported by previous

studies on the species ecology which demonstrated the occurrence of the pest in the American tropics.[43,44] In southern Europe, subtropical dry forests can be particularly suitable for *S. eridania* with a changing climate condition (RCP6.0 and 8.5). The total P10 unsuitability of the Benin Republic (Fig. 1) currently could help to explain why extensive field sampling and pheromone trapping efforts conducted in the country the past 2 years did not discover the pest again. This leads to an assumption that initial accidental introduction of the pest to the country did not survive long with the difficult weather conditions. Conversely, the country is suitable for MTP but further outbreaks can only be explained by migration from Central Africa (Fig. 2). Most of west Africa would become unsuitable in the event of climate change (RCP6.0 and 8.5; Fig. 1), suggesting that the increase in temperature will be deadly to SAW in contrast to the cool climates of southern and western Europe and of Asia and Australia. This could explain why SAW is listed as an A1 quarantine pest by the European Food Safety Authority (EFSA).[11] SAW is already confirmed in west (Nigeria) and central Africa (Cameroon and Gabon).

4.3 Parasitoid habitat suitability

Tropical dry, moist and humid forests are suitable environments for *T. remus*, except large parts of rainforests in the Congo basin under current climates. Tropical shrubland can be suitable for

the egg parasitoid on the Indian subcontinent and parts of east-ern Africa. *T. remus* can also survive climates of the subtropical dry forests of Southern Europe in the event of global warming (RCP6.0 and 8.5). Almost all rainforests in Latin America will become suitable with increased temperature regimes as the cli-mate changes (RCP6.0 and 8.5).[45,46] The habitat suitability of *T. pretiosum* almost mirrors that of the first egg parasitoid *T. remus*, except that southern parts of North America are suitable and southeastern Asia is unsuitable for the former. This parasitoid is a ubiquitous insect present almost everywhere.[47] In contrast to *T. remus*, *T. pretiosum* can establish almost all over the Congo basin in current climates. The bioclimate envelop used in the cur-rent models shows least suitability of *T. pretiosum* with indications that the egg parasitoid will not survive in tropical dry and moist forests in southern Africa. The egg-larval parasitoid *C. insularis* has the most limited geographic range compared to all other par-asitoids considered in this study. All of Europe and large parts of Middle Africa are unsuitable for this egg-larval parasitoid. How-ever, *C. insularis* offers a good opportunity for the biocontrol of SAW on Madagascar (in the event of the introduction of this pest to the island). The *C. marginiventris* models predict unsuitable por-tions of the Indian subcontinent and of coastal West African ecol-ogies close to Central Africa.[48] Likewise, Australia is only suitable to the larval parasitoid in its eastern parts. High temperatures (RCP8.5) will tangibly decrease the establishment capabilities of *C. marginventris* in the tropical moist and rain forests of Africa but not in the subtropical humid forests of southern Europe (RCP6.0 and 8.5).[49,50]

Our models show that the climate suitability of the parasitoids match well that of SAW (Figs 1, 3, 4 and S1–S5). Most native and current invaded regions suitable for SAW are also suitable for the four selected parasitoids combined (Figs 3 and S5). Only the climates of the southernmost parts of the Sahel and small por-tions of southern Europe are suitable for the SAW parasitoids. The ensemble suitability for the selected parasitoids will decrease under the RCP6.0 and 8.5 climate change scenarios (Fig. S5) partic-ularly in the Congo basin and on the Indian subcontinent. How-ever, most climates of East Asia (east and south-central China) and of the insular regions of southeast Asia will remain suitable to the parasitoids despite climate change. On the other hand, the P10 climate suitability range shift of the four parasitoids (Fig. 4) suggests potential for biological control-based long term management of the pest, as opposed to the worst-case scenario of the MTP map (Fig. S6) with maximal distribution for the pest and limited suitability for biocontrol.

Overall, the egg parasitoids might be excellent candidates for inundative biological control, the releases of large numbers of parasitoids (e.g. Trichogramma spp.), as opposed to inoculative biological control.[51] The present study demonstrates that all the considered parasitoids are generally good candidate biological control agents of SAW worldwide, except they will not be efficient in specific habitats of northern Latin America, West Africa and the Congo basin under current climate conditions (Fig. 4). However, we anticipate that additional management methods should com-plement biological control, particularly in changing climate condi-tions (RCP6.0 and 8.5).[15,52]

5 CONCLUSIONS

It is likely that SAW detection in west and central Africa occurred shortly after its invasion of the region. It may not be a severe prob-lem outside its native range for the moment but may compromise

crop yields in specific hotspots in the coming years. We anticipate that the spread of the pest east and south from Cameroon and Gabon may happen any time, provided there are suitable path-ways. We demonstrated that all the considered parasitoids might be generally good candidates for biological control of SAW glob-ally, except they will not establish in specific habitats. The egg par-asitoids can be excellent candidates for inundative biological control against SAW. The current work is another demonstration that the guild of parasitoids shared between SAW and FAW[53,54] represents a perfect opportunity to pursue further work for bio-control of both pests by the studied parasitoids. The interpreta-tion of the models in this study is based only on bioclimatic suitability thresholding, and output data are only as good as the input data available. Hence, more work is needed to validate these findings in local contexts, taking microclimatic conditions into account. This would contribute to calibration of the model inputs for more precise predictions and aid better interpretations of outputs. In addition, this paper does not consider the efficacy of individual parasitoids or intraguild competition between and among these and other natural enemies present in a given envi-ronment. The present work is one important step towards devel-oping biocontrol of these two important pests, newly introduced and established on the African continent.

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

SUPPORTING INFORMATION

Supporting information may be found in the online version of this article.

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