

Biogeography of cereal stemborers and their natural enemies: forecasting pest management efficacy under changing climate

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Abstract

Background: Climate warming presents physiological challenges to insects, manifesting as loss of key life-history fitness traits and survival. For interacting host–parasitoid species, physiological responses to heat stress may vary, thereby potentially uncoupling trophic ecological relationships. Here, we assessed heat tolerance traits and sensitivity to prevailing and future maximum temperatures for the cereal stemborer pests, *Chilo partellus*, *Busseola fusca* and *Sesamia calamistis* and their endoparasitoids, *Cotesia sesamiae* and *Cotesia flavipes*. We further used the machine learning algorithm, Maximum Entropy (MaxEnt), to model current and potential distribution of these species.

Results: The mean critical thermal maxima (CT_{max}) ranged from $39.5 \pm 0.9^\circ\text{C}$ to $44.6 \pm 0.6^\circ\text{C}$ and from $46.8 \pm 0.7^\circ\text{C}$ to $48.5 \pm 0.9^\circ\text{C}$ for parasitoids and stemborers, with *C. sesamiae* and *Ch. partellus* exhibiting the lowest and highest CT_{max} respectively. From the current climate to the 2050s scenario, parasitoids recorded a significant reduction in warming tolerance compared with their hosts. Habitat suitability for all stemborer–parasitoid species was spatially heterogeneous under current and future climatic scenarios. *Cotesia sesamiae*, *C. flavipes* and *B. fusca* exhibited significant habitat loss, whereas *Ch. partellus* and *S. calamistis* showed a significant habitat gain under future 2050s predictions. Model metrics based on mean area under the curve ranged from 0.72 to 0.84 for all species, indicating a good predictive performance of the models.

Conclusion: These results suggest *C. sesamiae* and *C. flavipes* may face survival constraints or extirpation compared with their pest hosts when environmental temperature reaches their upper thermal limits earlier, likely reducing pest regulation through density-mediated effects. The results demonstrate potential destabilization of stemborer–parasitoid trophic systems potentially compromising biocontrol efficacy under climate warming.

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Keywords: biogeography; climate change; host–parasitoid interaction; MaxEnt; warming tolerance

1 INTRODUCTION

Evidence of anthropogenic global climate change is rapidly being experienced, with the increased magnitude and frequency of global climate ‘presses’ and ‘pulses’ such as droughts, floods and heatwaves.^{1,2} Global carbon dioxide concentrations and mean surface temperatures are projected to increase by 540–970 p.p.m. and 1.4–5.8°C, respectively, by 2100.^{3,4} Such scenarios will have deleterious effects on biodiversity, community structure, composition and function, species geographic range and ecosystem function.^{3–5} Given that approximately 70% of the population in sub-Saharan Africa (SSA) depends on subsistence agriculture and natural pest suppression (for example, natural substances) for sustainable agricultural livelihoods, climate warming presents a significant threat to crop productivity and natural pest regulation.^{6,7}

Interactions between insects and their natural enemies are controlled by environmental factors.^{6,8} Among these, temperature

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and relative humidity (RH) have key roles affecting organismal reproduction, development, abundance, parasitism, functional responses, geographic distribution and overall survival.^{3,9–11} The geographical range limit of an insect species is dependent on its ecological tolerance to environmental conditions.¹² Hence, determination of ecological tolerance allows for better prediction of pest species biogeographical patterns.¹² Although a poleward shift in species distribution has been predicted with climate warming,^{13,14} tropical regions nevertheless remain vulnerable to pest insect outbreaks relative to temperate regions owing to optimal temperature and food resources.¹⁵ Thus, predictive models should also extend to tropical areas given their vulnerability to new invasions.

Cereal crops, such as sorghum (*Sorghum bicolor* L. Moench) and maize (*Zea mays* L.) are significant food crops in SSA.^{16,17} However, lepidopteran stemborers, mostly *Chilo partellus* (Swinhoe), *Busseola fusca* (Fuller) and *Sesamia calamistis* (Hampson) represent a significant pest pressure on cereal food crop production.^{16,18} This is exacerbated by the recent addition of the devastating invasive leaf defoliator, fall armyworm *Spodoptera frugiperda* (J.E. Smith), a significant biosecurity threat, affecting food security resilience in SSA.¹⁹ The distribution of stemborer species reportedly varies among different agroecological zones and regions.¹⁵ For example, although native to Asia, *Ch. partellus* has since spread across Africa, mostly in lowland to high altitude, highland tropical and humid transitional areas.^{15,20–23} *Busseola fusca* is, however, indigenous to Africa and predominant in cooler higher altitudes (above 600 m.a.s.l.) in East and southern Africa, at 2000 m.a.s.l. or above in central Africa and in dry lowland savanna in West Africa.^{16,24,25} *Sesamia calamistis*, also indigenous to Africa, is widely present across 33 SSA countries, albeit at lower populations.^{26,27} Naturally, these stemborer populations are modulated by natural enemies through density-dependent factors. For example, the larval parasitoids, *Cotesia sesamiae* (Cameron) and *Cotesia flavipes* Cameron (Hymenoptera: Braconidae) exert significant biotic pressure on these stemborers.^{28–30} In particular, *C. sesamiae*, is an endoparasitoid of the whole lepidopteran cereal stemborer complex,²⁹ and is native to Africa, whereas *C. flavipes*, which prefers *Ch. partellus*, is native to Asia but was introduced into African agroecosystems in the 1990s.³⁰ Both parasitoid species are efficacious, accounting for between 32% and 55% of stemborer reduction in agroecosystems.^{16,31}

The effect of climate warming may manifest in different ways and at different magnitudes with the potential of destabilizing co-evolved trophic interactions.⁶ Similarly, because of the direct effects of temperature on organismal metabolism and activity, differential effects of high temperature across trophic levels may affect phenological synchrony,^{8,32} or activity time syncs owing to different thermal sensitivity.³ Thus, the strength and effect of stemborer–parasitoid interactions may be mediated by temperature.^{18,33,34} For example, empirical evidence suggests insects on different trophic levels respond differentially to temperature stress, both in terrestrial³⁵ and aquatic environments³⁶ with negative effects on biological control.³⁷ Furthermore, temperature-induced changes in the abundance and distribution of herbivore hosts may reduce the success of parasitoids in insect pest management. In this regard, the outcome is partly dependent on the ability of the parasitoids to improve their host-searching capacity and extension of their geographical range.³⁸ Nevertheless, overwhelming evidence suggests that parasitoids at higher trophic levels may suffer thermal stress resulting in decreased longevity, fecundity and mobility.⁶ Given the economic importance of pest

stemborer herbivores (*Ch. partellus*, *B. fusca* and *S. calamistis*) and their natural enemies (*C. sesamiae* and *C. flavipes*), predicting the outcomes of their interactions under climate warming is of paramount importance for pest management practitioners. Although previous studies looked into thermal tolerances of stemborers and their larval parasitoids,^{35,39,40} the results have not been incorporated into models to predict their future interactions under climate warming.

Recent predictions of insect pests' biogeographical patterns have centred on the use of models,^{22,41,42} particularly species distribution models (SDMs).⁴³ SDMs use spatial occurrence data combined with environmental data to predict spatial patterns of environmental suitability and distribution of a particular species.⁴³ Occurrence ('presence') data usually consist of latitude and longitude coordinates where the species of interest is present. In addition, environmental data consist of environmental descriptors such as abiotic measurements of temperature and rainfall, as well as biotic factors such as the presence or absence of other interacting species (for example, predators, parasitoids, competitors, food sources).⁴³ Various SDMs have been used in species biogeographical modelling.^{44,45} Among these models, MaxEnt and GARP have been reported as more robust, providing stronger predictions using presence-only data.^{45,46} Whereas GARP predicts a species' spatial presence, MaxEnt also estimates the spatial probability of occurrence, thus is a key methodology in species distribution modelling.⁴⁷

Temperature-driven phenology models based on species distribution records and phenology data have been used to forecast the potential distribution of *Ch. partellus* in Africa.²² In addition, the models have also been used to predict the distribution and abundance of *Ch. partellus* and *C. flavipes* in Ethiopia,⁴⁸ *Ch. partellus* and *B. fusca* and their natural enemies (*C. flavipes* and *C. sesamiae*) along Kilimanjaro and Taita Hills gradients in the East African region¹⁵ and recently *Ch. partellus*, *B. fusca*, *S. calamistis*, *C. sesamiae* and *C. flavipes* in Kenya and Tanzania.⁴⁹ However, no studies have predicted the abundance and distribution of these species with respect to southern Africa given that the region is projected to be drier (10% less rainfall)^{50–52} and warmer (+3 to 4°C) by 2100.^{1,53–55} These abiotic shocks present challenges to pest–natural enemy interaction outcomes and pest management.^{36,54} Using MaxEnt, we thus predicted the current and future distribution of indigenous stemborer species, *B. fusca* and *S. calamistis*, exotic *Ch. partellus*, their indigenous larval parasitoid, *C. sesamiae* and exotic *C. flavipes* in southern Africa. We used warming tolerance (WT) as a key determinant of climate warming sensitivity for all the study species with respect to southern Africa using thermal limits to activity (critical thermal maxima) and environmental mean temperatures (mean maximum) under current and future climatic conditions. We hypothesize that thermal sensitivity between stemborer pests and their natural enemies is dissimilar and that there is asynchrony in abundance and distribution between these two interacting trophic levels. This information is important in conducting pest risk assessments as well as designing, planning and developing improved pest management systems under climate warming.

2 MATERIALS AND METHODS

2.1 Study insects and rearing conditions

The initial colony of *C. sesamiae* was obtained from the South African Sugarcane Research Institute (SASRI), South Africa, whereas *C. flavipes*, *B. fusca*, *S. calamistis* and *Ch. partellus* colonies

were obtained from the International Centre of Insect Physiology and Ecology (ICIPE), Kenya. These organisms had been in culture for more than 20 generations with regular augmentation with wild populations to minimize inbreeding depression. The *C. sesamiae* colony was generated from parasitized *S. calamistis* larvae, whereas the *C. flavipes* colony was obtained from parasitized *Ch. partellus* larvae. Both colonies were maintained in climate chambers (HPP 260; Memmert) at $28 \pm 1^\circ\text{C}$, $65\% \pm 10\%$ RH and a 12:12 h light/dark photoperiod on an artificial diet⁵⁶ in 30-ml plastic vials with perforated screw-cap lids. Parasitoid cocoons were maintained according to species, under similar optimal conditions in open Petri dishes placed in Bugdorm rearing cages (240 cm³; Bugdorm-BD43030F; Megaview Science) until eclosion. Eclosed parasitoids had access to food (25% honey and water from a cotton wick) ad libitum until they were used in experiments as 24–48 h old adults. *Ch. partellus* and *S. calamistis* pupae were maintained in open Petri dishes in rearing cages under the same optimum conditions as parasitoids ($28 \pm 1^\circ\text{C}$, $65\% \pm 10\%$ RH), whereas *B. fusca* pupae were maintained at $25 \pm 1^\circ\text{C}$, $75\% \pm 10\%$ RH and a 12:12 h light/dark photoperiod in climate chambers until adult eclosion. Following emergence, adult stem-borers had access to 25% sugar-water from moistened cotton wads. Wax papers folded into pleats were placed in the rearing cages as an oviposition substrate for gravid females. To maintain uniformity among test insects, eggs were harvested after every 12 h, and transferred to an artificial diet⁵⁶ where they were allowed to hatch into larvae that were later used in subsequent experiments. In all cases, sixth instar larvae (last instar developmental stage) were used in critical thermal maxima (CT_{max}) assays for all stem-borer species.

2.2 Critical thermal maxima (CT_{max}) determination

Ten individual sixth instar larvae of *Ch. partellus*, *B. fusca* and *S. calamistis* and adults (24–48 h old) of *C. sesamiae* and *C. flavipes* were randomly placed in a series of test tubes ('organ pipes') connected to a programmable water bath (Lauda Eco Gold, Lauda) and subjected to constant heating rates. In all cases, assays started at a set point (optimum temperature: 28°C for all stem-borers and parasitoids except for *B. fusca* at 25°C) for 10 min (to allow insect temperature equilibration) before increasing the temperature at a rate of $0.25^\circ\text{C min}^{-1}$ until CT_{max} was recorded. CT_{max} was defined as the upper temperature at which each insect lost coordinated muscle function, which was regarded as a lack of response to mild prodding.⁵⁷

2.3 Statistical analyses

CT_{max} data analyses were conducted in STATISTICA, version 13.2 (StatSoft). Data were first checked for normality and equality of variance using the Shapiro–Wilk and Hartley–Bartlett tests, respectively. CT_{max} data met assumptions of constant variance and were analysed using one-way analysis of variance (ANOVA) with CT_{max} as the dependent variable and species as the categorical factor. Tukey–Kramer's post hoc tests were used to separate statistically heterogeneous groups.

2.4 Determination of warming tolerance

Warming tolerance, regarded as a measure of an insect's sensitivity to climate warming was calculated using standardized methods, and derived from our CT_{max} values.^{54,58} The mean temperature of the warmest (T_{max}) quarter for both current and 2050 climate scenarios was downloaded from WorldClim (<https://www.>

TABLE 1. Bioclimatic variables and their contribution used to model areas suitable for *Chilo partellus*, *Busseola fusca*, *Sesamia calamistis*, *Cotesia sesamiae* and *Cotesia flavipes*

Variable	Percentage contribution				
	<i>B. fusca</i>	<i>C. partellus</i>	<i>C. sesamiae</i>	<i>C. flavipes</i>	<i>S. calamistis</i>
Average annual precipitation	36.5		10.6	0.6	24.4
Average annual temperature	1.8	7.7	6	3.4	9.5
Mean diurnal temperature range	5.2	17.9	5.7	5.3	0.3
Mean temperature of the wettest quarter	4.8	5.3	15.6	8.2	1.6
Temperature annual range		41.4			
Precipitation of the wettest month	27.6	4.8	2.3		37.3
Precipitation seasonality	1.1	0.6		1.1	6.2
Temperature seasonality	21.8	12.1	22.8	18.6	17.7
Elevation	1.3	10.3	37	62.8	3
Number of significant variables	8	8	7	7	8

Note: Selected variables were limited to those with $r \geq 0.9$ within the area of model development.

Table 2. Summary statistical results using one-way ANOVA showing effects of species (*Cotesia sesamiae*, *Cotesia flavipes*, *Busseola fusca*, *Sesamia calamistis* and *Chilo partellus*) on critical thermal maxima (CT_{max})

Trait	Effect	SS	DF	MS	F	p-value
CT_{max}	Intercept	86 722.66	1	86 722.66	241 647	<0.001
	Species	150.16	1	150.16	418.4	<0.001
	Error	13.64	38	0.36		

Abbreviations: DF, degrees of freedom; MS, variance; SS, the sum of squares due to the source.

worldclim.org/data/bioclim.html) version 2.1⁵⁹ and mapped over the national boundary map for southern Africa in ArcGIS version 10.3 (ESRI). The WorldClim platform comprises a set of data layers derived from interpolations of mean monthly weather data from various global meteorological stations with a 30 arc-seconds of grid resolution.⁶⁰ The raster data sets were clipped to southern Africa using ArcGIS (ESRI). *WT* was calculated using the raster calculator function from ArcToolbox in ArcGIS using the following formulae:

$$WT = CT_{\max} - T_{\max}$$

where *WT* is the warming tolerance, CT_{\max} is the critical thermal maximum and T_{\max} is the mean temperature of warmest quarter.

As a result, *WT* plotted onto the southern African map layer was used to generate current and future scenarios (2050s) maps.

2.5 Presence records for stemborers and their parasitoids in southern Africa

Occurrence records of stemborers (*Ch. partellus*, *B. fusca* and *S. calamistis*) and larval parasitoids (*C. sesamiae* and *C. flavipes*) were obtained from previous physical surveys conducted in southern African countries.^{61–67}

2.6 Model environmental variables

Predictor climatic variables, based on temperature and precipitation were downloaded from WorldClim version 2.1 (www.worldclim.org)⁵⁹ at a spatial resolution of 2.5 arc-minutes (approximately 5 km at the equator). The current bioclimatic variables were derived from the annual means for the period 1970–2000, whereas future variables were based on annual means for the 20-years period 2041–2060.⁵⁹ All 19 bioclimatic variables may not necessarily determine the potential habitat distribution of the study insect species; therefore, they were first subjected to multicollinearity analysis using Pearson's correlation in R, and further selected based on the variables that best described the ecology of lepidopteran stemborers and their parasitoids. When two variables had a Pearson's coefficient value of ($r \geq 0.9$), only one variable from such pair considering its relative importance in determining stemborers and parasitoids distribution and their predictive power (percentage contribution) was selected for

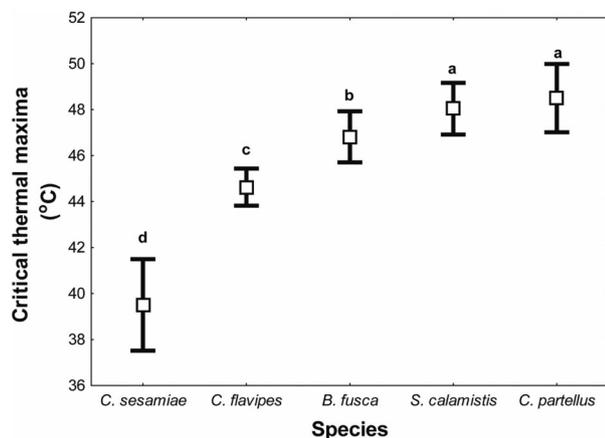


FIGURE 1. Species differences in critical thermal maxima for maize stemborers and their parasitoids. Error bars represent 95% confidence limits ($N = 20$). Means with the same letter are not significantly different from each other.

model development. As a result, from the 19 bioclimatic variables, a total of 8 bioclimatic variables and elevation were used in the development and simulation of the MaxEnt model. These were: average annual precipitation, average annual temperature, mean diurnal temperature range, mean temperature of the wettest quarter, temperature annual range, precipitation of the wettest

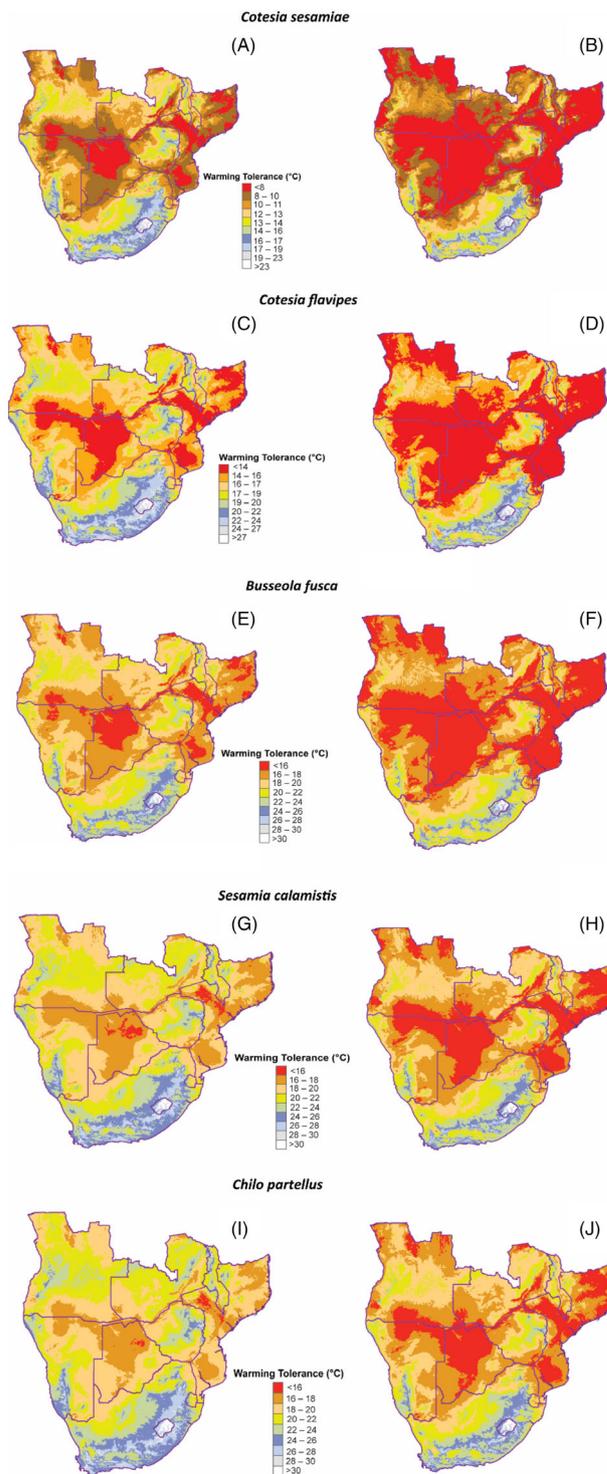


FIGURE 2. Warming tolerances for *Cotesia sesamiae*, *Cotesia flavipes*, *Busseola fusca*, *Sesamia calamistis* and *Chilo partellus* under current (A, C, E, G and I) and future (B, D, F, H and J) thermal conditions.

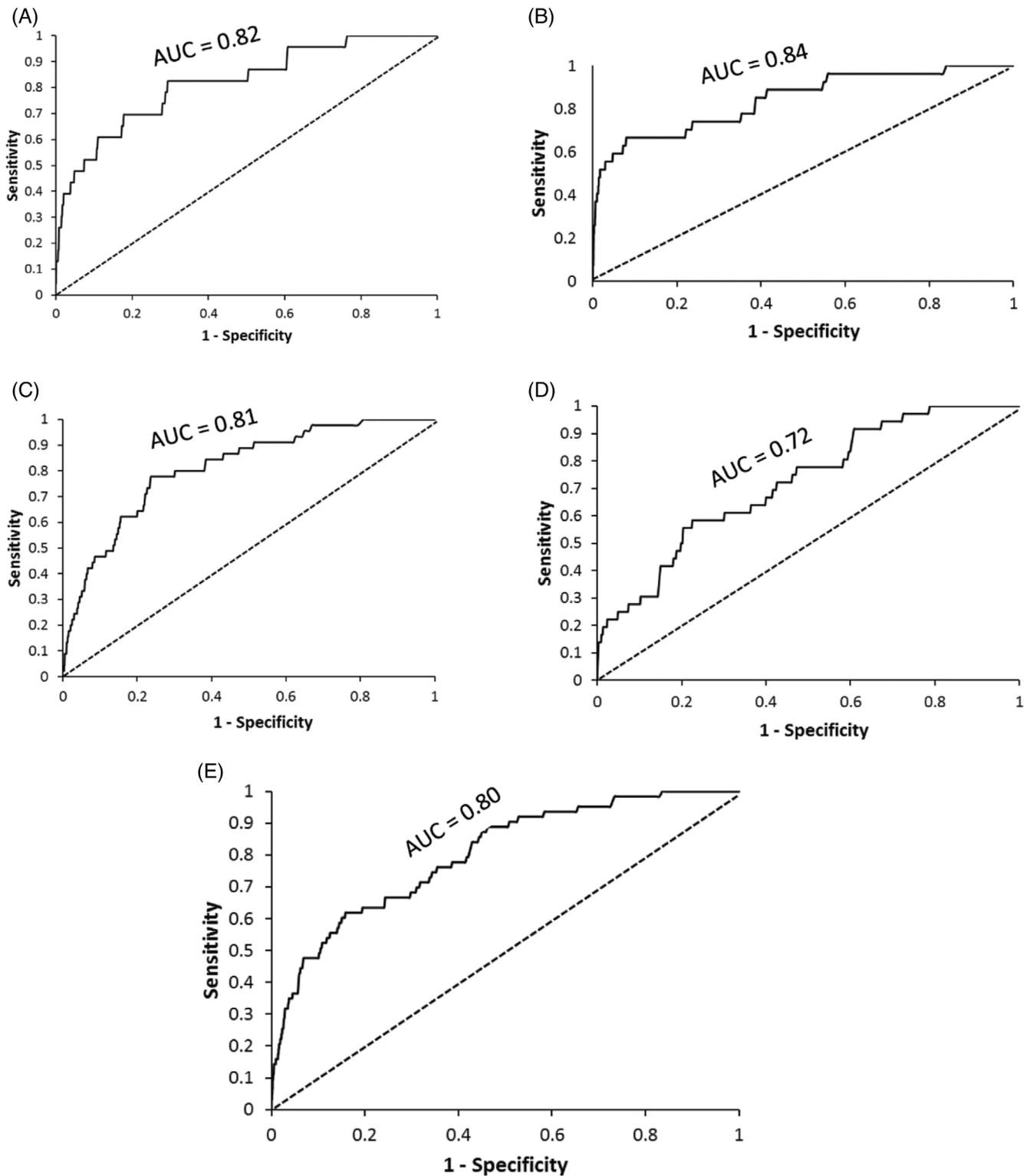


FIGURE 3. Receiver operating characteristic (ROC) curve and area under the curve (AUC) of the MaxEnt model for (A) *Cotesia sesamiae*, (B) *Cotesia flavipes*, (C) *Busseola fusca*, (D) *Sesamia calamistis* and (E) *Chilo partellus*.

month, precipitation seasonality, temperature seasonality and elevation (Table 1), as well as the Digital Elevation Model (DEM) from the NASA Shuttle Radar Topography Mission provided at 30 m pixel size (SRTM 30).⁶⁸ The DEM was resampled to the spatial resolution of the bioclimatic variables to match the pixel size for

use in the MaxEnt. These bioclimatic variables were considered as potential predictors of the stemborer and parasitoid habitat distribution based on their biological significance to species distributions, habitat modelling and ability to define eco-physiological tolerances of the study species.⁶⁹ Although most of the variables

were hinged on temperature and precipitation, elevation was also taken into consideration because the distribution of stemborers and their parasitoids is dependent on altitude.^{15,49,62} The final selection of predictor variables used for each species was based on the initial jack-knife test (Table 1). Variables that had the least training gain when used in isolation were dropped from the model.

At the same resolution, the aforementioned eight bioclimatic variables for future climatic conditions were also downloaded from WorldClim 2.1 for the Shared Socioeconomic Pathway 2 (SSP2-4.5) 2041–2060 climate scenario.^{59,70} SSP2-4.5 is termed the 'middle of the road' scenario characterized by intermediate greenhouse gas emissions, which are expected to start declining by 2050 but will not reach net zero by 2100. Thus, temperatures are expected to rise by approximately 2°C between 2041 and 2060.^{71,72} The elevation variable was maintained across the current and future climate scenarios because it was assumed that the altitude would not change significantly in the future to influence the results of this study.

2.7 Species distribution model

The MaxEnt model, a tool used to predict the distribution of a species from presence-only data and environmental variables, and effective with small sample sizes,⁷³ was used as the principal SDM to determine the potential habitat distribution and climate change impacts on *Ch. partellus*, *B. fusca*, *S. calamistis*, *C. sesamiae* and *C. flavipes* in southern Africa. The model was run using presence-only data.⁴⁶ The presence data sets for each species were split into training (75%) and validation (25%), and the number of iterations was set at 5000. The kernel density estimator, that is the 'kde2d' function of the MASS package⁷⁴ using the 'block' sampling approach in R⁷⁵ was used to generate the bias file. 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.⁷⁴ It is important to correct for sampling bias, particularly where collection of the data may be biased toward settlement areas, roads or easily accessible areas.⁷⁶ The MaxEnt modelling approach allows the inclusion of bias files in the model, which facilitates the choice of background data with similar bias. Furthermore, the optimum tuning and parameter settings for the MaxEnt models were derived from the 'ENMevaluate' function in the package ENMeval⁷⁷ available in R software.⁷⁵ This approach calculates multiple metrics to aid in selecting optimum model settings that balance goodness-of-fit and model complexity.⁷⁷ The following model parameters were derived for each pest and parasitoid using 'ENMevaluate' from the models with the lowest change in the Akaike information criterion ($\Delta AICc = 0$): linear (L), quadratic (Q), product (P), threshold (T), hinge (H) and regularized multiplier (RM). In addition, multivariate environmental similarity surface (MESS) analysis together with clamping, extrapolate and fade with clamping were also used for all the models. 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,⁷⁸ in our case in future scenarios for which occurrence reference data are unavailable.

A projection file containing predictor variables for the 2041–2060 climate scenario was uploaded to MaxEnt to perform the future projections using the current models. Model performance was assessed quantitatively using the area under the curve (AUC) statistic. The AUC was derived from threshold-independent receiver operating characteristic (ROC) analysis, significant in

assessing the discriminative power of the model.^{69,73} The ROC curve is a plot of true positives against false positives with AUC values between 0 and 1. An AUC closer to 1 indicates a high predictive capability of the model.⁷⁹ In addition, using the AUC metrics to evaluate the models has the advantage of being

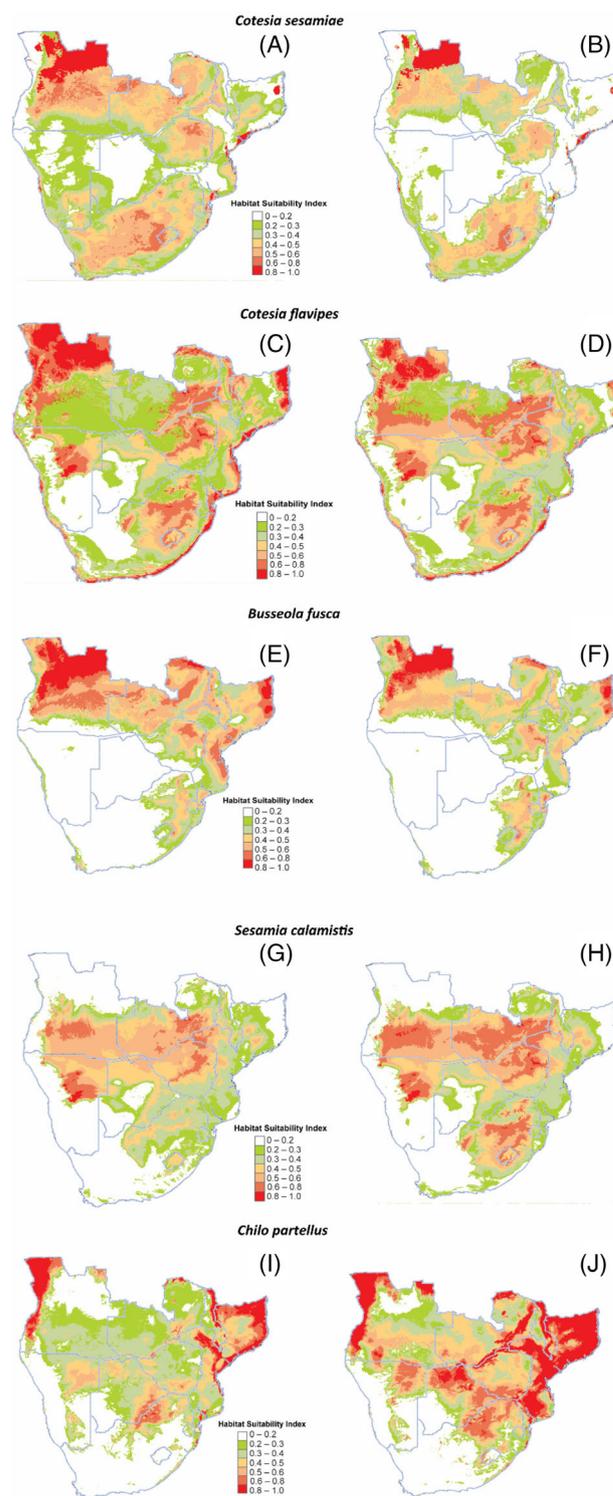


FIGURE 4. Predicted habitat suitability model for *Cotesia sesamiae*, *Cotesia flavipes*, *Busseola fusca*, *Sesamia calamistis* and *Chilo partellus* under current (A, C, E, G and I) and future (B, D, F, H and J) climatic conditions.

threshold-independent, and as such does not require decisions regarding thresholds of what constitutes a prediction of presence versus a prediction of absence. This was very relevant in this study because the occurrence points of the different pests and parasitoids varied spatially across the study area.^{80,81}

The ASCII outputs from MaxEnt were converted to GEOTIFF binary maps depicting suitable and unsuitable habitats based on the ten-percentile training presence logistic threshold.

3 RESULTS

3.1 Critical thermal maxima

Heat tolerance (CT_{max}) varied significantly across species ($p < 0.001$) (Table 2). The mean CT_{max} values for *C. sesamiae*, *C. flavipes*, *B. fusca*, *S. calamistis* and *Chilo partellus* were 39.5 ± 0.9 , 44.6 ± 0.6 , 46.8 ± 0.7 , 48.0 ± 0.8 and $48.5 \pm 0.9^\circ\text{C}$ respectively (Figure 1). *Ch. partellus* recorded the highest CT_{max} , although this heat tolerance did not differ significantly from that of *S. calamistis* (Figure 1). *Cotesia sesamiae* recorded the lowest CT_{max} (Figure 1), whereas *C. flavipes* and *B. fusca* were intermediate, although *B. fusca* had significantly higher CT_{max} . However, CT_{max} values for both *C. flavipes* and *B. fusca* were significantly different from those of *C. sesamiae*, *S. calamistis* and *Ch. partellus* (Figure 1).

3.2 Warming tolerances for stemborers and parasitoids

WT values under current climatic conditions were 7.65 to 23.94°C (*C. sesamiae*), 12.77 – 29.06°C (*C. flavipes*), 14.96 – 31.25°C (*B. fusca*), 16.18 – 32.47°C (*S. calamistis*) and 16.64 – 32.93°C (*Ch. partellus*), with *C. sesamiae* and *Ch. partellus* recording the lowest and highest WT ranges, respectively (Figure 2A,C,E,G,I). Similarly, projected WT values by 2050 were 5.38 – 23.03°C (*C. sesamiae*), 10.5 – 28.15°C (*C. flavipes*), 12.69 – 30.34°C (*B. fusca*), 13.91 – 31.56°C (*S. calamistis*) and 14.37 – 32.02°C (*Ch. partellus*) (Figure 2B,D,F,H,J). Although all species showed a reduction in projected WT, *Ch. partellus* exhibited highest projected WT range, whereas the generalist stemborer parasitoid *C. sesamiae* recorded the lowest WT range.

3.3 Model performance

The ROC is the good measure of model performance with widespread use in species distribution modelling. MaxEnt model outputs for parasitoids and stemborers showed strong goodness-of-fit (AUCs 0.72–0.84) (Figure 3), indicating that the model showed good predictive performance for suitable and unsuitable habitat differentiation for stemborer and parasitoid occurrence.⁶⁹

3.4 Stemborer and parasitoid habitat suitability

The highly suitable habitats for *C. sesamiae* and *C. flavipes* in the present include most parts of Angola, Zambia, Zimbabwe and

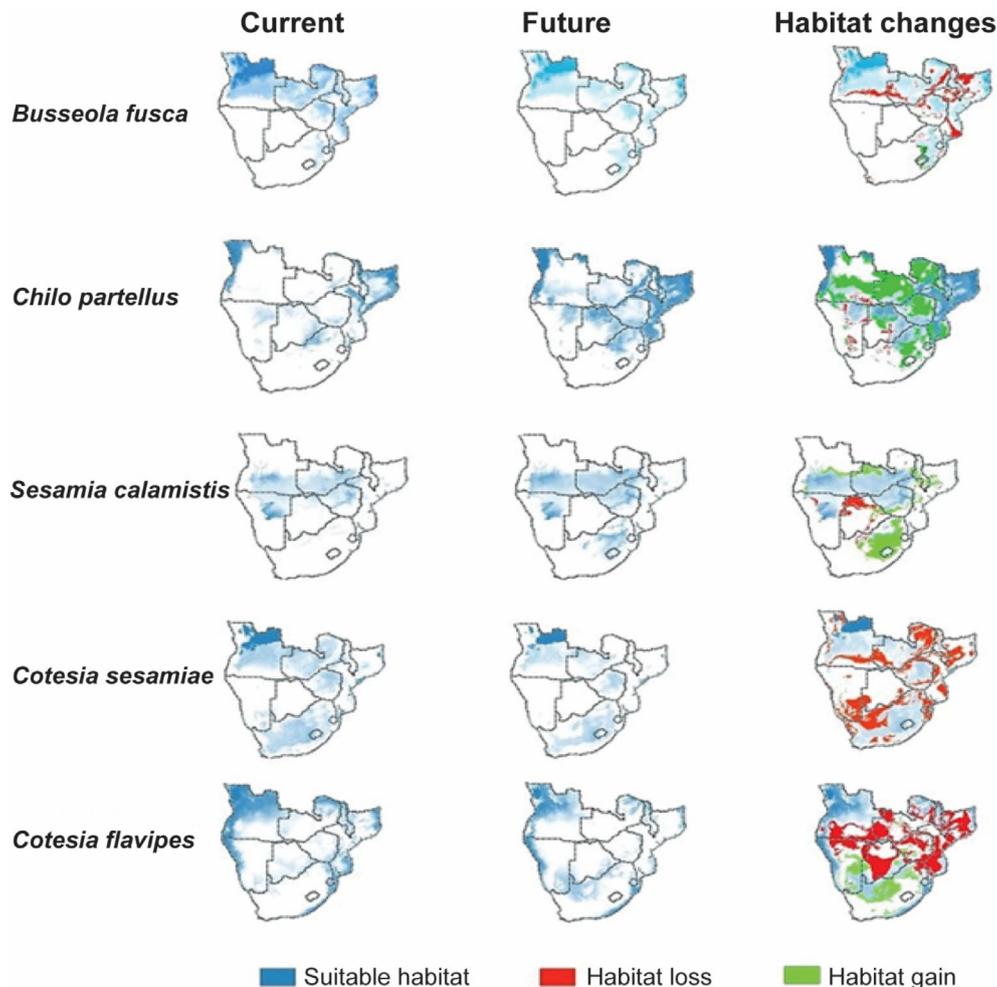


FIGURE 5. Habitat shifts (loss or gain) for *Busseola fusca*, *Chilo partellus*, *Sesamia calamistis*, *Cotesia sesamiae* and *Cotesia flavipes* due to changing climatic conditions.

Table 3. Changes in suitable habitats for *Chilo partellus*, *Busseola fusca*, *Sesamia calamistis*, *Cotesia sesamiae* and *Cotesia flavipes*

Species	Current (km ²)	Future (km ²)	Loss (km ²)	Gain (km ²)	Net change (km ²)
<i>Busseola fusca</i>	3 281 696.33	2 852 341	485 767.7	56 412.48	-429 355.13
<i>Chilo partellus</i>	2 755 862.33	4 155 005	119 134.6	1 518 277	1 399 142.61
<i>Sesamia calamistis</i>	2 193 018.97	2 670 806	187 833.7	665 621.1	477 787.39
<i>Cotesia sesamiae</i>	4 014 634.51	2 685 027	1 336 515	6907.07	-1 329 608.01
<i>Cotesia flavipes</i>	4 347 853.28	3 223 629	1 639 882	515 658	-1 124 224.36

South Africa, whereas most parts of Namibia and Botswana dominate as least suitable habitats (Figure 4A,C). For stemborers, Botswana, Namibia, southern Angola, southern and western parts of Zimbabwe and South Africa are not suitable for *B. fusca* at present (Figure 4E). Using current predictions, *S. calamistis* remains mostly confined to central parts of Angola and Zambia as well as northern parts of Zimbabwe, whereas *Ch. partellus* is mostly confined to western Angola, eastern Malawi and northern parts of Mozambique (Figure 4G,I). Habitat distributions for both parasitoids and stemborers evaluated under a future climate (2050) were spatially heterogeneous (Figure 4). As such, the greater parts of the terrestrial ecosystems are projected to be significantly suitable for both parasitoids and their herbivore stemborer hosts (Figure 4). Although parasitoids (*C. sesamiae* and *C. flavipes*), noctuids (*B. fusca* and *S. calamistis*) and crambid (*Ch. partellus*) showed changes in future distribution, *C. sesamiae* *C. flavipes* and *B. fusca* exhibited a reduction in suitable habitats by 2050 (Figures 4B,D,F and 5; Table 3). By contrast, *S. calamistis* recorded an increase in suitable habitats by 2050 extending into northern parts of Zambia and eastern parts of South Africa (Figures 4H and 5; Table 3). Likewise, *Ch. partellus* showed a significant increase in suitable habitats by 2050 with most parts of Mozambique, western Angola, eastern Malawi, northern parts of Botswana and Zimbabwe dominating (Figure 4J; Table 3). Although current climate showed Lesotho being unsuitable for *Ch. partellus*, 2050's projection showed sporadic occurrences indicating habitat gain for this invasive insect species (Figure 4I,J). Comparison of the parasitoids' future distribution showed more habitat gain for *C. flavipes* than for congeneric *C. sesamiae* (Figure 4B,D; Table 3).

4 DISCUSSION

Climate warming is altering ecosystems by shifting species performance, biogeographic ranges and trophic interaction outcomes.⁵ Our results demonstrate differential spatiotemporal distribution of host stemborer–natural enemy habitat suitability, and by inference their numbers under current and future climate warming scenarios. In particular, we show that some previously pest-unsuitable habitats will be more optimal under climate warming. For example, the range of *Ch. partellus* will increase by 2050. By contrast, habitats for antagonist parasitoids species are expected to decrease under climate warming, probably reducing the biotic pressure on stemborer pests. For example, the range of *C. sesamiae* is expected to dwindle with warming, probably offsetting stemborer pest management. This study thus provides novel context-specific southern African insights into the potential effects of climate warming on the spatial distribution of key larval parasitoids and their herbivorous hosts, and may help inform efficacious pest management under changing climates.

Insect species potentially survive projected warmer climate environments through either having higher basal stress tolerance^{82,83} or remodelling their thermal phenotypes.^{54,84} However, increasing evidence suggest that insects' acclimation response ratios are low and as such, phenotypic plasticity may be ecologically insufficient to cushion insects against climate change.^{85,86} Thus, high basal heat tolerance remains far more ecologically relevant in cushioning climate warming effects than phenotypic plasticity (see discussions in Kelley⁸² and Wan and Yang⁸³). Our basal heat tolerance results varied across species with invasive *Ch. partellus* exhibiting the highest CT_{max} overall. This indicates that *Ch. partellus* has inherent high basal heat tolerance relative to other stemborer and *Cotesia* parasitoid species, and this may confer fitness and survival advantage under projected climate warming⁸². However, this differential thermal sensitivity to high temperature may result in disruption of stemborer–parasitoid trophic interactions and biological control efficacy.⁵ Similarly, the efficacy of parasitoids is dependent on adult performance vis-à-vis host-searching ability (activity), population establishment, persistence, reproduction and development.⁵⁴ The current study demonstrates that both *C. sesamiae* and *C. flavipes* stop activity at approximately 39.5 and 44.6°C respectively, showing lower basal heat tolerance than their stemborer hosts. This likely translates into a spatial or temporal activity mismatch between the two levels, and may affect pest parasitism. Furthermore, because the generalist parasitoid *C. sesamiae* had lower heat tolerance than the more specific *C. flavipes*,^{29,30,40} there is a higher likelihood of future stemborer biological control programmes being negatively affected, albeit more for *S. calamistis* and *B. fusca* than for *Ch. partellus*.

Stemborer–parasitoid phenological mismatch can arise when ovipositing parasitoid adults and their respective susceptible stemborer developmental stages occur asynchronously.⁵ Most parasitoid species rely on plant chemical cues to locate their hosts, but their activity can be altered by temperature stress resulting in reduced parasitoid recruitment and parasitism rates.^{5,8,58} In addition, high temperatures can negatively influence parasitoid efficacy through top-down effects, for example by impacting behavioural activities such as flying and foraging.^{8,58} Although all stemborer and parasitoid species tested here showed a decrease in *WT* values from the current climatic conditions to the 2050s, both *Cotesia* parasitoids exhibited a greater reduction in *WT* than their host stemborer species, suggesting increased chances of deleterious effects during extreme weather events. Although southern Africa is projected to be warmer and drier,^{50,51,54} there is a higher likelihood of more stress exposure for parasitoids relative to their hosts. This asymmetrical stress exposure elicits major physiological and ecological constraints to the parasitoids, influencing key activity traits, for example host-searching capacity, oviposition rates and dispersal. In

particular, *C. sesamiae* and *C. flavipes* may face greater constraints on survival than *B. fusca*, *S. calamistis* and *Ch. partellus* with warming temperatures, resulting in a stemborer–natural enemy mismatch that may affect pest management.

Selection of the correct climatic variables based on the ecological aspects of a target species is fundamental in precisely modelling its spatiotemporal potential distribution.⁶⁹ The key bioclimatic variables used in this study were primarily hinged on temperature and precipitation. Previous studies showed that temperature and RH are key abiotic factors mediating insect physiological fitness, survival, distribution and the population dynamics of stemborers and their natural enemies.^{15,23,40,48,87} Thus, average annual precipitation, precipitation in the wettest month and temperature annual range were the key driving factors for the distribution of *B. fusca*, *S. calamistis* and *Ch. partellus* respectively, whereas elevation and temperature seasonality showed a significant distribution impact on parasitoids (*C. sesamiae* and *C. flavipes*).

Our results add to the current literature detailing shifts in the spatiotemporal distribution of pest insects with climate change.^{45,49,69,88,89} In particular, Jendritzki et al.⁴⁹ projected a significant decrease in parasitoid (*C. sesamiae* and *C. flavipes*) populations relative to their hosts (*B. fusca*, *Ch. partellus* and *S. calamistis*) and a decrease in parasitism in East Africa. The current results showed that climate change may have significant species-dependent impacts on the distribution of parasitoids and their stemborer hosts. For example, parasitoids (*C. sesamiae* and *C. flavipes*) and *B. fusca* showed a significant reduction in future suitable habitats, whereas *S. calamistis* and *Ch. partellus* showed a 30% and 55% increase in future habitat suitability respectively. Although *C. sesamiae* and *C. flavipes* have been reported to reduce stemborer densities between 32% and 55% in *Z. mays* and *S. bicolor*,^{16,31} the results suggest disruption of biological control programmes as a result of a mismatch in biogeography between the pests and their parasitoids, in agreement with Jendritzki et al.⁴⁹ Lepidopteran stemborers reportedly account for 5%–75% of cereal yield losses in SSA.^{16,17} As a result, this may negatively affect cereal production systems, resilience and food security in SSA. This may be exacerbated by the notion that approximately 70%–80% of African populations rely on subsistence agriculture, and natural enemy antagonists for pest control.^{15,49,90} Previous studies have projected increased numbers of generations and geographic expansion of *Ch. partellus* from dry lowland to the higher elevated areas of southeastern African countries.^{22,91} In addition, Mwalusepo et al.¹⁵ predicted an increase in climatic suitability for *Ch. partellus* with increased extension to moist mid-altitude and highland transitional areas of the East African region. This is consistent with current results indicating a projected gain in *Ch. partellus*-suitable habitats in southern Africa. Specifically, *Ch. partellus* showed a significant range expansion, potentially including Angola, Zambia, Zimbabwe, Malawi, Mozambique, South Africa and Lesotho. Given that *Ch. partellus* key host plants (maize and sorghum) are grown in these countries on both small- and large-scale farms, there is a greater likelihood of frequent and severe pest outbreaks. Supported by other non-crop wild plant hosts,⁶⁶ this may support *Ch. partellus* pest proliferation that may increase pest populations. Although indigenous *B. fusca* and *S. calamistis* exhibited projected habitat loss and a lower habitat gain than *Ch. partellus* respectively, exotic *Ch. partellus* may competitively outcompete and displace the native species, in keeping with the findings of Mutamiswa et al.²³ As a co-evolved endoparasitoid of

Ch. partellus, *C. flavipes* may be expected to follow its host for survival.¹⁵ In Ethiopia, model studies predicted that *C. flavipes* distribution may coincide greatly with *Ch. partellus* potential distribution with parasitoid density projected to be high in areas where host density is high.⁴⁸ However, this may not be the case under projected climate change in southern Africa because *C. flavipes* exhibited suitable habitat loss, whereas its host showed habitat gain. This implies that the parasitoid may not be able to follow the host in all its projected distribution areas, hence negatively affecting biological control under climate warming. Although *C. sesamiae* exhibited a greater projected reduction in suitable habitats, as well as being a generalist compared with its congener, this may potentially impact its ecological roles as a stemborer antagonist.

In conclusion, this study documents the projected regional spatiotemporal distribution of lepidopteran cereal stemborers and their natural enemies under climate change. Our model indicates: (1) more significant geographic expansion of exotic *Ch. partellus* relative to other indigenous stemborer species (*B. fusca* and *S. calamistis*) and larval parasitoids (*C. sesamiae* and *C. flavipes*); and (2) a more significant reduction in suitable habitats for associated parasitoids relative to their herbivore hosts. This infers potential success of *Ch. partellus* amidst warming habitats, and coupled with underperforming parasitoids owing to climate warming, *Ch. partellus* may thus dominate SSA ecosystems in the future (also see Mutamiswa et al.²³). In addition, *C. sesamiae* and *C. flavipes* parasitoids may not match the geographic expansion and/or activity timing of their host species, and hence is a potential spatiotemporal mismatch under projected climate warming.⁹² This will in all likelihood compromise future biological control programmes. Overall, the study underlies the importance of climate warming in influencing trophic interactions outcomes, with implications for biological pest control and potentially food security.

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CONFLICT OF INTEREST

All authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

Data largely from public sources of data. The rest is available upon request

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