



Uncertainties in the effectiveness of biological control of stem borers under different climate change scenarios in Eastern Africa

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Received: 6 September 2021 / Accepted: 4 March 2023
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Abstract

Climate change (CC) is expected to significantly affect biodiversity and ecosystem services. Adverse impacts from CC in the Global South are likely to be exacerbated by limited capacities to take adequate adaptation measures and existing developmental challenges. Insect pests today are already causing considerable yield losses in agricultural crop production in East Africa. Studies have shown that insects are strongly responding to CC by proliferation, shift in distribution, and by altering their phenology, which is why an impact on agriculture can be expected. Biological control (BC) has been proposed as an alternative measure to sustainably contain insect pests, but few studies predict its efficacy under future CC. Using the species maximum entropy modeling (Maxent) approach, we predict the current and future distribution of three important lepidopteran stem borer pests of maize in Eastern Africa, i.e., *Busseola fusca* (Fuller, 1901), *Chilo partellus* (Swinhoe, 1885), and *Sesamia calamistis* (Hampson, 1910), and two parasitoids that are currently used for BC, i.e., *Cotesia flavipes* (Cameron, 1891) and *Cotesia sesamiae* (Cameron, 1906). Based on these potential distributions and data collected during household surveys with local farmers in Kenya and Tanzania, also future maize yield losses are predicted for a business-as-usual scenario and a sustainable development scenario. We found that BC of the stem borer pests by *C. flavipes* and *C. sesamiae* will be less effective under more severe CC resulting in a reduced ability to curb maize yield losses caused by the stem borers. These results highlight the need to adapt BC measures to future CC to maintain its potential for environmentally friendly pest management strategies. The findings of this research are thus of particular relevance to policymakers, extension officers, and farmers in the region and will aid the adaptation of smallholder agricultural practices to the impacts of CC.

Keywords Kenya · Tanzania · Stem borer pests · Integrated pest management · Species distribution modeling · Maxent

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1 Introduction

Anthropogenic climate change (CC) will have substantial impacts on human–environment interactions, including the provisioning of important ecosystem services (IPCC 2014). Countries in the Global South are predicted to be more exposed to the impacts of CC (Christensen et al. 2007), as they often lack the financial, institutional, and human resources to cope with climatic and environmental change (Abeygunawardena et al. 2009). Many African countries are particularly vulnerable (WMO 2019; Boko et al. 2007), and it is expected that the effects of CC will significantly constrain economic and social development of the continent (AFDB et al. 2019; Baarsch et al. 2020; Boko et al. 2007).

Agriculture continues to play an important role in many developing East African economies, and in particular in Kenya and Tanzania where the agricultural sector contributes significantly to national GDP and constitutes a major source of labor (ILO 2021; Salami et al. 2010; World Bank 2021). Still more than half of the working population is employed in the agricultural sector (World Bank 2021). Agricultural activity is dominated by smallholder farmers (Salami et al. 2010) who typically cultivate small plots and primarily produce for home consumption. They are vulnerable to external shocks, such as extreme weather events, market fluctuations, or pest and disease outbreaks (Morton 2007; Salami et al. 2010). Synthetic pesticides are of limited relevance to most smallholder farmers, mainly because of financial constraints, limited availability, and lack of training (Kamau et al. 2018; Naidoo et al. 2010; Williamson et al. 2008), whereas traditional methods of pest control still play an important role (Abate et al. 2000).

An eminent threat to agricultural production and food systems is CC (FAO et al. 2020; IPCC 2019; Thornton et al. 2014) which will have direct effects on food security in East Africa and beyond (Anya et al. 2012; FAO et al. 2020; Sundström et al. 2014). Given that CC presumably impacts the distribution of insect pests (Stange and Ayres 2010), it is likely that crop health and yields will be affected, too. Hence, effective, sensible, and anticipatory management and mitigation are ever more important to minimize adverse impacts of CC on agriculture. This will not only be essential when trying to build a resilient food system that can secure nutrition for the local population, but also with regard to environmental degradation and the sustainable use of land resources. Integrated pest management (IPM), aiming at promoting healthy crops while minimizing disruptions to the environment and ecosystems (Barzman et al. 2015), can be an alternative or complementary approach to pesticide-based crop protection (Bale et al. 2008; Barzman et al. 2015). One approach in IPM is biological control (BC) that uses biological agents to control harmful organisms (Bale et al. 2008; FAO 2021a).

Even though a number of studies are predicting the future distribution of pest species under CC (Lantschner et al. 2018), little is known about the impact of CC on the distribution of important BC agents. As species' responses to CC differ (Ladányi and Horváth 2010), it is possible that established interactions of species used in BC programs will be disrupted as a consequence of a changing climate (Mwalusepo et al. 2015a; Skendžić et al. 2021; Thomson et al. 2010). Such climate-induced disruptions may render established BC relationships ineffective and impair proven strategies of IPM (Guimapi et al. 2020; Thomson et al. 2010). We therefore investigate the distribution of maize borers in Kenya and Tanzania in relation to their parasitoid BC agents to predict future prevalence. Given that maize is a staple crop in sub-Saharan Africa (SSA) and the most important crop in Kenya and Tanzania (ITA 2021; FAO 2021b), we also investigate the role of BC in reducing stem borer-associated maize yield losses under different CC scenarios.

2 Materials and methods

2.1 Species and presence records

Insect pests are damaging crops and cause considerable yield losses (De Groot 2002; Gofitshu et al. 2017; Kfir et al. 2002; Oerke 2006; Youdeowei 1989). Recent studies show that pest insects are sensitive to temperature and strongly respond to CC (Ladányi and Horváth 2010; Lehmann et al. 2020; Mwalusepo et al. 2015a; Stange and Ayres 2010) by altering their distribution, abundance, and phenology (Biber-Freudenberger et al. 2016; Godefroid et al. 2020; Lehmann et al. 2020; Mwalusepo et al. 2015a; Skendžić et al. 2021; Urvois et al. 2021). This comes with all the inherent consequences for agricultural production leading to new challenges for pest management (Biber-Freudenberger et al. 2016; Godefroid et al. 2020; Lehmann et al. 2020; Mwalusepo et al. 2015a; Skendžić et al. 2021; Urvois et al. 2021). This study investigates the potential current and future habitat suitability and distribution of three important maize pests in East Africa, the lepidopteran stem borers *Busseola fusca* (Fuller), *Sesamia calamistis* (Hampson) (both Lepidoptera: Noctuidae), and *Chilo partellus* (Swinhoe) (Lepidoptera: Crambidae) (CABI 2021a; De Groot 2002; Kfir et al. 2002). *Busseola fusca* attacks different cereal crops, in particular maize and sorghum (CABI 2021a; Kfir et al. 2002). It is native to Africa and widely established across the central, eastern, and southern parts of the continent (CABI 2021a). The invasive stem borer *C. partellus*, native to Asia (CABI 2021a), is a major pest of maize, sorghum, and pearl millet but also infests other important crops (CABI 2021a). It has a high adaptive capacity and tolerates a wide range of environmental conditions (CABI 2021b; Mutamiswa et al. 2017). Hence, *C. partellus* is a competitive colonizer, that now is widely present across Africa, and has been reported to increasingly displace certain native African stem borer species (CABI 2021a; Kfir et al. 2002; Mutamiswa et al. 2017). *Sesamia calamistis* attacks maize, sorghum, pearl millet, rice, wheat, and sugarcane (CABI 2021a). Indigenous to Africa, it is widely distributed throughout SSA (CABI 2021a). Despite its presence in East Africa, *S. calamistis* is of less importance there to maize production than *B. fusca* and *C. partellus* (Cugala and Omwega 2001; Nsami et al. 2001; Tamiru et al. 2007).

Among the BC agents used in IPM, larval parasitoid species have been reported to efficiently control open-field crop pests and are widely used in the containment of stem borers (Bale et al. 2008; Cugala and Omwega 2001; Dejen et al. 2013). We therefore predict the potential distribution of the gregarious larval endoparasitoids *Cotesia sesamiae* (Hampson) and *Cotesia flavipes* (Hampson) (both Hymenoptera: Braconidae) (CABI 2021b) that are used as BC agents of stem borer pests in South, Central, and East Africa (Dejen et al. 2013; Kaiser et al. 2017; Overholt et al. 1997). Being native to Pakistan (CABI 2021b), *C. flavipes* has been introduced in Kenya in 1993 as part of a BC program of *C. partellus* (Kfir et al. 2002; Omwega et al. 2006). It however attacks a broad range of insect pests (CABI 2021b), including *B. fusca* and *S. calamistis*. Its use has been successful in controlling the spread of stem borers in many countries of SSA (Kaiser et al. 2017; Overholt et al. 1997). The endoparasitoid *C. sesamiae* is indigenous to Africa and widely distributed across SSA (CABI 2021b). Even though *C. sesamiae* is less frequently used in BC programs, it can effectively suppress the spread of different lepidopteran pests, including *C. partellus*, *B. fusca*, and *S. calamistis* (CABI 2021a; Kaiser et al. 2017).

Presence records for the five species (*B. fusca*, 477; *C. partellus*, 251; *S. calamistis*, 260; *C. flavipes*, 190; *C. sesamiae*: 190) were obtained from several sources, reflecting different levels of extent and intensity of sampling efforts. Central to our research were data from a 2018

household survey conducted by researchers from the International Centre of Insect Physiology and Ecology (*icipe*) under the cooperative project “Adaptation for Food Security and Ecosystem Resilience in Africa” (AFERIA) of *icipe*, the University of Helsinki, and the University of York. The coordinates of the surveyed households that reported species presence were used for the species distribution modeling (SDM) exercise in this study. These data were complemented by occurrence points downloaded from the Global Biodiversity Information Facility (GBIF) and data obtained from *icipe*’s the “Climate Change Impacts on Ecosystem Services and Food Security in Eastern Africa” (CHIESA) project that was implemented between 2011 and 2015. Additional presence points emanated from *icipe*’s “Integrated pest management strategy to counter the threat of invasive fall armyworm to food security in Eastern Africa” (FAW-IPM) project.

2.2 Environmental variables

All environmental variables used for the SDM were downloaded in 2.5 arc minutes resolution from WorldClim version 2.1 (Coupled Model Intercomparison Project Phase 6 (CMIP6)) (Fick and Hijmans 2017). WorldClim provides data for 19 bioclimatic variables, which are derived from temperature and rainfall data and hence constitute biologically meaningful indicators for species distribution. Global data for the bioclimatic variables is available for past, present, and future climate scenarios (Fick and Hijmans 2017). Current bioclimatic variables are based on the averages of the years 1970–2000, whereas future bioclimatic variables are derived from extrapolations and comprise the averages of the 20-year periods 2021–2040, 2041–2060, 2061–2080, and 2081–2100 (Fick and Hijmans 2017). Future bioclimatic data is available for different General Circulation Models (GCMs) and Shared Socioeconomic Pathways (SSPs). Since the distribution of stem borers is altitude-dependent (Cugala and Omwega 2001; Mwalusepo et al. 2015a), elevation was included as an additional environmental variable in this study. Elevation data was also retrieved from WorldClim and is based on Shuttle Radar Topography Mission (SRTM) elevation data (Fick and Hijmans 2017). For a description of the environmental variables used for modeling, check the supplementary materials.

For the projection of the SDMs onto future climatic conditions, the bioclimatic variables were downloaded for three selected GCMs (CanESM5, CNRM-CM6-1, and MIROC6) that have been found to appropriately describe future climate in East Africa. The four SSPs describe different trajectories in future global development that entail different degrees of CC adaptation and mitigation. The SSPs are linked to distinct Representative Concentration Pathways (RCPs) that determine the levels of radiative forcing that are associated with the development trajectories and largely determine the intensity of CC. Accordingly, SSP1-2.6 represents an optimistic narrative of sustainable future global development, while SSP5-8.5 illustrates the worst-case emission scenario that neglects CC mitigation and will require extensive adaptation measures (Riahi et al. 2016). Given that an insight into both, the nearer future and longer-term climatic conditions, are relevant for farmers in the region, the periods 2041–2060 and 2081–2100 were considered.

2.3 Distribution modeling approach

The open-source software Maxent for modeling species niches and distributions is one of the most popular tools used among experts. We modeled the species distribution with Maxent using the “kuenm” package (Cobos et al. 2019) in R.

Maxent applies a machine-learning technique for maximum entropy modeling (Phillips et al. 2006). It uses a collection of georeferenced presence-only records of a species and a set of relevant environmental variables (Phillips et al. 2006).

Maxent builds a model based on the distribution of maximum entropy and a set of constraints provided by the environmental variables that predicts habitat suitability for each grid cell (Phillips et al. 2006). Each cell in the study area is assigned a probability value between 0 and 1 that categorizes habitat suitability, with 0 indicating no habitat suitability and 1 marking cells that provide a perfectly suitable habitat (Phillips et al. 2006). Maxent furthermore allows to project habitat suitability onto new environments in space and time (Elith et al. 2010). The projection into different geographical settings might reveal habitats where a species has not been detected yet, whereas projection in time can provide information on the potential distribution of species in the past or future, which is of particular relevance in predicting the potential effects of CC on species (Franklin 2010). For projecting species distribution, the model is trained based on a sample of presence-only points and current data of selected environmental variables. Based on additional environmental data that characterize habitats in different geographic areas or represent past or future environmental conditions, the model of the current distribution can be used to forecast habitat suitability elsewhere or under future environmental conditions, respectively (Phillips 2017).

In this study, we model the species' potential current and future distribution. By including three GCMs from CMIP6, we account for the inherent uncertainties of climate projection modeling (Beaumont et al. 2008). Future habitat suitability constitutes an ensemble average across several GCMs that was obtained by calculating mean suitability rasters according to SSP and time period. The suitability maps were then converted into species distribution maps by application of four selected suitability threshold levels. For each CC scenario according to SSP and time period, three habitat suitability maps were calculated, one for each GCM. For each habitat suitability map, four threshold levels were applied to categorize species presence or absence. As a result, 12 distribution maps were available per scenario and species, which were then stacked and calculated in their sum to show areas where, based on the different GCMs and thresholds, the presence of the species is more or less likely.

2.4 Estimation of yield loss and BC efficacy

Using the distribution data of the three stem borer species, associated maize yield losses were calculated. Data on maize yields in the study region were downloaded from the MapSPAM data center (IFPRI 2020) (see supplementary materials). Maize yield losses in the study area were quantified via the AFERIA household survey that assessed data from smallholder households in 12 villages in Taita Hills and the southeastern slope of Mount Kilimanjaro. Taita Hills are situated in southeastern Kenya, at an elevation ranging from 700 to 2000 m above sea level (m.a.s.l), between latitude 3°25' S and longitude 38°20' E. The southeastern slope of Mount Kilimanjaro is located in northeast Tanzania in the Pangani River Basin ranging from 700 to 1800 m.a.s.l, between latitude 3°4' S and longitude 37°4' E. At least 15 farmers were selected per village, and one respondent was interviewed per household following the protocol of Mwalusepo et al. (2015b) to assess farmers' perception of yield losses by stem borers. Respondents were able to distinguish these losses from others caused by abiotic stresses as stem borer-infested maize plants have typical and visible feeding traces of stem borer larvae on their leaves. To attribute the yield losses to *S. calamistis* and/or *B. fusca* or *S. calamistis* and/or *C. partellus*, the researchers referred to

their altitude distribution found in the field (Mwalusepo et al. 2018; 2015a): *Chilo partellus* is mostly present at low and *B. fusca* mostly at higher altitudes, whereas *S. calamistis* is present at all altitudes. In parallel, during the household survey, each maize field of each respondent was surveyed to confirm the main stem borer species present.

A sample of 225 household was surveyed out of which 208 households reported maize yield losses by *S. calamistis*, and 206 and 197 by *B. fusca* and *C. partellus*, respectively. The respondents were furthermore asked to quantify the yield losses by stem borers in percent. Based on these survey data, we calculated 95% confidence intervals (CIs) for maize yield losses, which were then used to predict current and future losses by stem borers. We predicted areas with high probability of maize yield losses by stem borers by multiplying species distribution maps with a raster carrying values on maize yields and a raster of yield losses caused by them (Eq. 1). Consequently, grid cells, where the stem borers are predicted to be present, and the cultivation of maize overlap are identified as areas with potential yield losses by the pests.

$$Y_{c,p} = A_{c,p} * M_c * L_p \quad (1)$$

where $Y_{c,p}$ represents yield losses (kg/ha) for each grid cell c and each stem borer species p , $A_{c,p} = \{1,0\}$ indicates each stem borer species' presence or absence for each grid cell, M_c indicates maize yield (kg/ha) for each cell, and L_p represents estimated yield losses by each stem borer (%). Furthermore, we predicted the current and future potential of using the parasitoids *C. flavipes* and *C. sesamiae* to control the pests and reduce maize yield losses. As part of the AFERIA household survey, respondents were asked for the potential of using the parasitoids to reduce maize yield losses caused by the stem borer species. Reduction potential was ranked by the respondents according to three different categories with rank 1, low (0–25%); rank 2, medium (25–75%); and rank 3, high (75–100%). For the calculation of the reduction potential, we used the mean value for each of the ranks, i.e., rank 1, 12.5%; rank 2, 50%; and rank 3, 87.5%. We calculated the 95% CI on maize yield loss reduction to project current and future loss reduction potential by the parasitoid species. We furthermore calculated the potential reduction of maize yield losses when using *C. flavipes* and *C. sesamiae* by multiplying the binary range maps of the natural enemy species with the maize yield loss and the reduction potential (Eq. 2). Accordingly, the areas where the presence of each parasitoid species overlaps with areas where maize yield losses by the stem borer pests occur were identified, and yield loss reduction was calculated as follows:

$$R_{c,e} = B_{c,e} * Y_{c,p} * P_e \quad (2)$$

where $R_{c,e}$ represents the potential reduction of yield losses (kg/ha) for each grid cell c by natural enemy e , $B_{c,e} = \{1,0\}$ indicates parasitoid presence or absence for each grid cell, $Y_{c,p}$ indicates maize yield losses (kg/ha), and P_e represents estimated potential yield losses reduction by the parasitoids (%).

2.5 Sampling bias

The presence points used for this research have to a large extent been collected within the scope of studies conducted in Kenya and Tanzania. However, it is not known whether the geographical concentration of presence records can be attributed to more favorable environmental conditions and hence greater habitat suitability for the species, or whether this agglomeration of presence points might be due to greater sampling efforts. Geographical

bias of occurrence data may, however, result in low-quality models (Phillips et al. 2009) and incorrect predictions of species distribution (Fourcade et al. 2014). In order to account for the potentially misleading uneven geographical distribution of the presence records used in SDM, a bias file was constructed. A sample of more than 700,000 presence coordinates of different insect species (Phillips et al. 2009) recorded on the African continent was downloaded from GBIF. Based on these records, a kernel density estimate map was constructed using the “MASS” package (Venables and Ripley 2002) in R and used to correct for potential sampling bias in the modeling process (compare Biber-Freudenberger et al. 2016; Fourcade et al. 2014).

2.6 Model calibration and best model selection

Apart from the inputs required to run Maxent, a wide variety of parameter settings can be individually adjusted to calibrate the best-performing model. For almost all parameters, in-built default settings have been validated by the developers of the software over a wide range of models. However, Morales et al. (2017) and Merow et al. (2013) indicate that the adoption of Maxent’s default settings may not necessarily produce the optimal species distribution model. According to Radosavljevic and Anderson (2014), the individual tuning of setting parameters for each species can lead to better performing models. In order to find the best-performing model for predicting habitat suitability for the species under current environmental conditions, we calibrated multiple models with different settings and inputs using the “kuenm” package (Cobos et al. 2019) in R that allows for automated model calibration and robust selection of the best-performing model. Accordingly, for each species, 279 models were calibrated using different sets of environmental variables (set 1, 19 bioclimatic variables and elevation; set 2, BIO1, BIO5, BIO6, BIO12, BIO13, BIO14, elevation; set 3, BIO5, BIO6, BIO13, BIO14, elevation), different values for the regularization multiplier (0.1, 1, and 10), and multiple combinations of feature classes (linear (l), product (p), quadratic (q), hinge (h), threshold (t)).

For all tested models, a random sample of 66.6% of presences was used as training data for building the models. The remaining 33.3% of the presence records was set aside for testing the models subsequently. The combination of parameters yielding the best-performing model for each species was identified considering statistical significance (partial receiver operating characteristics (pROC)), predictive ability (omission rate (OR) at 5%), and complexity (Akaike information criterion (AICc)). The model with the best selected settings was used for modeling (see supplementary materials).

3 Results

3.1 Habitat suitability under current and future climatic conditions

The mean area under the ROC curve (AUC) values of training data (over 15 replicate model runs) for all five species are above 0.98 (supplementary materials) which confirms excellent performance of our models.

The probability of habitat suitability was modeled for each species for current climatic conditions and different CC scenarios. The current habitat suitability in the study area and predicted future suitability for the period 2081–2100 are shown in Fig. 1. SSP1-2.6 which describes sustainable global development with low challenges in

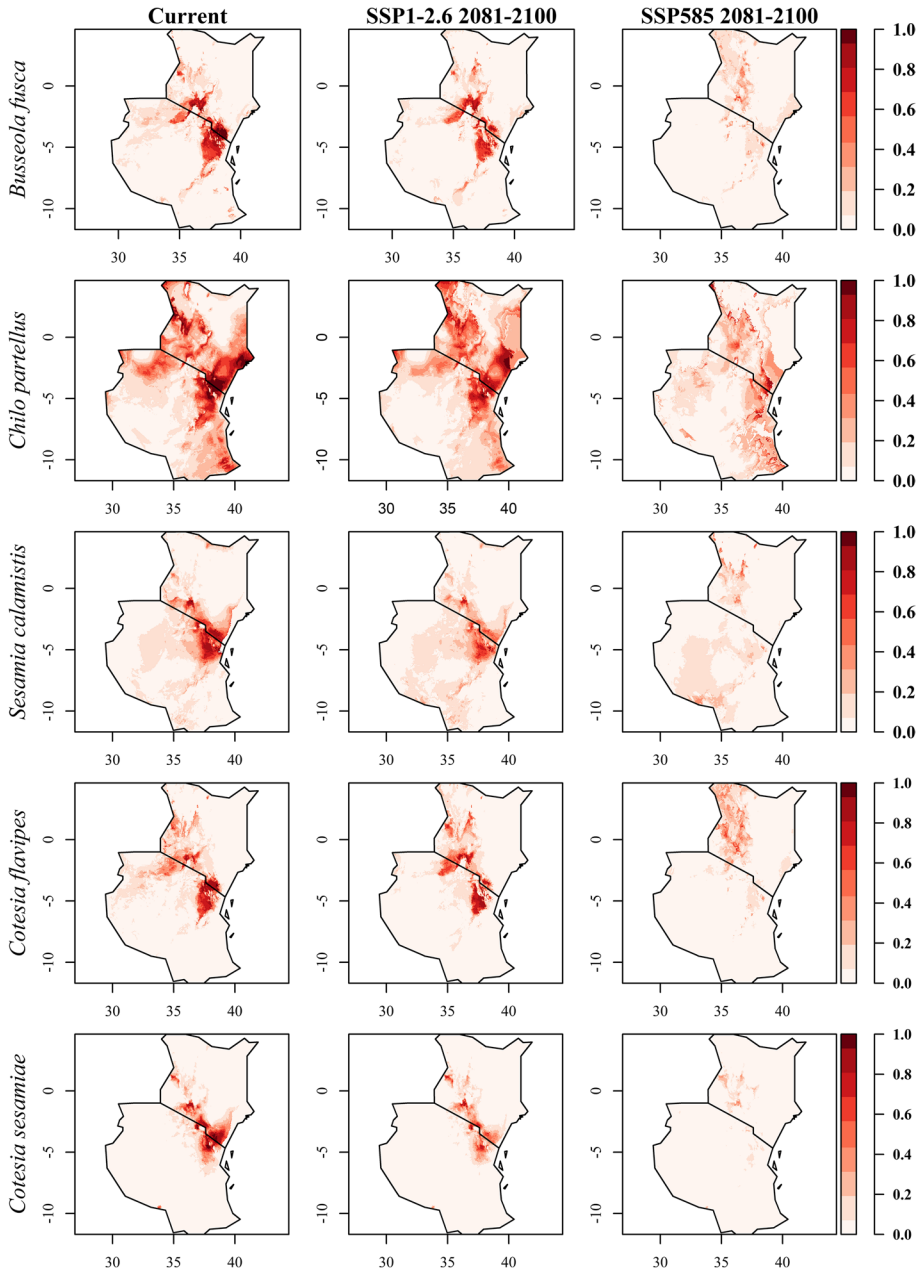


Fig. 1 Probability of habitat suitability under current climatic conditions and in 2081–2100 for SSP1-2.6 and SSP5-8.5 calculated as multi-model average from GCMs CanESM5, CNRM-CM6- 1, and MIROC6. Probability of habitat suitability ranges between 0 (low probability of suitable habitat) and 1 (perfectly suitable habitat). Grid cells with great suitability carry high probability values and are displayed in dark red, whereas cells with low suitability show low probability values and are colored in lighter red and white

mitigation and adaption is contrasted with the worst-case scenario SSP5-8.5 to demonstrate the changes in suitable habitats according to two opposing scenario pathways (results for SSP2-4.5 and SSP3-7.0, as well as for all scenarios in 2041–2060 are available in supplementary materials). Under current climatic conditions, high suitability for *B. fusca* is predicted in the border areas of Kenya and Tanzania but is forecasted to decline under both projected pathway scenarios. While under SSP1-2.6, habitat suitability is predicted to decrease only in areas with currently very high suitability, in scenario SSP5-8.5, habitat suitability declines at a significantly higher rate and across the whole study region. Regions that are now highly suitable are predicted to become largely unsuitable for the stem borer under this scenario. It is therefore to be expected that under more severe CC, the associated changes in habitat suitability will have considerable adverse effects on *B. fusca*. A similar observation can be made from the projections of habitat suitability for *S. calamistis*. At present, the border regions of both countries show relatively high habitat suitability, which is predicted to decline in the future under both SSPs. However, in case of SSP5-8.5, the decline in habitat suitability is dramatic for the period 2081–2100, indicating that habitat, which is currently highly suitable, will become largely unsuitable. Furthermore, overall habitat suitability in the study area will decrease remarkably, and areas providing suitable habitats for *S. calamistis* will be restricted to only a few scattered localities. Current and predicted future habitat suitability for *B. fusca* and *S. calamistis* is noticeably lower than for the invasive *C. partellus*, reflecting the greater tolerance for a wide range of environmental conditions and high adaptability of the latter species that also facilitates its successful invasion into new environments. Current probability of habitat suitability for *C. partellus* is high to very high across large areas of the study region. Yet also this invasive stem borer is predicted to be impacted by changing future climate under the shown SSPs. While for SSP1-2.6 areas with very high habitat suitability are forecasted to slightly decrease, these are predicted to be considerably reduced under scenario SSP5-8.5. Hence, also for *C. partellus*, habitat suitability is likely to be more adversely impacted under more severe CC. Habitat suitability for the natural enemies *C. flavipes* and *C. sesamiae* is also predicted to decline in the future under both SSPs. This decline is, however, less pronounced under SSP1-2.6. Areas of currently very high suitability for *C. flavipes* will shrink. For SSP5-8.5 in 2081–2100, areas that are highly suitable at present will become unsuitable, while regions of medium suitability will establish in northwestern Kenya. Currently there is only limited habitat suitability for the native *C. sesamiae* concentrating in the border region of Kenya and Tanzania. However, suitability is predicted to further decline for the considered time period and both SSPs. Under the pessimistic scenario SSP5-8.5, only a few scattered regions of medium suitability will remain. Accordingly, under severe CC, large parts of the study region are predicted to become unsuitable for *C. sesamiae*. Furthermore, habitat suitability for the native species *B. fusca*, *S. calamistis*, and *C. sesamiae* will be more adversely impacted by severe CC than for the non-native ones, i.e., *C. partellus* and *C. flavipes*.

In this study, different suitability threshold levels were selected (balance training omission, predicted area and threshold values Cloglog threshold (thereafter bto), maximum training sensitivity plus specificity Cloglog threshold (mtss), equal training sensitivity and specificity Cloglog threshold (etss), 10th percentile training presence Cloglog threshold (tp)) to convert habitat suitability maps into binary species range maps (for specific values see supplementary materials).

Selection of several threshold values has advantages over application of a single threshold, as it considers the inherent uncertainties.

The potential distribution of the stem borer and parasitoid species under current climatic conditions as well as for the CC scenarios SSP1-2.6 and SSP5-8.5 in 2081–2100 varies significantly (Fig. 2). Among the stem borers, the invasive *C. partellus* is predicted to be currently the most widely distributed, whereas the distribution of the native stem borers concentrates around the border area of the study region. The modeled current distribution of the parasitoids is less widespread than for the stem borers. Under future CC, the distribution of all five species is predicted to slightly shift or decrease for SSP1-2.6. Areas that currently show high likelihood of species presence are less likely to inhabit them in the future. For SSP5-8.5, a significant reduction in the distribution of all five species is forecasted. Under the worst-case scenario, *C. sesamiae* becomes extremely rare in the study region, while the distribution of *C. flavipes* will shift towards northwestern Kenya.

The predicted presence of the stem borer species is reduced across the entire study area.

3.2 Pest impact on maize yields

We calculated 95% CIs of maize yield losses for each stem borer species based on the AFERIA household survey data (cf. Section 2.4 for further explanations). With an average loss of 28.72% [95% CI 26.65, 30.79], yield losses by *C. partellus* are the highest, followed by *B. fusca* with an average loss of 27.86% [95% CI 25.77, 29.96], and *S. calamistis* with 27.25% [95% CI 24.9, 29.59]. Predicted mean current and future yield losses by the three stem borers are shown as mean value and for suitability threshold level bto (Fig. 3) (for minimum and maximum losses, as well as losses for SSP2-4.5 and SSP3-7.0, time period 2041–2060, and thresholds mtss, etss, and tp, see supplementary materials).

Compared to current levels, maize losses are predicted to slightly decrease for *B. fusca* in SSP1-2.6 while remaining relatively stable for *C. partellus* and *S. calamistis*. Yield losses by all three species are predicted to decrease significantly until 2081–2100 under pathway SSP5-8.5. This decrease can be attributed to the notable decline in habitat suitability (Fig. 1), which is projected to result in reduced future species presence in the study area (Fig. 2). Hence, maize yield losses associated with the stem borer species are expected to decline under more severe CC while remaining at a higher level for SSP1-2.6. Nevertheless, the degree of yield losses largely depends on the suitability threshold applied (see supplementary materials), with bto showing a remarkably larger area with predicted yield losses.

3.3 Future role of BC in reducing maize yield losses by stem borers

Based on the household survey data, *C. flavipes* is with 53.68% [95% CI 50.2, 57.16] slightly more effective in reducing yield losses by stem borers than *C. sesamiae* with 51.39% [95% CI 47.84, 54.93]. The potential of using the natural enemies *C. flavipes* and *C. sesamiae* to reduce maize yield losses caused by the stem borer species varies depending on the two scenarios SSP1-2.6 and SSP5-8.5 in 2081–2100 (Figs. 4 and 5) (for minimum and maximum reduction potential, as well as possible reduction of

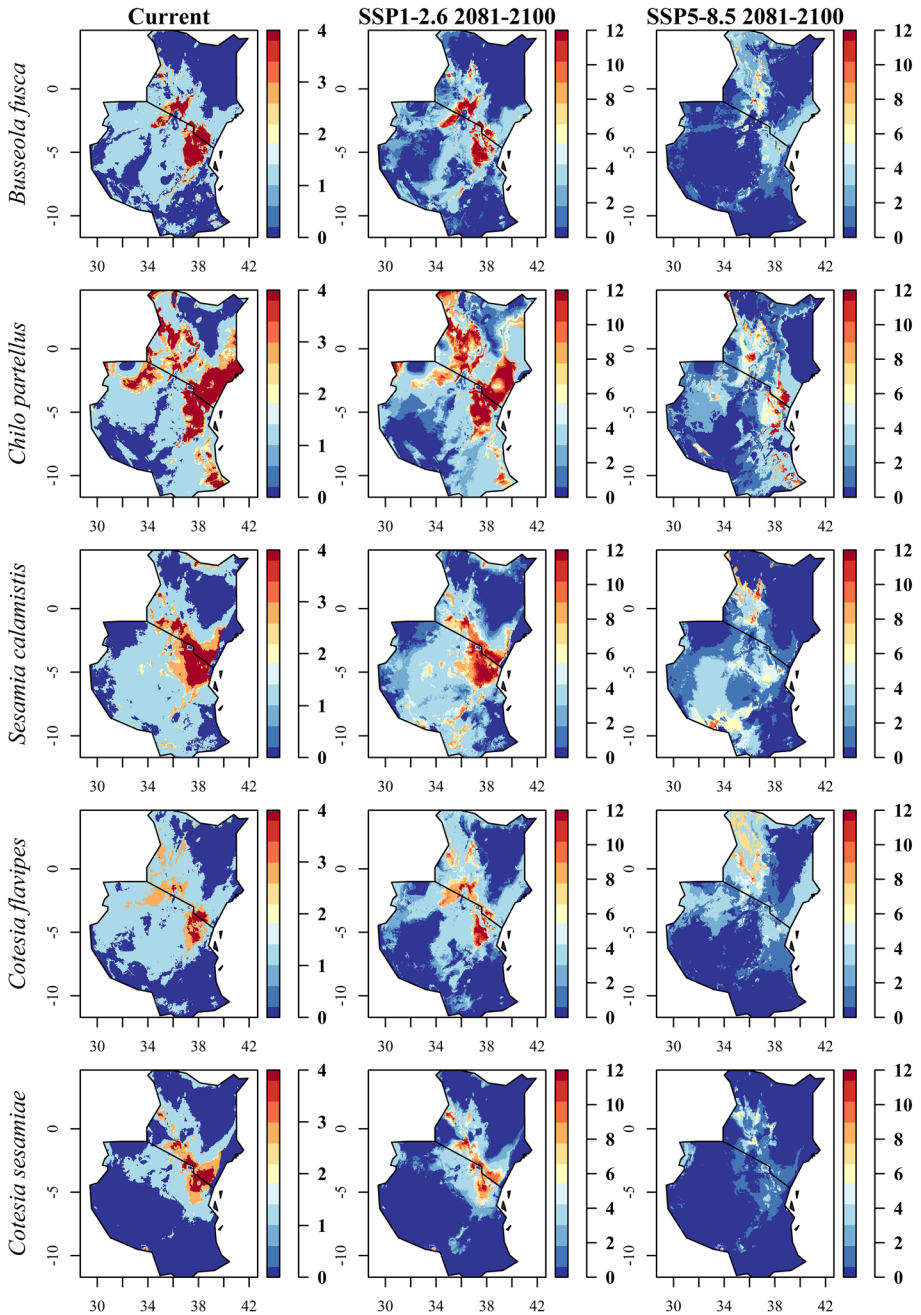


Fig. 2 Sum of 4 binary range maps (current distribution) and 12 binary range maps (future distribution) obtained by application of 4 threshold levels, with each binary layer showing either species presence (1) or absence (0). Predicted species distribution under current climatic conditions and for pathways SSP1-2.6 and SSP5-8.5 for period 2081–2100. Grid cells where predicted species presence is likely are colored in red and orange, whereas grid cells where presence is less likely are colored in blue

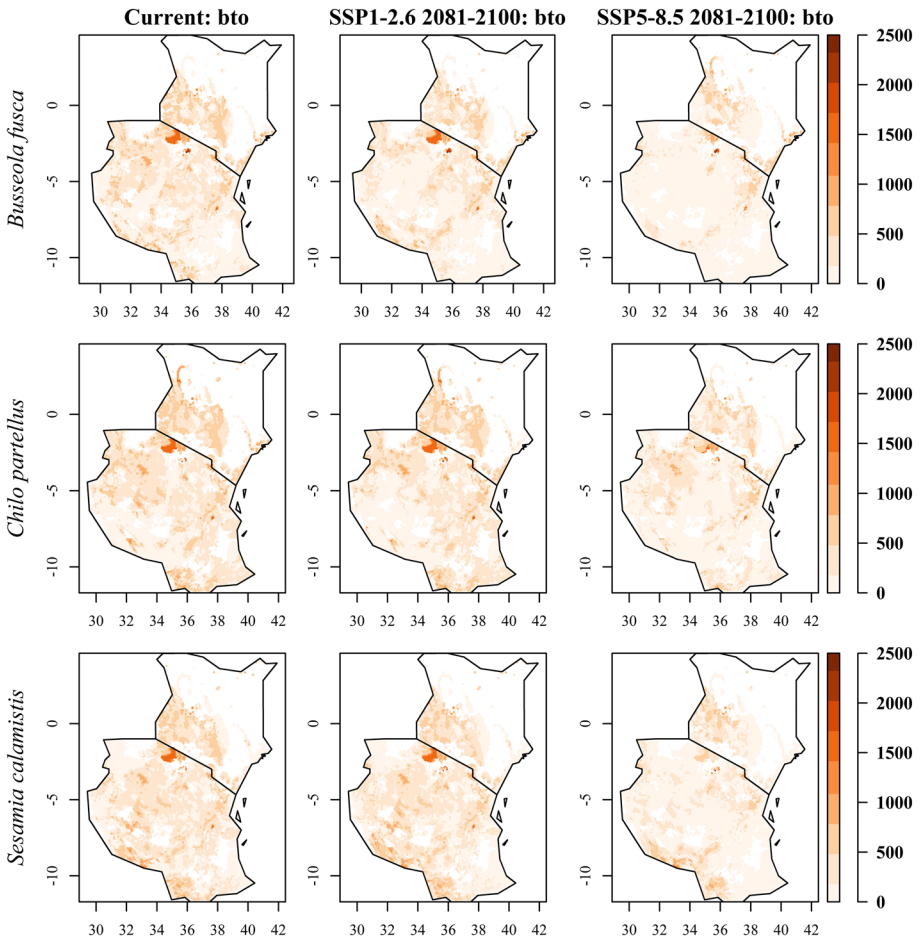


Fig. 3 Predicted mean maize yield losses (in kg/ha) by the stem borers *B. fusca*, *C. partellus*, and *S. calamistis* under current climatic conditions and in 2081–2100 for SSP1-2.6 and SSP5-8.5 for suitability threshold bto. Grid cells with high predicted yield losses are colored in darker orange to brown, whereas cells where maize yield losses by the species are low are colored in lighter orange and white

yield losses by BC for SSP2-4.5 and SSP3-7.0, time period 2041–2060, and thresholds mtss, etss, and tp, see supplementary materials). In general, *C. flavipes* has a greater potential to reduce *B. fusca*-associated maize yield losses than *C. sesamiae*. Yet, its potential to reduce losses by *B. fusca* is predicted to decline for both developmental pathways, especially for SSP5-8.5. Furthermore, *C. flavipes* is predicted to be more effective in reducing maize yield losses caused by the invasive *C. partellus* than *C. sesamiae*. For both BC agents, the potential to reduce maize yield losses by *C. partellus* is predicted to decline. Whereas SSP1-2.6 entails a less significant decrease, the worst-case scenario SSP5-8.5 is predicted to result in a remarkably lower reduction potential. The same is true for containing maize yield losses caused by *S. calamistis*;

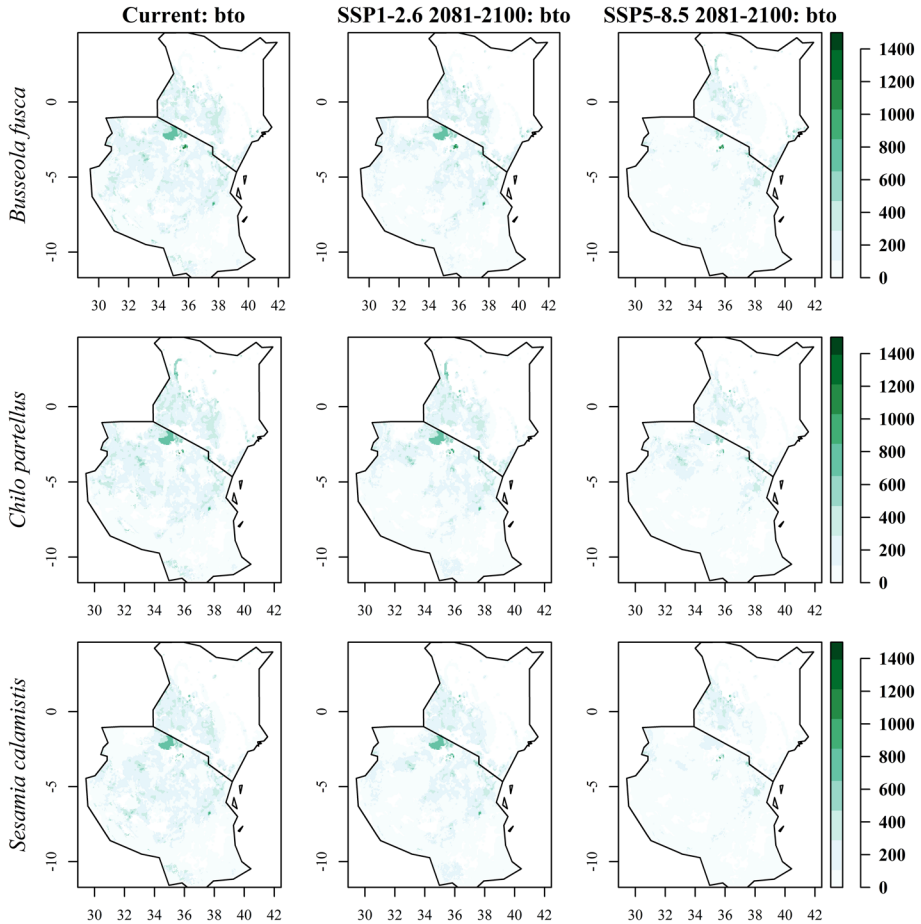


Fig. 4 Predicted mean reduction of maize yield losses (in kg/ha) by *B. fusca*, *C. partellus*, and *S. calamistis* through the use of *C. flavipes* under current climatic conditions and in 2081–2100 for SSP1-2.6 and SSP5-8.5 for suitability threshold bto. Grid cells where parasitoid application significantly reduces the amount of maize yield losses caused by the stem borer are colored in darker green, whereas cells with lower predicted reduction of maize yield losses are colored in lighter green and white

here also *C. flavipes* shows a higher reduction potential. However, areas in which stem borer-caused maize yield losses can be reduced by BC with the two parasitoids are predicted to decline under the studied CC scenarios. While the reduction potential by *C. flavipes* is predicted to be significantly reduced under SSP5-8.5, the BC potential of *C. sesamiae* will have almost entirely vanished under that scenario. Analyzing the predictions for the future effectiveness of using the two natural enemy species to reduce maize yield losses by the three stem borers in the study region, we therefore conclude that the more severe CC will be, the more pronounced is the decrease in the BC reduction potential of the two *Cotesia* species.

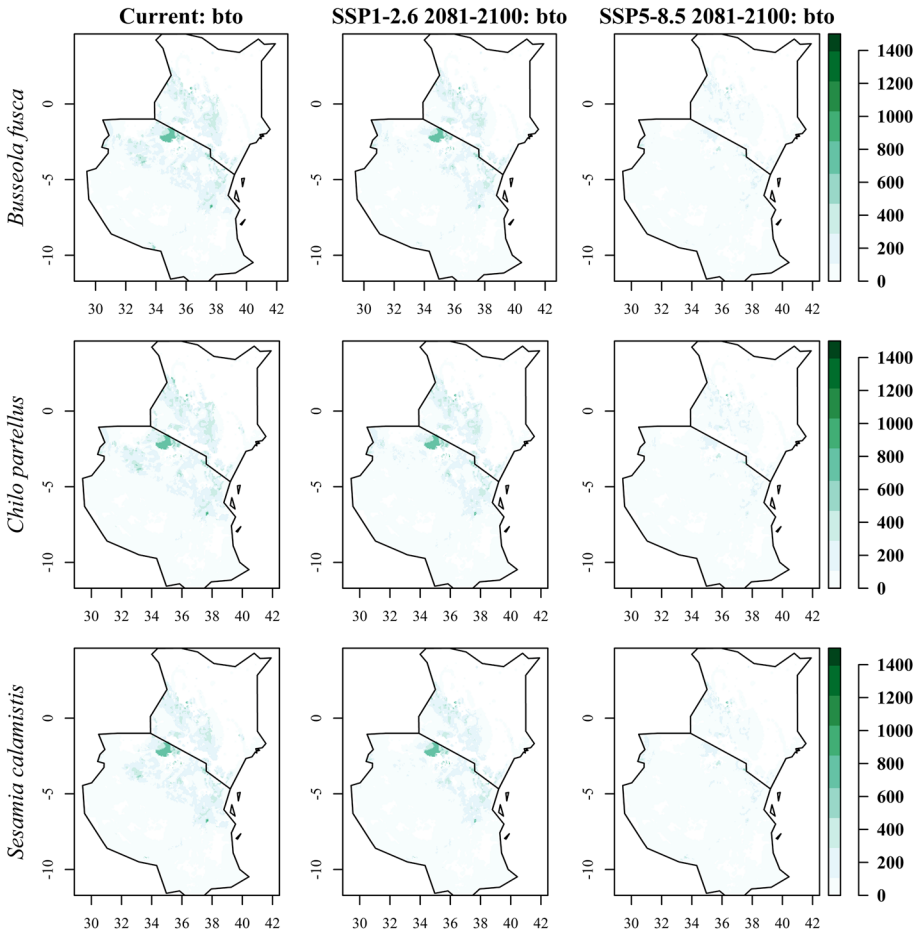


Fig. 5 Predicted mean reduction of maize yield losses (in kg/ha) by *B. fusca*, *C. partellus*, and *S. calamistis* through the use of *C. sesamiae* under current climatic conditions and in 2081–2100 for SSP1-2.6 and SSP5-8.5 for suitability threshold bto. Grid cells where parasitoid application significantly reduces the amount of maize yield losses caused by the stem borer are colored in darker green, whereas cells with lower predicted reduction of maize yield losses are colored in lighter green and white

4 Discussion and conclusions

The three studied maize stem borers and their two associated larval parasitoids are very likely to respond to CC, regardless of the respective change scenario. The uncertainties inherent when making predictions on future climate and environmental conditions were considered by investigating species distribution using different CC models, socioeconomic pathways, and time periods. Under all investigated CC scenarios, habitat suitability is going to change, and the species are predicted to adjust their distribution. We also found that all species' future distribution strongly depends on the magnitude of CC. More severe CC is predicted to cause a notable decrease in the presence of the stem borers, which will result in a decline in predicted maize yield losses associated with the pests, yet this

not to say that stem borer-inflicted yield losses will completely vanish but rather will be reduced. Moreover, this decline in yield losses is, however, predicted to be accompanied by a decreasing potential to reduce losses caused by stem borers through the impact of *C. flavipes* and *C. sesamiae*. The distribution of the two natural enemies is forecasted to significantly decline under severe CC, which may render established mechanisms of BC ineffective or not viable. This finding is of direct relevance to farmers in the study area that will benefit from the control of stem borers by the parasitoids, as they will likely need to adjust their pest management strategies in the future. Although the analyzed pest species will most likely become less relevant to farmers under CC, other pest species may appear and which also have to be managed. However, managing these new pests will be even more of a challenge as the farmers do not know them yet nor how to contain them to avoid crop damage. Consequently, any effective pest management strategy therefore needs to be assessed in the context of climate change.

For the calculation of maize yield losses, we assumed that the maize yield in the study area remains constant over time.

Yet, the introduction of improved crop varieties with higher resilience to climate variability and attack by stem borers, the emergence of higher-yielding varieties or changes in productivity could affect future yields (Bänziger et al. 2006; IFPRI 2016). We also did not consider the impact of CC on maize plants and yields themselves and assume that the geographic distribution of maize cultivation and yields remains constant over time, despite changing environmental conditions. Though maize plants will be affected by CC, consequently the suitability of certain regions in Africa for maize production might change (Tito et al. 2018). This may impair maize cultivation in some areas while enabling it in others (Jones and Thornton 2003; Luhunga 2017). The potential shift in habitat suitability for maize may create new overlaps with the distribution of pests and parasitoids, which in turn impacts yields, yield losses, and opportunities for BC.

When investigating the impact of CC on pests and agricultural crops, it is also important to determine how climate variability affects the crop species. Moreover, stem borers not only damage maize but a whole range of cereal crops (CABI 2021a). Considering the potential impact of stem borers on food security, it would therefore be of great interest to investigate their relevance for other important staple crops, in particular sorghum and millet whose cultivation in the region is currently pushed forward as for their greater drought resilience (Burke et al. 2009; CSIRO 2021; IFAD 2017).

Other studies have also assessed the potential future distribution of pests and other species under future CC. Our findings are in line with Thomson et al. (2010) outlining that CC influences interactions between herbivores and natural enemies, e.g., by resulting in a mismatch in their distribution, which can reduce the effectiveness of using natural enemies for pest control. Mwalusepo et al. (2015a) investigated the impact of temperature change on the future distribution of maize stem borers and their BC agents at a local scale along Mount Kilimanjaro and the Taita Hills of Tanzania and estimated the impact on maize yields. They confirm that temperature is a key factor in determining the distribution of stem borer pests and their natural enemies, corroborating results from our study. Yet, Mwalusepo et al. (2015a) predict a worsening of pest impact on maize production along the two mountain gradients, whereas we forecast, especially for the more distant future (2081–2100), stem borer-associated maize yield losses to decline under the impact of more severe CC. Furthermore, Mwalusepo et al. (2015a) predict a geographical disruption in the distribution of stem borers and their natural enemies, with decreased but also increased levels of BC at higher and lower altitudes, respectively. In contrast, we conclude that the studied BC relationships will become less effective and even unviable under future CC. The discrepancies

in the findings of our study and the research by Mwalusepo et al. (2015a) stem from the different modeling approaches applied and inputs used. Mwalusepo et al. (2015a) predict species distribution based on temperature-driven phenology models, whereas our research employs a correlative method for SDM that uses maximum entropy density estimations. One advantage of the latter method is that it allows to incorporate the range in potential modeling outputs by assigning habitat suitability as a probability value, thereby also considering uncertainty. Furthermore, Mwalusepo et al. (2015a) analyze potential future species distribution according to different levels of altitude in the study area. Our study, however, included elevation as homologous to the bioclimatic variables into model calibration and does not distinguish modeling outputs based on elevation but draws conclusions on country level. However, dynamically downscaled regional climate models (RCMs), as used by Mwalusepo et al. (2015a), provide data at a finer resolution and capture mesoclimatic dynamics more accurately which potentially results in better simulations of regional climate than coarse resolution GCMs (Beaumont et al. 2008; Giorgi 2019). In our study, we explicitly used data for the bioclimatic variables in 2.5 arc minutes resolution which is based on the latest version of GCMs from CMIP6. This approach is reasonable when examining the effects of climatic changes, i.e., changes in temperature and precipitation, on species distribution.

We focused our study at three stem borer pests and two important natural enemy species. The emergence of new pests or BC agents as a result of CC was not part of this study though. For instance, the 2016 introduction into Africa and subsequent wide spread of the neotropical fall armyworm (FAW), *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae) (Goergen et al. 2016), initially lead to spectacular increases in maize losses and near suppression of all other lepidopteran stem borer species in the FAW affected countries (Hailu et al. 2021; Sokame et al. 2021). This new pest will probably also modify the expected changes in the distribution and abundance of the here modeled stem borers and their parasitoids. Such developments pose new challenges for pest management that will, among others, require the adaption of BC strategies. It is hence of great interest to investigate the distribution of a broader range of pests and their natural enemies to obtain a more holistic picture on relevant insect pests, their impact on staple crop production, and the potential of BC to be able to offer more concrete advice to farmers (Biber-Freudenberger et al. 2016). We found that the invasive stem borer *C. partellus* and the exotic parasitoid *C. flavipes* are and will be more widely distributed under CC, indicating that they are less sensitive to CC. Hence, research on invasive pests and possibilities for their containment, e.g., via BC, needs to be intensified. For that, modeling could be indefinitely repeated using presence data for all species of interest. Given the low agricultural productivity in the region and the prevailing deficiencies in the food system (IFPRI 2016), we demonstrate that maize stem borers are and to a certain extent will continue to be a threat to food security in the future. Therefore, effective control measures need to be applied to mitigate their proliferation and reduce associated yield losses. Empowering relevant actors to anticipate changes in insect distribution triggered by CC will be essential in building a more resilient food system that is less prone to external shocks (Bottrell and Schoenly 2018).

We believe our results to be of high relevance for farmers, extension officers, and policymakers in Kenya and Tanzania, as they provide estimations not only of future pest distributions, but also of associated yield losses and the potential of BC to contain these pests. Hence, this study can serve as a blueprint to identify future pests as well as their potential natural enemies in East Africa and beyond, which will help farmers to adjust their farming and pest management strategies to changing environmental conditions. As anticipatory and effective pest management is fundamental in reducing yield losses, policymakers and

extension officers could support farmers in adapting their practices to increase the resilience of local agricultural systems. To our knowledge, this is one of very few studies that combine the prediction of future pest species distribution with the potential of BC under different CC scenarios while also considering the impact on maize, which is the most important crop in the study area. Pesticide-based pest control measures are increasing in importance; however, sustainable methods of pest control need to be promoted to avoid adverse impacts on health and the environment. The examined BC relationships have been proven effective at present, but we forecasted that their potential under future CC will substantially decline. Assuring the continued efficacy of BC to avoid dis-adoption, increasing skepticism among farmers and turn towards synthetic pesticides, is key in building a sustainable and environmentally friendly food system. We therefore suggest an increasing consideration of pest species as well as the potential of different BC strategies under varying environmental and climatic conditions.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10584-023-03514-3>.

Acknowledgements The authors acknowledge additional data that help finetune model outputs collected by Sizah Mwalusepo and Boaz Musyoka under the CHIESA and AFERIA projects, respectively, both supported by the Ministry for Foreign Affairs of Finland. We additionally acknowledge valuable inputs by Dr. Powell Mponela of CIAT/ZEF.

Author contribution Ines Jendritzki wrote the manuscript and conducted the analyses; Henri E. Z. Tonnang and Paul-André Calatayud contributed through data provision; Henri E. Z. Tonnang, Paul-André Calatayud, Christian Borgemeister, and Tino Johansson critically revised the manuscript; and Lisa Biber-Freudenberger supervised the data analysis, data interpretation, and manuscript development.

Funding Open Access funding enabled and organized by Projekt DEAL. Ines Jendritzki was supported by the Volkswagen Foundation with the grant number VW-94832 under the funding initiative “Knowledge for Tomorrow-Cooperative Research Project in sub-Saharan Africa on Resource, their Dynamics, and Sustainability.” Financial support was also provided through the project “LANUSYNCON—At the Science Policy Interface: LANd Use SYnergies and CONflicts within the framework of the 2030 Agenda (01UU2002),” funded by the German Federal Ministry of Education and Research (BMBF).

Data availability Presence records used for this research constitute a collection of records downloaded from GBIF (<https://www.gbif.org/>) and data points provided through various projects by *icipe*. All presence records are available in a.csv in the supplementary materials. Data for relevant environmental variables used for species distribution modeling, i.e., bioclimatic variables and elevation, can freely be accessed and downloaded from WorldClim (<https://www.worldclim.org/>). All modeling outputs of this research, i.e., predictions on habitat suitability, distribution, maize yield losses by stem borers, and estimated potential of biological control to reduce stem borer-associated maize yield losses, can be accessed in TIF format through the ZEF Data Portal (<https://daten.zef.de/geonetwork/srv/get/catalog.search#/home>).

Materials availability Not applicable.

Code availability R script made available

Declarations

Ethics approval Does not apply

Consent to participate The authors declare that any person named as co-author of this manuscript is aware of the fact and has agreed to being named.

Consent for publication All authors involved in this research explicitly expressed their consent for the research to be published.

Conflict of interest The authors declare no competing interests.

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