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Climate change and ecological intensification of agriculture in sub-Saharan Africa – A systems approach to predict maize yield under push-pull technology

Nikolaos Alexandridis[a,1,*], Benjamin Feit[b,1], Job Kihara[c], Tim Luttermoser[d], Wilhelm May[a], Charles Midega[e,f], Ingrid Öborn[g], Katja Poveda[d], Gudeta W. Sileshi[h,i], Beyene Zewdie[j], Yann Clough[a,2], Mattias Jonsson[b,2]

[a] *Centre for Environmental and Climate Science (CEC), Lund University, Lund, Sweden*
[b] *Department of Ecology, Swedish University of Agricultural Sciences (SLU), Uppsala, Sweden*
[c] *International Center for Tropical Agriculture (CIAT), Nairobi, Kenya*
[d] *Department of Entomology, Cornell University, Ithaca, NY, USA*
[e] *Poverty and Health Integrated Solutions (PHIS), Kisumu, Kenya*
[f] *Unit for Environmental Sciences and Management, IPM Program, North-West University, Potchefstroom, South Africa*
[g] *Crop Production Ecology, Swedish University of Agricultural Sciences (SLU), Uppsala, Sweden*
[h] *Department of Plant Biology and Biodiversity Management, Addis Ababa University, Addis Ababa, Ethiopia*
[i] *School of Agricultural, Earth and Environmental Sciences, University of KwaZulu-Natal, Pietermaritzburg, South Africa*
[j] *Department of Ecology, Environment and Plant Sciences, Stockholm University, Stockholm, Sweden*

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ABSTRACT

Assessing effects of climate change on agricultural systems and the potential for ecological intensification to increase food security in developing countries is essential to guide management, policy-making and future research. 'Push-pull' technology (PPT) is a poly-cropping design developed in eastern Africa that utilizes plant chemicals to mediate plant–insect interactions. PPT application yields significant increases in crop productivity, by reducing pest load and damage caused by arthropods and parasitic weeds, while also bolstering soil fertility. As climate change effects may be species- and/or context-specific, there is need to elucidate how, in interaction with biotic factors, projected climate conditions are likely to influence future functioning of PPT. Here, we first reviewed how changes in temperature, precipitation and atmospheric CO_2 concentration can influence PPT components (i.e., land use, soils, crops, weeds, diseases, pests and their natural enemies) across sub-Saharan Africa (SSA). We then imposed these anticipated responses on a landscape-scale qualitative mathematical model of maize production under PPT in eastern Africa, to predict cumulative, structure-mediated impacts of climate change on maize yield. Our review suggests variable impacts of climate change on PPT components in SSA by the end of the 21st century, including reduced soil fertility, increased weed and arthropod pest pressure and increased prevalence of crop diseases, but also increased biological control by pests' natural enemies. Extrapolating empirical evidence of climate effects to predict responses to projected climate conditions is mainly limited by a lack of mechanistic understanding regarding single and interactive effects of climate variables on PPT components. Model predictions of maize yield responses to anticipated impacts of climate change in eastern Africa suggest predominantly negative future trends. Nevertheless, maize yields can be sustained or increased by favourable changes in system components with less certain future behaviour, including higher PPT adoption, preservation of field edge density and agricultural diversification beyond cereal crops.

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[*] Correspondence to: The Ecology Building, Sölvegatan 37, 22362 Lund, Sweden.
E-mail address: nikos.alexandridis@cec.lu.se (N. Alexandridis).

[1] These authors share first authorship

[2] These authors share senior authorship

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1. Introduction

Climate change, as a major driver of changes in physical and biological systems, is one of the most significant challenges humanity is facing in the 21st century (Nolan et al., 2018; IPCC, 2022). Continued accumulation of greenhouse gases in the planet's atmosphere is projected to raise global average temperatures, change the amount and distribution of rainfall, and increase the frequency and intensity of extreme weather events (IPCC, 2022). The extent to which climate change will affect agricultural systems, and whether current agricultural practices and their adaptations to climate change will provide food security in the future, are questions that warrant investigation. This is particularly the case in developing countries which, despite carrying the least responsibility for the climate crisis, will likely be affected the most (IPCC, 2022). These countries often face a multitude of challenges on top of climate change, such as rapid population growth, resource scarcity, food and nutrition insecurity, land degradation and stagnating yields, biodiversity loss and need for transformative change of the agriculture and food systems (e.g. van Ittersum et al., 2016; Giller, 2020; Giller et al., 2021). Ecological intensification through agricultural diversification, where additional crops are cultivated in space and time, and stronger provision of ecosystem services, such as bolstering soil fertility and natural pest and weed control, has been advocated as a sustainable approach to reduce yield gaps (Kleijn et al., 2019; Tamburini et al., 2020). However, climate change can alter species' functional traits and ecological interactions, with important population, community and ecosystem-level consequences (Tylianakis et al., 2008; Hevia et al., 2017). Anticipating the performance of ecologically intensified cropping systems under climate change is thus required to strengthen the evidence base for sustainable food production.

In sub-Saharan Africa (SSA), lepidopteran stemborer species, including *Chilo partellus* and *Busseola fusca*, are among the main arthropod pests of cereal crops, and cause significant yield losses (Kfir et al., 2002). In research and development efforts spanning over a decade, a team of cross-disciplinary scientists in eastern Africa developed a stimulo-deterrent pest control approach specific for lepidopteran stemborer species, known as 'push-pull' technology (PPT) (Khan et al., 2016). In this system, plant chemicals, including primary and secondary metabolites that mediate plant–insect interactions and thereby effectively control the pests, are deployed through polycropping. In the initial version, maize or sorghum are intercropped with molasses grass (*Melinis minutiflora*) or silverleaf desmodium (*Desmodium uncinatum*), which emit semiochemicals that are repellent ('push') to the pests. The field is surrounded by Napier grass (*Pennisetum purpureum*), which emit attractive volatile organic compounds ('pull') (Khan et al., 2008; Midega et al., 2015a, 2015b). Gravid stemborer moths are repelled from crop plants and subsequently attracted to and trapped on the border grass, where the young larvae have low survival rates (Midega et al., 2011). Originally developed to mitigate the effects of lepidopteran stemborers, PPT with *Desmodium* intercrops has also proven effective against parasitic *Striga* weeds, and the highly damaging invasive fall armyworm *Spodoptera frugiperda*, which has rapidly spread across the African continent since its introduction in 2016 (Midega et al., 2018). Under current conditions, PPT effectively controls all of these major pests and bolsters soil fertility, resulting in significant crop yield increases (Khan et al., 2008; Niassy et al., 2022). In efforts to improve ecological resilience, and extend the benefits of the technology to drier areas in the region, new companion plants have been identified and incorporated into the system. In a series of on-station and on-farm evaluations, *Brachiaria* cv Mulato II and greenleaf desmodium (*Desmodium intortum*) were found to be more drought- and heat-tolerant than the initial companion plants used in the technology. This variant of the original system, dubbed 'climate-smart PPT', retains the technology's benefits, including effectiveness against target pests and weeds (Midega et al., 2015a, 2015b; Midega et al., 2018).

Thus far, climate-smart PPT remains a robust system that delivers pest management and yield benefits through a variety of mechanisms, including significant improvement in soil health through nitrogen (N) fixation, enhanced soil organic carbon (C) and phosphorus (P) availability, moisture conservation and soil arthropod abundance and diversity (Khan et al., 2008; Ndayisaba et al., 2020), thus also contributing to climate change adaptation and mitigation (Ndayisaba et al., 2022). The benefits are realised in a range of agro-ecological zones in the region (Midega et al., 2015a, 2015b). Nevertheless, as climate change impacts may be species- and/or context-specific, there is need to elucidate how, in interaction with biotic factors, changes are likely to influence functioning of the technology in the future. As the effectiveness of PPT is dependent on multi-level species interactions (Khan et al., 2016), any effect of the environment on these interactions is likely to affect the functioning of this cropping system. Impacts are expected to propagate through complex ecological networks, including feedback loops back into affected components. It is therefore essential to synthesize available understanding and fill knowledge gaps on how climate change can influence separate PPT components (i.e., land use, soils, crops, weeds, diseases, pests and their natural enemies), and the long-term effectiveness of the technology through system-wide feedbacks.

Here, we anticipate climate change effects on PPT in maize production, using a mixed methods approach. First, we review projected impacts of changes in temperature, precipitation and atmospheric CO_2 concentration on PPT components. Although PPT is currently mostly applied in eastern Africa, we review effects across SSA, with the goal of informing ongoing dissemination of PPT and other measures of ecological intensification in the region. Our review has three primary objectives: a) identify types of pertinent evidence that is available across disciplines and assess their utility for predicting climate change effects on PPT components, b) examine how methodological considerations can facilitate or hamper such evidence-based prediction, and c) identify gaps in the knowledge base about climate responses of PPT components, as well as the methodologies that can generate such knowledge. Secondly, based on expert knowledge, we develop a qualitative mathematical model (Levins, 1998) for a holistic representation of maize production under PPT in eastern Africa. Mechanistic modelling can increase the reliability of predictions of climate change impacts on agroecosystems, by explicitly representing confounding ecological interactions (Cuddington et al., 2013). Reviewed responses of PPT system components to climate change are imposed on the model to predict cumulative, structure-mediated impacts on maize yield, allowing us to identify interventions with a potential to sustain PPT maize yields in eastern Africa under projected climate conditions. Ultimately, we aim to provide the knowledge and methodological basis for reliable predictions of climate change impacts on PPT and other measures of ecological intensification across SSA.

2. Methods

2.1. Review of climate change impacts on PPT components

Our distinct objectives of classifying available evidence, reviewing methodological advances or constraints, and identifying knowledge gaps across disciplines, can be achieved most efficiently by a scoping review (Munn et al., 2018). Scoping studies "aim to map rapidly the key concepts underpinning a research area and the main sources and types of evidence available, and can be undertaken as stand-alone projects in their own right" (Mays et al., 2004). Unlike systematic reviews, scoping studies address broad topics that involve a variety of study designs (Arksey and O'Malley, 2005). We performed a mixed methods review, iteratively employing database search, reference chaining and expert consultation, in order to maximize the breadth of the reviewed literature (Depraetere et al., 2020). The scope of the review was determined a priori, in order to represent the complexity of PPT systems in SSA. Reviewed components include climate, belowground processes, crop yield and use of land, weeds, plant diseases, crop pests and their natural enemies.

2.2. Qualitative model predictions of maize yield under PPT

Qualitative mathematical modelling can predict the direction of a system's response to perturbations based solely on knowledge of the system's structure (Dambacher et al., 2003). For the development of qualitative mathematical models, we elicited expert knowledge of the maize push-pull system in eastern Africa through a participatory modelling approach (Fulton et al., 2015). System experts participated in an initial and a follow-up workshop aimed at unanimous identification of key system components and their interactions at the landscape scale (see Section 5.2). Uncertainties were noted for model verification through analysis of alternative system structures. Direct effects among

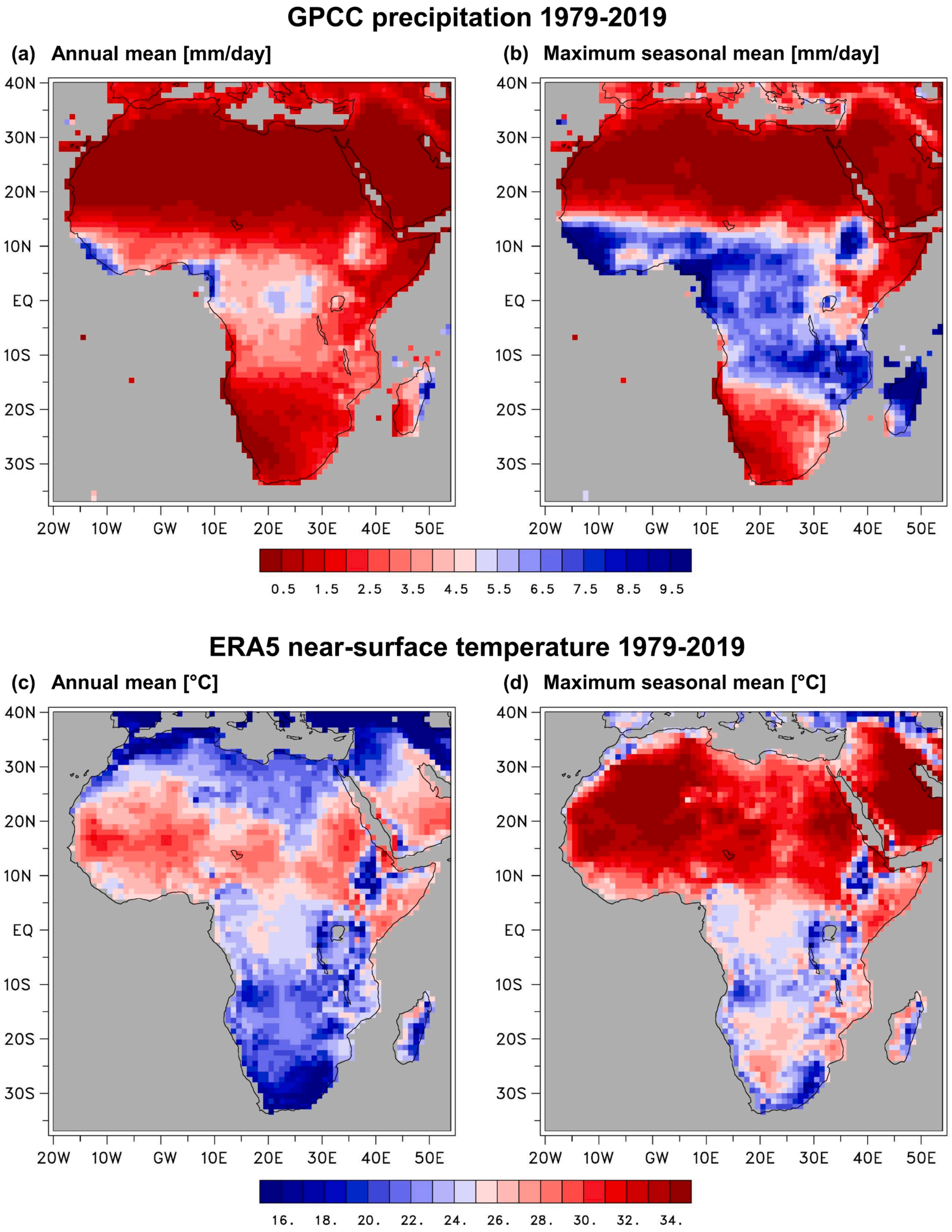

Fig. 1. Precipitation from the Global Precipitation Climatology Centre (GPCC) data set for the period 1979–2019 (Schneider et al., 2018) (upper panels) and near-surface temperatures from the ERA5 data set for the period 1979–2019 (Hersbach et al., 2020) (lower panels). (a) Annual mean precipitation [mm/day], (b) maximum seasonal mean precipitation over 3-month periods [mm/day], (c) annual mean near-surface temperatures [°C] and (d) maximum seasonal mean near-surface temperatures over 3-month periods [°C].

system components were combined into a signed digraph (network depicting the direction and sign of interactions) for each alternative system structure (Alexandridis et al., 2021). The matrix representation of a signed digraph is a qualitatively specified (i.e., consisting of 0, −1 and 1) community matrix (linearization of a Lotka–Volterra equation at an equilibrium point) (Puccia and Levins, 1985). Standard analysis of the qualitative matrix for each alternative structure (Dambacher et al., 2002) assessed the system's stability potential and equilibrium response of maize yield to climate change. Climate change was imposed on each model as sustained increases or decreases in system components, based on reviewed impacts of climate change on each PPT component (see Section 5.3).

3. Climate in sub-Saharan Africa

3.1. Main climate characteristics

The geographic location and large extent of the African continent, ranging approximately from 35° N to 35° S, and bordering the Atlantic Ocean to the west and the Indian Ocean to the east, lead to high climate variability. In particular, African climate is governed by high seasonal variations associated with seasonal shifts of the intertropical convergence zone.

Mean annual precipitation is high (3–6 mm/day) in some of the coastal areas affected by the monsoon during local summer, i.e., Guinea and Cameroon coasts in the west and the eastern coast of Madagascar (Fig. 1a). Other areas with high rainfall include central Africa, the Ethiopian Highlands and parts of eastern Africa. Little annual rainfall occurs in the north and south-west of the continent and in the Horn of Africa. The geographic distribution of maximum seasonal mean rainfall has a similar structure, with high values ranging between 5 and 10 mm/day (Fig. 1b).

Annual mean temperatures are highest in the northern part of the continent, reaching 30 °C in the Sahel (Fig. 1c). In the southern part, except for South Africa, annual mean temperatures range between 20 and 25 °C. In South Africa, as well as several other mountainous or coastal regions, annual mean temperatures range between 15 and 20 °C. Similar to annual mean temperatures, the highest maximum seasonal mean temperatures are found in the northern part of the continent, where they are generally above 30 °C (Fig. 1d). Maximum seasonal mean temperatures also reach 30 °C on the Horn of Africa. In the central and southern parts of the continent, maximum seasonal mean temperatures are markedly lower, ranging between 18 and 25 °C in several regions.

3.2. Recent climate trends

Consistent with ongoing global warming, annual mean near-surface temperatures have increased over the entire African continent between 1981 and 2012 (Hartmann et al., 2013). Over most of SSA, near-surface temperatures have increased by more than 0.2 °C/decade, with slightly smaller increases in the Congo Basin and Madagascar. Larger increases, generally between 0.4 and 0.6 °C/decade, have been observed in northern Africa.

Annual mean rainfall has also shown notable trends over most of the African continent in recent decades. According to Maidment et al. (2015), annual rainfall has increased in western Africa, the Sahel and southern Africa, and decreased in eastern Africa, over the period 1983–2010. Changes typically range between 0.2 and 0.5 mm/day/decade. Similar patterns can be identified in several data sets, and are thus considered to be robust, but local details and estimated magnitude of trends vary.

3.3. Projected future changes in climate

Atmospheric concentrations of certain greenhouse gases, i.e., carbon dioxide (CO_2), methane and nitrous oxide, have been increasing due to anthropogenic emissions, and are likely to keep changing in the future. The nature of these changes depends on the underlying emission scenarios, which are in turn governed by different socio-economic development paths. The concept of Shared Socio-economic Pathways (SSPs) has been developed to describe five different narratives, resulting in varying challenges for adaptation to and mitigation of future climate change (O'Neill et al., 2017). Combined with different values of cumulative radiative forcing, these SSPs result in mitigation scenarios, which have been used for future climate projections (O'Neill et al., 2016). To facilitate the assessment of regional climate changes in the 6th Assessment Report of the Intergovernmental Panel on Climate Change (IPCC), Iturbide et al. (2020) divide mainland Africa into eight regions, six of which cover SSA (Table 1).

The 6th Assessment Report of the IPCC includes an atlas of regional climate projections, including the six climate regions of mainland SSA (Iturbide et al., 2021). All regions show similar warming at the end of the 21st century, for both winter and summer seasons, with values ranging between 1 °C and 4.8 °C for different climate scenarios (Table 2). Area means of changes in precipitation vary somewhat by region and season (Table 3). In all cases, however, projected changes increase with the strength of climate forcing. In western and eastern Africa, mean rainfall is projected to increase in winter and summer seasons. At the end of the 21st century, strong climate forcing is associated with rainfall increases of about 7% in western, 11% in central and 19–24% in eastern Africa. In southern Africa, in contrast, mean rainfall is projected to decrease by 6–20%.

Changes in climate means are accompanied by changes in climate extremes. Annual daily maximum temperatures are projected to increase up to 4–6 °C by the end of the 21st century, with highest values predicted for the Sahel and southern Africa (Collins et al., 2013). The number of tropical nights (i.e., days with minimum temperatures above 20 °C) is projected to increase between 70 and 100 days, with the highest numbers for regions with a pronounced dry season. Nikulin et al. (2018) link global warming of 2 °C by the end of the 21st century to higher intensity of precipitation on wet days by up to 1 mm/day, over much of the African continent. Heavy precipitation events (defined as the annual maximum of precipitation accumulated over five days) are similarly projected to increase by a maximum of 10–20 mm in western Africa, in particular the southern part, and the central tropics.

4. Climate change impacts on push-pull components

4.1. Anticipated impacts on below-ground processes

Climate change is expected to have varied influences on soil conditions, beneficial organisms and susceptibility of crops to infestation by soil pests and pathogens (Rosenzweig et al., 2001). Extreme weather variabilities attributed to climate change can alter the ecology, distribution and trophic interactions of soil organisms (Ziska and McConnell, 2016). Well-designed, replicated and controlled manipulative

Table 1
Division of mainland sub-Saharan Africa (SSA) into 6 climate regions.

Region	Acronym	Intra-regional climate variation
Western Africa	WAF	Wet south, semi-arid north (Sahel)
Central Africa	CAF	Wet south and centre, semi-arid north (Sahel)
North Eastern Africa	NEAF	Wet west (Ethiopian Highlands), dry east (Horn of Africa)
South Eastern Africa	SEAF	Relatively wet eastern coasts and western mountains
West Southern Africa	WSAF	Relatively cold coasts
East Southern Africa	ESAF	Relatively cold south and wet coasts

For details, see Iturbide et al. (2020).

Table 2
Changes in annual mean temperature [°C] at the end of the 21st century (2081–2100) with respect to the recent past (1995–2014) for different Shared Socio-economic Pathways (SSPs), in each SSA climate region (see Table 1). Values represent the median and 10th-90th percentile range of changes simulated by individual climate models.

Region	SSP1-2.6	SSP2-4.5	SSP3-7.0	SSP5-8.5
WAF	1.1 (0.5–1.8)	2.1 (1.6–3.1)	3.3 (2.4–4.2)	4.0 (2.8–6.1)
CAF	1.1 (0.5–1.7)	2.1 (1.4–3.0)	3.3 (2.2–4.6)	4.0 (2.3–5.8)
NEAF	1.1 (0.6–1.8)	2.1 (1.6–3.0)	3.2 (2.4–4.3)	4.0 (3.0–5.5)
SEAF	1.0 (0.5–1.6)	2.0 (1.6–2.9)	3.1 (2.4–4.1)	3.8 (2.8–5.3)
WSAF	1.1 (0.6–2.0)	2.5 (1.8–3.5)	3.9 (3.0–5.0)	4.8 (3.6–6.6)
ESAF	1.2 (0.6–1.9)	2.3 (1.7–3.1)	3.6 (2.7–4.6)	4.5 (3.3–6.2)

Table 3
Changes in annual mean precipitation [%] at the end of the 21st century (2081–2100) with respect to the recent past (1995–2014) for different Shared Socio-economic Pathways (SSPs), normalized by the means for the recent past, in each SSA climate region (see Table 1). Values represent the median and 10th-90th percentile range of changes simulated by individual climate models.

Region	SSP1-2.6	SSP2-4.5	SSP3-7.0	SSP5-8.5
WAF	1.8 (−6.1 to 9.0)	3.7 (−7.5 to 13.0)	4.6 (−11.3 to 16.9)	7.1 (−14.5 to 20.8)
CAF	2.9 (0.6–4.7)	5.8 (1.2–9.4)	8.0 (4.3–14.7)	11.4 (2.9–18.4)
NEAF	4.8 (0.2–15.9)	10.1 (−1.0 to 22.4)	16.2 (5.8–33.8)	24.1 (3.8–34.6)
SEAF	3.6 (−0.3 to 12.5)	6.6 (−2.4 to 15.5)	13.1 (1.1–23.1)	18.6 (1.4–28.2)
WSAF	-2.6. (−9.0 to 3.4)	-2.2 (−8.3 to 4.0)	-7.1 (−16.7 to 2.0)	-7.6 (−16.6 to 2.7)
ESAF	-1.9 (−9.9 to 3.5)	-1.2 (−7.6 to 3.5)	-2.1 (−13.1 to 4.8)	-0.4 (−16.9 to 8.1)

experiments studying the interactive effects of multiple climate-change factors over timescales longer than one season are lacking in Africa. Therefore, much of the knowledge we have today is based on field and laboratory studies that focus on one or two factors and is drawn from microclimate influences of agricultural practices and multi-locational or -seasonal studies representing different climates.

4.1.1. Impacts on soil nutrients and organic matter

Higher incidence of heavy precipitation can result in loss of soil organic matter and nutrients through increased soil erosion, surface flooding and waterlogging (ITPS, 2015; Chen et al., 2020). A meta-analysis of data from experimental warming studies shows that warming accelerates loss of plant litter mass by 6.8%, soil respiration by 9.0% and dissolved organic C leaching by 12.1% (Lu et al., 2013). Another meta-analysis shows that long-term ($\geq$ 5 years) warming by 0.3–5.1 °C reduces the recalcitrant C pool by 14%, by stimulating microbial utilization (Chen et al., 2020). A temperature increase of 1 °C may decrease turnover times by 4–11% and 8–16% for the intermediate and stabilized fractions, respectively (Hakkenberg et al., 2008). While most below-ground effects of climate change are directly linked to rainfall and temperature, increasing atmospheric CO_2 concentration is expected to stimulate nitrogenase enzyme activity (Gibson et al., 1982), and thereby also nitrogen fixation (Tissue et al., 1996).

4.1.2. Impacts on soil microbial communities

Soil microbial communities play a vital role in the cycling of carbon and nutrients (Castro et al., 2010; Classen et al., 2015). Changes in temperature, precipitation and CO_2 concentration can impact soil food webs both directly and indirectly, by altering plant growth, structure and physiology (Pritchard, 2011; Classen et al., 2015).

Decomposition of soil organic matter, soil respiration, and microbial biomass generally increase with temperature (Classen et al., 2015). The effect of temperature is often studied using experimental warming in the field or in the laboratory. However, temperature changes can be coupled with changes in air and soil moisture (Classen et al., 2015). It is, therefore, not surprising that experiments exploring only the effects of temperature show inconsistent results. For example, in the USA, Castro et al. (2010) found higher fungal abundance in plots with 3 °C warming, while bacterial abundance increased in plots combining warming and elevated (+300 ppm) CO_2, but decreased in warmer plots under ambient atmospheric CO_2. As a result of species' different climate preferences, temperature variations can prompt changes in species sorting within underground microbial communities (Grönemeyer and Reinhold-Hurek, 2018).

Microbial community composition and structure have also been shown to be sensitive to experimental changes in precipitation regime and across precipitation gradients (Evans and Wallenstein, 2014). Castro et al. (2010) indicate that changes in precipitation tend to have much greater effects on community composition than warming and CO_2 enrichment. Furthermore, long-term effects of precipitation fluctuations may also lead to selection of tolerant phenotypes. For example, Evans and Wallenstein (2014) found that a decade of exposure to more frequent drying-rewetting stress resulted in a greater proportion of taxa exhibiting stress tolerance, compared to communities exposed to the ambient precipitation regime.

Elevated atmospheric CO_2 commonly stimulates the flow of organic C into the soil system, increases root production and exudation, but decreases plant litter quality (Pritchard, 2011). Global meta-analyses show that CO_2 enrichment enhances mycorrhizal and N-fixing relationships (Treseder, 2004; Alberton et al., 2005), but the effects of warming are highly variable (Pritchard, 2011). Both warming and CO_2 enrichment have been found to enhance fungal metabolic pathways relative to bacterial pathways. Whether a shift towards fungal dominance will increase soil-borne disease incidence in the future remains an open question (Pritchard, 2011).

4.1.3. Impacts on soil fauna

Soil (micro-, meso- and macro-) fauna are responsible for transformation of plant litter, maintenance of soil physical properties, recycling of nutrients, protection of nutrients and organic matter in soil biostructures and for natural pest control (Lavelle et al., 2002; Sileshi and Mafongoya, 2006). When richness of functional groups, such as litter transformers and predators, is reduced by changes in land use or climate, essential ecosystem functions may also suffer. Soil fauna is sensitive to warming. Unfortunately, studies investigating effects of climate change on soil fauna in African cropping systems are rare. Predictions thus need to be based predominantly on studies conducted in other climatic regions. In a two-year mesocosm experiment evaluating the effects of a 3.5 °C temperature increase on a grassland soil community in Scotland, Briones et al. (2009) observed total disappearance of surface-dwelling earthworms, a decrease in the abundance of larger oligochaetes and Prostigmata mites, but an increase in fungivorous mites. A meta-analysis encompassing studies from Europe and North America found that enchytraeid worm populations will decline precipitously if soil temperatures rise above the threshold of 16 °C (Briones et al., 2007). In line with these findings, a study from Kenya found macrofauna species richness to decline by 27% in response to experimentally increased temperatures by 2.2 °C; however, mesofauna species richness simultaneously increased by 63% (Ayuke et al., 2019). Higher biomass productivity under warmer and wetter conditions enhanced the abundance and activity of fungal-feeding collembola involved in organic matter decomposition (Muturi et al., 2011; Coyle et al., 2017; Zagatto et al., 2019).

4.2. Anticipated impacts on crop yields and land use

Impacts of climate change on crop yields (mass harvested per unit area) and agricultural land use are difficult to predict, in part due to investment in adaptation. Warmer climates might lead to specific crops being grown at higher altitudes in order to maintain the cultivated area (Ruf et al., 2015; Schroth et al., 2016). In temperate regions, an alternative option would be to shift growing to a cooler season, but this is not possible in tropical areas, where heat stress will become a major challenge for many crops. Breeding for heat stress and drought tolerance, along with short duration varieties, is a long-term adaptation strategy that needs to be combined with adaptive cropping practices and improved institutional capacity (Challinor et al., 2007).

4.2.1. *Impacts on maize*

Simulations of current maize varieties and agricultural practices under projected mid-21st century climate conditions indicate an overall yield reduction of 10% in Africa (Lobell et al., 2011). This prediction hides enormous variability, as, for instance, maize yields are predicted to increase in Côte d'Ivoire, Lesotho and Somalia, and remain constant in Equatorial Guinea and Liberia. Despite large inter- and intra-country variability, maize yields are predicted to decrease overall in each SSA region (Jones and Thornton, 2003). This reduction is mostly driven by higher maximum temperatures, delayed onset of rainy seasons and higher evapotranspiration, which negate any positive effects of higher rainfall.

The importance of maize for food security in SSA motivates a prioritization of adaptation strategies to preserve the area under maize cultivation (Cairns et al., 2013). Declines in maize cultivation may still occur in areas predicted to suffer the strongest negative impacts of higher temperatures and more variable rainfall patterns, i.e., lowland and dry mid-altitudes of western and southern Africa (Tesfaye et al., 2015). In view of potential decreases in maize yield, making climate resilient germplasm accessible to farmers requires breeding for drought- and heat-tolerant varieties, strengthening of seed systems and higher availability of credit for seed providers and farmers (Cairns et al., 2013). In addition, offsetting climate-induced reductions in maize yield calls for management practices that reduce evapotranspiration and increase soil moisture, such as reduced tillage, retention of residues, intercropping or crop rotations and water harvesting (Kuyah et al., 2021).

4.2.2. *Impacts on sorghum*

Sorghum yield is predicted to decline in western Africa under climate scenarios of rising mean annual temperatures beyond 2 °C (Sultan et al., 2013), irrespective of any positive effects of higher rainfall or CO_2 fertilization (Sultan et al., 2014; Amouzou et al., 2019). Similar predictions are generated by models of sorghum yield in eastern and southern Africa, with the exception of nutrient-poor soils, where projected climate changes lead to higher yields (Turner and Rao, 2013). Management practices in sorghum cultivation are predicted to outweigh negative impacts of climate change on yield (Adam et al., 2020), suggesting limited direct climate impacts on the crop's cultivation area.

4.2.3. *Impacts on arable weeds and weed competition*

Suboptimal climate conditions for crop plants can reduce their ability to compete with a diverse pool of weeds, some of which may expand their geographic range (McDonald et al., 2009), and profit in growth and reproduction in response to projected climate change (Peters and Gerowitt, 2014). Maize and sorghum use the Hatch–Slack (or C_4) pathway of carbon fixation. The Calvin cycle (or C_3) pathway appears to be overrepresented among major weeds in SSA (Rodenburg et al., 2011). Higher mean temperature and drought occurrence are expected to favour C_4 over C_3 plants (Goodman, 2004), creating an advantage for maize and sorghum over weeds. However, this advantage can be reduced or reversed by higher atmospheric CO_2 concentrations (Bazzaz and Carlson, 1984; but see Watling and Press, 1997).

CO_2 fertilization is expected to enhance rhizome and tuber growth of perennial weeds, impeding their effective control (Patterson, 1995). Increasingly erratic rainfall patterns with higher drought and flood occurrence (Giannini et al., 2008) should favour parasitic weeds that are adapted to low rainfall (e.g., *Striga hermonthica*) or flooded conditions (e.g., *Rhamphicarpa fistulosa*) (Rodenburg et al., 2010). *Striga* weeds in particular infect a variety of crops in SSA, and are expected to be favoured by higher soil degradation caused by more frequent climate extremes (Rodenburg et al., 2011). Projected climate change can also expand the geographic distribution of parasitic weeds towards higher latitudes and altitudes (Patterson et al., 1999), although the geographic range of parasitic weeds may be primarily dictated by the range of their host crop plants (Phoenix and Press, 2005). Finally, the effectiveness of existing herbicides might also be reduced under projected climate conditions (Rodenburg et al., 2011).

4.3. *Anticipated impacts on arthropod crop pests*

Effects of climate change on arthropod crop pests are highly dependent on individual pest species' responses to changes in climate variables and the current climatic conditions in the respective regions. As studies combining field data with predictive modelling of temperature effects are rare, current predictions have to rely on laboratory data. In addition, the effects of rainfall on pest populations remains largely unexplored, due to both the paucity of studies explicitly investigating such effects and the lack of knowledge about the mechanistic details of precipitation effects on pest development. Nevertheless, the available data suggests that arthropod pests in SSA will likely increase in abundance in response to climate change mainly due to range expansions and increased survival.

4.3.1. *Temperature impacts*

Arthropods are constrained in their growth and development by the temperature of their environment, and show distinct temperature niches defined by a temperature optimum, along with lower and upper tolerance limits (Pörtner and Farrell, 2008; Régnière et al., 2012; Gullan and Cranston, 2014; Feit et al., 2021). Climate change in SSA will likely increase temperatures above lower tolerance limits for some arthropod pest species in areas of higher altitude or southern latitude, but might also be pushing temperatures above upper tolerance limits in areas that are already hot (Deutsch et al., 2018). Overall, we expect that arthropod pests in SSA will increase in abundance via three different mechanisms: a) range expansion of pests to higher altitudes or higher southern latitudes (Yonow et al., 2017); b) increased pest densities, survival and/or crop damage due to higher temperatures (Sseruwagi et al., 2004; Reji and Chander, 2008; Jeremiah et al., 2015; Mwalusepo et al., 2015) and c) spatiotemporal mismatch of pests and their natural enemies, leading to reduced biological control (Mwalusepo et al., 2015). Although we expect this to be true for most of SSA, arthropod pests in western and central Africa, in particular, might experience the least change or even a decrease in abundance, given that current average temperatures are already between 25 and 30 °C, and an increase in temperature above 30 °C could surpass the upper temperature limit of many pests. This has already been reported for some pests of maize (Barfield and Ashley, 1987; Sokame et al., 2020; Viswajyothi et al., 2020) and pests feeding on multiple crops, such as the desert locust *Schistocerca gragaria* (Hamilton, 1950).

Field data combined with predictive modelling indicate range expansions to higher altitudes for stemborers *Chilo partellus* and *Busseola fusca* (Mwalusepo et al., 2015), the most important pests of maize and sorghum in SSA before the invasion of fall armyworm to the region (Abate et al., 2000). However, as studies combining field data with predictive modelling remain rare, laboratory data become a key source of information to predict impacts of temperature changes on arthropod pests. For instance, laboratory experiments indicate that increases in temperature lead to higher fecundity and faster development in the pink stemborer *Sesamia inferens* (Viswajyothi et al., 2020), and higher relative growth rate for several species, such as the invasive fall armyworm *Spodoptera frugiperda* and the stemborers *B. fusca*, *C. partellus*, and *Sesamia calamistis* (Sokame et al., 2020). On the other hand, temperatures above upper tolerance limits have been demonstrated to reduce growth and survival parameters, with the exact thresholds varying between pest species (Hamilton, 1950; El-Nahal et al., 1978; Baxendale, 1983; Barfield and Ashley, 1987; Oduor et al., 1995; Sokame et al., 2020; Viswajyothi et al., 2020). Naturally, assessments of temperature effects carried out under laboratory conditions have their limitations. For instance, they often represent constant temperatures, and not the fluctuations typical of natural conditions. Furthermore, temperature effects were in most studies investigated independently of other relevant factors, such as host availability, rainfall patterns and interactions with other organisms. Nevertheless, we consider these data informative when trying to assess the direct effect of temperature on insect pest growth and development.

4.3.2. Precipitation impacts

Changes in long-term rainfall patterns and short-term precipitation events are both likely to influence the development and population growth of pest species, and thus their impact on agricultural production. However, the direction and magnitude of precipitation effects on invertebrates is highly variable and typically species-specific (Barnett and Facey, 2016). Consequently, precipitation effects on agricultural pests must be assessed at a species level, based on the respective life history traits. This becomes particularly evident by reports that even pest species of very similar biology can show contrasting responses to changes in rainfall patterns. For instance, effects of higher precipitation on populations of lepidopteran stemborer species can be either positive, with *B. fusca* benefitting from high rainfall and accompanying humidity (Van Rensburg et al., 1987; Ntiri et al., 2019), or negative, with both *C. partellus* and *S. calamistis* benefitting from dryer climates (Ntiri et al., 2019).

Unfortunately, knowledge of the effects of precipitation on the majority of economically important arthropod pest species in SSA is rudimentary and, further compounding the problem, often contradictory. For example, populations of the invasive fall armyworm have been reported to benefit from higher precipitation in some studies (Murúa et al., 2006; Nboyine et al., 2020), while others found that egg populations are highest during dry spells (Dequech et al., 2013), and that both pupae and larvae experience an increased risk of drowning after rainfall events (Sims, 2008; Early et al., 2018). To a large part, our current lack of understanding of the effects of rainfall on pest populations stems from the paucity of studies explicitly investigating such effects. In addition, we often lack knowledge about the mechanistic details of precipitation effects on pest development. Further research addressing both these issues is imperative in order to generate precise and reliable predictions of potential changes in pest pressure because of shifting rainfall patterns.

4.4. Anticipated impacts on crop diseases

Climate change is predicted to affect the spread and severity of crop diseases in SSA. In particular, diseases that rely on transmission via insect vectors might profit from the expected increase in pest densities, as a result of higher temperatures and precipitation (see Section 4.3). Consequently, future climate conditions are likely to further increase the spread of diseases, such as maize lethal necrosis (Isabirye and Rwomushana, 2016), a serious threat to maize production in SSA (Beyene et al., 2017; Marenya et al., 2018). Certain diseases that do not exclusively rely on vector transmission might also increase in spread and severity due to more suitable climate conditions. For example, wheat stem rust *(Puccinia graminis)*, leaf rust *(Puccinia recondite*), stripe rust *(Puccinia striiformis*) and powdery mildew (*Blumeria graminis)* are predicted to cause a 72% decline in wheat yield by 2090 under higher air temperature and/or lower precipitation compared to current conditions (Liu et al., 2008; Adhikari et al., 2015). In contrast, climate change might decrease the prevalence of certain currently common diseases, such as sorghum ergot caused by *Claviceps africana*, whose severity decreases with increasing temperature and reduced humidity (Adhikari et al., 2015).

Changes in temperature, precipitation, CO_2 and ozone concentrations are expected to affect microbial communities in the soil pathosystem. While temperatures above 25 °C, along with sufficient moisture, are expected to enhance the growth and reproduction of fungi (Karuri et al., 2017), it is unclear whether pathogenic fungi would also increase. In the absence of empirical data, it is difficult to predict these effects in African cropping systems, and any attempt to generalize will be challenging, as the effects of climate change will differ by pathosystem and geographic region. It is also extremely difficult to model these changes, because pre-existing uncertainties are exacerbated when downscaling projected climate data to the level of plants or plant parts and organs, where fungi typically operate. The main difficulties in predicting crop diseases in the future include finding suitable data on current epidemics to construct good empirical models, the uncertainties associated with climate models, and the inability to predict other changes that may occur, such as possible adaptations of plants and/or pathogens and shifts in agricultural practices (Elad and Pertot, 2014).

4.5. Anticipated impacts on biological control by generalist predators and parasitoids

Effects of climate change on biological control are likely to be highly context specific. Predators within a system often differ in their climatic niches (Feit et al., 2021), and predictions of higher predation rates with increasing temperatures will largely hinge on the thermal tolerance of natural enemies (Pörtner and Farrell, 2008). The fitness of predators and parasitoids could be altered by changes in prey quality and size due to climate change, while the susceptibility of prey to predators and parasitoids could be modified through changes in their phenological matching (Thomson et al., 2010). However, we expect such effects to be stronger for specialised groups of parasitoids than for generalistic predators, so that parasitoids are likely to adapt to the new environment. Predictions based on the general patterns for predation and parasitism discussed below are extremely uncertain. There is an urgent need for studies of predation and parasitism under realistic climate change scenarios, particularly in African cropping systems.

4.5.1. Temperature impacts

Predators of crop pests include a wide range of invertebrates, such as spiders, ants, predatory beetles and true bugs, as well as vertebrates, such as birds and bats. Most of these predators tend to be relatively generalistic, adapting their prey choice to prey availability, even though certain groups of predators prefer prey with certain body sizes or other traits (e.g., lady beetles preferring aphids and other soft-bodied invertebrates). The most direct measure of the impact of predator communities on pest populations are estimates of predation rates (Birkhofer et al., 2017). Unfortunately, there is extremely limited information available from any part of the world on how temperature affects predators and predation rates in the crops considered here (see Ahmed et al., 2013 for a rare example outside Africa).

For now, predictions of how changes in ambient temperature will affect predation rates have to rely on general patterns found under current conditions in regions of contrasting temperatures. For instance, Roslin et al. (2017) demonstrated predation rates by arthropod predators to increase, both with warmer temperatures associated with decreasing latitude towards the tropics, and with decreasing altitude. Predation rates by mammals and birds were found to remain largely stable. Similarly, Hodkinson (2005) found predation pressure to decline with colder temperatures associated with increasing elevation. Based on such studies, we can predict that increasing temperatures resulting from climate change will likely lead to higher average predation rates by arthropod predators, but that predation by birds and mammals will likely remain unaffected.

In contrast to predators, parasitoids kill their prey when their larvae feed and develop on or within the body of a host. Consequently, life histories of parasitoids and their hosts are closely linked, particularly through seasonal and geographical synchrony between parasitoid activity and host availability (Godfray, 1994). As climate change impacts both parasitoids and pests directly but also indirectly by altering their interactions (Jeffs and Lewis, 2013), predicting the consequences of climate change on the biocontrol potential of parasitoids remains challenging. Nevertheless, climate change has the potential to disrupt pest-parasitoid temporal and/or geographical synchronization, by interfering with developmental times of insect pests, or by raising temperatures above upper tolerance limits for parasitoids but not for pests (Ovaskainen et al., 2013; Tougeron et al., 2020). Since synchronization between parasitoids and pests is of pivotal importance for their interaction, the potential for natural biological control might be reduced and outbreaks of pests which had been controlled by parasitoids might become more common. However, through evolutionary pressure, parasitoids are expected to employ several strategies to adapt to these changes. For instance, adjustments in parasitoid diapause and other behavioural and physiological modifications could retain synchrony with hosts, so that parasitoid attack rates are maintained (Tougeron et al., 2020). Indirect support for the potential of parasitoids to adapt to increasing temperatures in the long term is provided by a study showing no consistent effect of either altitude or temperature on parasitoid richness in Kenya (Mailafiya et al., 2010).

4.5.2. *Precipitation impacts*

Evidence for links between predation or parasitoid attack rates and precipitation is even more scant than fro temperature. It has been shown that parasitoid attack rates on caterpillars across northern and southern America are unaffected by variation in average precipitation levels, but that they decline with increasing precipitation variability (Stireman et al., 2005). The latter pattern was driven by more specialized parasitic wasps, whereas more generalized tachinid flies were unaffected by rainfall variability (Stireman et al., 2005). Since predators tend to be more generalized in their trophic preferences than parasitoids, we can predict that predation rates are likely more robust to changes in both average levels of rainfall and rainfall variability.

5. Modelling maize yield under push-pull in eastern Africa

5.1. *From direct to interactive impacts of climate change*

Complex interactions between PPT system components render each component's response to climate change conditional on changes elsewhere in the system. Here, we investigate such indirect effects of climate change on maize yield under PPT in eastern Africa at the landscape scale. Eastern Africa (North and South Eastern Africa in Table 1) is PPT's region of origin, and hosts the majority of farmers currently practicing PPT (Midega et al., 2015a, 2015b). We build qualitative mathematical models of alternative system structures, and impose increases or decreases on system components, depending on the sign of their reviewed responses to climate change in eastern Africa (reviewed response signs are the same in North and South Eastern Africa). The resulting response of maize yield to projected climate change represents not only direct climate impacts, but also impacts propagating through the system's structure.

Our review suggests variable impacts of climate change on PPT components in eastern Africa (Table 4). Higher mean temperature and rainfall values, as well as higher climate extremes by the end of the 21st century, are likely to reduce soil fertility, due to soil erosion and loss of organic carbon. Higher evapotranspiration and delayed onset of rainy seasons are predicted to reduce maize yields, but maize and other cereals' role as staple crops is likely to retain the area dedicated to cereal cultivation. Adverse conditions for maize plants are expected to create a competitive advantage for a diverse pool of weeds, particularly those that benefit from land degradation, such as *Striga* spp. Disease incidence is more difficult to anticipate, but higher vector densities and destabilization of soil pathosystems could increase the prevalence of maize diseases under climate change. Maize pests are expected to benefit from future increases in rainfall and temperature, due to range expansion, higher activity and potential mismatch with natural enemies. Information regarding climate change impacts on pests' natural enemies is limited, but it suggests positive responses of predation rates caused by higher temperature.

Table 4
Reviewed predictions of climate-induced change in each push-pull system component and modelled responses of maize yield to each changing system component in eastern Africa. Symbols ○, ⊖, ⊕ and ? indicate no change, decreasing, increasing and ambiguous responses, respectively.

System component	Climate-induced change in system component	Maize yield response to changing system component
Maize yield	⊖	⊖
Striga	⊕	⊖
Stemborer	⊕	⊖
Fall armyworm	⊕	?
Stemborer natural enemies	⊕	⊕
Fall armyworm natural enemies	⊕	?
Generalist natural enemies	⊕	⊕
Soil fertility	⊖	⊖
Cereal crop cultivation	○	⊖[a]
Grassland proportion	?	?
Field edge density	?	⊕[a]
PPT adoption	?	⊕[a]

[a] In response to a hypothetical increase in changing system component.

5.2. *System structure*

The version of system structure that generated consensus among participants in workshops for expert knowledge elicitation (Fig. 2) is based on maize yield and its reduction by maize-consuming *Striga* weeds, stemborer and fall armyworm pests. These interactions are represented as negative effects on yield and positive effects on maize consumers. Similar consumption interactions occur between the two pests and their specialist and generalist natural enemies. Fall armyworm also has a consumption interaction with stemborers, due to predation and cannibalism on stemborer larvae (Midega et al., 2018). The negative element of this interaction is reinforced by reduced stemborer attack rates on maize heavily infested by fall armyworm (Hailu et al., 2021; Mutyambai et al., 2022). Fall armyworm is also attacked by stemborer parasitoids without the emergence of progeny (Sokame et al., 2021). Being a sink for these stemborer specialist enemies, fall armyworm has a negative effect on them. Finally, *Striga* infestation enhances stemborer oviposition on maize (Mohamed et al., 2007), there is thus a positive effect of *Striga* on stemborers.

The numerous factors controlling soil fertility (see Section 4.1) have a direct positive effect on maize yield and a negative effect on *Striga* infestation (Ekeleme et al., 2014). Cereal crops provide hosts for both *Striga* and stemborers (Midega et al., 2015a, 2015b), thus cereal cultivation at the landscape scale has a positive effect on the two components. Grasslands provide resources and refuge to stemborers, *Striga* and all natural enemies (e.g., Khan et al., 1997), hence a positive effect in the direction of these components from the landscape proportion of grasslands. A similar effect originates from landscape density of field edges (overall, not only PPT fields), but only for natural enemies (e.g., Mailafiya et al., 2011; Midega et al., 2014). Note that all these landscape characteristics affect fall armyworm in a similar way. However, as all considered land uses, including cultivation of non-cereal crops, can be beneficial to fall armyworm, a change in any one of them will be

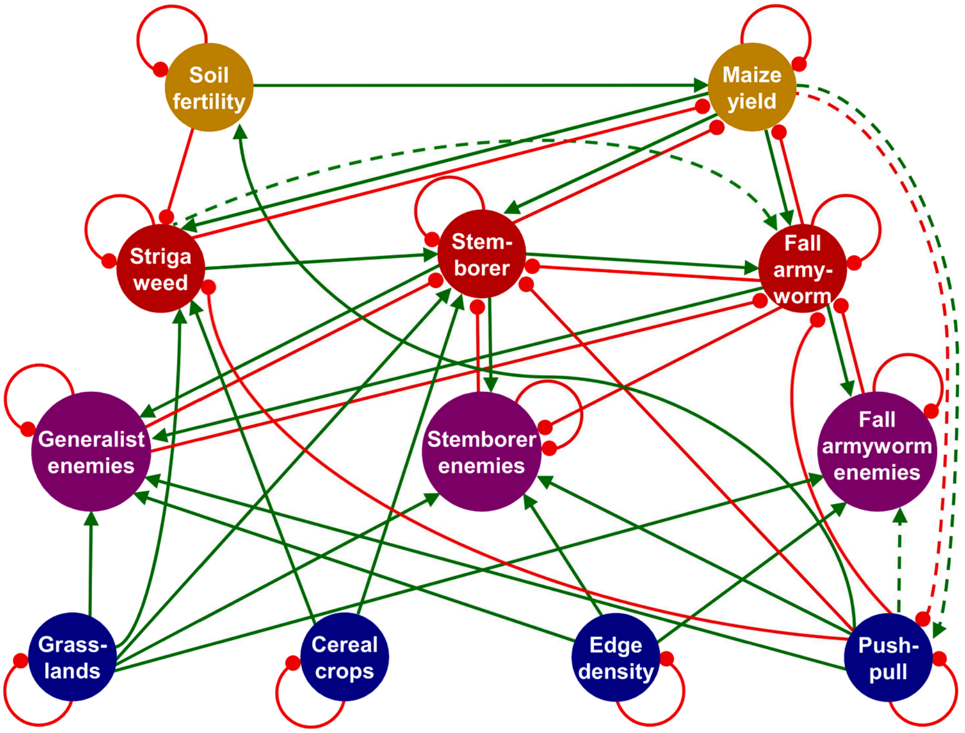

Fig. 2. Signed digraph model of landscape-scale maize push-pull systems in eastern Africa. Top to bottom and left to right, nodes represent: in yellow, crop-related system components of soil fertility and maize yield; in dark red, weed and pest components abundance of *Striga*, stemborer and fall armyworm; in purple, abundance of generalist and specialist natural enemies on stemborer and fall armyworm; in blue, land use components of grasslands and cereal crops land cover, density of field edges and local extent of PPT adoption. Green links ending in arrows and red links ending in filled circles represent positive and negative direct effects, respectively. Dashed links indicate uncertain interactions examined through analysis of models of alternative system structures (see main text for details).

compensated by changes in other landscape components; hence land use changes have no direct effect on fall armyworm.

The extent of PPT adoption in maize cultivation affects many system components through the physical, chemical and biological effects of the technology. PPT has a direct negative effect on *Striga*, stemborer (Khan et al., 2008; Midega et al., 2015a, 2015b) and fall armyworm (Midega et al., 2018; Sobhy et al., 2022), and a positive effect on stemborer specialist (Midega et al., 2009) and generalist natural enemies (Midega et al., 2006) and on soil fertility (Drinkwater et al., 2021). All system components have negative self-effects caused by various processes, such as dependence on external input, accumulation of waste products, territoriality or behavioural inhibition of reproduction (Levins, 1998).

We addressed uncertainty about component interactions, specifically centred on fall armyworm and PPT, by analysing models of alternative system structures (Fig. 2). These two system components form particularly active research areas, with new knowledge constantly being generated. First, enhancement of stemborer oviposition by *Striga* infestation could extend to fall armyworm oviposition on maize. Second, specialist natural enemies of fall armyworm could be enhanced by PPT adoption, similarly to stemborer specialist enemies. We assessed the effect of these potential interactions on system behaviour, by adding positive direct effects from *Striga* to fall armyworm and from PPT adoption to specialist fall armyworm enemies, both independently and in combination. Finally, PPT adoption by farmers is controlled by complex socioeconomic processes (Murage et al., 2015), ideally represented explicitly by social-ecological models. Here, we approximate these effects by directly linking PPT adoption to maize yield. In two versions of the model, we added a negative and a positive effect from maize yield to PPT adoption, assuming that higher yields either reduce or increase farmers' motivation to adopt the technology.

5.3. *Predicted impacts on maize yield*

All alternative hypotheses of system structure result in models with a high potential for stability (i.e., able to maintain their structure following a perturbation), except when higher maize yield enhances PPT adoption (see Table A7 in Appendix A). Consequently, transitory changes to components of these systems (or pulse perturbations, such as droughts or floods) are likely to be fully absorbed, while sustained changes (or press perturbations, such as land use trends or climate change) can push system components towards new equilibrium levels (Dambacher et al., 2003). Model predictions of the direction of such equilibrium responses of maize yield to reviewed impacts of climate change through different PPT components are consistent across alternative system structures (see Tables A8–13 in Appendix A).

Climate change in eastern Africa will have contrasting impacts on the system through different components (Table 4). A direct or disease-induced reduction in maize yield is sustained following internal system interactions, with the same response triggered by soil fertility deterioration and higher *Striga* infestation. Increasing stemborer abundance also reduces maize yield, but higher activity of stemborer specialist and generalist natural enemies is predicted to enhance yields. In contrast, an increase in fall armyworm or higher activity of its specialist enemies will, respectively, also antagonize or release stemborers, leading in both cases to ambiguous responses of maize yield.

Lower landscape-level cultivation of cereal crops would reduce stemborer populations, thus increasing maize yield, but our review suggests no such change in eastern Africa. Future trends of field edge density, grassland amount and push-pull adoption are more difficult to anticipate. Higher overall density of field edges in the landscape should also lead to higher maize yield, by enhancing stemborer specialist enemies and suppressing fall armyworm, in spite of also enhancing *Striga*. However, smallholder fields are already relatively small in most SSA countries. Similarly, increasing grassland proportion in the landscape enhances *Striga* and suppresses fall armyworm. However, in lack of a clear response by the stemborer, impacts of varying grassland proportion on maize yield remain ambiguous. In contrast, higher adoption of PPT is predicted to enhance maize yield, mainly through soil fertility improvement and *Striga* suppression.

The cumulative, structure-mediated impact of climate change on maize yield depends on the strength of single impacts through each system component. Qualitative analysis of combined impacts can indicate the degree to which different components force yield responses in each direction (Dambacher et al., 2003). When we also consider the flexibility of components' reviewed response to climate change, it appears that favourable changes in PPT adoption, and to a lesser extent cultivation of cereals and field edge density, have the potential to tip the balance towards positive responses of maize yield. Consequently, increasing PPT adoption, while retaining field edge density and limiting additional cereals cultivation, are agricultural strategies with the potential to counterbalance otherwise negative cumulative impacts of climate change, towards sustained or higher future maize yields in eastern Africa.

6. Conclusions and Perspectives

Available evidence of climate change impacts on PPT components stem from diverse methodologies. Climate projections and the respective responses of crop yields typically result from analysis of mechanistic models of cumulative impacts. Although generally reliable, model predictions can be confounded by little understood externalities, such as uncertainty about emission scenarios and potential adaptation of farming systems or value chains to climate change. Predictions of pest responses to climate change stem less from modelling or field observations, and more from laboratory experimentation. Experiments have the advantage of controlled conditions, but limited inference potential regarding the behaviour of complex real-world systems (Wernberg et al., 2012). Inference can be more challenging for PPT components that feature limited experimental or modelling research. For instance, conclusions from the study of microclimate influences of agricultural practices on below-ground processes cannot be easily projected to future climate conditions. Predicted impacts of climate change on weeds and pest predators or parasitoids similarly rely on observed patterns under contrasting climate conditions, which are difficult to extrapolate.

Extrapolating empirically or experimentally derived predictions of climate change impacts on PPT components is mainly constrained by limited understanding of the mechanisms behind these impacts and their potential interactions. For instance, interactive effects of multiple aspects of climate change on soil conditions over long timescales have not been adequately explored in SSA. In the case of crop diseases, limited understanding stems from a lack of data on previous epidemics, as well as difficulties in downscaling climate projections to microclimates relevant for disease incidence. Predictions of weed pressure under future conditions would benefit from experiments on climate change impacts on crop-weed interactions. Basic information is similarly lacking on the mechanisms behind direct effects, especially of precipitation, and interactive climate effects on arthropod pests and their predation or parasitoid attack rates.

Using review outputs as input to holistic agroecosystem models enhances the robustness of predictions about the effectiveness of PPT under different scenarios of climate and land use change. Any attempt to predict agricultural impacts of climate change across SSA, and anticipate the climate resilience of ecological intensification measures such as PPT, has to deal with high spatiotemporal variability, involving case-specific scales and levels of organization. Dividing SSA into climate regions facilitates this task, despite persistent intra-regional differences. Predictions of climate change impacts on PPT could further benefit from similar categorizations that combine multiple explanatory and response variables. The complexity of the involved phenomena may require more systematic aggregation approaches, such as the use of archetype analysis (Oberlack et al., 2019; Alexandridis et al., 2022).

Qualitative mathematical models allow for holistic system representations (Levins, 1998), thus reducing the risk of unexpected consequences of agricultural practices (Sterman, 2010). Adopting locally-adapted combinations of some of the identified maize yield-enhancing strategies, which include higher PPT adoption, preservation of field edge density and diversifying agriculture to increase the share of crops other than cereals, shows robust potential to safeguard maize yields in view of overwhelmingly negative predicted impacts of climate change. Furthermore, model analysis suggests promising areas for future research, by indicating under-studied system interactions with a relatively strong influence on model predictions. Specifically, the mechanisms behind PPT adoption appear to be a fruitful avenue for both empirical research and explicit representation within integrated social-ecological models, potentially also investigating impacts that feed back into climate change.

Holistic models of agroecosystems can explore trade-offs of climate change adaptation measures, such as limiting the cultivation of cereal crops to sustain or increase maize yields. Cereal production in sub-Saharan Africa needs to triple by 2050 to meet the needs created by a growing population and higher standards of living (van Ittersum et al., 2016). So far, increases in cereal production have mainly been achieved through area expansion, and to some extent through higher yields (Giller et al., 2021). However, further increasing cultivated land is neither sustainable nor possible; thus enhancing the yield of present farmland dominated by smallholder farming is the preferable route ahead. Achieving this goal will require transformative change in terms of policy and economic incentives for farmers to invest in agriculture, as well as other options for employment and income (Giller, 2020).

Ecological intensification measures, such as PPT or agroforestry, show great potential for sustainable improvement of livelihoods (MacLaren et al., 2022) in regions with low access to inputs (Barrett and Bevis, 2015) and adverse agronomic conditions (Tittonell and Giller, 2013). As different measures are locally embedded in similar agroecosystems, our review can provide the knowledge basis for assessing climate resilience of ecological intensification in general, and guide relevant research across SSA. The example of PPT demonstrates the benefits of complementing this knowledge basis with holistic agroecosystem models. The resulting increase in PPT predictive reliability and policy effectiveness can be achieved outside eastern Africa with minor changes to the model. This work can be a blueprint for models predicting the resilience of other measures of ecological intensification across SSA and around the world.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

No data was used for the research described in the article.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2023.108511.

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