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Push-pull cropping and ecosystem functioning in sub-Saharan African smallholder systems

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Cover: Illustration of key thesis components: landscape structure, cropping systems, soils, natural enemies, and pest dynamics. (Illustration: Grace Mercy Amboka)

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Abstract

Ecological intensification aims to sustain crop yields by enhancing ecosystem functions, yet its performance across the diverse environments of sub-Saharan Africa is not well understood. Drawing on data from four East African countries, this thesis investigates how push-pull (PP) cropping system interacts with soil conditions and landscape structure to influence natural enemy communities, lepidopteran pest regulation and *Striga* weed suppression. Across countries, natural enemy communities were dominated by ants, and the overall abundance and diversity of natural enemies varied with landscape heterogeneity, cropping season and elevation. However, landscape effects were only present in Kenya. The push-pull system increased natural enemy abundance only in landscapes with high forest cover, while reduced crop cover, greater grass cover and configurational heterogeneity tended to reduce natural enemy abundance. Reduced crop cover, greater grass cover and configurational heterogeneity were also associated with lower pest damage, most likely due to mechanisms other than predation. PP cropping increased pest suppression in Uganda and Ethiopia, whereas no effects were detected in Kenya or Rwanda, although pest damage varied with seasons in Rwanda. At the soil level, PP fields with high *Desmodium* cover had elevated SOM, N, and P, but responses differed among countries. Field age produced divergent soil trajectories, with some older PP fields showing acidification and others accumulating SOM. *Striga* weed suppression demonstrated context dependency: PP was most effective in uniformly nutrient-poor or physically constrained soils, while in countries with limited soil variation or low seedbank pressure, soil interactions could not be detected. These findings highlight that PP is a context-dependent system whose effectiveness varies across ecological gradients. Aligning PP with local agroecological conditions is therefore essential for achieving consistent and sustainable outcomes in smallholder farming systems.

Keywords: biocontrol, ecological intensification, fall armyworm, landscape, natural enemies, pests, soil fertility, stemborer, *Striga*

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Abstract

Ekologisk intensifiering syftar till att upprätthålla goda skördenivåer genom att förbättra ekosystemens funktioner, men hur väl detta fungerar i de varierande miljöerna i Afrika söder om Sahara är fortfarande dåligt känt. Med utgångspunkt i data från fyra östafrikanska länder undersöker denna avhandling hur odlingssystemet push-pull (PP) samverkar med jordförhållanden och landskapsstruktur för att påverka samhällen av naturliga fiender, reglering av skadegörande fjärilslarver och ogräset *Striga*. Samhällena av naturliga fiender dominerades av myror, och artrikedomen varierade med landskapets heterogenitet, odlingssäsong och höjd över havet. Landskapseffekter påvisades dock endast i Kenya. Där ökade push-pull förekomsten av naturliga fiender endast i landskap med hög skogstäckning, medan minskad grödtäckning, större grästäckning och konfigurationsheterogenitet tenderade att minska förekomsten av naturliga fiender. Minskad grödtäckning, större grästäckning och konfigurationsheterogenitet var också förknippad med lägre skadegörarnivåer, mest troligt på grund av andra mekanismer än predation. PP-odling minskade skadegörarangreppen i Uganda och Etiopien, medan inga effekter påvisades i Kenya eller Rwanda, även om skadegörarangreppen varierade med årstiderna i Rwanda. PP-fält med hög *Desmodium*-täckning (en av samodlingsväxterna i PP) hade förhöjda nivåer av SOM, N och P, men responsen skiljde sig mellan länder. Vissa äldre PP-fält visade försurning medan andra ackumulerade SOM. Bekämpning av *Striga*-ogräs var kontextberoende: PP var mest effektiv på enhetligt näringsfattiga fält eller med begränsande markfysik, medan i länder med begränsad variation i markförhållanden eller med liten fröbank påvisades inget markberoende. Dessa resultat visar att PP är ett kontextberoende odlingssystem vars effektivitet varierar över ekologiska gradienter. Att anpassa PP efter lokala agroekologiska förhållanden är därför avgörande för att uppnå pålitliga och hållbara resultat i småbrukarsystem.

Keywords: biologisk bekämpning, ekologisk intensifiering, höstarmélarv (Spodoptera frugiperda), landskap, naturliga fiender, skadegörare, markbördighet, stamborrare, *Striga* (häxaört)

Dedication

To that little beautiful African girl `*Achalugo*´ who dared to dream...
This is for her...for every moment she was told it was too hard,
too far, too big for someone like her…
and still chose to rise, to learn, and to believe.

To my adorable nieces and nephews…
May you never stop dreaming, daring, and doing!

This is for the smallholder farmers who welcomed me into their fields,
whose resilience and wisdom shaped every chapter of this work.

Contents

List of publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I. Grace Mercy Amboka; Maryselah Nelima; Charles A.O. Midega; Daniel Munyao Mutyambai; Benjamin Feit; Mattias Jonsson (2025). Elevation and grassland cover shape natural enemy communities in Kenyan maize crops. International Journal of Tropical Insect Science. https://doi.org/10.1007/s42690-025-01670-w

II. GM. Amboka, M. Jonsson, C. Apel, D. Meinhof, A. Liepa, F. Chidawanyika, A. Detebo, F. Librán-Embid, EA. Martin, I. Steffan-Dewenter, M. Peters, J. Zhang, M. Thiel, M. Otim, J. Mugisha, GB. Bahta, F. Maina, A. Murage, B. Feit, AS. Dahlin. Soil property responses to push-pull cropping in East Africa (Submitted)

III. GM. Amboka, M. Jonsson, C. Apel, D. Meinhof, A. Liepa, F. Chidawanyika, A. Detebo, F. Librán-Embid, EA. Martin, I. Steffan-Dewenter, M. Peters, J. Zhang, M. Thiel, M. Otim, J. Mugisha, GB. Bahta, B. Feit, AS. Dahlin. Inconsistent effects of push-pull cropping and soil fertility on *Striga* weeds and pest damage across four East African countries (manuscript)

IV. GM. Amboka, B. Feit , C. Apel, D. Meinhof, A. Liepa, F. Chidawanyika, A. Detebo, F. Librán-Embid, EA. Martin, I. Steffan-Dewenter, M. Peters, J. Zhang, M. Thiel, M. Otim, J. Mugisha, GB. Bahta, AS. Dahlin, M. Jonsson. Context-dependent pest regulation in East African maize systems: landscape structure, seasonality and cross-country variation in Push-pull cropping performance. (manuscript)

The contribution of Grace Mercy Amboka to the papers included in this thesis were as follows:

I. Main author. Performed the data analysis and wrote the first version of the manuscript. Reviewed and edited the final version of the manuscript with support from the co-authors.

II. Main author. Planned and designed the experiment with the other co-authors. Collected data with contributions from the other coauthors, performed the data analysis, and wrote the first version of the manuscript. Reviewed and edited the final version of the manuscript with support from the co-authors.

III. Main author. Planned and designed the experiment with the other co-authors. Collected data with contributions from the other coauthors, performed the data analysis, and wrote the first version of the manuscript. Reviewed and edited the final version of the manuscript with support from the co-authors.

IV. Main author. Planned and designed the experiment with the other co-authors. Collected data with contributions from the other coauthors, performed the data analysis, and wrote the first version of the manuscript. Reviewed and edited the final version of the manuscript with support from the co-authors.

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Abbreviations

FAO	Food and Agriculture Organisation of the United Nations
FAOSTAT	Food and Agriculture Organisation of the United Nations Statistics
FAW	Fall armyworm
GDP	Global Domestic Product
IPM	Integrated pest management
PP	Push-pull technology
SNH	Semi-natural habitat
SSA	Sub-Saharan Africa

1. Introduction

1.1 From conventional to ecological intensification

For thousands of years, agriculture has been the cornerstone of human societies, influencing livelihoods, economies and landscapes globally. This traces back to the Neolithic period, characterised by stone tools and the domestication of plants and animals, and extends through the invention of plough-based cropping and irrigation systems in Mesopotamia (Ellis, 2000; Grigg, 1974). With the growing population and rising food demand, conventional agricultural intensification emerged as the key strategy, aiming to increase productivity per unit area of land (Bailey-Serres et al., 2019; Ellis, 2000).

The Green Revolution marked the height of conventional intensification, spurring economic growth and livelihood improvement for many farming households (Evenson & Gollin, 2003). It promoted large-scale monocultures of improved crop varieties of staples such as maize, wheat and rice, combined with synthetic mineral fertiliser, chemical pesticide inputs and irrigation (Pingali, 2012). While this strategy strengthened global food security, it came at a cost, posing serious challenges to sustainability. The expansion of large-scale monocultures and heavy dependence on synthetic external inputs led to biodiversity loss, soil degradation, water depletion and contamination, raising concerns about their long-term sustainability (Foley et al., 2011). In particular, the ecological cost of synthetic pesticides was epitomised by Rachel Carson's *Silent Spring* in 1962 (Paull, 2013). Carson raised concerns that the indiscriminate use of chemicals such as DDT (dichlorodiphenyltrichloroethane) was causing widespread damage to wildlife, resulting in "a spring without voices," where birdsongs and other signs of life were silenced by environmental contamination. *Silent Spring* sparked a global debate on the hidden costs of conventional intensification, marking a turning point in environmental consciousness worldwide.

The growing awareness of ecological damage arising from the Green Revolution prompted a renewed focus on more environmentally friendly approaches. The principles of agroecology, which focus on applying ecological principles and concepts in crop production, intensified in the late 20th century (Gallardo-López et al., 2018). Although the practices themselves are much older, rooted in the knowledge and traditions of different indigenous farming communities worldwide (Pimbert et al., 2021), the term agroecology only began to appear in the literature in the 1920s (Gliessman, 1990; Klages, 1928). Building on these ecological principles, the concept of Integrated Pest Management (IPM) gained prominence as a crucial alternative framework. IPM was first formally proposed in the late 1950s (Stern, 1959), and by the late 1970s, it had become a pivotal and widely adopted strategy for using ecological approaches to manage invertebrate pests, weeds and pathogens (R. F. Smith et al., 1976). This move signified a shift from calendar-based pesticide application to a more ecologically informed pest control approach.

The early 21st century witnessed the emergence of new concepts such as sustainable intensification (Pretty et al., 2011; Rockström et al., 2017) and ecological intensification (Bommarco et al., 2013; Tittonell, 2014), in response to the ecological costs of conventional intensification. Both approaches aimed to enhance crop productivity while reducing negative externalities, put emphasis on ecological functions, and integration of local knowledge with scientific innovations. Together, they reflect a paradigm shift in how intensification is viewed in modern agriculture.

Ecological intensification is gaining momentum as the world strives to achieve global food security without compromising ecosystem health, in line with the Sustainable Development Goals (Mishenin et al., 2021; Shahmohamadloo et al., 2021). This approach harnesses ecosystem functions that directly support agricultural productivity, such as pollination, natural pest control, and soil fertility (Krupek et al., 2022). Unlike the conventional approaches, ecological intensification positions biodiversity not as a constraint but as a critical asset to productive agroecosystems (Bommarco et al., 2013). Its effective application, however, goes beyond the local field scale. At the landscape scale, increasing habitat availability and heterogeneity could enhance the abundance of beneficial organisms, such as natural enemies, pollinators, and the ecological services they provide (Clarkson et al., 2022; Marja et al., 2022). This could reduce on-farm pesticide use, enhancing in situ biodiversity above and below ground, and promoting crop productivity over time, thus a win-win strategy.

1.2 Biodiversity and ecosystem functions in agroecosystems

At the core of ecological intensification is biodiversity, specifically in reference to species richness, evenness and functional traits. Biodiversity provides multiple ecosystem functions, such as weed and pest control, pollination, and nutrient cycling, that directly or indirectly promote sustainable agricultural productivity (Altieri & Nicholls, 2018; Jonsson et al., 2017). Natural enemies of crop pests, including arthropod predators, parasitoids, pathogens (i.e. bacteria and fungi), amphibians, and birds, help to suppress pest populations, thereby reducing the need for chemical pesticides (Avalos et al., 2020). Pollinators such as bees, flies, as well as bats and birds, enhance the reproductive success of insect and animal-pollinated crops, contributing to yield (Mphethe et al., 2025; Requier et al., 2023).

Similarly, soil fauna, such as earthworms, termites, microorganisms (bacteria, archaea, fungi), are vital in nutrient cycling, decomposition of organic matter, and improving soil structure, which enhances soil aeration and water movement (Edwards & Arancon, 2022; Traoré et al., 2022). Vegetation biodiversity at both the local field and landscape scale also contributes substantially to ecosystem functions (Beillouin et al., 2021). Agricultural practices such as mixed cropping, agroforestry and crop rotation increase crop heterogeneity, which can help with weed suppression, reduce soil erosion, and promote steady yield (Kumari et al., 2024; Scott-Brown et al., 2025). At the landscape level, natural and seminatural habitats such as hedgerows, grass meadows, and trees act as sources for these beneficial organisms, enabling spillover into farmlands, as well as providing corridors for their movement (Petit & Landis, 2023). Therefore, at both local and landscape scales, biodiversity promotes ecosystem functioning by reducing reliance on chemical inputs, increasing agroecosystems' resilience to environmental perturbations, and enhancing overall sustainability. Among these processes, natural enemies play a critical role in pest regulation. Characterising the structure, composition, and environmental drivers of natural enemy communities is essential for sustaining effective biological control in agroecosystems.

1.3 Natural enemy community structure and ecological importance

The community structure, encompassing diversity, abundance, and functional composition of natural enemies (i.e. ants, parasitoid wasps, spiders, and predatory beetles), is central in regulating pest populations in agroecosystems (Jonsson et al., 2017; Ratto et al., 2022). Their presence in the agroecological systems can reduce crop pests by up to 90%, highlighting both ecological and economic benefits (Martin et al., 2013). Diverse communities of natural enemies enhance biological control through complementary foraging strategies and temporal stability in pest suppression (Laubmeier et al., 2023; Mesmin et al., 2022). Moreover, structurally complex natural enemy assemblages can strengthen the agroecosystems´ resilience to environmental disturbances and management changes by increasing their capacity to regulate pests (Rusch et al., 2015). However, these communities can be influenced by both local factors, such as cropping systems, and landscape-scale factors, including habitat composition, configuration, and elevation (Debinski, 2023; Karp et al., 2018). Notably, elevation represents a particularly important environmental gradient that shapes biodiversity patterns, physiological adaptations and species interactions (Kunene et al., 2022; Paudel et al., 2021). Assessing how multi-scale drivers affect natural enemy community structure is essential for promoting sustainable, ecologically based pest management strategies.

1.4 Elevation gradient and natural enemies

Elevation is an important environmental gradient influencing biodiversity and is increasingly important as species shift upward in response to climate change (Jacobsen, 2020; McCain & Garfinkel, 2021). Elevation changes are associated with variations in temperature, oxygen availability, humidity, and vegetation structure, which in turn influence the organismal physiology (Khaliq et al., 2023), diversity and spatial distribution (M. A. Smith et al., 2023), habitat selection (Uhey et al., 2022) and species interactions (Sam et al., 2023; Wang et al., 2024). In agricultural landscapes, these climatic and vegetation shifts have significant implications for natural enemy communities that provide pest control services (Herrera-Alsina et al., 2025; Uhey et al., 2022).

Studies across elevational gradients document clear shifts in the diversity and abundance of arthropod natural enemies, such as ants (Kunene et al., 2022; Munyai & Foord, 2012), spiders (Måsviken et al., 2023), and parasitoid wasps (Randall, 2025). Lower warmer elevations tend to support greater species richness and activity, while higher elevations often harbour more endemic or cold-tolerant taxa (Herrera-Alsina et al., 2025; Hodkinson, 2005). These compositional changes reflect physiological constraints, such as developmental time and reproductive capacity (Helms, 2023), and resource availability (Rödder et al., 2021). Such shifts in community composition create distinct ecological niches; for example, predatory ants may dominate at low elevations, while specific spider taxa may become more prominent at higher elevations, depending on climatic and habitat conditions (Kunene et al., 2022; Nogueira et al., 2021). Understanding the structural shifts of natural enemy communities along the elevation gradient is crucial for predicting spatial variation in pest regulation and designing adaptive, climate-resilient pest management strategies.

1.5 Smallholder farming in sub-Saharan Africa

Agriculture contributes approximately 20% of sub-Saharan Africa's GDP, and employs most of its population. However, food insecurity remains a persistent problem since an estimated 90% of the production comes from smallholder, low-input, rainfed systems (Boda et al., 2024; Khan et al., 2014). These farms, often typically under two hectares, are heavily reliant on ecosystem functions such as pollination, pest control and soil fertility (Drinkwater & Snapp, 2022; Morizet-Davis et al., 2023), due to their low input nature. To manage risks and enhance crop productivity, smallholder farmers often practice mixed cropping, which enhances ecosystem functioning (Rapsomanikis, 2015). However, the sustainability of these systems is increasingly threatened by rapid population growth (Beegle et al., 2016), land-use change (Bununu et al., 2023; Molotoks et al., 2021), and climate-related pressures (Alexandridis et al., 2023). Developing sustainable smallholder farms remains a pressing goal as many of the communities relying on these systems continue to face undernutrition, food insecurity, and poverty (Khan et al., 2014).

1.6 Importance of maize and sorghum in sub-Saharan Africa

Cereal production in sub-Saharan Africa is largely dominated by maize (*Zea mays* [L.]), accounting for about 40% of the total cereal output in Africa (Erenstein et al., 2022; FAO, 2025a). Maize is the most widely cultivated staple cereal crop, supporting the food security and livelihood of nearly a quarter of a billion people (Erenstein et al., 2022). Between 2020 and 2025, maize production in SSA has marginally declined from 87.5 to about 84 million tons (FAO, 2025a). Despite maize's vulnerability to crop failure, i.e. severely reduced or negligible yield due to its specific biological needs during growth, it remains central to SSA smallholder farmers' food systems (Asfaw et al., 2024; Ragasa et al., 2025).

Sorghum (*Sorghum bicolor* [L.]), on the other hand, while less dominant when compared to maize, plays an increasingly important role in enhancing food security across SSA, particularly in arid and semi-arid regions (Hadebe et al., 2017; Orr et al., 2016). Unlike maize, sorghum is well-adapted to heat and drought, among other multiple biotic and abiotic stresses, making it more resilient to climate change (Huang, 2018; Tari et al., 2013). These traits make sorghum a strategic crop for vulnerable farming communities in SSA. Approximately 65% of sorghum is utilised for food consumption, while the remaining is used for other non-food purposes, such as animal feed and fuel (Orr et al., 2016). Africa remains the top producer of sorghum at about 28.5 million tons in 2024, led by Nigeria (7 million tons), Sudan (5.3 million tons), and Ethiopia (4.1 million tons) (Charyulu et al., 2024; IGC Report, 2024). Ethiopia exemplifies sorghum's potential in the region as it is currently East Africa's top producer. Research shows that while the total area planted to sorghum may decrease, overall output can still increase due to gains in productivity (Charyulu et al., 2024). For this reason, sorghum's climate resilience could offer an essential buffer against food insecurity and environmental shocks (Tari et al., 2013).

1.7 Constraints to cereal production in sub-Saharan Africa

Cereal production in sub-Saharan Africa is severely limited by a combination of both abiotic and biotic factors. These factors are often interconnected and are exacerbated by climate change, poor agricultural practices and socioeconomic challenges.

1.7.1 Biotic constraints

Insect pests

Among the major biotic stresses are insect pests such as maize stalk stem borers, *Busseola fusca* (Noctuidae), sorghum stem borers *Chilo partellus* Swinh (Pyralidae) (Khan et al., 2006) and fall armyworm *Spodoptera frugiperda* (Day et al., 2017). Stem borers and FAW pose a serious threat, with estimated yield losses ranging from 0 to 100 %, and are therefore considered among the worst biotic constraints in the region (De Groote, 2002; De Groote et al., 2020). The corn leaf aphid (*Rhopalosiphum maidis*) and greenbug (*Schizaphis graminum*) are sap-feeding pests on both crops, which can lead to stunted growth, leaf discolouration, and reduced yield (Gonçalves et al., 2020; Royer et al., 2015). The sorghum midge (*Stenodiplosis sorghicola*) is a key pest of sorghum, whose larvae feed on developing sorghum seeds in the flower spikelets, resulting in significant yield losses (Okosun et al., 2021). Termites also cause economic losses to many crops globally due to their polyphagous nature, causing damage to the roots and lower stems (Otieno, 2018; Rana et al., 2021). Other below-ground pests include soil pests, such as rootworms, wireworms, cutworms and white grubs, which attack roots and seedlings, causing stunted growth and wilting, potentially killing the plant (Okosun et al., 2021).

Birds

Birds are also a major pest of maize and sorghum in the region (De Mey et al., 2012; Mey & Demont, 2013). The Red-billed Quelea (*Quelea quelea*) is one of the most damaging avian pests in Africa, with its preferred diets consisting of sorghum and millet (DLCO-EA, 2022; FAO, 2025b). Other significant bird pests include village weavers (*Ploceus cucullatus*), doves and pigeons, especially species like the African mourning dove (*Streptopelia decipiens*), Rose-ringed Parakeet (*Psittacula krameri*), Red Bishop (*Euplectes orix*) and crows (Mey & Demont, 2013; Mofokeng & Shargie, 2016). These birds cause damage by forming massive flocks in the fields, devouring either the planted seeds or the seeds on the stalks (Raheem et al., 2021). Moreover, they are highly adaptable, and their migratory nature makes it difficult for farmers to predict and prevent attacks. As much as traditional control methods, such as human "bird scarers," are being used, they are labour-intensive and often ineffective against massive bird flocks (Hiron et al., 2014).

Weeds

Weeds likewise pose a significant constraint to cereal production in sub-Saharan Africa, with some species causing substantial yield losses (Tittonell & Giller, 2013). The most problematic weed is *Striga* spp., also known as the "witchweed", a parasitic plant known to attach to cereal roots like maize and sorghum, hindering their growth (Orr et al., 2016). *Striga hermonthica* and *Striga asiatica* are the key species in the region (Reynolds et al., 2015). Under severe infestation, *Striga* alone can cause yield losses of up to 100% in maize, depending on crop variety, growth stage and environmental conditions (Hayelom, 2014; Khan et al., 2002). In some cases, smallholder farmers have been forced to abandon severely infested fields, reducing available land for cultivation (Atera & Itoh, 2011). Other non-parasitic weeds include: Johnsongrass (*Sorghum halepense*), witchgrass (*Panicum capillare*), spear grass (*Imperata cylindrica*), crabgrass (*Digitaria sanguinalis*), goosegrass (*Eleusine indica*), pigweed (*Amaranthus spp.*), lambsquarters (*Chenopodium album*), purple nutsedge (*Cyperus rotundus*), and common purslane (*Portulaca oleracea*), which are major threats during the first few weeks of the crop's growth (Gharde et al., 2018; Silberg et al., 2019). The competition from these weeds can lead to significant yield losses if not properly managed.

Diseases (fungi, bacteria and viruses)

In addition to insect pests and weeds, diseases caused by fungi, bacteria and viruses have constrained the production of maize and sorghum. For example, fungal diseases such as the northern corn leaf blight (*Setosphaeria turcica*), cause lesions on the leaves, reducing the plant's photosynthetic capacity (Li et al., 2024), sorghum downy mildew (*Peronosclerospora sorghi*) and sooty stripe (*Ramulispora sorghi*), cause leaf discolouration and stunting growth (Jeger et al., 1998; Perumal et al., 2008), and charcoal rot (*Macrophomina phaseolina*), which infects the stalk, cause it to rot, and the plants to lodge and die prematurely (Rajput et al., 2023). Bacterial diseases include bacterial stalk rot (*Erwinia chrysanthemi*), which causes the stalks to rot and collapse (Ullah et al., 2025). Viral diseases include maize streak virus (MSV) and maize dwarf mosaic virus (MDMV), which are transmitted by insects and cause leaf streaking, mottling, and severe stunting (Emeraghi et al., 2021; Massawe et al., 2018). The MDMV is also linked to maize lethal necrosis (MLN), which has caused a widespread cereal failure in SSA, leading to food insecurity (Mahuku et al., 2015).

1.7.2 Abiotic constraints

Degraded soils

Low soil fertility and water stress are among the most significant abiotic constraints to maize and sorghum production in the region. African soils are old, strongly weathered and inherently less fertile (Jones et al., 2013; Managa & Nkobole, 2016). This is reflected in continent-wide assessments such as the Soil Atlas of Africa, which document the widespread occurrence of highly leached nutrient-poor soil types like Ferralsols and Acrisols across vast areas of the continent (Jones et al., 2013),

The poor soil fertility is a multifaceted issue encompassing both soil chemistry and physics. The most significant soil chemical challenge is the lack of essential plant nutrients. Key among these is the depletion of critical nutrients such as nitrogen (N), phosphorus (P), and potassium (K). This depletion is primarily driven by continuous cultivation without sufficient nutrient replenishment, a process commonly referred to as crop nutrient mining (Ikazaki et al., 2024; Maes et al., 2023). Furthermore, the depletion of these nutrients is severely exacerbated by low soil organic matter (SOM) content. First, SOM plays a crucial role in soil chemistry by providing a reservoir of low-release nutrients, particularly N and P, through mineralisation (Laub et al., 2025). Secondly, SOM improves cation exchange capacity (CEC), the soil's ability to hold onto positively charged essential nutrients (like K^+, Ca^{2+}, Mg^{2+}), thereby preventing their leaching (Ayongwa, 2011). Lastly, SOM helps buffer soil pH against extreme acidity or alkalinity (Vanlauwe & Giller, 2006). The limited use of organic inputs (i.e. manure and crop residues) and inorganic inputs (synthetic fertiliser) also exacerbates soil infertility (Maes et al., 2023). This low or complete lack of fertiliser and soil amendments means that crop productivity is particularly dependent on often severely depleted soil fertility, leading to continuous cycles of low yield and continued nutrient mining (Laub et al., 2025; Zou et al., 2022).

The physical properties of soils are also a limiting factor in the region. Decades of desertification and soil erosion caused by deforestation and poor land management have stripped away nutrient-rich topsoil, removing essential plant nutrients and soil organic carbon (SOC). The loss of topsoil and SOC leads to the breakdown of soil aggregates and poor soil structure, resulting in compacted soils, which simultaneously hinders air exchange, root growth, and microbial activities. These degraded soils have low water infiltration, retention and drainage capacity, meaning rainwater is either lost as runoff or percolates too rapidly for effective root uptake. As a result, plants may experience alternating periods of drought stress and waterlogging, both of which reduce nutrient availability and impair root function. Such conditions not only constrain crop growth but also create favourable conditions for parasitic weeds like *Striga*, which thrives in low nitrogen and low carbon soils under water stress. The combined loss of soil carbon and poor water regulation thus perpetuates a cycle of degradation and vulnerability of cereal crops in the region (Ikazaki et al., 2024). Moreover, water stress alone can cause substantial yield losses, with maize being most vulnerable from pre-tassel emergence through the early grain filling stage, a period during which drought can reduce grain yield by up to 90% under extreme stress (NeSmith & Ritchie, 1992; Omokpariola et al., 2025).

Climate change

Climate change also serves as an abiotic constraint in cereal production in SSA by altering the physical conditions of the agricultural environment, making them increasingly unsuitable for crop growth. As highlighted in the introductory statement of this section, climate change intensifies the constraints mentioned earlier through thermal stress, drought and flooding (Kotir, 2011; Omokpariola et al., 2025). The rising global temperatures lead to higher frequency and intensity of heat waves, and generally higher average temperatures across the growing season. This increased heat can impact the plant physiology by accelerating growth and shortening the life cycle, particularly during the crucial flowering and grain filling stages (Tran et al., 2025). Such compression of the growth period reduces photosynthetic efficiency and pollination success, leading to smaller grain size and overall lower yields. Maize is highly susceptible to heat stress, with studies showing substantial yield decline associated with even the slightest increase in mean temperature (Adhikari et al., 2015; Liu et al., 2025).

Climate change also disrupts predictable rainfall patterns, leading to both drought and floods. Drought is one of the most severe abiotic stresses affecting SSA's predominantly rainfed agriculture. The reduced and erratic rainfall causes prolonged dry spells and soil moisture deficit during critical growing stages (Alimagham et al., 2024). Water scarcity limits nutrient absorption and reduces turgor pressure, resulting in stunted growth, poor grain filling and permanent wilting. Furthermore, drought also exacerbates existing soil acidity and heavy metal toxicity by concentrating solutes, further inhibiting nutrient uptake and plant development. Studies estimate that drought can cause yield declines of up to 30% in arid and semiarid zones of SSA (Omokpariola et al., 2025; Onyeaka et al., 2024). Conversely, climate change increases the frequency and intensity of rainfall, which leads to flooding. Heavy downpour accelerates soil erosion, washing away fertile topsoil and essential nutrients, leaving behind infertile soils (Kotir, 2011), while waterlogging leads to soil anoxia that deprives roots of oxygen, root damage, increases seed mortality, and nutrient leaching (Bedasa et al., 2025; Tran et al., 2025). Collectively, these processes reduce soil fertility and crop productivity, underscoring the urgent need for adaptive strategies to buffer smallholder farming systems against climate variability.

1.7.3 Socio-economic constraints

Beyond abiotic and biotic limitations, socioeconomic factors also significantly limit maize and sorghum productivity in SSA. Smallholder farmers often face limited access to essential agricultural inputs, credit and extension services (Ferris et al., 2014; Gómez y Paloma, 2020). Additionally, poor infrastructure, particularly poor road networks and storage facilities, leads to substantial post-harvest loss (Nyambo et al., 2022), while weak market systems create unstable prices, discouraging farmers from adopting new farming technologies (Chianu et al., 2008). When combined with biotic and abiotic stressors, these socioeconomic issues present a major barrier to improving cereal production and require broader institutional and policy-level interventions.

1.8 Strategies to improve crop productivity in sub-Saharan Africa

Improving maize and sorghum yield in SSA requires a multifaceted approach that combines both elements of conventional and ecological intensification to address agronomic, environmental, and socioeconomic constraints. Conventional intensification includes, for example, the use of high-yielding, pest-resistant and drought-tolerant seed varieties, which can significantly increase yields (Tandzi & Mutengwa, 2020). To achieve this, plant breeding efforts must be tailored to specific agroecological zones to maximise their potential. In parallel, ecological intensification focusing on utilising ecosystem functions to boost productivity should be encouraged. A critical part of this is utilising crop diversification strategies, such as crop rotation and intercropping (Bommarco et al., 2013; Jaworski et al., 2023). These strategies play a vital role in sustaining soil fertility and boosting productivity by leveraging biodiversity (Dainese et al., 2019; Kebede, 2021).

Integrated pest and weed management (IPM) strategies further contribute to sustainable production. The use of biological control agents, such as predatory arthropods and parasitoids, can greatly reduce losses from pests such as FAW and stemborers (Hassanali et al., 2008). One example of an IPM and weed management system is the push-pull technology (Pickett et al., 2014), which will be discussed in detail in the following section. Beyond pest and weed management, improving on-farm practices, i.e. mixed cropping, mulching, infrastructure and market access can reduce post-harvest losses and increase profitability. Moreover, investing in extension services, farmer training, and digital tools remains essential for disseminating agronomic knowledge (Hazell & Rahman, 2014). Collectively, these diverse interventions enhance the sustainability and resilience of cereal production and improve food security across sub-Saharan Africa.

1.8.1 The push-pull technology

Push-pull (PP) is a promising ecological intensification strategy developed for smallholder farmers in Africa, designed to address insect pests, parasitic weeds and limited soil fertility that constrain cereal yields (Khan et al., 2006; Pickett et al., 2014). Originally developed to manage the stemborer moths and parasitic *Striga* weeds, it has since proven effective against the invasive fall armyworms (FAW), which have plagued maize production across the region since 2016 (Cheruiyot et al., 2021; Midega et al., 2018). The PP system intercrops maize or sorghum with *Desmodium* spp., a 'push' intercrop, and the field is surrounded with *Brachiaria* or *Pennisetum* spp. grasses as a “pull” border crop (Pickett et al., 2014). The system has also been adapted and intensified to include high-value vegetable crops within the cereal component (Chidawanyika et al., 2025). *Desmodium* suppresses pests through multiple mechanisms: releasing semiochemicals that influence FAW and stemborer behaviour and attract natural enemies, and physically trapping and killing larvae, demonstrating that PP effectiveness arises from interacting chemical and mechanical pathways (Da Silva et al., 2022; Erdei et al., 2024; Odermatt et al., 2025).

Beyond pest control, *Desmodium* roots exude allelopathic compounds that induce suicidal germination in *Striga* (Khan et al., 2002; Kountche et al., 2019). As a legume, it also enhances soil fertility by fixing atmospheric nitrogen and contributing organic matter that increases SOC, P, and N (Kuyah et al., 2023; Meena et al., 2018). *Desmodium's* dense foliage improves moisture retention and reduces erosion, while both the intercrop and border grasses serve as valuable livestock fodder (Hassanali et al., 2008). Across diverse agroecological zones, PP has consistently shown improved pest and weed management, soil fertility and an increase in crop yield (Luttermoser et al., 2023; Midega et al., 2018; Ndayisaba et al., 2021).

1.8.2 Drivers of variability in push-pull performance

Despite the demonstrated success of the PP technology across many sites in East Africa, yields under the system remain highly variable (Khan et al., 2014). A large-scale study spanning three East African countries, for instance, found that maize yields in PP fields ranged widely from approximately 2 to 6 tonnes per hectare (t/ha) (Midega et al., 2018). This variability suggests that the performance of PP is shaped not only by its capacity to suppress pests and weeds but also by broader environmental and management factors. Challenges such as drought, nutrient deficiencies, and competition from non-parasitic weeds often constrain yields in ways that PP alone cannot fully address. Understanding the contextual factors shaping PP performance is therefore critical, particularly in smallholder farming systems where resource limitations and environmental heterogeneity are common. This section highlights two key drivers of PP variability, namely soil fertility and landscape structure and how they interact with the system.

1.8.3 Soil fertility as a driver of push-pull effectiveness

Soil fertility and crop vulnerability

Low soil fertility is a major limiting factor for crop production in smallholder systems and fundamentally shapes plant vulnerability to pests and weeds.

Adequate nutrient availability supports plant growth, biomass production and the development of structural and biochemical defences (Chrysargyris et al., 2017; Roosta, 2024). When soils are deficient in essential nutrients such as N, P or K, plant growth is stunted, physiological resilience is reduced, and their natural defences are weakened (Tripathi et al., 2022). As a result, plants become more susceptible to insect pests, e.g. FAW and parasitic weeds, e.g. *Striga* and are less likely to recover from damage. This leads to significant yield losses, and these dynamics highlight an important indirect link between soil fertility, pest and weed pressure, and the potential success of the PP system.

Soil fertility as a determinant of PP system performance

The performance of the PP system is closely tied to the underlying soil fertility conditions. The intercrop *Desmodium*, for instance, requires adequate plant nutrients to grow vigorously, suppress weeds, and perform its ecological functions, including the production of important secondary metabolites (Erdei et al., 2024; Venkatasai et al., 2025). In fertile soils, *Desmodium* can perform its functions more effectively, strengthening pest and *Striga* suppression and improving crop growth (Herms & Mattson, 1992; Saleem et al., 2023).

The mechanisms underlying PP effectiveness may also differ across fertility gradients. In low soil fertility conditions, yield gains are likely driven primarily by biological N fixation and weed suppression, alleviating nutrient limitation and competition, whereas in moderately fertile soils, improved pest regulation through enhanced ecological functioning may play a larger role. This functional flexibility helps explain why PP can perform well across a range of soil types, while also contributing to the observed variability in outcomes.

Push-pull contribution to soil fertility: benefits and constraints

A core feature of PP is its capacity to enhance soil fertility over time. The primary benefit arises from the intercrop *Desmodium*, a legume that fixes atmospheric nitrogen into the soil, contributes root biomass and leaf litter, and improves soil organic matter content, leading to enhanced soil structure and water retention (Nair et al., 2021; Ndayisaba et al., 2021). However, the soil-improving benefits of the system are not immediate. Soil fertility recovery is a gradual process that may take several seasons before substantial improvements become noticeable. This slow trajectory may not align with the immediate needs of smallholder farmers facing acute food insecurity. Moreover, the process of N fixation itself requires other essential nutrients, particularly P, because it is energy demanding and depends on P-rich adenosine triphosphate (ATP) and adequate P availability for effective nodulation (Zhong et al., 2023). In soils that are already critically depleted of P or other micronutrients, the system's ability to fix N and improve soil health may be severely limited without the addition of external amendments.

Trade-offs and competition under low-fertility conditions

Although *Desmodium* contributes to long-term soil restoration, it can also compete with the main crop for water and nutrients, especially in low-fertility or drought-prone environments (Suárez et al., 2022; Vazeux-Blumental et al., 2025). To mitigate these risks, *Desmodium* biomass management is recommended, as competition is always seen when the *Desmodium* grow beyond its designated rows (Pickett et al., 2014). These synergistic and antagonistic interactions between soil fertility and the PP system need to be considered. The successful upscaling of the PP system thus requires adaptive management strategies that actively mitigate resource competition and use supplementary inputs to bridge the gap between the immediate needs of food-insecure farmers and the system's long-term soil health benefits.

1.8.4 Landscape structure and pest regulation in push-pull systems

Agricultural landscapes consist of complex mosaics of crop fields, interspersed with seminatural habitats (SNH) such as grassland and forest (Macfadyen et al., 2021; Macfadyen & Muller, 2013). At broader spatial scales, two components of landscape structure, composition (types and proportions of different land cover) and configuration (their spatial arrangement), shape ecological processes by determining resource availability and the movement of organisms, including pests and natural enemies (Marja et al., 2022). Because many insects disperse over large distances, landscape structure can strongly influence local pest regulation.

Although SNH provides natural enemies with essential resources, such as food and shelter, thereby enhancing biological control (Zhang et al., 2021), they may also benefit pest species, leading to variable outcomes across regions and farming systems (Daelemans et al., 2023; González et al., 2022). As a result, the net effect of landscape complexity on pest suppression is not universally positive. Instead, outcomes could depend on pest traits, crop type, and on-farm management (Dainese et al., 2019; Karp et al., 2018). This variability underscores the importance of evaluating PP within its landscape context.

Landscape composition

Agricultural landscapes with a high proportion of SNH generally support greater abundance and richness of natural enemies due to increased availability of alternative prey and nesting sites (Dassou et al., 2023; Hohlenwerger et al., 2022). By sustaining these beneficial organisms, such habitats enhance natural pest regulation in adjacent crop fields (Marja et al., 2022; Tortosa et al., 2023). As mentioned earlier, greater SNH cover does not guarantee improved pest suppression (Dainese et al., 2019; Karp et al., 2018). Thus, the net outcome of landscape composition depends on how it interacts with farm-level management, including PP.

In contrast, simplified landscapes dominated by monocultures often lose key SNH and field margins, reducing habitat for natural enemies and increasing susceptibility to pest outbreaks, which may lead to greater pesticide use (Zhao et al., 2015). A growing body of work shows that low landscape complexity can weaken biological control effectiveness (Carbonne et al., 2022; Feit et al., 2021), underscoring the importance of maintaining or restoring habitat diversity at the landscape scale to support resilient pest control services.

Landscape Configuration

Beyond composition, landscape configuration also plays a critical role in shaping pest regulation dynamics (Duarte et al., 2018; Haan et al., 2020). Features such as field size and shape, edge density, distance between habitats and connectivity influence the movement and interaction of pests and their natural enemies. In smallholder farming systems characterised by fine-grained heterogeneity, natural enemies' spillover into fields can be enhanced (Haan et al., 2020).

One key configuration metric is edge density, which describes the degree of landscape fragmentation and complexity (Macfadyen & Muller, 2013). Higher edge density increases the connectivity between crops and adjacent SNH, promoting the movement of natural enemies and improving pest suppression (Grande et al., 2020; Rand et al., 2006). Conversely, landscapes with low edge density, typical of large contiguous monocultures, reduce connectivity while enabling rapid pest buildup (Furlong & Zalucki, 2010). These patterns underscore the value of integrating configuration-based landscape planning with farm-level practices to design functionally connected, ecologically resilient agroecosystems.

Landscape context and the effectiveness of PP

The effectiveness of local interventions such as PP depends on how they interact with surrounding landscape features, particularly in smallholder systems characterised by heterogeneous land use. A crucial concept illustrating this interaction is the *Intermediate Landscape Complexity Hypothesis*, which proposes that habitat manipulations such as flower strips or PP systems tend to be most effective in landscapes of intermediate complexity, where they supplement but do not replace existing ecological processes (Tscharntke et al., 2012). In highly simplified landscapes, local interventions may be insufficient to restore ecological balance, whereas in very complex landscapes, additional interventions may provide limited gains because natural regulation is already high, or because SNH also supports pest populations.

Empirical evidence globally supports this context dependency. Studies from Africa show that landscape complexity can enhance pest suppression by attracting beneficial insects (Brévault et al., 2025; Macfadyen et al., 2021). Research from other regions supports this broader pattern; for example, Jonsson *et al*. (2015) found that flower strips were more effective at attracting beneficial insects in a more complex landscape. However, while these studies point to a generally positive relationship, other studies have reported neutral or negative effects of landscape complexity (Dainese et al., 2019; Karp et al., 2018). Assessing these multiscale interactions is essential for designing resilient strategies that enhance natural pest regulation while maximising PP performance.

2. Aims

This thesis investigates how local (soil fertility and cropping systems) and landscape-scale (composition, configuration, and elevation) factors shape natural enemy communities and assesses how these multiscale drivers influence the performance of push-pull cropping systems in suppressing lepidopteran pest damage and *Striga* weeds. The specific objectives of the thesis were to :

- Assess how elevation and grassland cover shape natural enemy communities in Kenyan maize crops (**Paper I**)
- Examine the soil property responses to push-pull cropping in East Africa (**Paper II**)
- Determine the effect of push-pull cropping and soil physical and chemical properties on *Striga* seed density and pest damage (**Paper III**)
- Evaluate how push-pull cropping and landscape structure influence the natural enemy community and pest control (**Paper IV**)

3. Materials and Methods

3.1 Overview of datasets

This thesis draws on data from two complementary research projects investigating arthropod biodiversity, landscape factors, soil fertility and the regulation of FAW, stemborer pests and *Striga* seed density in East African smallholder agroecosystems. Data for **Paper I** were collected under the Resilient Push-Pull project in Kenya, focusing on how elevation and grassland cover shape natural enemy communities in maize cropping systems.

Data for **Papers II-IV** were obtained from a large-scale regional study under the Horizon 2020 UPSCALE project, in collaboration with national partners across five East African countries: Ethiopia, Kenya, Rwanda, Uganda, and Tanzania. In this study, I examined the effects of soil fertility, cropping systems and landscape structures on the performance of push-pull technology across four countries: Ethiopia, Kenya, Rwanda, and Uganda. Data from Tanzania could not be analysed due to practical challenges.

3.2 Study area and field selection

The data for **Paper I** were collected in western Kenya between September 2019 and July 2020. Twenty-four smallholder maize fields located across six counties (Bungoma, Homabay, Kisumu, Trans-Nzoia, Uasin-Gishu, and Vihiga (Figure 1a) were selected along an elevational gradient of 1050-2000 meters above sea level (masl).

In **Papers II-IV**, data were collected between March 2022 and March 2023 across four East African countries: Ethiopia's eastern Amhara region (Dawachefa and Kalu districts), Kenya's western region (Homabay, Kisumu, Siaya, Vihiga counties), Rwanda's north-eastern region (Gatsibo district), and Uganda's south-eastern region (Kamuli, Kisozi, Namwendwa, Namutumba, Namasagali district) (Figure 1b). A total of 128 fields were selected, with 32 fields per country. The general study regions within each country were determined based on soil maps (Jones et al., 2013). Subsequently, the specific fields were preselected using existing GIS-based landcover maps and verified through ground truthing to ensure suitability.

The experimental design followed a paired approach, where each pair was located within 10 to 50 meters of each other, and, where possible, on the same farm, to reduce soil and management variability (Tittonell et al., 2005). In each country, 16 fields were under push-pull (PP) cropping, and 16 were non-push-pull (NPP) control fields. In the PP fields, maize was intercropped with *Desmodium* in Kenya, Rwanda and Uganda, while in Ethiopia, sorghum was intercropped with *Desmodium*. The NPP control fields primarily consisted of sole-cropped maize, though a few were intercropped with other crops, depicting the diverse farming practices in the region. In Kenya, two fields included common beans and one with groundnuts (3 fields); in Rwanda, two included bananas, and one each with cassava, beans, and potatoes (5 fields); and in Uganda, three had common beans, three with cassava, and one each with soybeans and sweet potatoes (8 fields). In Ethiopia, all NPP were solely planted with sorghum. The sizes of the fields varied between 100m^2 and 1500m^2, with Rwanda having smaller fields due to its hilly terrain.

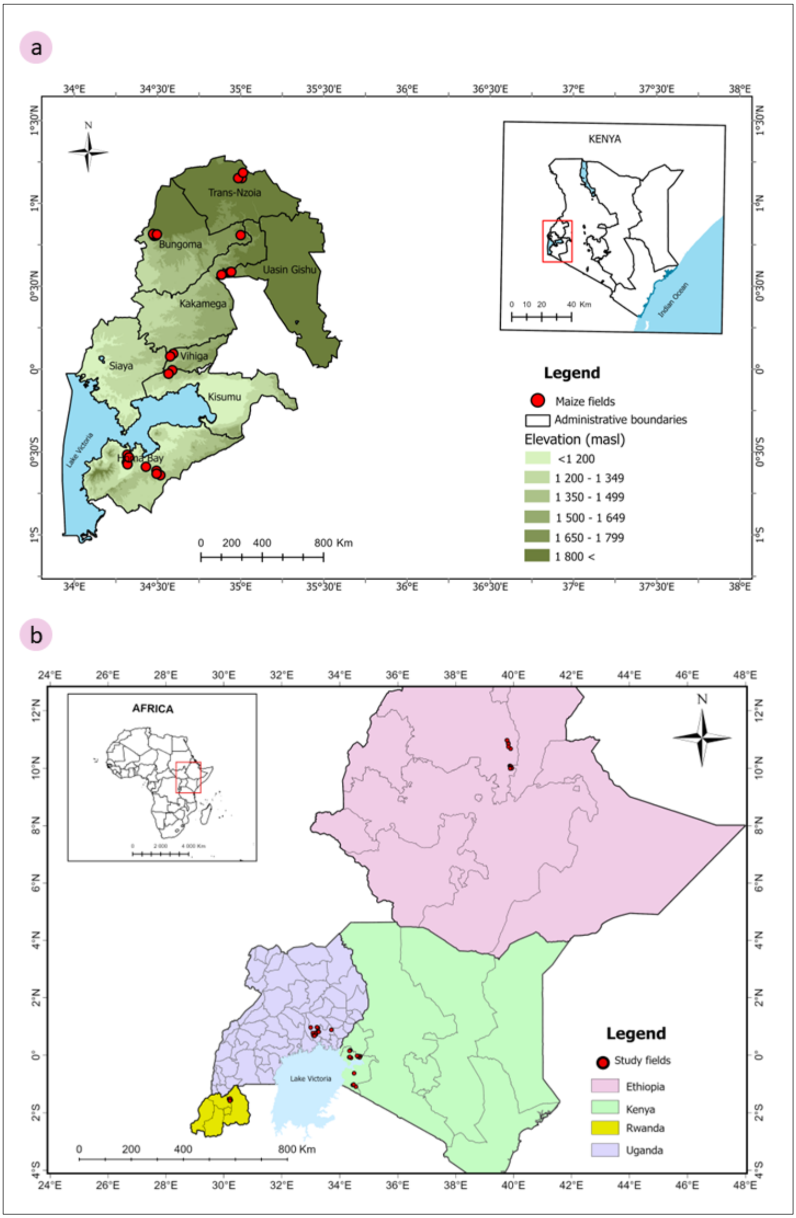


Figure 1: Map of the study area in East Africa. (a) maize fields located along an elevation gradient in western Kenya, and (b) sorghum and maize fields in Ethiopia, Kenya, Rwanda, and Uganda.

3.3 Estimation of landscape structure

For **Paper I**, grass cover composition was quantified by establishing a 1 km radius buffer around the centre of each field. This spatial scale is considered appropriate for studying the population dynamics of arthropod predators in agricultural landscapes (Lu et al., 2022; Rusch et al., 2016), to quantify grass cover composition. The buffers were created in ArcGIS using high-resolution satellite imagery from Google Earth (2017). Within each buffer, grassland areas were manually mapped, and the percentage cover of grass was calculated, ranging from 5% to 30%.

For **Paper IV**, landscape data from the 96 fields across the three countries (Kenya, Rwanda and Uganda) were used to investigate the effect of cropping system and landscape structures on natural enemy abundance and pest-related leaf damage. Land cover surrounding each field was estimated using detailed crop classifications derived from Sentinel-2 and PlanetScope satellite data. The classification was based on field data collected in June 2022. A MaxNDVI image composite was created, and a Random Forest classification was subsequently applied to generate a high-resolution land cover map. These maps were harmonised and reclassified into 8 distinct land cover types (bare soil, built-up, cropland, forest, grassland, shrubland, flooded vegetation, and water). For areas outside the extent of the detailed classification map but still within the studied landscape, the reclassified ESA WorldCover 2021 dataset was used to fill data gaps.

Landscape metrics were computed using software ESRI ArcGIS Pro 3.2.0, using a 1000 m radius buffer centred on each field. Landscape composition was expressed as the proportion of each land cover type relative to the total landscape. Landscape configuration was quantified using edge density, calculated as the total length of all edge lengths (boundaries between different land cover types) divided by the total landscape area.

3.4 Overview of the dominant soil types

The study region spans a range of agroecological zones, with diverse soil types underpinning variation in agricultural conditions and productivity across the region (**Papers II** and **III**). The Amhara region of Ethiopia is characterised by dominant Vertisols and Leptosols. Western Kenya features a combination of Plinthic Acrisols and Eutric Gleysols, reflecting both well-drained and periodically waterlogged conditions. In Rwanda's Gatsibo district, Umbric Ferralsols and Regosols are predominant, while in south-eastern Uganda, Acrisols, Nitisols, and Ferralsols dominate (Jones et al., 2013).

3.5 Climatic conditions

All four countries experience bimodal rainfall, with annual precipitation ranging between 1150 and 1650 mm and a mean annual temperature between 19.0 and 24°C. In Ethiopia, the East Amhara region receives short rains (Bega season) from February to May, and long rains (Kiremt season) from June to September. The region receives an average of 1,113 mm of rainfall annually and has a mean annual temperature of 20.1°C (Dessalegn & Akalu, 2015; Tiku et al., 2025) . In western Kenya, long rains occur from March to May, followed by short rains from October to December. The region receives about 1,500 mm of rainfall annually, with a mean annual temperature of 24°C (Hession & Moore, 2011; Indeje et al., 2001). Similarly, both eastern Rwanda and South-eastern Uganda experience long rains from March to May and the short rains from September to November. Eastern Rwanda receive approximately 1,170 mm of rainfall annually and has a mean annual temperature of 19°C (Rwema et al., 2025; Siebert et al., 2019), while south-eastern Uganda receives around 1,197 mm of rainfall annually and a mean annual temperature of 22.8°C (Hession & Moore, 2011; Nsubuga et al., 2014).

3.6 Data collection

3.6.1 Arthropod sampling and identification

In **Paper I**, ground-dwelling arthropods were sampled over two consecutive planting seasons: the short rainy season (September to December 2019), where sixteen fields were sampled and the long rainy season (March to July 2020), where all twenty-four fields were sampled. There was only one maize cropping season at the highest elevations, which motivated the different number of fields between seasons. Sampling across seasons was critical to account for the variability in arthropod populations throughout the year (Fischer et al., 2022). Arthropod populations are not static, as their abundance and composition can fluctuate in response to environmental changes such as rainfall and temperature (Fischer et al., 2022; Høye, 2020), life cycles, phenology (Gerlich et al., 2025), resource availability (Achury et al., 2022; Farooq et al., 2022), and farm management practices (Brusse et al., 2024). Sampling in each field was carried out twice using six wet pitfall traps, which were placed at least three rows from the field edges, and 5-10 meters (m) apart. To capture the insects, traps were filled to two-thirds with water and a few drops of unscented detergent to break the water's surface tension (Yi et al., 2012). After approximately 24 (±3) hours of exposure, traps were collected and all specimens retrieved. The specimens were then preserved in 70% ethanol and stored at -35°C. All arthropods were later identified to the genus level; only arthropod predators and parasitoids were selected for statistical analyses to assess the impacts of elevation and grassland cover.

In **Paper IV**, arthropods were sampled using a combination of wet pitfall traps and sweep netting to capture both ground-dwelling and foliage-dwelling taxa. Sampling spanned two consecutive planting seasons in Kenya, Rwanda and Uganda. Within each field, sampling was conducted twice per season. Three parallel transects were established along the maize rows in each field. The first transect was placed 1m from the field edge, while the second and third transects were positioned 2 to 4 m inward from the previous one, maintaining consistent spacing. Four wet pitfall traps were installed on the first 2 transects (2 traps per transect) using a double cup method. Each trap was placed at a position corresponding to 25% of the transect distance from each end of the transect, with the rim level to the ground surface to ensure unobstructed access for the arthropods. Traps were filled to two-thirds of their volume with a preservative solution of water and ethylene glycol, plus a few drops of unscented detergent. Each trap was covered with a clear plexiglass sheet, positioned 3cm above the ground to reduce rainfall interference and catch unwanted small mammals. The traps were left in the field for seven days. In total, four wet pitfall traps were installed per field. After the exposure period, the traps were removed, and all specimens were collected. For sweep netting, arthropods were collected along each established transect, performing 25 sweeps per transect (one left-to-right loop was considered one sweep). All specimens from both sampling methods were preserved in 70% ethanol and stored at -40°C. Arthropods were identified to the family level in each country, with only arthropod predators and parasitoid taxa included in subsequent statistical analyses.

Figure 2: Arthropod sampling in a maize field in Rwanda (a) wet pitfall trap installation, (b) specimen collection after seven days, and (c) an insect captured by sweep netting (Photos: Grace M. Amboka).

3.6.2 Soil measurement, sampling and analysis

Field-saturated soil water infiltration rates and soil penetration resistance were measured, and soil samples were collected from both PP and NPP fields in **Papers II** and **III**.

Field-saturated water infiltration

The infiltration rate was measured at three locations per field using a double-ring infiltrometer (20/30 cm inner/outer diameter). The measurements were conducted on level ground between maize rows. Readings were recorded for approximately 2.5 hours, or until the infiltration rate had stabilised. The average of the three determinations was taken as indicative of the soil's saturated hydraulic conductivity under field conditions (Figure 3a).

Soil penetration depth

Soil penetration depth was measured once during the sampling season using a portable static cone penetrometer (Wile, Tuusula, Finland). Measurements were taken under standardised soil moisture conditions after significant rainfall followed by drainage to field capacity. For each reading, the depths at which penetration resistance reached 200 psi (favourable to satisfactory root penetration) and 300 psi (satisfactory to poor conditions) were recorded, along with the maximum depth reached by the rod. Ten measurements were collected per field, converted to metres, and averaged to estimate the field's maximum penetration depth (Figure 3b). Soil penetration data were not available for the Ugandan fields.

Soil sample collection, preparation and laboratory analyses

Composite soil samples (0-20 cm depth) were collected from 20 soil cores (2.5 cm diameter) taken in a zig-zag pattern across the field and then homogenised for laboratory analysis. The samples were air-dried indoors on trays, and aggregates were crushed. The soil was subsequently sieved through a 2 mm mesh, and the resulting fine fraction was homogenised for further analysis (Figure 3c-e).

The prepared soil samples underwent comprehensive laboratory analysis to determine twenty additional physical and chemical properties. Soil texture was analysed at Makerere University in Kampala, Uganda, using the hydrometer method (Bouyoucos, 1962). A complete soil chemical analysis was performed at Crop Nutrition Laboratories in Nairobi, Kenya, using the procedures described by Pansu and Gautheyrou (2006). Chemical properties were assessed through standard laboratory methods. Soil pH and electrical conductivity (EC) were measured potentiometrically. Plant available nutrients including phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), sulphur (S), sodium (Na), iron (Fe), manganese (Mn), boron (B), copper (Cu), and zinc (Zn) were extracted using Mehlich 3 solution and quantified with inductively coupled plasma optical emission spectroscopy (ICP-OES). Soil organic matter was analysed using the Walkley-Black method and converted to organic carbon, based on the assumption that SOM contains 58% carbon. Total N was determined using the Kjeldahl method. The carbon-to-nitrogen ratio (C: N ratio) and cation exchange capacity (CEC) were subsequently calculated from the analytical data.

3.6.3 *Striga* seed bank assessment

Striga seed bank and husk density were determined in the soil at Makerere University. This was done through wet sieving followed by flotation in sucrose solution, following Berner´s protocol (Berner et al., 1997). The isolated seeds and husks were counted under a light dissecting microscope at 30X magnification (**Paper III**).

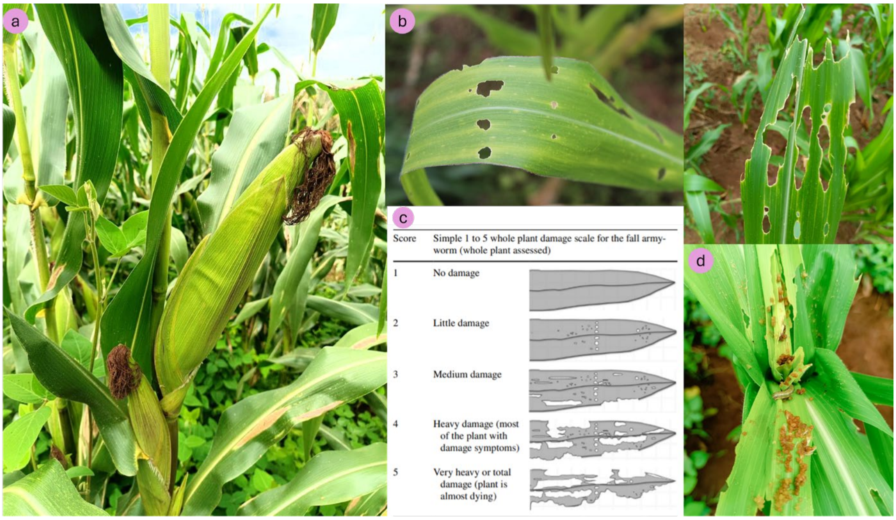
3.6.4 Pest damage assessment

In both PP and NPP fields, leaf damage caused by FAW and stemborers was recorded (**Papers III-IV**). Along each transect, seven maize plants were systematically selected; every second plant was tagged for subsequent field observations, resulting in a total of 21 tagged plants per field. Damage was recorded on all the leaves of each tagged plant (Figure 4a-d). Leaf damage was scored using a simple scale ranging from 1 to 5 (Toepfer et al., 2021). Due to the difficulty in visually distinguishing damage caused by FAW and stem borers, the score represented the combined damage by both pest groups. Leaf damage from non-targeted pests (wilting, breakage, livestock feeding, or other insect infestations) was also recorded but excluded from subsequent analyses, ensuring that the damage estimate specifically represented FAW and stem borer activity.

3.6.5 Field-level agronomic and management data

Field-level data were collected to characterise management practices and crop attributes. In each PP field, *Desmodium* coverage was visually estimated and scored between 20% and 100%. Information on field age (number of growing seasons since establishment) and fertiliser use (manure or mineral, recorded as applied or not applied) was obtained from the farmers through a questionnaire. Across countries, the age of the PP fields ranged from 6 months to 14 years, with the oldest fields in Kenya and the youngest in Uganda. *Desmodium* cover showed the greatest variation in Kenya and Uganda (20% to 100%), moderate in Rwanda (50% to 100%), and uniform in Ethiopia (75%). Manure application was most frequent in Rwanda, while mineral fertiliser use was highest in Kenya and absent in Ethiopia (**Paper II**).

Figure 3: Field soil measurements and laboratory processing (a) water infiltration, (b) soil compaction, (c) sample collecting (d) crushing and sieving, and (e) weighing and sub-sampling (Photos: Grace M. Amboka)



Score	Simple 1 to 5 whole plant damage scale for the fall army-worm (whole plant assessed)
1	No damage
2	Little damage
3	Medium damage
4	Heavy damage (most of the plant with damage symptoms)
5	Very heavy or total damage (plant is almost dying)

Figure 4: FAW and stemborer damage in maize fields (a) push-pull field, (b) pest-induced leaf damage, (c) FAW damage severity scored using the Toepfer et al. (2021) visual scale, and (d) maize whorl damage by FAW larvae (Photos: Grace M. Amboka).

3.7 Statistical analyses

All statistical analyses were conducted in R version 4.4.0 (R Core Team, 2024).

Common statistical procedures

To ensure consistency across analyses, all models were checked for multicollinearity and selected based on the same information-theoretic approach. Multi-collinearity among predictors was assessed using Variance Inflation Factors (VIFs), calculated with the vif function in the fmsb package (Minato Nakazawa, 2024). Only variables with VIF < 3 were retained, indicating no significant collinearity (Zuur et al., 2010). Interaction terms were excluded when strong correlations were detected among predictors. Model selection was performed for competing models on Akaike's Information Criterion (ΔAICc<2) using the dredge function in the *MuMIn* package (Kamil Bartoń, 2024). When multiple competing models met this criterion, model averaging was conducted using the model. avg function, otherwise the single best model was retained (Burnham et al., 2010). Model fit checks were performed using the simulateResidual function in the *DHARMa* package (**Papers I-IV**).

Paper I

Generalised linear mixed models (GLMMs) were used to assess the effects of elevation and surrounding grassland cover on the predator communities. Data from two sampling rounds per season were pooled, and four key diversity metrics were calculated for each field using the *vegan* package (Oksanen et al., 2025): Shannon diversity index, species richness, Pielou's evenness, and overall abundance. Data from both seasons were combined to increase statistical power. Field identity was included as a random factor to account for the non-independence of observations within the same field. Models were fitted with the appropriate error distribution: negative binomial distribution for species richness and abundance, beta for evenness, and a Gaussian for Shannon diversity, using the *lme4* and *MASS* packages. Multicollinearity assessment and model selection were conducted as outlined in the common statistical procedures section.

To assess the effects of elevation and grassland cover on natural enemy community composition, Non-Metric Multidimensional Scaling (NMDS) was performed on the Bray-Curtis dissimilarity matrix using the metaMDS function in the package *vegan* (Oksanen et al., 2025). Differences in community composition among predefined categories of elevation and grassland cover were tested using permutational multivariate analysis of variance (PERMANOVA) with the adonis function. The assumption of homogeneity of multivariate dispersion was confirmed first using the betadisper function before PERMANOVA. Pairwise comparisons were subsequently conducted to identify specific group differences (Anderson, 2005).

Paper II

Generalised linear models (GLMs) were used to evaluate twenty physicochemical soil properties associated with push-pull (PP) and non-push-pull (NPP) cropping systems and analysed separately for each country. The effects of cropping systems (PP vs. NPP) and fertiliser type (manure or mineral) on soil properties were evaluated. The percentage of clay was included as a covariate, as clay content directly influences soil properties, but is independent of the cropping system. For PP fields, separate GLMs were fitted to examine the effect of field age, *Desmodium* cover, and fertiliser application on the twenty soil variables. Model selection and collinearity diagnostics followed the procedures described in the common statistical procedures section above.

Paper III

Generalised linear mixed models were applied to test the effects of the cropping system and soil physicochemical properties on *Striga* seed density and leaf damage. Models were fitted with the appropriate error distribution: negative binomial or Poisson on *Striga* seed density and Gaussian for leaf damage, using the *lme4* and *MASS* packages. The field pair was included as a random factor.

Before model fitting, six key physicochemical properties were selected per country (CEC, N, P and pH, water infiltration rates, and soil compaction depth), and summarised using principal component analysis (PCA), with the prcomp function in the package *stats*. The CEC was used as a proxy for exchangeable cations and clay content, while total N and P were included as they are limiting in all the countries, with concentrations way below the critical thresholds (FAO, 2007; NAAIAP, 2014). Soil pH was included because it directly influences nutrient availability for plant uptake. The first two principal components (PC1 and PC2) were included as predictors in the GLMMs.

In Ethiopia, PC1 captured a gradient from high soil pH and CEC to low P availability, while PC2 represented a gradient from greater soil penetration depth to lower N content and reduced infiltration capacity. In Kenya, PC1 captured a gradient from high pH, P, and CEC to low infiltration rates, while PC2 represented a gradient from greater soil penetration depth to lower N content. In Rwanda, PC1 captured a gradient from high CEC and N content to lower pH, while PC2 represented a gradient from higher P availability to lower infiltration capacity and reduced soil penetration depth. In Uganda, PC1 captured a gradient from high pH, CEC, P, and N, while PC2 represented a gradient from high infiltration capacity and N content to lower P availability. Multicollinearity assessment and model selection were conducted as outlined in the common statistical procedures section.

Paper IV

Generalised linear mixed models were applied to test the effects of the landscape structure, cropping system and season on natural enemy abundance, richness and leaf damage. Models were fitted with the appropriate error distribution: negative binomial or Poisson on natural enemy abundance and richness, and leaf damage was modelled using linear mixed models fitted with *lme4* and *MASS* packages. The field pair was included as a random factor.

Before model fitting, four landscape variables within a 1000m buffer (forest, grass, cropland cover and edge density) were summarised using principal component analysis (PCA), with the prcomp function in the package stats. The first two principal components (PC1 and PC2) were then included as the landscape predictors in the GLMMs. In Kenya, PC1 captured a gradient from high cropland cover to high grass cover and edge density, while PC2 represented high cropland to high forest cover. In Rwanda, PC1 ranged from high cropland cover to high grass and forest cover, whereas PC2 represented a gradient from low to high grass cover and edge density. In Uganda, PC1 captured the gradient from high cropland cover to high forest cover and edge density, while PC2 ranged from low grass cover to high forest cover. Multicollinearity assessment and model selection were conducted as outlined in the common statistical procedures section.

4. Results and Discussion

This thesis shows that the push-pull (PP) system enhances key ecosystem functions, including soil fertility, natural enemy diversity, and the suppression of pests and *Striga* weed. However, these benefits are shaped by soil conditions, landscape structure, and seasonal dynamics, making PP performance context-dependent across East Africa. Understanding how these field-to-landscape-scale interactions mediate PP outcomes is essential for promoting cropping systems that sustain ecosystem services and productivity in sub-Saharan African agroecosystems.

The results show that natural enemy communities were shaped by environmental context. At the field scale, elevation influenced natural enemy composition, with higher elevations exhibiting lower evenness, while grass cover showed a weak positive effect on richness. The higher elevation was dominated by *Myrmicaria* ants while the lower elevation supported a broader mix of genera, including *Aphaenogaster*, *Crematogaster*, *Odontomachus*, and *Pachycondyla* ants, along with *Allonemobius* crickets and *Lycosa* spiders (**Paper I**). The performance of the PP system varied across countries, with natural enemy responses and pest damage affected differently by landscape structure and differed between the long and short rainy seasons in different countries (**Paper IV**). In Kenya, natural enemy responses and pest damage varied with landscape structure, with PP field in more complex, grass-rich or forested landscapes showing higher natural enemy activity and reduced pest damage. Uganda showed consistently lower pest damage under PP, with neither landscape nor season influencing the relative effectiveness of PP, while in Rwanda cropping system effect depended on season, with higher natural enemy abundance and richness, along with lower pest damage observed during the short rainy season. These findings highlight the importance of habitat complexity, seasonal climatic variation and more stable system performance in shaping biocontrol potential.

At the soil level, PP cropping improved several physicochemical properties compared to NPP systems, particularly in relation to *Desmodium* cover, though effects varied between countries. For example, PP fields with high *Desmodium* cover had high N, P, and SOM (**Paper II**), highlighting the benefits of integrating *Desmodium* within the cereal fields. In **Paper III**, the effect of PP on *Striga* seed density and pest damage was inconsistent across countries. In Uganda, PP consistently suppressed *Striga* seed density independent of soil conditions, while in Rwanda, PP interacted with soil properties and showed no effect in Ethiopia and Kenya, while pest damage was reduced in Ethiopia and Uganda (**Paper III**). These patterns demonstrate that PPs' effectiveness is context-dependent, with soil fertility only explaining variation in Rwanda.

To strengthen natural regulation of fall armyworm, stem borers and *Striga* under PP, management needs to be aligned with local ecological conditions such as conserving forest remnants, maintaining grassy edges and hedgerows, or promoting agroforestry in Kenya; improving soil fertility in Rwanda through practices like adding organic amendments or manure to reduce *Striga* proliferation; timing PP establishment ahead of the short rainy season to maximize on the natural enemy activity to suppress pest; and ensuring vigorous *Desmodium* and trap grasses in Uganda (**Papers I** to **IV**).

4.1 Effect of elevation, landscape structure and seasonality on natural enemies and pest damage

In **Paper I,** across both long and short rainy seasons, a total of 1317 natural enemies were collected, representing 60 families and 174 genera. It was found that ants (Hymenoptera| Formicidae) dominated the community (52%), followed by omnivorous crickets (Orthoptera| Trigonidiidae; 10%) and spiders (Araneae| Lycosidae; 9%) In **Paper IV**, natural enemy communities were substantially larger due to a longer sampling period, with 33,934 individuals collected in Kenya and 20,697 in Rwanda across both long and short rainy seasons, representing 119 families in Kenya and 64 in Rwanda. Like **Paper I**, ants dominated the natural enemy assemblages, accounting for 52% of individuals in Kenya and 67% in Rwanda. Crickets (Orthoptera: Gryllidae) were the second most abundant group, comprising 27% of individuals in Kenya and 7% in Rwanda, respectively. Spiders were also well represented, particularly Lycosidae in Kenya (6%) and Salictidae in Rwanda (10%). The dominance of ants in our study mirrors patterns in tropical agroecosystems, where ants frequently dominate (Schultheiss et al., 2022).

The importance of ants in pest control in sub-Saharan Africa has been examined in a few studies. For example, Dassou *et al*. (2021) and Koffi *et al*. (2020) showed that predatory ants such as *Pheidole* and *Campotonus* could effectively control the invasive FAW in maize fields in Benin and

Ghana. Despite these benefits, certain ant taxa, such as *Crematogaster,* can defend plant sucking aphids against other natural enemies, potentially exacerbating pest problems (Wills & Landis, 2018). Nevertheless, ants´ abundance in most tropical agroecosystems makes them possible allies in IPM, even though studies on their role in pest suppression are still limited in the region.

4.1.1 Effects of elevation on natural enemy diversity and community composition

Natural enemy communities responded to elevation changes (**Paper I**). It was found that natural enemy evenness declined significantly with increasing elevation (Figure 5), while richness and total abundance showed no clear elevational trends. The reduced evenness at higher elevations might be due to cooler climatic conditions and reduced resource availability (Ceia-Hasse et al., 2023), which together may limit the establishment of more diverse communities. In contrast, lower elevation supported a more diverse and evenly distributed community, likely due to higher plant productivity and resource availability (Farooq et al., 2022; Pilar et al., 2020), which can sustain a broader range of natural enemy species.

Apart from affecting evenness, elevation also shifted community composition (**Paper I**). Notably, *Myrmicaria* ants became increasingly dominant above 1600 meters above sea level (masl), while ants from the genera *Pachycondyla*, *Odontomachus*, and *Crematogaster* were more common at lower elevations ranging between ~1200 to 1500 masl. Such taxa-specific turnover is consistent with elevational filtering documented in other tropical and temperate systems (Kunene et al., 2022; Måsviken et al., 2023), suggesting that elevation acts as a major determinant of species distribution through its influence on thermal tolerance, habitat structure, and resource dynamics. Dominance by a few species at high elevations (such as *Myrmicaria*) may reduce functional redundancy, compromising pest control services, whereas the more even communities at lower elevations are likely to be more stable in the event of environmental perturbations (Lefcheck et al., 2015; Loreau & De Mazancourt, 2013).

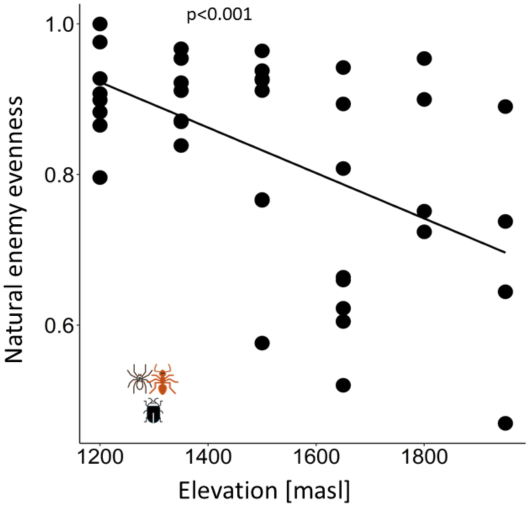


Figure 5: Relationship between elevation and natural enemy evenness in Kenya. Points represent individual field sites, and the fitted line shows the significant negative relationship predicted by the linear regression ($p < 0.05$, Wald z-tests).

4.1.2 Landscape heterogeneity and season as drivers of natural enemy communities

Papers I and **IV** demonstrated that landscape structure, particularly the amount of semi-natural habitat, played an important but context-dependent role in shaping natural enemy communities. In **Paper I,** even though grassland cover explained less variation in community composition than elevation, it still influenced community composition during the long rainy season. It was found that maize fields embedded in >20% grass cover supported higher richness of natural enemy assemblages, whereas landscapes with <10% grass cover were dominated by a single genus. This suggests that grasslands and other semi-natural habitats can provide essential resources and refuges that help maintain diverse natural enemy assemblages (Farooq et al., 2022; Pilar et al., 2020).

Paper IV demonstrated seasonal and landscape structural effects on natural enemy abundance and richness. In Kenya, an interaction between landscape structure gradient and PP fields was observed, with PP fields supporting higher natural enemy abundance than NPP fields in more forested (and less cropped) landscapes, while no difference in abundance was detected in low-forest areas (Figure 6a; Table 1). Contrary there was a non-significant negative relationship between natural enemy abundance and landscape, as they tended to decline with increasing grassland cover and edge density and with reduced cropland cover. Natural enemy richness was significantly affected by seasons, with fewer taxa recorded in the short rainy season. Increasing forest cover also showed a positive but non-significant effect on richness in both PP and NPP fields, indicating that forested landscapes may provide complementary resources and microhabitats that enhance natural enemy communities.

These landscape-dependent patterns are consistent with broader evidence that forested and heterogeneous landscapes increase natural enemy activity. Forested landscapes, for instance, are known to provide cooler microclimates, structural complexity and litter, supporting richer predator communities (Clarkson et al., 2022; Hohlenwerger et al., 2022). These trends align with evidence from empirical and meta-analytic studies showing that landscape complexity, particularly semi-natural habitats such as grasslands and forest patches, can enhance natural enemy richness, abundance, and pest control, although effects are not consistent across all systems (Karp et al., 2018; Marja et al., 2022).

In addition to landscape gradients, seasonal changes also modulated natural enemy abundance and richness in Kenya (**Papers I** and **IV**). Evidence from **Paper I** shows that the positive influence of grass cover on natural enemy composition in Kenya was significant during the long rains, when increased rainfall and vegetation growth enhance floral resources, alternative prey, and microhabitat availability (Achury et al., 2022). In **Paper IV**, natural enemy abundance and richness significantly declined from the long to the short rainy season. Short rainy seasons in Kenya are often associated with shorter crop duration and lower resource availability, because smallholder farmers tend to plant early maturing maize varieties to cope with the shorter and more variable rainfall (Lila, 2023; Rutsaert & Donovan, 2023).

In Rwanda, however, landscape structure did not modulate PP effectiveness. Instead, PP performance was mainly driven by seasonal variation. Natural enemy abundance and richness were high during the short rainy season (**Paper IV**), showing that PP effectiveness in Rwanda is linked to climatic seasonality rather than landscape composition. The short rainy season coincides with the major cropping season, characterised by high maize and bean biomass, dense vegetation cover and stable humidity (NISR, 2021). These conditions likely enhance resource availability and create favourable microhabitat conditions for predators and parasitoids, thereby strengthening biological control during this period.

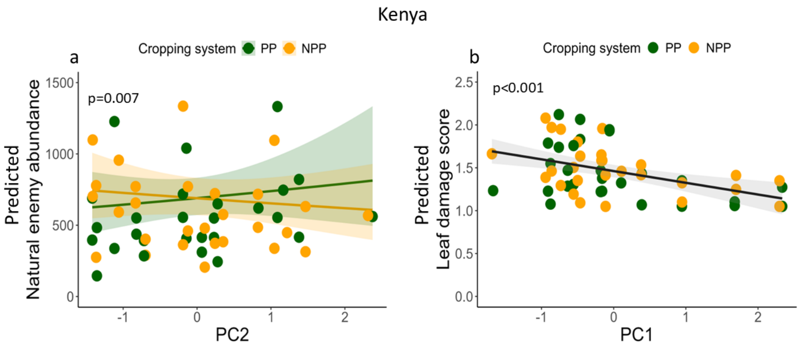


Figure 6: Averaged model-predicted associations along PC2 (cropland-forest cover gradient), and PC1(cropland-grassland gradient and landscape heterogeneity) in Kenya. a) Abundance per field and b) Pest damage per field. All predictions are derived from model-averaged GLMMs and are back-transformed to the response scale, with 95% confidence intervals. Points represent individual field sites.

4.1.3 Pest pressure across landscapes, cropping systems, and seasons

In **Paper IV**, landscape structure, seasonality and cropping system each emerged as key drivers of pest damage, with landscape structure being more influential in Kenya, seasonality in Rwanda and the cropping system in Uganda. In Kenya, pest damage declined along gradients of high grass cover and greater landscape heterogeneity, suggesting that cropland-dominated landscapes experienced higher pest pressure (Figure 6b). Since natural enemy abundance also declined along these gradients, although not significantly, other mechanisms are likely contributing to reduced pest damage. One possibility is that specialised parasitoids, which were not captured by our sampling methods, likely benefited from grasslands and suppressed pest populations (Bianchi et al., 2006; Landis et al., 2000). Additionally, bottom-up approaches, such as reduced resource concentration in a more heterogeneous landscape, may have a limited pest population and thereby reduce pest damage (Andow, 1991; Tscharntke et al., 2005).

Empirical studies in the Kenyan PP systems have shown that landscape complexity can influence both pest pressure and natural enemy responses, indicating that PP performance can be shaped by its surrounding landscape context rather than functioning in isolation (Midega et al., 2014b). While these patterns align with studies showing that heterogeneous landscapes and non-crop habitats often enhance natural enemy activity and reduce herbivore abundance, global syntheses also demonstrate that landscape effects are not universally consistent across systems (Karp et al., 2018).

In Rwanda, the performance of PP to suppress pest damage was mainly modulated by seasons. Pest damage significantly declined during the short rainy season compared to the long rainy season, indicating that seasonality played an important role in Rwanda (Figure 7). Decline in pest damage during the short rainy season may be attributable to the observed increased natural enemy abundance and richness, which helps keep pest populations in check.

In Uganda, the cropping system was the primary driver of pest damage, with significantly lower damage observed in PP fields compared to NPP fields (Figure 8). These reductions appeared relatively insensitive to landscape gradients or seasonal variation, suggesting that the core PP mechanisms, *Desmodium* repulsion, trap-grass attraction, and enhanced microhabitat conditions for natural enemies functioned more reliably under Ugandan conditions. This clear association between low pest damage and PP aligns with previous studies showing effective PP-mediated suppression of FAW, stemborers and *Striga* in Uganda (Hailu et al., 2018; Midega et al., 2018).

The results in **Papers I** and **IV** revealed that PP effects on natural enemies and pest damage are context dependent. In Kenya, landscape structure was the dominant driver; in Rwanda, seasonal climatic conditions had the strongest influence; and in Uganda, the PP system consistently suppressed leaf damage. This context dependency reinforces growing evidence that biological control outcomes in African agroecosystems are shaped by locally specific interactions of climate, landscape, and farming practices rather than a single overarching driver (Abbas et al., 2022; Sánchez et al., 2022).

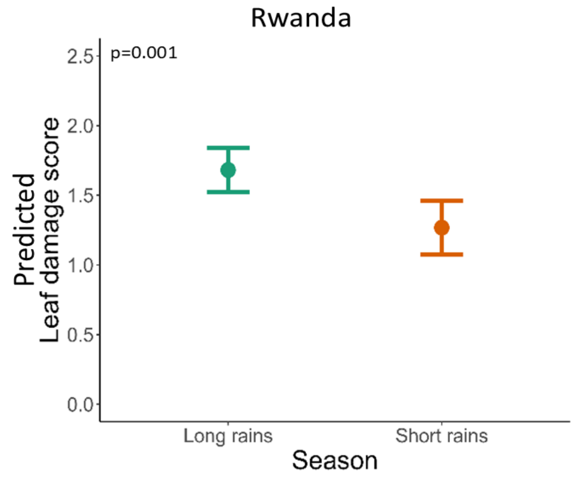


Figure 7: Averaged model-predicted associations between cropping seasons (long and short rainy seasons) and pest damage per field in Rwanda. All predictions are derived from model-averaged GLMMs and are back-transformed to the response scale, with 95% confidence interval.

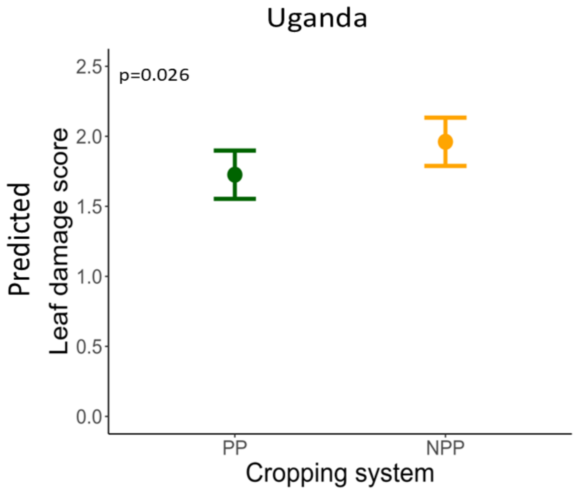


Figure 8: Averaged model-predicted associations between cropping system (push-pull and non-push-pull) and pest damage per field in Uganda. All predictions are derived from model-averaged GLMMs and are back-transformed to the response scale, with 95% confidence interval.

Table 1: Statistical output of the final GLMM for natural enemy abundance, richness and pest damage in relation to cropping system, landscape principal components and cropping season in Kenya, Rwanda and Uganda. Estimates (Est. ± SE), z values and associated p-values are shown. Significant p-values are shown in **bold**.

Country	Response	Predictor	Est+ Std.Error	z value	Pr (>|z|)
Kenya	Abundance	Intercept	6.53 ± 0.09	66.71	<0.001
		Short-rainy season	-0.39 ± 0.12	3.65	**<0.001**
		PP	0.00 ± 0.10	0.02	0.98
		PC2	-0.12 ± 0.09	1.33	0.18
		PC2:PP	0.28 ± 0.10	2.70	**0.01**
		PC1	-0.09 ± 0.08	1.22	0.22
	Richness	Intercept	3.23 ± 0.05	70.20	<0.001
		Short-rainy season	-0.27 ± 0.06	-4.60	**<0.001**
		PP	0.03 ± 0.06	-0.54	0.59
		PC2	0.04 ± 0.04	0.97	0.33
		PC2:PP	-0.05 ± 0.06	0.86	0.39
	Damage	Intercept	1.46 ± 0.04	39.65	<0.001
		PC1	-0.14 ± 0.04	-3.68	**<0.001**
Rwanda	Abundance	Intercept	5.52 ± 0.13	42.97	<0.001
		Short-rainy season	0.45 ± 0.17	2.66	**0.008**
	Richness	Intercept	2.39 ± 0.05	43.42	<0.001
		Short-rainy season	0.48 ± 0.06	8.00	**<0.001**
		PP	0.03 ± 0.07	-0.44	0.66
		PP: short-rainy season	-0.05 ± 0.08	0.55	0.58
	Damage	Intercept	1.68 ± 0.08	0.40	<0.001
		Short-rainy season	-0.41 ± 0.12	3.47	**0.001**
		PP	-0.12 ± 0.12	0.94	0.35
		PP: short-rainy season	-0.32 ± 0.15	2.13	**0.03**
Uganda	Damage	Intercept	1.78 ± 0.10	8.26	<0.001
		PP	-0.23 ± 0.10	2.22	**0.03**

4.2 Soil properties, push-pull performance, *Striga* and pest outcomes

4.2.1 Variation in baseline soil characteristics across sites

As expected, soils varied widely in texture and physicochemical properties, reflecting East Africa's agroecological diversity (**Paper II**; Table 2). Soils in Uganda and Rwanda were generally lighter and more acidic, while those in Ethiopia and Kenya were heavier, with cation exchange capacity (CEC) values exceeding the productivity threshold of 15 meq 100 g^{-1}. This threshold refers to the concentrations of extractable nutrients in the soil, above which the addition of more nutrients is unlikely to result in a significant economic yield increase (FAO, 2007; NAAIAP, 2014). Infiltration rates were highest in Kenya and Uganda. Available P and total N concentrations were generally below agronomic recommendations in all countries, except in some Ethiopian fields where P and base cation levels were exceptionally high. Boron and zinc deficiencies were consistent across all countries, suggesting widespread micronutrient limitations, a pattern also reported in a meta-analysis study across sub-Saharan Africa (Sileshi et al., 2019). Establishing these soil conditions lays the foundation for interpreting cross-country differences in PP outcomes underpinning the context-dependent effects of PP on soil fertility, *Striga* suppression, and pest regulation (**Paper III**).

4.2.2 Soil fertility differences between cropping systems

Although some differences in CEC and micronutrient concentrations were observed between PP and NPP fields, particularly lower CEC and micronutrients in Ethiopian and slightly higher Fe in Kenyan PP fields, there were no significant differences in SOM, total N and available P in any of the four countries (**Paper II**). Rwanda and Uganda showed no detectable differences between PP and NPP fields across key fertility indicators. This contrasts with earlier studies in Rwanda reporting PP-associated improvements in N, P, and SOC (Ndayisaba et al., 2021, 2022). Such inconsistencies likely reflect regional differences in soil type (Jones et al., 2013).

Table 2: Minimum, Maximum and Median values of selected soil chemical properties across countries

Country	**Ethiopia**			**Kenya**			**Rwanda**			**Uganda**			
Soil properties	Min	Max	Med	Min	Max	Med	Min	Max	Med	Min	Max	Med	Critical values[a]
Sand %	23	53	43	29	75	57	37	81	73	43	75	55	-
Silt %	18	44	28	10	38	20	11	49	23	7	45	35	-
Clay %	23	41	32	11	39	25	2	38	6	2	20	10	-
pH	7	8.8	7.4	4.9	7.3	6	4.6	6.18	5.7	5.1	6.7	6.0	>5.5
EC (uS/cm)	34.8	209	57.3	12.5	214	35.9	13.3	65.6	36.6	17.6	68.4	34.3	>80
CEC (meq/100g)	34.7	79.1	53.9	4.2	46.2	12.9	3.9	20.6	6.6	4.3	17.6	12.8	>15
SOM %	1.5	4.0	2.66	1.9	4.72	3.23	2	3.85	2.6	2.5	4.5	3.7	-
N %	0.1	0.17	0.12	0.1	0.2	0.16	0.1	0.18	0.1	0.1	0.17	0.1	>0.2
C:N	8.25	17.7	11.9	9.4	15.2	12.3	12.4	16	14.4	13.9	18.1	15.3	-
P (ppm)	2.64	323	24.1	1.8	76.2	13.8	4.8	88	30.1	3.1	80.2	5.6	>30
Ca (ppm)	5010	13700	7775	468	5810	1220	367	2320	544	290	2550	1600	>400
K (ppm)	248	933	547.5	42.7	760	178	52.6	468	88.4	45.4	369	140	>94
Mg (ppm)	612	1770	892.5	77.6	1140	216	53.1	476	123	51	321	222.5	>120
S (ppm)	14.2	41.8	17.9	5.2	17.4	10.7	7.4	23.8	10.1	8.81	14.6	12.4	>20

[a] Critical values (FAO, 2007; NAAIAP, 2014) refer to the threshold concentrations of extractable nutrients in the soil, above which the addition of more nutrients is unlikely to result in a significant economic yield increase. Minimum, Maximum and Median lowest, highest, and middle values recorded for each soil variable across all observations.

4.2.3 Effects of *Desmodium* cover on soil fertility

In **Paper II**, *Desmodium* cover emerged as an important determinant of soil fertility in PP fields, although its effect varied across countries. Higher *Desmodium* cover correlated with increased SOM, CEC, N, K, and S levels in Kenya and Uganda, reflecting its contribution to organic matter inputs and nutrient enrichment (Meena et al., 2018). In Rwanda, greater *Desmodium* coverage was instead associated with higher P availability (Figure 9), supporting its capacity to enhance P mobilisation (White et al., 2021). Phosphorus mobilisation is crucial, especially in agricultural systems, because P is often bound in forms that are unavailable to the plants (Zhong et al., 2023). Thus, increasing the pool of plant-available P can substantially improve P uptake, root growth and crop productivity in the highly acidic soils common in Rwanda. Greater P availability also enhances overall nutrient uptake because well-developed root systems are better able to explore the soil profile and access other nutrients and micronutrients. Moreover, adequate P alleviates energy limitations within the plant, supporting metabolic processes that facilitate the assimilation and transport of multiple nutrients. Collectively, these improvements contribute to stronger plant growth and greater resilience under nutrient-limited conditions (Divito & Sadras, 2014; X. Tang et al., 2021). Ethiopia was excluded from the analysis due to a lack of variation in *Desmodium* cover. These country-specific patterns highlight that the soil fertility benefits of *Desmodium* are context-dependent and shaped by underlying soil properties and local conditions.

4.2.4 Soil property changes across push-pull field ages

In **Paper II**, older PP fields showed contrasting patterns across countries. In Kenya, fields older than 4 years showed signs of acidification and nutrient depletion (K, B), likely driven by long-term biomass export from *Desmodium* harvest and repeated application of ammonium-based fertilisers (Shi et al., 2019; Sileshi et al., 2019). These patterns suggest that without balanced nutrient replenishment, older PP fields may become increasingly nutrient-limited over time.

In Uganda, however, older PP fields (~4 years) exhibited higher C:N ratios, indicative of gradual SOM accumulation, which may reflect lower biomass export, slower decomposition rates, or sustained inputs from *Desmodium* litter (Meena et al., 2018). This is consistent with reports that

Ugandan farmers tend to maintain PP fields for many years because of their perceived reliability and yield benefits (Chepchirchir et al., 2018). Such long-term maintenance, together with the generally consistent management practices documented by Chepchirchir et al. (2018), likely contributes to SOM build-up and may help explain the stable PP performance in *Striga* suppression and pest reduction observed in **Paper III.** Limited variation in field age in Rwanda and no variation in Ethiopia prevented assessment of field age effects in those countries.

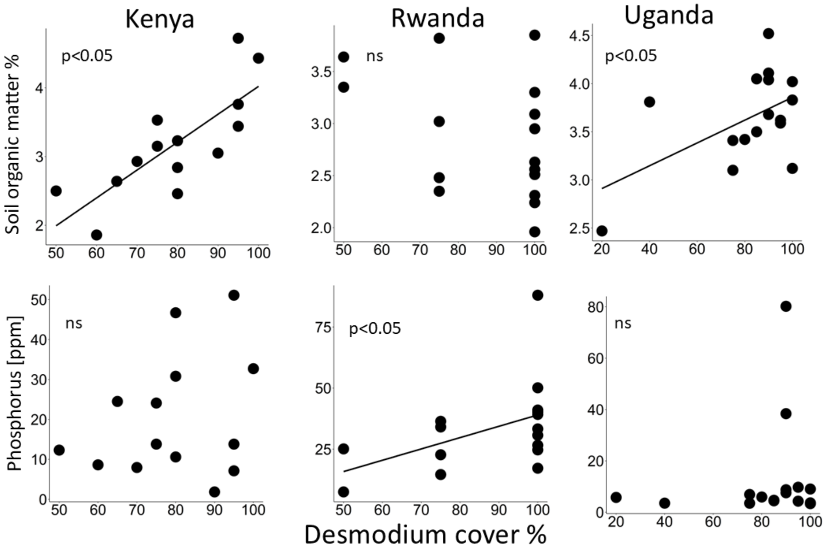


Figure 9: Relationships between *Desmodium* cover and (a) soil organic matter (SOM), (B) phosphorus in PP fields across Kenya, Rwanda, and Uganda. Linear regression models were used to assess the associations, with fitted lines shown in each panel. Significance levels are indicated as follows: $p < 0.05$, and (ns) not significant ($p \geq 0.1$).

4.2.5 Influence of clay content on soil fertility

Clay content emerged as a strong determinant of soil fertility as clay-rich soils were positively associated with SOM, N, S, CEC, Ca, and Mg (**Paper II**). This pattern is consistent with the well-established role of clay in enhancing nutrient retention and water-holding capacity (Kome et al., 2019). However, clay content did not differ between PP and NPP fields, indicating that the observed nutrient differences were likely driven by broader field and management-level contexts.

4.2.6 Effects of manure and mineral fertiliser application

In **Paper II**, we found that manure and fertiliser use contributed to variation in soil conditions across fields, although the specific soil responses were strongly context dependent. In Uganda, manure use increased CEC, Ca, Zn, and N, reflecting its well-established role in replenishing micronutrients and enhancing nutrient retention, functions that are particularly valuable in the nutrient-depleted and weathered soils common across sub-Saharan Africa (Mkhabela, 2006; Sileshi et al., 2025). When applied in adequate quantities, manure can also contribute to SOM build-up, improve biological activity, and buffer acidity, thus making it an essential amendment for rehabilitating degraded soils (Bayu et al., 2005).

In Kenya, however, manure use was related to lower pH and CEC, suggesting possible targeted application to already degraded soils, where baseline infertility can obscure potential benefits (Das et al., 2017; Gross & Glaser, 2021). Mineral fertiliser use in Kenya further contributed to declines in soil pH and base cation levels, consistent with the acidifying effects of ammonium-based inputs widely used in the region (Sileshi et al., 2019). Among the four countries, Kenya had the highest number of farmers applying mineral fertiliser. Despite the potential acidification issues of some mineral fertilisers, these inputs remain important in supplying nutrients to severely depleted soils. These findings underscore the need for balanced nutrient management strategies that integrate both organic and mineral inputs, especially in degraded African soils, where they offer complementary benefits. However, constraints related to manure availability, fertiliser affordability, and input quality continue to limit farmers' ability to apply these amendments at the rates needed to sustain or increase soil health and long-term productivity.

4.2.7 Effects of push-pull and soil fertility on *Striga* seed bank

In **Paper III**, the interactive effect of cropping system and soil fertility on *Striga* seed bank density was assessed. The analysis revealed that the effect of PP on *Striga* seed density varied among countries, with the clearest interactions observed in Rwanda. Lower *Striga* seed density under PP occurred only in soils that were less acidic but low in N and CEC, or in soils with high P availability, shallow exploitable depth and slower water infiltration (Figure 10). These results suggest that PP's benefits were strongest in nutrient-poor or P-rich but physically constrained soils, consistent with previous studies in the region showing that *Striga* suppression by PP is most effective under nutrient-poor conditions (Khan et al., 2010; Sileshi et al., 2025).

In Uganda, PP significantly reduced *Striga* seedbank density, and this strong main effect likely reflects the uniformly low soil fertility, particularly severe P limitation across fields. Under such nutrient-constrained conditions, where *Striga* infestation is typically most severe, the allelopathic suppression by *Desmodium* becomes especially effective (Khan et al., 2002; Kountche et al., 2019). This pattern aligns with the baseline soil conditions reported in **Paper II**, where Ugandan soils were moderately acidic, lighter and nutrient-limited, but showed comparatively less variation across fields than those in the other countries. Such relatively homogenous soil conditions likely contributed to the uniform PP response.

In contrast to Uganda, neither cropping system nor soil fertility played a detectable role in shaping *Striga* seed banks in Ethiopia and Kenya. Ethiopian fields had extremely low *Striga* seed density levels, ranging from 0 to 3 *Striga* seeds per 50grams of soil, likely due to high alkaline soils, creating unfavourable conditions for *Striga* emergence (C. Tang et al., 1999). In Kenya, *Striga* seedbank density also showed no clear response to soil gradients or cropping systems, which contrasts with previous studies showing strong benefits of the PP system on above-ground *Striga* count (Luttermoser et al., 2023; Midega et al., 2018). These differences are likely due to methodological and contextual differences. Whereas earlier research focused on above-ground *Striga* counts in well-managed, long-established PP fields, our study assessed the seed bank as a measure influenced by multi-year legacy effects and was also conducted across fields with more variable management histories, both of which can mask current management impacts (Murage et al., 2015; Roobroeck et al., 2023).

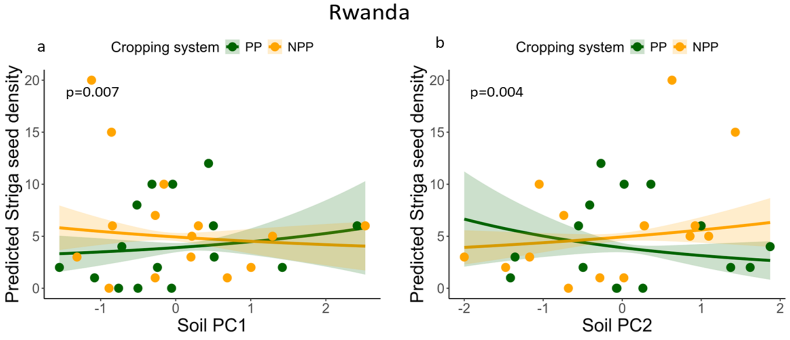


Figure 10: Averaged model-predicted relationship between soil PC1 (high CEC and N, low pH), PC2 (high P infiltration capacity and soil penetration depth).The regression lines indicate model-predicted relationships based on GLMM model averaging of the best support models

4.2.8 Effects of push-pull and soil fertility on pest damage

In **Paper III**, the analysis also revealed that the effect of PP on pest damage varied among countries. In Ethiopia and Uganda, PP consistently reduced pest damage, and these effects appeared independent of underlying soil conditions (Figure 11). We found no evidence that soil fertility gradients further enhanced the reduction of leaf damage associated with PP in any of the countries. This pattern reflects PP's fundamental mechanism of volatile-mediated repellence and attraction (Erdei et al., 2024; Lang et al., 2024), rather than soil-driven processes. The observed independence from soil fertility suggests that the production and emission of these key volatiles by the companion crops *Desmodium* and border grass (*Brachiaria* or *Pennisetum* spp.) could be robust across soil fertility gradients present in Ugandan and Ethiopian fields.

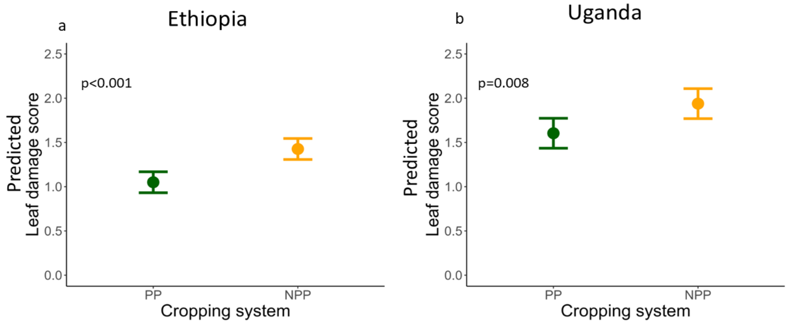


Figure 11: Averaged model-predicted associations between cropping systems and leaf damage by FAW and stem borers in (a) Ethiopia and (b) Uganda. Values represent GLMM estimates (means ± 95% confidence intervals), derived from model averaging of the best-supported models.

In Kenya and Rwanda, we found no evidence that PP or soil fertility gradients enhanced leaf damage reduction, suggesting that unmeasured local factors may have overshadowed the chemical cues central to PP's performance. Landscape features and management practices can strongly influence habitat structure and semiochemical dynamics outcomes (Dassou et al., 2023), and **Paper IV** shows that in Kenya, leaf damage decreased with increasing grass cover and landscape heterogeneity, indicating that landscape complexity can override field-level treatment effects. In Rwanda, seasonality played a dominant role in shaping pest damage, suggesting that landscape and seasonality drivers, rather than soil fertility of the cropping system, govern pest outcomes in Kenya and Rwanda. By contrast, previous studies in Kenya consistently reported significant reductions in FAW and stemborer damage under PP systems (Khan et al., 2006; Midega et al., 2018). The variable results for PP effects on pest damage and *Striga* suppression are explained by different underlying factors: soil conditions were more important to *Striga* responses, whereas pest control was more independent of soil conditions.

5. Conclusion and recommendations

This thesis advances our understanding of how ecological processes shape pest regulation, weed suppression, and soil health within East African smallholder agroecosystems. By integrating natural enemy communities, landscape structure, soil properties, and cropping systems, this thesis provides a comprehensive synthesis of the multi-scale drivers that influence the performance of the push-pull (PP) system. These findings show the context-dependent nature of PP performance and demonstrate how multiple ecological and agronomic factors jointly shape outcomes for smallholder farmers (Catford et al., 2022). Rather than functioning as a "one-size-fits-all" intervention, PP emerges as a system whose performance varies in strength across ecological gradients. Consequently, the effectiveness and long-term resilience of PP depend on how well it is aligned with local agroecological contexts, underscoring the need for site-specific implementation to achieve consistent and sustainable outcomes.

To sustain effective pest regulation in agricultural systems, natural enemy communities are essential. Across the study region, natural enemy communities were consistently dominated by ants, yet their abundance and richness shifted markedly with changes in elevation, landscape complexity, and seasonal conditions (**Papers I** and **IV**). Higher elevations were characterised by more uneven communities dominated by a few genera, whereas lower elevations supported more even and diverse assemblages (**Paper I**). Landscape gradients exerted contrasting influences on natural enemy communities. Natural enemy abundance increased along the forest-cover gradient, whereas landscapes with higher grass cover and greater edge density showed a non-significant tendency toward lower abundance and richness (**Paper IV**). These patterns reveal that landscape effects on natural enemy communities are more nuanced than commonly assumed. Hence, the role of semi-natural habitats in strengthening natural enemy communities appears to be context-dependent rather than universally beneficial within these smallholder systems. Therefore, given the inconsistent landscape effects observed in this thesis, landscape management should be guided by local evidence rather than the general assumption about increased habitat complexity.

In **Paper IV**, pest damage from key maize pests (fall armyworms and stemborers) was influenced by landscape heterogeneity, cropping system, and seasonal dynamics. Structurally simple landscapes experienced higher pest pressure, whereas more heterogeneous landscapes showed reduced pest damage. These patterns did not correspond to changes in natural enemy abundance, suggesting that predators were not the primary mechanism. Instead, landscape effects may reflect processes such as resource concentration, where pests can be reduced by decreasing cropland. Seasonal changes altered both pest pressure and natural enemy abundance, demonstrating that pest control outcomes cannot be uncoupled from broader climatic cycles, since temperature and rainfall influence insect physiology and dispersal, as well as cropping decisions (Rutsaert & Donovan, 2023; Terblanche et al., 2024). Notably, PP consistently reduced pest damage in only two countries, suggesting that its volatile-mediated pest-repelling mechanism is robust to underlying soil differences. Because the landscape structure did not clearly mediate pest damage through natural enemies, field-level practices such as cropping decisions and diversification may offer more practical leverage points for farmers.

In contrast, PP's suppression of *Striga* showed context-dependent patterns, with soil properties moderating its effectiveness in only one country (**Paper III**). The results show that PP can be particularly effective under uniformly low soil fertility or physically constrained soils, where *Striga* pressure is typically high, and *Desmodium's* suppressive mechanism may have greater influence (Khan et al., 2010). However, in countries with limited soil variation or low *Striga* pressure, interactions between PP and soil could not be detected, likely because the absence of strong soil gradients or existing seedbank legacies obscured moderating effects. These findings highlight that *Striga* suppression is shaped not only by the PP mechanism itself but also by soil processes and long-term field management. Thus, integrated soil fertility management combining organic amendments, adequate fertiliser inputs, and protection of soil organic matter is essential. Ensuring farmers have access to quality *Desmodium* seed and clear guidance on establishment and biomass management will further strengthen outcomes.

In **Paper II**, high *Desmodium* cover emerged as a contributor to soil fertility within PP fields, by enhancing soil organic matter, nutrient concentrations, and P availability. Field age further modulated soil fertility, with some PP fields showing gradual nutrient depletion over time, likely due to biomass export and fertilisation practices, while others showed gradual accumulation of SOM under consistent management. These findings highlight the importance of balanced nutrient management and of recognising the long-term consequences of biomass utilisation and fertiliser choice in PP systems. Because *Desmodium* plays a central role in PPs' soil-improving functions, biomass should not be excessively harvested, as residue retention supports soil organic matter, nutrient availability, and the long-term soil-improving functions of PP. Fertiliser choice should avoid practices that contribute to soil acidification or nutrient depletion over time.

Based on these insights, tailoring PP interventions to local agroecological conditions remains important, particularly regarding soil fertility. Although PP often performed independently of soil variation, pairing the system with targeted soil amendments may be beneficial in areas with severely degraded soils. Furthermore, strengthening smallholder farmers' knowledge and reliable inputs is also crucial. Farmer training on pest and weed ecology, *Desmodium* and pull-crop management, soil fertility, and core PP principles, alongside improved access to quality *Desmodium* seeds, trap grasses, and appropriate fertiliser sources, will help reduce implementation failures. Finally, consideration of long-term soil trajectories through nutrient budgeting to optimise on fertiliser use and monitoring can help prevent gradual acidification or nutrient depletion that may undermine PP’s long-term benefits.

In conclusion, this thesis reveals how biodiversity, soils and landscapes jointly shape the success of PP as an ecological intensification strategy in East African smallholder farming systems. Yet much remains to be uncovered about the subtle interactions that govern life within these agroecosystems.

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6. Future perspective

Papers I and **IV** investigated natural enemy communities, pest damage and performance of push-pull (PP) systems across gradients of elevation, landscape structure, and two contrasting seasons in East African smallholder farms. However, the study captured only a subset of the ecological and management variability characteristic of smallholder systems in sub-Saharan Africa, which limits broader generalisation of landscape-pest-enemy relationships. While landscape structure and seasonality explained some of the observed context dependency, a substantial proportion of variation in pest damage and PP performance remained unexplained. Future research should therefore extend beyond landscape composition alone to examine additional drivers of context dependence, including within-field management practices (e.g. crop variety choice, *Desmodium* density, biomass removal, fertiliser use), pest pressure history, and climatic variability. To advance mechanistic understanding, future studies should identify which specific habitat elements (e.g. forests, grasslands, field margins) and landscape configurations meaningfully support natural enemies, and how these interact with local field conditions such as crop phenology, management intensity, and seasonal dynamics to influence pest populations and PP performance. Studies that explicitly link landscape structure to natural enemy behaviour, pest colonisation dynamics, and crop damage will be crucial for clarifying when and why landscape effects translate into effective biological control. Long-term monitoring that integrates seasonal variability and farmer management will further help determine under which conditions landscape structure amplifies, dampens, or becomes decoupled from pest suppression in heterogeneous smallholder systems

Paper II examined how *Desmodium* cover and field age shape soil fertility within PP systems, showing that *Desmodium* contributes to increased SOM, nutrient availability, and P mobilisation, while long-term management determines whether soils accumulate or lose fertility over time. Although soil types were considered during field selection, the study captured only part of the soil diversity present across regions where PP is implemented. Future research should therefore investigate PP performance across a wider range of soil constraints and management histories, including differences in biomass utilisation, fertiliser regimes, and *Desmodium* varieties. Such work would help disentangle how management decisions interact with inherent soil properties to shape long-term soil trajectories and crop performance under

Paper III demonstrated that soil conditions influence the effectiveness of PP in suppressing *Striga*, with soil moderation detected in only one country and the strongest effects occurring in uniformly low-fertility or physically constrained soils. However, the study captured only a subset of the soil and *Striga* variability present across PP-growing regions. Future research should examine PP performance across broader gradients of soil fertility, subsoil constraints, and *Striga* seedbank densities, while also accounting for land-use history, seedbank legacy effects, and variation among *Striga* ecotypes. The role of soil microbial communities also warrants further investigation, as interactions between *Desmodium*, rhizosphere microbes, and nutrient cycling may contribute to geographic variation in PP effectiveness.

Finally, future work would benefit from integrative approaches that explicitly link multiple drivers of context dependence, landscape structure, soil fertility, management practices, and seasonal variability to crop yield outcomes. Structural equation modelling or similar frameworks could help disentangle direct and indirect pathways through which PP influences yields via pest suppression, weed control, soil fertility, and biodiversity. Such integrative analyses would strengthen our ability to predict where and when PP delivers the greatest benefits and guide its adaptation and scaling across diverse smallholder farming systems.

References

Abbas, A., Ullah, F., Hafeez, M., Han, X., Dara, M. Z. N., Gul, H., & Zhao, C. R. (2022). Biological Control of Fall Armyworm, Spodoptera frugiperda. *Agronomy*, *12*(11), 2704. https://doi.org/10.3390/agronomy12112704

Achury, R., Clement, L., Ebeling, A., Meyer, S., Voigt, W., & Weisser, W. W. (2022). Plant diversity and functional identity alter ant occurrence and activity in experimental grasslands. *Ecosphere*, *13*(10), e4252. https://doi.org/10.1002/ecs2.4252

Adhikari, U., Nejadhashemi, A. P., & Woznicki, S. A. (2015). Climate change and eastern Africa: A review of impact on major crops. *Food and Energy Security*, *4*(2), 110–132. https://doi.org/10.1002/fes3.61

Alexandridis, N., Feit, B., Kihara, J., Luttermoser, T., May, W., Midega, C., Öborn, I., Poveda, K., Sileshi, G. W., Zewdie, B., Clough, Y., & Jonsson, M. (2023). Climate change and ecological intensification of agriculture in sub-Saharan Africa – A systems approach to predict maize yield under push-pull technology. *Agriculture, Ecosystems & Environment*, *352*, 108511. https://doi.org/10.1016/j.agee.2023.108511

Alimagham, S., Van Loon, M. P., Ramirez-Villegas, J., Adjei-Nsiah, S., Baijukya, F., Bala, A., Chikowo, R., Silva, J. V., Soulé, A. M., Taulya, G., Tenorio, F. A., Tesfaye, K., & Van Ittersum, M. K. (2024). Climate change impact and adaptation of rainfed cereal crops in sub-Saharan Africa. *European Journal of Agronomy*, *155*, 127137. https://doi.org/10.1016/j.eja.2024.127137

Altieri, M., & Nicholls, C. (2018). *Biodiversity and Pest Management in Agroecosystems* (0 edn). CRC Press. https://doi.org/10.1201/9781482277937

Andow, D. A. (1991). Vegetational Diversity and Arthropod Population Response. *Annual Review of Entomology*, *36*(1), 561–586. https://doi.org/10.1146/annurev.en.36.010191.003021

Asfaw, D. M., Asnakew, Y. W., Sendkie, F. B., Abdulkadr, A. A., Mekonnen, B. A., Tiruneh, H. D., & Ebad, A. M. (2024). Analysis of constraints and opportunities in maize production and marketing in Ethiopia. *Heliyon*, *10*(20), e39606. https://doi.org/10.1016/j.heliyon.2024.e39606

Avalos, S., González, E., Mangeaud, A., & Valladares, G. (2020). Caterpillar-parasitoid food webs and biological control in two extensive crops. *Biological Control*, *143*, 104184. https://doi.org/10.1016/j.biocontrol.2019.104184

Ayongwa, G. C. (2011). *Understanding the diverse roles of soil organic matter in the cereal – Striga hermontica interaction* [Wageningen University]. chrome-extension://efaidnbmnnnibpcajpcglclefindmkaj/https://edepot.wur.nl/161327

Bailey-Serres, J., Parker, J. E., Ainsworth, E. A., Oldroyd, G. E. D., & Schroeder, J. I. (2019). Genetic strategies for improving crop yields. *Nature*, *575*(7781), 109–118. https://doi.org/10.1038/s41586-019-1679-0

Bayu, W., Rethman, N. F. G., & Hammes, P. S. (2005). The Role of Animal Manure in Sustainable Soil Fertility Management in Sub-Saharan Africa: A Review. *Journal of Sustainable Agriculture*, *25*(2), 113–136. https://doi.org/10.1300/J064v25n02_09

Bedasa, Y., Gemechu, A., Bedemo, A., Gebissa, B., & Xiuguang, B. (2025). Impacts of climate and non-climate factors on cereal crop yield in East Africa: A generalized method of moments (GMM) panel data analysis. *Journal of Agriculture and Food Research*, *21*, 101829. https://doi.org/10.1016/j.jafr.2025.101829

Beegle, K., Christiaensen, L., Dabalen, A., & Gaddis, I. (2016). *Poverty in a Rising Africa*. Washington, DC: World Bank. https://doi.org/10.1596/978-1-4648-0723-7

Beillouin, D., Ben-Ari, T., Malézieux, E., Seufert, V., & Makowski, D. (2021). Positive but variable effects of crop diversification on biodiversity and ecosystem services. *Global Change Biology*, *27*(19), 4697–4710. https://doi.org/10.1111/gcb.15747

Berner, D. K., Winslow, M. D, & Awad, A. E. (1997). *Striga research methods*. The Pan-African *Striga* Control Network (PASCON) and the International Institute of Tropical Agriculture.

Bianchi, F. J. J. A., Booij, C. J. H., & Tscharntke, T. (2006). Sustainable pest regulation in agricultural landscapes: A review on landscape composition, biodiversity and natural pest control. *Proceedings of the Royal Society B: Biological Sciences*, *273*(1595), 1715–1727. https://doi.org/10.1098/rspb.2006.3530

Boda, C. S., Akorsu, A. D., Armah, F. A., Atwiine, A., Byaruhanga, R., Chambati, W., Ekumah, B., Faran, T., Hombey, C. T., Isgren, E., Jerneck, A., Mazwi, F., Mpofu, E., Ndhlovu, D., Ocen, L., & Sibanda, M. (2024). Visions of sustainable development and the future of smallholder farmers in sub-Saharan Africa (and beyond). *Frontiers in Sustainable Food Systems*, *8*. https://doi.org/10.3389/fsufs.2024.1357574

Bommarco, R., Kleijn, D., & Potts, S. G. (2013). Ecological intensification: Harnessing ecosystem services for food security. *Trends in Ecology & Evolution*, *28*(4), 230–238. https://doi.org/10.1016/j.tree.2012.10.012

Bouyoucos, G. J. (1962). Hydrometer Method Improved for Making Particle Size Analyses of Soils[1]. *Agronomy Journal*, *54*(5), 464–465. https://doi.org/10.2134/agronj1962.00021962005400050028x

Brévault, T., Sow, A., Coulibaly, M., Mboh, M., & Maïga, D. S. (2025). *Integrating Landscape Complexity and Agroecological Maize Crop Management to Mitigate Fall Armyworm Incidence in West Africa*. Elsevier BV. https://doi.org/10.2139/ssrn.5347187

Brusse, T., Thénard, J., Marrec, R., & Caro, G. (2024). *Farming practices in the landscape have an impact on grassland arthropods, in addition to local conditions and land cover*. Ecology. https://doi.org/10.1101/2024.11.25.625040

Bununu, Y. A., Bello, A., & Ahmed, A. (2023). Land cover, land use, climate change and food security. *Sustainable Earth Reviews*, *6*(1). https://doi.org/10.1186/s42055-023-00065-4

Burnham, K. P., Anderson, D. R., & Anderson, D. R. (2010). *Model selection and multimodel inference: A practical information-theoretic approach* (2. ed., [4. printing]). Springer.

Carbonne, B., Bohan, D. A., Foffová, H., Daouti, E., Frei, B., Neidel, V., Saska, P., Skuhrovec, J., & Petit, S. (2022). Direct and indirect effects of landscape and field management intensity on carabids through trophic resources and weeds. *Journal of Applied Ecology*, *59*(1), 176–187. https://doi.org/10.1111/1365-2664.14043

Catford, J. A., Wilson, J. R. U., Pyšek, P., Hulme, P. E., & Duncan, R. P. (2022). Addressing context dependence in ecology. *Trends in Ecology & Evolution*, *37*(2), 158–170. https://doi.org/10.1016/j.tree.2021.09.007

Ceia-Hasse, A., Boieiro, M., Soares, A., Antunes, S., Figueiredo, H., Rego, C., Borges, P. A. V., Conde, J., & Serrano, A. R. M. (2023). Drivers of Insect Community Change along the Margins of Mountain Streams in Serra da Estrela Natural Park (Portugal). *Insects*, *14*(3), 243. https://doi.org/10.3390/insects14030243

Charyulu, D. K., Afari-Sefa, V., & Gumma, M. K. (2024). Trends in Global Sorghum Production: Perspectives and Limitations. In E. Habyarimana, M. A. Nadeem, F. S. Baloch, & N. Zencirci (Eds), *Omics and Biotechnological Approaches for Product Profile-Driven Sorghum Improvement* (pp. 1–19). Springer Nature Singapore. https://doi.org/10.1007/978-981-97-4347-6_1

Chepchirchir, R. T., Macharia, I., Murage, A. W., Midega, C. A. O., & Khan, Z. R. (2018). Ex-post economic analysis of push-pull technology in Eastern Uganda. *Crop Protection*, *112*, 356–362. https://doi.org/10.1016/j.cropro.2018.07.001

Cheruiyot, D., Chidawanyika, F., Midega, C. A. O., Pittchar, J. O., Pickett, J. A., & Khan, Z. R. (2021). Field evaluation of a new third generation push-pull technology for control of *striga* weed, stemborers, and fall armyworm in western Kenya. *Experimental Agriculture*, *57*(5–6), 301–315. https://doi.org/10.1017/S0014479721000260

Chianu, J. N., Mairura, F., Ekise, I., & Chianu, J. N. (2008). *Farm input marketing in western Kenya: Challenges and opportunities*. *3*, 167–173.

Chidawanyika, F., Omuse, E. R., Agutu, L. O., Pittchar, J. O., Nyagol, D., & Khan, Z. R. (2025). An Intensified Cereal Push-Pull System Reduces Pest Infestation and Confers Yield Advantages in High-Value Vegetables. *Journal of Crop Health*, *77*(1), 40. https://doi.org/10.1007/s10343-024-01107-3

Chrysargyris, A., Drouza, C., & Tzortzakis, N. (2017). Optimization of potassium fertilization/nutrition for growth, physiological development, essential oil composition and antioxidant activity of Lavandula angustifolia Mill. *Journal of Soil Science and Plant Nutrition*, *ahead*, 0–0. https://doi.org/10.4067/S0718-95162017005000023

Clarkson, J., Borah, J. R., Baudron, F., & Sunderland, T. C. H. (2022). Forest Proximity Positively Affects Natural Enemy Mediated Control of Fall Armyworm in Southern Africa. *Frontiers in Forests and Global Change*, *5*. https://doi.org/10.3389/ffgc.2022.781574

Da Silva, V. F., Dos Santos, A., Silveira, L. C. P., Tomazella, V. B., & Ferraz, R. M. (2022). Push-pull cropping system reduces pests and promotes the abundance and richness of natural enemies in brassica vegetable crops. *Biological Control*, *166*, 104832. https://doi.org/10.1016/j.biocontrol.2021.104832

Daelemans, R., Hulsmans, E., Laenen, E., Remy, S., Beliën, T., & Honnay, O. (2023). Direct and indirect effects of management and landscape on biological pest control and crop pest infestation in apple orchards. *Journal of Applied Ecology*, *60*(1), 181–192. https://doi.org/10.1111/1365-2664.14319

Dainese, M., Martin, E. A., Aizen, M. A., Albrecht, M., Bartomeus, I., Bommarco, R., Carvalheiro, L. G., Chaplin-Kramer, R., Gagic, V., Garibaldi, L. A., Ghazoul, J., Grab, H., Jonsson, M., Karp, D. S., Kennedy, C. M., Kleijn, D., Kremen, C., Landis, D. A., Letourneau, D. K., … Steffan-Dewenter, I. (2019). A global synthesis reveals biodiversity-mediated benefits for crop production. *SCIENCE ADVANCES*.

Dassou, A. G., Idohou, R., Azandémè-Hounmalon, G. Y., Sabi-Sabi, A., Houndété, J., Silvie, P., & Dansi, A. (2021). Fall armyworm, Spodoptera frugiperda (J.E. Smith) in maize cropping systems in Benin: Abundance, damage, predatory ants and potential control. *International Journal of Tropical Insect Science*, *41*(4), 2627–2636. https://doi.org/10.1007/s42690-021-00443-5

Dassou, A. G., Laura Estelle Loko, Y., Toffa, J., Gbèmavo, C., Adjahossou, N., Tchakpa, C., Agboyi, L. K., Sanon, A., Dansi, A., & Brévault, T. (2023). Within-field crop diversity and landscape complexity decrease the abundance of fall armyworm larvae in maize cropping systems. *Biological Control*, *183*, 105260. https://doi.org/10.1016/j.biocontrol.2023.105260

Day, R., Abrahams, P., Bateman, M., Beale, T., Clottey, V., Cock, M., Colmenarez, Y., Corniani, N., Early, R., Godwin, J., Gomez, J., Moreno, P. G., Murphy, S. T., Oppong-Mensah, B., Phiri, N., Pratt, C., Silvestri, S., & Witt, A. (2017). Fall Armyworm: Impacts and Implications for Africa. *Outlooks on Pest Management*, *28*(5), 196–201. https://doi.org/10.1564/v28_oct_02

De Groote, H. (2002). Maize Yield Losses from Stemborers in Kenya. *International Journal of Tropical Insect Science*, *22*(02), 89–96. https://doi.org/10.1017/s1742758400015162

De Groote, H., Kimenju, S. C., Munyua, B., Palmas, S., Kassie, M., & Bruce, A. (2020). Spread and impact of fall armyworm (Spodoptera frugiperda J.E. Smith) in maize production areas of Kenya. *Agriculture, Ecosystems & Environment*, *292*, 106804. https://doi.org/10.1016/j.agee.2019.106804

De Mey, Y., Demont, M., & Diagne, M. (2012). Estimating Bird Damage to Rice in Africa: Evidence from the Senegal River Valley. *Journal of Agricultural Economics*, *63*(1), 175–200. https://doi.org/10.1111/j.1477-9552.2011.00323.x

Debinski, D. M. (2023). Insects in Grassland Ecosystems. In *Rangeland Wildlife Ecology and Conservation* (pp. 897–929). Springer, Cham. https://doi.org/10.1007/978-3-031-34037-6_26

Dessalegn, O. G., & Akalu, D. S. (2015). The impacts of climate change on African continent and the way forward. *Journal of Ecology and The Natural Environment*, *7*(10), 256–262. https://doi.org/10.5897/JENE2015.0533

Divito, G. A., & Sadras, V. O. (2014). How do phosphorus, potassium and sulphur affect plant growth and biological nitrogen fixation in crop and pasture legumes? A meta-analysis. *Field Crops Research*, *156*, 161–171. https://doi.org/10.1016/j.fcr.2013.11.004

DLCO-EA. (2022). *Quelea birds control operation in Ethiopia* [Deseart Locust Control Organisation for East Africa]. https://dlco-ea.org/quelea-birds-control-operation-in-ethiopia-december-2022/#:~:text=The%20Red%E2%80%93billed%20quelea%20is,cereals%20in%20Sub%2DSaharan%20Africa.

Drinkwater, L. E., & Snapp, S. S. (2022). Advancing the science and practice of ecological nutrient management for smallholder farmers. *Frontiers in Sustainable Food Systems*, *6*, 921216. https://doi.org/10.3389/fsufs.2022.921216

Duarte, G. T., Santos, P. M., Cornelissen, T. G., Ribeiro, M. C., & Paglia, A. P. (2018). The effects of landscape patterns on ecosystem services: Meta-analyses of landscape services. *Landscape Ecology*, *33*(8), 1247–1257. https://doi.org/10.1007/s10980-018-0673-5

Edwards, C. A., & Arancon, N. Q. (2022). Earthworms, Soil Structure, Fertility, and Productivity. In C. A. Edwards & N. Q. Arancon, *Biology and Ecology of Earthworms* (pp. 303–334). Springer US. https://doi.org/10.1007/978-0-387-74943-3_10

Ellis, F. (2000). *Peasant economics: Farm households and agrarian development* (2. ed., reprinted). Cambridge Univ. Press.

Emeraghi, M., Achigan-Dako, E. G., Nwaoguala, C. N. C., & Oselebe, H. (2021). Maize streak virus research in Africa: An end or a crossroad. *Theoretical and Applied Genetics*, *134*(12), 3785–3803. https://doi.org/10.1007/s00122-021-03914-y

Erdei, A. L., David, A. B., Savvidou, E. C., Džemedžionaitė, V., Chakravarthy, A., Molnár, B. P., & Dekker, T. (2024). The push–pull intercrop Desmodium does not repel, but intercepts and kills pests. *eLife*, *13*, e88695. https://doi.org/10.7554/eLife.88695

Erenstein, O., Jaleta, M., Sonder, K., Mottaleb, K., & Prasanna, B. M. (2022). Global maize production, consumption and trade: Trends and R&D implications. *Food Security*, *14*(5), 1295–1319. https://doi.org/10.1007/s12571-022-01288-7

FAO (Ed.). (2007). *Mapping biophysical factors that influence agricultural production and rural vulnerability*. FAO. https://www.fao.org/4/a1075e/a1075e00.htm

FAO. (2025a). *FAOSTAT*. Food and Agriculture Organisation of the United Nations. https://www.fao.org/faostat/en/#data/QCL

FAO. (2025b). *One pest, many risks: Quelea birds and the case for safer control* [Food and Agriculture Organisation]. https://www.fao.org/one-health/highlights/quelea-birds-and-the-case-for-safer-control/en#:~:text=Each%20year%2C%20enormous%20flocks%20of,rice%20and%20wheat%20within%20hours.

Farooq, M. O., Razaq, M., & Shah, F. M. (2022). Plant diversity promotes species richness and community stability of arthropods in organic farming. *Arthropod-Plant Interactions*, *16*(6), 593–606. https://doi.org/10.1007/s11829-022-09920-1

Feit, B., Blüthgen, N., Daouti, E., Straub, C., Traugott, M., & Jonsson, M. (2021). Landscape complexity promotes resilience of biological pest control to climate change. *Proceedings of the Royal Society B: Biological Sciences*, *288*(1951), 20210547. https://doi.org/10.1098/rspb.2021.0547

Ferris, S., Robbins, P., Best, R., Seville, D., & Buxton, A. (2014). *Linking Smallholder Farmers to Markets and the Implications for Extension and Advisory Services*. International Institute for Environment and Development. chrome-extension://efaidnbmnnnibpcajpcglclefindmkaj/https://agritech.tnau.ac.in/

dmi/2013/pdf/MEAS%20Discussion%20Paper%204%20-%20Linking%20Farmers%20To%20Markets%20-%20May%202014.pdf

Fischer, C., Gerstmeier, R., & Wagner, T. C. (2022). Seasonal and temporal patterns of rainfall shape arthropod community composition and multi-trophic interactions in an arid environment. *Scientific Reports*, *12*(1), 3742. https://doi.org/10.1038/s41598-022-07716-0

Foley, J. A., Ramankutty, N., Brauman, K. A., Cassidy, E. S., Gerber, J. S., Johnston, M., Mueller, N. D., O’Connell, C., Ray, D. K., West, P. C., Balzer, C., Bennett, E. M., Carpenter, S. R., Hill, J., Monfreda, C., Polasky, S., Rockström, J., Sheehan, J., Siebert, S., … Zaks, D. P. M. (2011). Solutions for a cultivated planet. *Nature*, *478*(7369), 337–342. https://doi.org/10.1038/nature10452

Furlong, M. J., & Zalucki, M. P. (2010). Exploiting predators for pest management: The need for sound ecological assessment. *Entomologia Experimentalis et Applicata*, *135*(3), 225–236. https://doi.org/10.1111/j.1570-7458.2010.00988.x

Gallardo-López, F., Hernández-Chontal, M. A., Cisneros-Saguilán, P., & Linares-Gabriel, A. (2018). Development of the Concept of Agroecology in Europe: A Review. *Sustainability*, *10*(4), 1210. https://doi.org/10.3390/su10041210

Gerlich, H. S., Holmstrup, M., Schmidt, N. M., & Høye, T. T. (2025). Phenological responses to climate change across taxa and local habitats in a high-Arctic arthropod community. *Ecological Monographs*, *95*(1), e1643. https://doi.org/10.1002/ecm.1643

Gharde, Y., Singh, P. K., Dubey, R. P., & Gupta, P. K. (2018). Assessment of yield and economic losses in agriculture due to weeds in India. *Crop Protection*, *107*, 12–18. https://doi.org/10.1016/j.cropro.2018.01.007

Gliessman, S. R. (1990). Agroecology: Researching the Ecological Basis for Sustainable Agriculture. In S. R. Gliessman (Ed.), *Agroecology* (Vol. 78, pp. 3–10). Springer New York. https://doi.org/10.1007/978-1-4612-3252-0_1

Gómez y Paloma, S. (with Riesgo, L., & Louhichi, K.). (2020). *The Role of Smallholder Farms in Food and Nutrition Security* (1st ed). Springer International Publishing AG. https://doi.org/10.1007/978-3-030-42148-9

Gonçalves, M. C., Ramos, A., Nascimento, T., Harakava, R., Duarte, A. P., & Lopes, J. R. S. (2020). Aphid transmission of maize yellow mosaic virus: An emerging polerovirus. *Tropical Plant Pathology*, *45*(5), 544–549. https://doi.org/10.1007/s40858-020-00374-5

González, E., Bianchi, F. J. J. A., Eckerter, P. W., Pfaff, V., Weiler, S., & Entling, M. H. (2022). Ecological requirements drive the variable responses of wheat pests and natural enemies to the landscape context. *Journal of Applied Ecology*, *59*(2), 444–456. https://doi.org/10.1111/1365-2664.14062

Grande, T. O., Aguiar, L. M. S., & Machado, R. B. (2020). Heating a biodiversity hotspot: Connectivity is more important than remaining habitat. *Landscape Ecology*, *35*(3), 639–657. https://doi.org/10.1007/s10980-020-00968-z

Grigg, D. B. (1974). *The Agricultural Systems of the World: An Evolutionary Approach* (1st edn). Cambridge University Press. https://doi.org/10.1017/CBO9780511665882

Haan, N. L., Zhang, Y., & Landis, D. A. (2020). Predicting Landscape Configuration Effects on Agricultural Pest Suppression. *Trends in Ecology & Evolution*, *35*(2), 175–186. https://doi.org/10.1016/j.tree.2019.10.003

Hadebe, S. T., Modi, A. T., & Mabhaudhi, T. (2017). Drought Tolerance and Water Use of Cereal Crops: A Focus on Sorghum as a Food Security Crop in Sub-Saharan Africa. *Journal of Agronomy and Crop Science*, *203*(3), 177–191. https://doi.org/10.1111/jac.12191

Hailu, G., Niassy, S., Zeyaur, K. R., Ochatum, N., & Subramanian, S. (2018). Maize–Legume Intercropping and Push–Pull for Management of Fall Armyworm, Stemborers, and Striga in Uganda. *Agronomy Journal*, *110*(6), 2513–2522. https://doi.org/10.2134/agronj2018.02.0110

Hassanali, A., Herren, H., Khan, Z. R., Pickett, J. A., & Woodcock, C. M. (2008). Integrated pest management: The push–pull approach for controlling insect pests and weeds of cereals, and its potential for other agricultural systems including animal husbandry. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *363*(1491), 611–621. https://doi.org/10.1098/rstb.2007.2173

Hayelom, B. T. (2014). *Advance research on Striga control: A review*. https://doi.org/10.5897/AJPS2014.1186

Hazell, P. B. R., & Rahman, A. (Eds). (2014). *New directions for smallholder agriculture* (1st ed). Oxford University Press.

Helms, J. A. (2023). Climate, geography, and the mating phenology of ants. *Insectes Sociaux*, *70*(1), 119–125. https://doi.org/10.1007/s00040-022-00888-y

Herms, D. A., & Mattson, W. J. (1992). The Dilemma of Plants: To Grow or Defend. *The Quarterly Review of Biology*, *67*(3), 283–335. https://doi.org/10.1086/417659

Herrera-Alsina, L., Parvanova, R., Guirguis, J., Bocedi, G., Trethowan, L., Lancaster, L. T., & Travis, J. M. J. (2025). Disentangling evolutionary, geometric and ecological components of the elevational gradient of diversity. *Evolution Letters*, *9*(1), 51–64. https://doi.org/10.1093/evlett/qrae048

Hession, S. L., & Moore, N. (2011). A spatial regression analysis of the influence of topography on monthly rainfall in East Africa. *International Journal of Climatology*, *31*(10), 1440–1456. https://doi.org/10.1002/joc.2174

Hiron, M., Rubene, D., Mweresa, C. K., Ajamma, Y. U., Owino, E. A., & Low, M. (2014). Crop damage by granivorous birds despite protection efforts by human bird scarers in a sorghum field in western Kenya. *Ostrich*, *85*(2), 153–159. https://doi.org/10.2989/00306525.2014.937368

Hodkinson, I. D. (2005). Terrestrial insects along elevation gradients: Species and community responses to altitude. *Biological Reviews*, *80*(3), 489–513. https://doi.org/10.1017/S1464793105006767

Hohlenwerger, C., Tambosi, L. R., & Metzger, J. P. (2022). Forest cover and proximity to forest affect predation by natural enemies in pasture and coffee plantations differently. *Agriculture, Ecosystems & Environment*, *333*, 107958. https://doi.org/10.1016/j.agee.2022.107958

Høye, T. T. (2020). Arthropods and climate change – arctic challenges and opportunities. *Current Opinion in Insect Science*, *41*, 40–45. https://doi.org/10.1016/j.cois.2020.06.002

Huang, R. (2018). Research progress on plant tolerance to soil salinity and alkalinity in sorghum. *Journal of Integrative Agriculture*, *17*(4), 739–746. https://doi.org/10.1016/S2095-3119(17)61728-3

IGC Report. (2024). https://www.sorghum-id.com/en/sorghum-continues-growing-worldwide/

Ikazaki, K., Nagumo, F., Simporé, S., & Barro, A. (2024). Understanding yield-limiting factors for sorghum in semi-arid sub-Saharan Africa: Beyond soil nutrient deficiency. *Soil Science and Plant Nutrition*, *70*(2), 114–122. https://doi.org/10.1080/00380768.2023.2279582

Indeje, M., Semazzi, F. H. M., Xie, L., & Ogallo, L. J. (2001). Mechanistic Model Simulations of the East African Climate Using NCAR Regional Climate Model: Influence of Large-Scale Orography on the Turkana Low-Level Jet. *Journal of Climate*, *14*(12), 2710–2724. https://doi.org/10.1175/1520-0442(2001)014%253C2710:MMSOTE%253E2.0.CO;2

Jacobsen, D. (2020). The dilemma of altitudinal shifts: Caught between high temperature and low oxygen. *Frontiers in Ecology and the Environment*, *18*(4), 211–218. https://doi.org/10.1002/fee.2161

Jaworski, C. C., Thomine, E., Rusch, A., Lavoir, A.-V., Wang, S., & Desneux, N. (2023). Crop diversification to promote arthropod pest management: A review. *Agriculture Communications*, *1*(1), 100004. https://doi.org/10.1016/j.agrcom.2023.100004

Jeger, Gilijamse, Bock, & Frinking. (1998). The epidemiology, variability and control of the downy mildews of pearl millet and sorghum, with particular reference to Africa. *Plant Pathology*, *47*(5), 544–569. https://doi.org/10.1046/j.1365-3059.1998.00285.x

Jones, A., Breuning-Madsen, H., Brossard, M., Dampha, A., Deckers, J., Dewitte, O., Gallali, T., Hallett, S., Jones, R., Kilasara, M., Le Roux, P., Michel, E., Montanarella, L., Ahmed, O., Thiombiano, L., Van Ranst, E., Yemefack, M., & Zougmoré, R. (2013). *Soil atlas of Africa.* Publications Office. https://data.europa.eu/doi/10.2788/52319

Jonsson, M., Kaartinen, R., & Straub, C. S. (2017). Relationships between natural enemy diversity and biological control. *Current Opinion in Insect Science*, *20*, 1–6. https://doi.org/10.1016/j.cois.2017.01.001

Jonsson, M., Straub, C. S., Didham, R. K., Buckley, H. L., Case, B. S., Hale, R. J., Gratton, C., & Wratten, S. D. (2015). Experimental evidence that the effectiveness of conservation biological control depends on landscape complexity. *Journal of Applied Ecology*, *52*(5), 1274–1282. https://doi.org/10.1111/1365-2664.12489

Kamil Bartoń. (2024). *MuMIn: Multi-Model Inference* (p. 1.47.5) [Data set]. https://doi.org/10.32614/CRAN.package.MuMIn

Karp, D. S., Chaplin-Kramer, R., Meehan, T. D., Martin, E. A., DeClerck, F., Grab, H., Gratton, C., Hunt, L., Larsen, A. E., Martínez-Salinas, A., O'Rourke, M. E., Rusch, A., Poveda, K., Jonsson, M., Rosenheim, J. A., Schellhorn, N. A., Tscharntke, T., Wratten, S. D., Zhang, W., … Zou, Y. (2018). Crop pests and predators exhibit inconsistent responses to surrounding landscape composition. *Proceedings of the National Academy of Sciences*, *115*(33). https://doi.org/10.1073/pnas.1800042115

Kebede, E. (2021). Contribution, Utilization, and Improvement of Legumes-Driven Biological Nitrogen Fixation in Agricultural Systems. *Frontiers in Sustainable Food Systems*, *5*, 767998. https://doi.org/10.3389/fsufs.2021.767998

Khaliq, I., Shahid, M. J., Kamran, H., Sheraz, M., Awais, M., Shabir, M., Asghar, M., Rehman, A., Riaz, M., Braschler, B., Sanders, N. J., & Hof, C. (2023). The role of thermal tolerance in determining elevational distributions of four arthropod taxa in mountain ranges of southern Asia. *Journal of Animal Ecology*, *92*(10), 2052–2066. https://doi.org/10.1111/1365-2656.13996

Khan, Z. R., Hassanali, A., Overholt, W., Khamis, T. M., Hooper, A. M., Pickett, J. A., Wadhams, L. J., & Woodcock, C. M. (2002). Control of witchweed Striga hermonthica by Intercropping with Desmodium spp., and the Mechanism Defined as Allelopathic. *Journal of Chemical Ecology*.

Khan, Z. R., Midega, C. A. O., Bruce, T. J. A., Hooper, A. M., & Pickett, J. A. (2010). Exploiting phytochemicals for developing a 'push-pull' crop protection strategy for cereal farmers in Africa. *Journal of Experimental Botany*, *61*(15), 4185–4196. https://doi.org/10.1093/jxb/erq229

Khan, Z. R., Midega, C. A. O., Pittchar, J. O., Murage, A. W., Birkett, M. A., Bruce, T. J. A., & Pickett, J. A. (2014). Achieving food security for one million sub-Saharan African poor through push–pull innovation by 2020. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *369*(1639), 20120284. https://doi.org/10.1098/rstb.2012.0284

Khan, Z. R., Pickett, J. A., Wadhams, L. J., Hassanali, A., & Midega, C. A. O. (2006). Combined control of Striga hermonthica and stemborers by maize–

Desmodium spp. Intercrops. *Crop Protection*, *25*(9), 989–995. https://doi.org/10.1016/j.cropro.2006.01.008

Klages, K. H. (1928). Crop Ecology and Ecological Crop Geography in the Agronomic Curriculum[1]. *Agronomy Journal*, *20*(4), 336–353. https://doi.org/10.2134/agronj1928.00021962002000040002x

Koffi, D., Kyerematen, R., Eziah, V. Y., Agboka, K., Adom, M., Goergen, G., & Meagher, R. L. (2020). Natural Enemies of the Fall Armyworm, Spodoptera frugiperda (J.E. Smith) (Lepidoptera: Noctuidae) in Ghana. *Florida Entomologist*, *103*(1), 85. https://doi.org/10.1653/024.103.0414

Kome, G. K., Enang, R. K., Tabi, F. O., & Yerima, B. P. K. (2019). Influence of Clay Minerals on Some Soil Fertility Attributes: A Review. *Open Journal of Soil Science*, *09*(09), 155–188. https://doi.org/10.4236/ojss.2019.99010

Kotir, J. H. (2011). Climate change and variability in Sub-Saharan Africa: A review of current and future trends and impacts on agriculture and food security. *Environment, Development and Sustainability*, *13*(3), 587–605. https://doi.org/10.1007/s10668-010-9278-0

Kountche, B. A., Jamil, M., Yonli, D., Nikiema, M. P., Blanco-Ania, D., Asami, T., Zwanenburg, B., & Al-Babili, S. (2019). Suicidal germination as a control strategy for *Striga hermonthica* (Benth.) in smallholder farms of sub-Saharan Africa. *PLANTS, PEOPLE, PLANET*, *1*(2), 107–118. https://doi.org/10.1002/ppp3.32

Krupek, F. S., Redfearn, D., Eskridge, K. M., & Basche, A. (2022). Ecological intensification with soil health practices demonstrates positive impacts on multiple soil properties: A large-scale farmer-led experiment. *Geoderma*, *409*, 115594. https://doi.org/10.1016/j.geoderma.2021.115594

Kumari, V. V., Balloli, S. S., Kumar, M., Ramana, D. B. V., Prabhakar, M., Osman, M., Indoria, A. K., Manjunath, M., Maruthi, V., Chary, G. R., Chandran, M. A. S., Gopinath, K. A., Venkatesh, G., Rao, M. S., Singh, V. K., & Timsina, J. (2024). Diversified cropping systems for reducing soil erosion and nutrient loss and for increasing crop productivity and profitability in rainfed environments. *Agricultural Systems*, *217*, 103919. https://doi.org/10.1016/j.agsy.2024.103919

Kunene, C., Foord, S. H., Scharff, N., Pape, T., Malumbres-Olarte, J., & Munyai, T. C. (2022). Ant Diversity Declines with Increasing Elevation along the Udzungwa Mountains, Tanzania. *Diversity*, *14*(4), 260. https://doi.org/10.3390/d14040260

Kuyah, S., Muoni, T., Bayala, J., Chopin, P., Dahlin, A. S., Hughes, K., Jonsson, M., Kumar, S., Sileshi, G. W., Dimobe, K., & Öborn, I. (2023). Grain legumes and dryland cereals contribute to carbon sequestration in the drylands of Africa and South Asia. *Agriculture, Ecosystems & Environment*, *355*, 108583. https://doi.org/10.1016/j.agee.2023.108583

Landis, D. A., Wratten, S. D., & Gurr, G. M. (2000). Habitat Management to Conserve Natural Enemies of Arthropod Pests in Agriculture. *Annual Review of Entomology*, *45*(1), 175–201. https://doi.org/10.1146/annurev.ento.45.1.175

Laub, M., Corbeels, M., MacLaren, C., Ndungu, S. M., Mucheru-Muna, M. W., Mugendi, D., Vanlauwe, B., Waswa, W., Yegon, R., & Six, J. (2025). Maize yield responses to soil organic carbon under integrated soil fertility management in tropical environments. *Agronomy for Sustainable Development*, *45*(6), 63. https://doi.org/10.1007/s13593-025-01054-x

Laubmeier, A. N., Tabassum, N., & Tenhumberg, B. (2023). Temperature fluctuation alters optimal predator community composition for anticipated biological control. *Frontiers in Ecology and Evolution*, *10*, 998396. https://doi.org/10.3389/fevo.2022.998396

Lefcheck, J. S., Byrnes, J. E. K., Isbell, F., Gamfeldt, L., Griffin, J. N., Eisenhauer, N., Hensel, M. J. S., Hector, A., Cardinale, B. J., & Duffy, J. E. (2015). Biodiversity enhances ecosystem multifunctionality across trophic levels and habitats. *Nature Communications*, *6*(1), 6936. https://doi.org/10.1038/ncomms7936

Li, P., Sohail, A., Zeng, F., Hao, Z., & Dong, J. (2024). Setosphaeria turcica, the Maize Leaf Blast Pathogen: Current Status and Infection Mechanisms. *Agronomy*, *14*(7), 1488. https://doi.org/10.3390/agronomy14071488

Lila, T. (2023). *Early maturity products popular among farmers in Kenya*. https://www.cimmyt.org/news/early-maturity-products-popular-among-farmers-in-kenya/

Liu, J., Wu, J., Jiang, D., Chen, S., Hao, M., Ding, F., Wu, G., & Liang, H. (2025). Research on the impact of climate change on food security in Africa. *Scientific Reports*, *15*(1), 31251. https://doi.org/10.1038/s41598-025-14560-5

Loreau, M., & De Mazancourt, C. (2013). Biodiversity and ecosystem stability: A synthesis of underlying mechanisms. *Ecology Letters*, *16*(s1), 106–115. https://doi.org/10.1111/ele.12073

Lu, A., Gonthier, D. J., Sciligo, A. R., Garcia, K., Chiba, T., Juárez, G., & Kremen, C. (2022). Changes in arthropod communities mediate the effects of landscape composition and farm management on pest control ecosystem services in organically managed strawberry crops. *Journal of Applied Ecology*, *59*(2), 585–597. https://doi.org/10.1111/1365-2664.14076

Luttermoser, T., Khan, Z. R., Midega, C. A. O., Nyagol, D., Jonsson, M., & Poveda, K. (2023). Are pests adapting to the push-pull system? Ecologically intensified farms in Kenya maintain successful pest control over time. *Agriculture, Ecosystems & Environment*, *347*, 108345. https://doi.org/10.1016/j.agee.2023.108345

Macfadyen, S., & Muller, W. (2013). Edges in Agricultural Landscapes: Species Interactions and Movement of Natural Enemies. *PLoS ONE*, *8*(3), e59659. https://doi.org/10.1371/journal.pone.0059659

Macfadyen, S., Tay, W. T., Hulthen, A. D., Paull, C., Kalyebi, A., Jacomb, F., Parry, H., Sseruwagi, P., Seguni, Z., Omongo, C. A., Kachigamba, D., Otim, M., Schellhorn, N., Polaszek, A., Colvin, J., & De Barro, P. (2021). Landscape factors and how they influence whitefly pests in cassava fields across East Africa. *Landscape Ecology*, *36*(1), 45–67. https://doi.org/10.1007/s10980-020-01099-1

Maes, O., Rembold, F., Callenius, C., & Van Eynde, E. (2023). *Saharan Africa: The role of fertilisers and soil health* (No. JRC135925). European Commission. https://publications.jrc.ec.europa.eu/repository/handle/JRC135925

Mahuku, G., Lockhart, B. E., Wanjala, B., Jones, M. W., Kimunye, J. N., Stewart, L. R., Cassone, B. J., Sevgan, S., Nyasani, J. O., Kusia, E., Kumar, P. L., Niblett, C. L., Kiggundu, A., Asea, G., Pappu, H. R., Wangai, A., Prasanna, B. M., & Redinbaugh, M. G. (2015). Maize Lethal Necrosis (MLN), an Emerging Threat to Maize-Based Food Security in Sub-Saharan Africa. *Phytopathology®*, *105*(7), 956–965. https://doi.org/10.1094/PHYTO-12-14-0367-FI

Managa, L. R., & Nkobole, N. (2016). Towards Climate-Smart Agricultural Approach: Prospect for Smallholder Farmers in Semi-Arid Regions. *Journal of Agriculture and Environmental Sciences*, *Vol. 5,*(No. 2,), 36–46. https://doi.org/10.15640/jaes.v5n2a5

Marja, R., Tscharntke, T., & Batáry, P. (2022). Increasing landscape complexity enhances species richness of farmland arthropods, agri-environment schemes also abundance – A meta-analysis. *Agriculture, Ecosystems & Environment*, *326*, 107822. https://doi.org/10.1016/j.agee.2021.107822

Martin, E. A., Reineking, B., Seo, B., & Steffan-Dewenter, I. (2013). Natural enemy interactions constrain pest control in complex agricultural landscapes. *Proceedings of the National Academy of Sciences*, *110*(14), 5534–5539. https://doi.org/10.1073/pnas.1215725110

Massawe, D. P., Stewart, L. R., Kamatenesi, J., Asiimwe, T., & Redinbaugh, M. G. (2018). Complete sequence and diversity of a maize-associated Polerovirus in East Africa. *Virus Genes*, *54*(3), 432–437. https://doi.org/10.1007/s11262-018-1560-5

Måsviken, J., Marquina, D., Norén, K., Dalén, L., & Dalerum, F. (2023). Elevational variation of spider and insect communities in the Swedish mountains. *Ecosphere*, *14*(6), e4540. https://doi.org/10.1002/ecs2.4540

McCain, C. M., & Garfinkel, C. F. (2021). Climate change and elevational range shifts in insects. *Current Opinion in Insect Science*, *47*, 111–118. https://doi.org/10.1016/j.cois.2021.06.003

Meena, R. S., Das, A., Yadav, G. S., & Lal, R. (Eds). (2018). *Legumes for Soil Health and Sustainable Management*. Springer Singapore. https://doi.org/10.1007/978-981-13-0253-4

Mesmin, X., Maret, M., Vincent, M., Daniel, L., Gardin, P., Raitif, J., Faloya, V., Cortesero, A.-M., & Le Ralec, A. (2022). Biological control at work: Demonstrating the complementary effects of natural enemies on two contrasting pests and the damage they cause. *Journal of Pest Science*, *95*(2), 653–667. https://doi.org/10.1007/s10340-021-01426-8

Mey, Y. D., & Demont, M. (2013). Bird damage to rice in Africa: Evidence and control. In M. C. S. Wopereis, D. E. Johnson, N. Ahmadi, E. Tollens, & A. Jalloh (Eds), *Realizing Africa's rice promise* (1st edn, pp. 241–249). CABI. https://doi.org/10.1079/9781845938123.0241

Midega, C. A. O., Jonsson, M., Khan, Z. R., & Ekbom, B. (2014b). Effects of landscape complexity and habitat management on stemborer colonization, parasitism and damage to maize. *Agriculture, Ecosystems & Environment*, *188*, 289–293. https://doi.org/10.1016/j.agee.2014.02.028

Midega, C. A. O., Pittchar, J. O., Pickett, J. A., Hailu, G. W., & Khan, Z. R. (2018). A climate-adapted push-pull system effectively controls fall armyworm, Spodoptera frugiperda (J E Smith), in maize in East Africa. *Crop Protection*, *105*, 10–15. https://doi.org/10.1016/j.cropro.2017.11.003

Minato Nakazawa. (2024). *fmsb: Functions for Medical Statistics Book with some Demographic Data* (p. 0.7.6) [Data set]. https://doi.org/10.32614/CRAN.package.fmsb

Mishenin, Y., Yarova, I., & Koblianska, I. (2021). Ecologically Harmonized Agricultural Management for Global Food Security. In M. K. Jhariya, R. S. Meena, & A. Banerjee (Eds), *Ecological Intensification of Natural Resources for Sustainable Agriculture* (pp. 29–76). Springer Singapore. https://doi.org/10.1007/978-981-33-4203-3_2

Mkhabela, T. S. (2006). A Review of the Use of Manure in Small-Scale Crop Production Systems in South Africa. *Journal of Plant Nutrition*, *29*(7), 1157–1185. https://doi.org/10.1080/01904160600767179

Mofokeng, M. A., & Shargie, N. G. (2016). Bird Damage and Control Strategies in Grain Sorghum Production. *International Journal of Agricultural and Environmental Research*, *2*(4), 264-269.

Molotoks, A., Smith, P., & Dawson, T. P. (2021). Impacts of land use, population, and climate change on global food security. *Food and Energy Security*, *10*(1). https://doi.org/10.1002/fes3.261

Morizet-Davis, J., Marting Vidaurre, N. A., Reinmuth, E., Rezaei-Chiyaneh, E., Schlecht, V., Schmidt, S., Singh, K., Vargas-Carpintero, R., Wagner, M., & Von Cossel, M. (2023). Ecosystem Services at the Farm Level—Overview, Synergies, Trade-Offs, and Stakeholder Analysis. *Global Challenges*, *7*(7), 2200225. https://doi.org/10.1002/gch2.202200225

Mphethe, V., Weier, S. M., Swanepoel, L. H., Parker, D., & Taylor, P. J. (2025). Perceived and actual ecosystem services by fruit bats, birds and primates in litchi orchards agroecosystems. *Journal of Applied Ecology*, 1365-2664.70168. https://doi.org/10.1111/1365-2664.70168

Munyai, T. C., & Foord, S. H. (2012). Ants on a mountain: Spatial, environmental and habitat associations along an altitudinal transect in a centre of endemism. *Journal of Insect Conservation*, *16*(5), 677–695. https://doi.org/10.1007/s10841-011-9449-9

Murage, A. W., Midega, C. A. O., Pittchar, J. O., Pickett, J. A., & Khan, Z. R. (2015). Determinants of adoption of climate-smart push-pull technology for enhanced food security through integrated pest management in eastern Africa. *Food Security*, *7*(3), 709–724. https://doi.org/10.1007/s12571-015-0454-9

NAAIAP. (2014). *Soil suitability evaluation for maize production in Kenya*. Ministry of Agriculture, Livestock and Fisheries.

Nair, P. K. R., Kumar, B. M., & Nair, V. D. (2021). Soil Organic Matter (SOM) and Nutrient Cycling. In P. K. R. Nair, B. M. Kumar, & V. D. Nair, *An Introduction to Agroforestry* (pp. 383–411). Springer International Publishing. https://doi.org/10.1007/978-3-030-75358-0_16

Ndayisaba, P. C., Kuyah, S., Midega, C. A. O., Mwangi, P. N., & Khan, Z. R. (2021). Intercropping desmodium and maize improves nitrogen and phosphorus availability and performance of maize in Kenya. *Field Crops Research*, *263*, 108067. https://doi.org/10.1016/j.fcr.2021.108067

Ndayisaba, P. C., Kuyah, S., Midega, C. A. O., Mwangi, P. N., & Khan, Z. R. (2022). Push-pull technology improves carbon stocks in rainfed smallholder agriculture in Western Kenya. *Carbon Management*, *13*(1), 127–141. https://doi.org/10.1080/17583004.2022.2035823

NeSmith, D. S., & Ritchie, J. T. (1992). Effects of soil water-deficits during tassel emergence on development and yield component of maize (Zea mays). *Field Crops Research*, *28*(3), 251–256. https://doi.org/10.1016/0378-4290(92)90044-a

Nogueira, A. A., Brescovit, A. D., Perbiche-Neves, G., & Venticinque, E. M. (2021). Beta Diversity along an Elevational Gradient at the Pico da Neblina (Brazil): Is Spider (Arachnida-Araneae) Community Composition Congruent with the Guayana Region Elevational Zonation? *Diversity*, *13*(12), 620. https://doi.org/10.3390/d13120620

Nsubuga, F. N. W., Olwoch, J. M., Rautenbach, C. J. deW., & Botai, O. J. (2014). Analysis of mid-twentieth century rainfall trends and variability over southwestern Uganda. *Theoretical and Applied Climatology*, *115*(1–2), 53–71. https://doi.org/10.1007/s00704-013-0864-6

Nyambo, P., Mavunganidze, Z., & Nyambo, V. (2022). *Sub-Saharan Africa Smallholder Farmers Agricultural Productivity: Risks and Challenges*. https://doi.org/10.1007/978-981-16-6771-8_25

Odermatt, D. M., Chidawanyika, F., Mutyambai, D. M., Schmid, B., Domeignoz Horta, L. A., Onjura, C. O., Tamiru, A., & Schuman, M. C. (2025). Desmodium volatiles in 'push-pull' cropping systems and protection against the fall armyworm, Spodoptera frugiperda. *eLife*, *13*, RP100981. https://doi.org/10.7554/eLife.100981.3

Okosun, O. O., Allen, K. C., Glover, J. P., & Reddy, G. V. P. (2021). Biology, Ecology, and Management of Key Sorghum Insect Pests. *Journal of Integrated Pest Management*, *12*(1), 4. https://doi.org/10.1093/jipm/pmaa027

Oksanen, J., Simpson, G. L., & Kindt, R. (2025). *Package 'vegan'* [Data set]. https://vegandevs.github.io/vegan/

Omokpariola, D. O., Agbanu-Kumordzi, C., Samuel, T., Kiswii, L., Moses, G. S., & Adelegan, A. M. (2025). Climate change, crop yield, and food security in Sub-Saharan Africa. *Discover Sustainability*, *6*(1), 678. https://doi.org/10.1007/s43621-025-01580-4

Onyeaka, H., Nwauzoma, U. M., Akinsemolu, A. A., Tamasiga, P., Duan, K., Al-Sharify, Z. T., & Siyanbola, K. F. (2024). The ripple effects of climate change on agricultural sustainability and food security in Africa. *Food and Energy Security*, *13*(5), e567. https://doi.org/10.1002/fes3.567

Orr, A., Mwema, C., Gierend, A., & Nedumaran, S. (2016). *Sorghum and Millets in Eastern and Southern Africa: Facts, Trends and Outlook*. ICRISAT Research Program Markets, Institutions and Policies, Working Paper Series No. 62.

Otieno, H. M. O. (2018). Impacts and Management of Termites (Isoptera: Termitidae) among Smallholder Farmers In East Africa. *Journal of Agriculture and Ecology Research International*, *16*(1), 1–12. https://doi.org/10.9734/JAERI/2018/44842

Pansu, M., & Gautheyrou, J. (2006). *Handbook of soil analysis: Mineralogical, organic and inorganic methods*. Springer.

Paudel, S., Kandel, P., Bhatta, D., Pandit, V., Felton, G. W., & Rajotte, E. G. (2021). Insect Herbivore Populations and Plant Damage Increase at Higher Elevations. *Insects*, *12*(12), 1129. https://doi.org/10.3390/insects12121129

Paull, J. (2013). The Rachel Carson Letters and the Making of Silent Springs. *Sage Open*, *3*(3), 2158244013494861. https://doi.org/10.1177/2158244013494861

Perumal, R., Nimmakayala, P., Erattaimuthu, S. R., No, E.-G., Reddy, U. K., Prom, L. K., Odvody, G. N., Luster, D. G., & Magill, C. W. (2008). Simple sequence repeat markers useful for sorghum downy mildew

(Peronosclerospora sorghi) and related species. *BMC Genetics*, *9*(1), 77. https://doi.org/10.1186/1471-2156-9-77

Petit, S., & Landis, D. A. (2023). Landscape-scale management for biodiversity and ecosystem services. *Agriculture, Ecosystems & Environment*, *347*, 108370. https://doi.org/10.1016/j.agee.2023.108370

Pickett, J. A., Woodcock, C. M., Midega, C. A., & Khan, Z. R. (2014). Push–pull farming systems. *Current Opinion in Biotechnology*, *26*, 125–132. https://doi.org/10.1016/j.copbio.2013.12.006

Pilar, F., Loïc, M., Emmanuel, D., & Sergio, R. (2020). Seasonal changes in arthropod diversity patterns along an Alpine elevation gradient. *Ecological Entomology*, *45*(5), 1035–1043. https://doi.org/10.1111/een.12881

Pimbert, M. P., Moeller, N. I., Singh, J., & Anderson, C. R. (2021). Agroecology. In M. P. Pimbert, N. I. Moeller, J. Singh, & C. R. Anderson, *Oxford Research Encyclopedia of Anthropology*. Oxford University Press. https://doi.org/10.1093/acrefore/9780190854584.013.298

Pingali, P. L. (2012). Green Revolution: Impacts, limits, and the path ahead. *Proceedings of the National Academy of Sciences*, *109*(31), 12302–12308. https://doi.org/10.1073/pnas.0912953109

Pretty, J., Toulmin, C., & Williams, S. (2011). Sustainable intensification in African agriculture. *International Journal of Agricultural Sustainability*, *9*(1), 5–24. https://doi.org/10.3763/ijas.2010.0583

Ragasa, C., Takeshima, H., Asante, S., Amare, M., Ma, N., Olanrewaju, O., & Duchoslav, J. (2025). Maize yield responsiveness and profitability of fertilizer: New survey evidence from six African countries. *Food Policy*, *133*, 102815. https://doi.org/10.1016/j.foodpol.2025.102815

Raheem, D., Dayoub, M., Birech, R., & Nakiyemba, A. (2021). The Contribution of Cereal Grains to Food Security and Sustainability in Africa: Potential Application of UAV in Ghana, Nigeria, Uganda, and Namibia. *Urban Science*, *5*(1), 8. https://doi.org/10.3390/urbansci5010008

Rajput, L. S., Kumar, S., Nataraj, V., Shivakumar, M., Pathak, K., Jaiswal, S., Mandloi, S., Agrawal, N., Ratnaparkhe, M. B., Kumawat, G., Maheshwari, H. S., & Pandey, V. (2023). Recent advancement in management of soybean charcoal rot caused by Macrophomina phaseolina. In *Macrophomina Phaseolina* (pp. 55–74). Elsevier. https://doi.org/10.1016/B978-0-443-15443-0.00023-1

Rana, A., Chandel, R. S., Verma, K. S., & Joshi, M. J. (2021). Termites in Important Crops and Their Management. *Indian Journal of Entomology*, *83*(3), 486–504. https://doi.org/10.5958/0974-8172.2021.00001.8

Rand, T. A., Tylianakis, J. M., & Tscharntke, T. (2006). Spillover edge effects: The dispersal of agriculturally subsidized insect natural enemies into adjacent natural habitats. *Ecology Letters*, *9*(5), 603–614. https://doi.org/10.1111/j.1461-0248.2006.00911.x

Randall, M. G. M. (2025). Tritrophic interactions in a changing climate: A seed-feeding moth and its larval ectoparasitoids along an elevational gradient. *Journal of Insect Conservation*, *29*(3), 38. https://doi.org/10.1007/s10841-025-00674-8

Rapsomanikis, G. (2015). *The economic lives of smallholder farmers: An analysis based on household data from nine countries*. Food and Agriculture Organization of the United Nations. https://openknowledge.fao.org/server/api/core/bitstreams/32709b4d-ed41-4b1e-9d37-91786824cb9e/content

Ratto, F., Bruce, T., Chipabika, G., Mwamakamba, S., Mkandawire, R., Khan, Z., Mkindi, A., Pittchar, J., Sallu, S. M., Whitfield, S., Wilson, K., & Sait, S. M. (2022). Biological control interventions reduce pest abundance and crop damage while maintaining natural enemies in sub-Saharan Africa: A meta-analysis. *Proceedings of the Royal Society B: Biological Sciences*, *289*(1988), 20221695. https://doi.org/10.1098/rspb.2022.1695

Requier, F., Pérez-Méndez, N., Andersson, G. K. S., Blareau, E., Merle, I., & Garibaldi, L. A. (2023). Bee and non-bee pollinator importance for local food security. *Trends in Ecology & Evolution*, *38*(2), 196–205. https://doi.org/10.1016/j.tree.2022.10.006

Reynolds, T. W., Waddington, S. R., Anderson, C. L., Chew, A., True, Z., & Cullen, A. (2015). Environmental impacts and constraints associated with the production of major food crops in Sub-Saharan Africa and South Asia. *Food Security*, *7*(4), 795–822. https://doi.org/10.1007/s12571-015-0478-1

Rockström, J., Williams, J., Daily, G., Noble, A., Matthews, N., Gordon, L., Wetterstrand, H., DeClerck, F., Shah, M., Steduto, P., De Fraiture, C., Hatibu, N., Unver, O., Bird, J., Sibanda, L., & Smith, J. (2017). Sustainable intensification of agriculture for human prosperity and global sustainability. *Ambio*, *46*(1), 4–17. https://doi.org/10.1007/s13280-016-0793-6

Rödder, D., Schmitt, T., Gros, P., Ulrich, W., & Habel, J. C. (2021). Climate change drives mountain butterflies towards the summits. *Scientific Reports*, *11*(1), 14382. https://doi.org/10.1038/s41598-021-93826-0

Roobroeck, D., Kimutai, G., Kanampiu, F., Ng'etich, W., Roing De Nowina, K., & Vanlauwe, B. (2023). Effective Striga control and yield intensification on maize farms in western Kenya with N fertilizer and herbicide-resistant variety. *Field Crops Research*, *296*, 108924. https://doi.org/10.1016/j.fcr.2023.108924

Roosta, H. R. (2024). The responses of pepper plants to nitrogen form and dissolved oxygen concentration of nutrient solution in hydroponics. *BMC Plant Biology*, *24*(1), 281. https://doi.org/10.1186/s12870-024-04943-7

Royer, T. A., Pendleton, B. B., Elliott, N. C., & Giles, K. L. (2015). Greenbug (Hemiptera: Aphididae) Biology, Ecology, and Management in Wheat and

Sorghum. *Journal of Integrated Pest Management*, *6*(1), 19–19. https://doi.org/10.1093/jipm/pmv018

Rusch, A., Birkhofer, K., Bommarco, R., Smith, H. G., & Ekbom, B. (2015). Predator body sizes and habitat preferences predict predation rates in an agroecosystem. *Basic and Applied Ecology*, *16*(3), 250–259. https://doi.org/10.1016/j.baae.2015.02.003

Rusch, A., Chaplin-Kramer, R., Gardiner, M. M., Hawro, V., Holland, J., Landis, D., Thies, C., Tscharntke, T., Weisser, W. W., Winqvist, C., Woltz, M., & Bommarco, R. (2016). Agricultural landscape simplification reduces natural pest control: A quantitative synthesis. *Agriculture, Ecosystems & Environment*, *221*, 198–204. https://doi.org/10.1016/j.agee.2016.01.039

Rutsaert, P., & Donovan, J. (2023). *Maize farmers acquire early-maturity seed across production environments*. CGIAR. https://www.researchgate.net/publication/373683616_Maize_farmers_acquire_early-maturity_seed_across_production_environments

Rwema, M., Safari, B., Laine, M., Sylla, M. B., & Roininen, L. (2025). Trends and Variability of Temperatures in the Eastern Province of Rwanda. *International Journal of Climatology*, e8793. https://doi.org/10.1002/joc.8793

Saleem, S., Mushtaq, N. U., Rasool, A., Shah, W. H., Tahir, I., & Rehman, R. U. (2023). Plant nutrition and soil fertility. In *Sustainable Plant Nutrition* (pp. 23–49). Elsevier. https://doi.org/10.1016/B978-0-443-18675-2.00009-2

Sam, K., Jorge, L. R., Koane, B., Amick, P. K., & Sivault, E. (2023). Vertebrates, but not ants, protect rainforest from herbivorous insects across elevations in Papua New Guinea. *Journal of Biogeography*, jbi.14686. https://doi.org/10.1111/jbi.14686

Sánchez, A. C., Jones, S. K., Purvis, A., Estrada-Carmona, N., & De Palma, A. (2022). Landscape complexity and functional groups moderate the effect of diversified farming on biodiversity: A global meta-analysis. *Agriculture, Ecosystems & Environment*, *332*, 107933. https://doi.org/10.1016/j.agee.2022.107933

Schultheiss, P., Nooten, S. S., Wang, R., Wong, M. K. L., Brassard, F., & Guénard, B. (2022). The abundance, biomass, and distribution of ants on Earth. *Proceedings of the National Academy of Sciences*, *119*(40), e2201550119. https://doi.org/10.1073/pnas.2201550119

Scott-Brown, A. S., Rial-Lovera, K., Giannitsopoulos, M. L., Rickson, J. R., Staton, T., Walters, K. F. A., & Burgess, P. J. (2025). Farmland trees and integrated pest management: A review of current knowledge and developing strategies for sustainable systems. *Ecological Solutions and Evidence*, *6*(3), e70087. https://doi.org/10.1002/2688-8319.70087

Shahmohamadloo, R. S., Febria, C. M., Fraser, E. D. G., & Sibley, P. K. (2021). The sustainable agriculture imperative: A perspective on the need for an agrosystem approach to meet the United Nations Sustainable Development Goals by 2030. *Integrated Environmental Assessment and Management*, *18*(5), 1199–1205. https://doi.org/10.1002/ieam.4558

Shi, R., Liu, Z., Li, Y., Jiang, T., Xu, M., Li, J., & Xu, R. (2019). Mechanisms for increasing soil resistance to acidification by long-term manure application. *Soil and Tillage Research*, *185*, 77–84. https://doi.org/10.1016/j.still.2018.09.004

Siebert, A., Dinku, T., Vuguziga, F., Twahirwa, A., Kagabo, D. M., delCorral, J., & Robertson, A. W. (2019). Evaluation of ENACTS-Rwanda: A new multi-decade, high-resolution rainfall and temperature data set—Climatology. *International Journal of Climatology*, *39*(6), 3104–3120. https://doi.org/10.1002/joc.6010

Silberg, T. R., Chimonyo, V. G. P., Richardson, R. B., Snapp, S. S., & Renner, K. (2019). Legume diversification and weed management in African cereal-based systems. *Agricultural Systems*, *174*, 83–94. https://doi.org/10.1016/j.agsy.2019.05.004

Sileshi, G. W., Jama, B., Vanlauwe, B., Negassa, W., Harawa, R., Kiwia, A., & Kimani, D. (2019). Nutrient use efficiency and crop yield response to the combined application of cattle manure and inorganic fertilizer in sub-Saharan Africa. *Nutrient Cycling in Agroecosystems*, *113*(2), 181–199. https://doi.org/10.1007/s10705-019-09974-3

Sileshi, G. W., Kuyah, S., Schuman, M. C., Chidawanyika, F., Muriithi, B. W., Midega, C. A. O., Olagoke, A., Otim, M. H., Mafongoya, P. L., & Martin, E. A. (2025). Opportunities for expansion of push-pull technology as an agroecological and sustainable intensification approach in Africa. *Npj Sustainable Agriculture*, *3*(1), 30. https://doi.org/10.1038/s44264-025-00069-x

Smith, M. A., Warne, C., Pare, K., Dolson, S., Loewen, E., Jones, K., & Janzen, D. H. (2023). Communities of Small Terrestrial Arthropods Change Rapidly Along a Costa Rican Elevation Gradient. In *Neotropical Gradients and Their Analysis* (pp. 255–307). Springer International Publishing. https://doi.org/10.1007/978-3-031-22848-3_10

Smith, R. F., Apple, J. L., & Bottrell, D. G. (1976). The Origins of Integrated Pest Management Concepts for Agricultural Crops. In J. L. Apple & R. F. Smith (Eds), *Integrated Pest Management* (pp. 1–16). Springer US. https://doi.org/10.1007/978-1-4615-7269-5_1

Stern, V. M. (1959). The integrated control concept. *Hilgardia*, *29*(2), 81-101.

Suárez, J. C., Anzola, J. A., Contreras, A. T., Salas, D. L., Vanegas, J. I., Urban, M. O., Beebe, S. E., & Rao, I. M. (2022). Influence of Simultaneous Intercropping of Maize-Bean with Input of Inorganic or Organic Fertilizer on Growth, Development, and Dry Matter Partitioning to Yield

Components of Two Lines of Common Bean. *Agronomy*, *12*(5), 1216. https://doi.org/10.3390/agronomy12051216

Tandzi, N. L., & Mutengwa, S. C. (2020). Factors Affecting Yield of Crops. In Amanullah (Ed.), *Agronomy—Climate Change and Food Security*. IntechOpen. https://doi.org/10.5772/intechopen.90672

Tang, C., Unkovich, M. J., & Bowden, J. W. (1999). Factors affecting soil acidification under legumes. III. Acid production by N_2 -fixing legumes as influenced by nitrate supply. *New Phytologist*, *143*(3), 513–521. https://doi.org/10.1046/j.1469-8137.1999.00475.x

Tang, X., Zhang, C., Yu, Y., Shen, J., Van Der Werf, W., & Zhang, F. (2021). Intercropping legumes and cereals increases phosphorus use efficiency; a meta-analysis. *Plant and Soil*, *460*(1–2), 89–104. https://doi.org/10.1007/s11104-020-04768-x

Tari, I., Laskay, G., Takács, Z., & Poór, P. (2013). Response of Sorghum to Abiotic Stresses: A Review. *Journal of Agronomy and Crop Science*, *199*(4), 264–274. https://doi.org/10.1111/jac.12017

Terblanche, J. S., Clusella-Trullas, S., & Lehmann, P. (2024). How climate change might impact insect movement via physiological mechanisms. *One Earth*, *7*(4), 608–622. https://doi.org/10.1016/j.oneear.2024.03.008

Tiku, T. W., Tarekegn, G. B., Sahlu, D., Teshebo, G. B., Enyew, F. B., Umer, Y., & Debele, S. E. (2025). Evaluating CMIP6 Precipitation Simulations Across Different Rainfall Regimes in the Amhara Region, Ethiopia. *Natural Hazards Research*, S266659212500023X. https://doi.org/10.1016/j.nhres.2025.03.002

Tittonell, P. (2014). Ecological intensification of agriculture—Sustainable by nature. *Current Opinion in Environmental Sustainability*, *8*, 53–61. https://doi.org/10.1016/j.cosust.2014.08.006

Tittonell, P., & Giller, K. E. (2013). When yield gaps are poverty traps: The paradigm of ecological intensification in African smallholder agriculture. *Field Crops Research*, *143*, 76–90. https://doi.org/10.1016/j.fcr.2012.10.007

Tittonell, P., Vanlauwe, B., Leffelaar, P. A., Shepherd, K. D., & Giller, K. E. (2005). Exploring diversity in soil fertility management of smallholder farms in western Kenya. *Agriculture, Ecosystems & Environment*, *110*(3–4), 166–184. https://doi.org/10.1016/j.agee.2005.04.003

Tortosa, A., Giffard, B., Sirami, C., Larrieu, L., Ladet, S., & Vialatte, A. (2023). Increasing landscape heterogeneity as a win–win solution to manage trade-offs in biological control of crop and woodland pests. *Scientific Reports*, *13*(1), 13573. https://doi.org/10.1038/s41598-023-40473-2

Tran, B.-L., Tseng, W.-C., & Chen, C.-C. (2025). Climate change impacts on crop yields across temperature rise thresholds and climate zones. *Scientific Reports*, *15*(1), 23424. https://doi.org/10.1038/s41598-025-07405-8

Traoré, S., Guébré, D., Hien, E., Traoré, M., Lee, N., Lorenz, N., & Dick, R. P. (2022). Nutrient cycling and microbial responses to termite and earthworm activity in soils amended with woody residues in the Sudano-Sahel. *European Journal of Soil Biology*, *109*, 103381. https://doi.org/10.1016/j.ejsobi.2021.103381

Tripathi, R., Tewari, R., Singh, K. P., Keswani, C., Minkina, T., Srivastava, A. K., De Corato, U., & Sansinenea, E. (2022). Plant mineral nutrition and disease resistance: A significant linkage for sustainable crop protection. *Frontiers in Plant Science*, *13*, 883970. https://doi.org/10.3389/fpls.2022.883970

Tscharntke, T., Klein, A. M., Kruess, A., Steffan-Dewenter, I., & Thies, C. (2005). Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. *Ecology Letters*, *8*(8), 857–874. https://doi.org/10.1111/j.1461-0248.2005.00782.x

Tscharntke, T., Tylianakis, J. M., Rand, T. A., Didham, R. K., Fahrig, L., Batáry, P., Bengtsson, J., Clough, Y., Crist, T. O., Dormann, C. F., Ewers, R. M., Fründ, J., Holt, R. D., Holzschuh, A., Klein, A. M., Kleijn, D., Kremen, C., Landis, D. A., Laurance, W., … Westphal, C. (2012). Landscape moderation of biodiversity patterns and processes - eight hypotheses. *Biological Reviews*, *87*(3), 661–685. https://doi.org/10.1111/j.1469-185X.2011.00216.x

Uhey, D. A., Bowker, M. A., Haubensak, K. A., Auty, D., Vissa, S., & Hofstetter, R. W. (2022). Habitat Type Affects Elevational Patterns in Ground-dwelling Arthropod Communities. *Journal of Insect Science*, *22*(4), 9. https://doi.org/10.1093/jisesa/ieac046

Ullah, G., Nisar, M., Rehman, F. U., Paree Paker, N., Hussain Munis, M. F., & Chaudhary, H. J. (2025). Mitigating maize stalk rot disease: Harnessing Bacillus subtilis PM57 and Bacillus cereus PM38 as biocontrol allies against Erwinia carotovora. *Microbial Pathogenesis*, *205*, 107556. https://doi.org/10.1016/j.micpath.2025.107556

Vanlauwe, B., & Giller, K. (2006). Popular myths around soil fertility management in sub-Saharan Africa. *Agriculture, Ecosystems & Environment*, *116*(1–2), 34–46. https://doi.org/10.1016/j.agee.2006.03.016

Vazeux-Blumental, N., Mathieu, L., Trabac, T., Palaffre, C., Lagardère, B., Carraretto, M., Bauland, C., Le Guilloux, M., Le Roux, C. P., Caïus, J., Marmagne, A., Enjalbert, J., Flutre, T., Le Cadre, E., Parnaudeau, V., Muller, D., Moënne-Loccoz, Y., Manicacci, D., & Tenaillon, M. I. (2025). Revival of traditional agricultural systems – A multidisciplinary on-farm survey of maize-bean intercropping reveals unexpected competition effects on beans. *PLANTS, PEOPLE, PLANET*, *7*(6), 1755–1770. https://doi.org/10.1002/ppp3.70049

Venkatasai, N. N., Shetty, D. N., Vinay, C. M., Sekar, M., Muthusamy, A., & Rai, P. S. (2025). A comprehensive review of factors affecting growth and secondary metabolites in hydroponically grown medicinal plants. *Planta*, *261*(3), 48. https://doi.org/10.1007/s00425-025-04619-y

Wang, S., Han, M., Wei, K., & Wang, X. (2024). Effects of temperature on reproduction and development of *Cyanopterus ninghais* (Hymenoptera: Braconidae), a larval parasitoid of *Monochamus alternatus* (Coleoptera: Cerambycidae). *Journal of Applied Entomology*, *148*(4), 415–423. https://doi.org/10.1111/jen.13232

White, K. E., Cavigelli, M. A., & Bagley, G. (2021). Legumes and nutrient management improve phosphorus and potassium balances in long-term crop rotations. *Agronomy Journal*, *113*(3), 2681–2697. https://doi.org/10.1002/agj2.20651

Wills, B. D., & Landis, D. A. (2018). The role of ants in north temperate grasslands: A review. *Oecologia*, *186*(2), 323–338. https://doi.org/10.1007/s00442-017-4007-0

Yi, Z., Jinchao, F., Dayuan, X., Weiguo, S., & Axmacher, J. C. (2012). A Comparison of Terrestrial Arthropod Sampling Methods. *Journal of Resources and Ecology*, *3*(2), 174–182. https://doi.org/10.5814/j.issn.1674-764x.2012.02.010

Zhang, J., You, S., Niu, D., Gavilanez Guaman, K. G., Wang, A., Saqib, H. S. A., He, W., Yu, Y., Yang, G., Pozsgai, G., & You, M. (2021). Landscape composition mediates suppression of major pests by natural enemies in conventional cruciferous vegetables. *Agriculture, Ecosystems & Environment*, *316*, 107455. https://doi.org/10.1016/j.agee.2021.107455

Zhao, Z.-H., Hui, C., He, D.-H., & Li, B.-L. (2015). Effects of agricultural intensification on ability of natural enemies to control aphids. *Scientific Reports*, *5*(1). https://doi.org/10.1038/srep08024

Zhong, Y., Tian, J., Li, X., & Liao, H. (2023). Cooperative interactions between nitrogen fixation and phosphorus nutrition in legumes. *New Phytologist*, *237*(3), 734–745. https://doi.org/10.1111/nph.18593

Zou, T., Zhang, X., & Davidson, E. A. (2022). Global trends of cropland phosphorus use and sustainability challenges. *Nature*, *611*(7934), 81–87. https://doi.org/10.1038/s41586-022-05220-z

Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems: *Data exploration*. *Methods in Ecology and Evolution*, *1*(1), 3–14. https://doi.org/10.1111/j.2041-210X.2009.00001.x

Popular science summary

Africa's smallholder farmers are farming on the edge. Nutrient-poor soils, rapid landscape degradation, and persistent pests like fall armyworm (FAW), stemborers and weeds like Striga continue to undermine cereal production, while many farmers are resource-poor, hence unable to afford costly fertilisers and pesticides. In response, ecological intensification practices that leverage ecological processes are becoming increasingly practical and climate-resilient alternatives.

One promising ecological intensification strategy is the push-pull (PP) cropping system, a mixed cropping approach that combines a repellent intercrop with an attractive border crop to manage pests. In this system, the leguminous intercrop *Desmodium* "pushes" stemborers and FAW away from the main crop, i.e. maize or sorghum, while the surrounding border of *Brachiaria* or *Pennisetum* spp. grass "pulls" them out of the field where their larvae have very low survival rates. Beyond repelling pests, *Desmodium* also attracts natural enemies, suppresses *Striga* through allelopathic root exudates that trigger suicidal germination, and improves soil fertility by fixing nitrogen and adding organic matter through its leaves and root biomass. However, the landscape and soil conditions under which PP delivers the most consistent and sustained benefit remain poorly understood. This thesis, therefore, examined how the type of cropping system, together with landscape-scale features including composition, configuration and elevation factors, shaped natural enemy communities. It also investigated how soil fertility and landscape structure influence the performance of the PP system in suppressing lepidopteran pest damage and Striga seed bank density.

Field work conducted across four East African countries revealed a high diversity of beneficial arthropods within cereal fields. Tens of thousands of natural enemies were recorded, dominated by ants but also including spiders, crickets, and other predators that support natural pest regulation. Their diversity and abundance varied with elevation, season, cropping system, and landscape structure. Higher elevations were dominated by certain taxa, making pest control services more vulnerable to environmental change. In contrast, lowland areas with greater plant productivity hosted more even natural enemy communities, which are more resilient and capable of sustaining pest suppression.

Landscape features played a nuanced role in shaping natural enemy communities. In Kenya, the PP cropping system increased natural enemy abundance only in landscapes with higher forest cover, while fields embedded in landscapes with more grass cover and high edge density tended to support fewer natural enemies, although this latter effect was weak and non-significant. These patterns indicate that semi-natural habitats do not function uniformly as ecological reservoirs, and their influence on natural enemies depends on local context. Importantly, the study did not find clear evidence that landscape gradients supporting or reducing natural enemies translated into corresponding changes in pest damage, suggesting that bottom-up mechanisms, such as resource concentration in the landscape, were more influential drivers of pest pressure.

Within the PP system, healthy *Desmodium* cover improved soil organic matter, nitrogen, and plant-available phosphorus, reinforcing the system's broader soil-enhancing functions. These plant-soil interactions are central to PP’s ecological performance: as soil fertility improves, crops grow more vigorously, become more resilient to stress, and benefit from enhanced nutrient cycling. However, this research also showed that these benefits are not guaranteed. When *Desmodium* biomass is regularly harvested for fodder or when fertilisers are applied in ways that acidify the soil, nutrient depletion can still occur. The long-term sustainability of PP, therefore, depends on management practices that maintain soil fertility, including balanced nutrient inputs and reducing biomass removal.

The performance of PP against *Striga* showed context-dependent patterns, with soil conditions moderating its effectiveness in only Rwanda. In degraded or nutrient-poor soils, where Striga pressure is typically highest, PP’s suppressive mechanisms appeared stronger. In countries with minimal soil variation or small *Striga* seedbanks, these soil-related patterns were more difficult to detect because the lack of clear gradients limited observable interactions. In contrast, PP’s ability to reduce pest damage was largely independent of soil conditions, although the strength of this effect was not consistent across countries.

The results of this thesis highlight that the success of PP as an ecological intensification practice is shaped by environmental context. Landscapes rich in biodiversity offer stronger natural pest control. Soils with specific nutrient limitations respond differently to PP’s ecological mechanisms. Seasonal patterns regulate the abundance of both pests and their natural enemies. And farmers’ management decisions determine whether soils improve or degrade over time. No single factor dictates outcomes; rather, it's the combination of seasons, soil, landscape, and management that governs how well PP performs.

Nature already provides many of the tools needed for sustainable agriculture. By understanding and fostering these ecological processes, farmers can build productive systems that rely less on costly inputs and more on biodiversity, healthy soils, and functional landscapes. Ecological intensification is not simply an alternative; it is a pathway toward farming that strengthens both ecosystems and livelihoods.

Populärvetenskaplig sammanfattning

Afrikas småbönder odlar på gränsen till vad systemen klarar av. Näringsfattiga jordar, snabb landskapsdegradering och ihållande problem med skadegörare som höstarmélarv (FAW), stamborrare och ogräs som Striga fortsätter begränsa spannmålsproduktionen, samtidigt som många bönder är resursfattiga och därför saknar möjlighet att bekosta dyra gödselmedel och bekämpningsmedel. Som ett svar på detta framstår ekologisk intensifiering som utnyttjar ekologiska processer som ett alltmer praktiskt och klimatresilient alternativ.

En lovande strategi för ekologisk intensifiering är push-pull-systemet (PP), ett samodlingssystem som kombinerar en avskräckande samodlingsgröda med en attraktiv kantgröda för att hantera skadegörare. I detta system skrämmer den baljväxtbaserade samodlingsgrödan *Desmodium* bort stamborrare och FAW från huvudgrödan, det vill säga majs eller durra, medan en omgivande kant av gräs som *Brachiaria* eller *Pennisetum* spp. Lockar dem ur fältet, där larvernas överlevnad är mycket låg. Utöver att stöta bort skadegörare lockar *Desmodium* även naturliga fiender, undertrycker ogräset Striga genom allelopatiska rotutsöndringar som utlöser självmordsgroning, samt förbättrar markbördigheten genom kvävefixering och tillförsel av organiskt material via blad och rotbiomassa. Trots detta är de landskaps- och markförhållanden under vilka PP ger de mest konsekventa och långsiktiga fördelarna fortfarande dåligt kända.Denna avhandling undersökte därför hur lokala odlingssystem, i samspel med landskapsfaktorer i större skala inklusive sammansättning, konfiguration och höjd över havet formar samhällen av naturliga fiender. Den analyserade även hur markbördighet och odlingssystem påverkar PP-systemets förmåga att minska skador från skadegörande fjärilslarver samt storleken på *Strigas* fröbank.

Fältarbete som genomfördes i fyra östafrikanska länder visade på en hög mångfald av nyttiga leddjur i spannmålsfälten. Tiotusentals naturliga fiender registrerades, dominerade av myror men även inkluderande spindlar, syrsor och andra rovdjur som bidrar till naturlig skadedjursreglering. Deras mångfald och abundans varierade med höjd över havet, säsong, odlingssystem och landskapsstruktur. Högre belägna områden hade dominerades av enskilda naturliga fiender, vilket gör skadedjursregleringen mer sårbar för miljöförändringar. I kontrast hyste låglandsområden med högre växtproduktion mer jämnt fördelade samhällen av naturliga fiender, vilka är mer resilienta och bättre på att upprätthålla skadedjurskontroll.

Det omgivande landskapet påverkade samhällen av naturliga fiender på ett nyanserat sätt. I Kenya ökade PP-systemet endast förekomsten av naturliga fiender i landskap med högre skogstäckning, medan fält som låg i landskap med mer gräsmarker och hög kantdensitet tenderade att stödja färre naturliga fiender, även om den senare effekten var svag och icke-signifikant. Dessa mönster indikerar att semi-naturliga habitat inte fungerar enhetligt som ekologiska reservoarer och att deras påverkan på naturliga fiender beror på lokal kontext. Viktigt är att studien inte fann tydliga bevis för att landskapsgradienter som stödjer eller minskar naturliga fiender ledde till motsvarande förändringar i skadedjursangrepp, vilket tyder på att bottom-up-mekanismer, såsom koncentration av födoresurser i landskapet, var mer inflytelserika faktorer för skadegörartrycket.

Inom PP-systemet förbättrade ett friskt och tätt *Desmodium*-täcke halten av markorganiskt material, kväve och växttillgängligt fosfor, vilket stärker systemets övergripande markförbättrande funktioner. Dessa mark-växt-interaktioner är centrala för PP:s ekologiska prestanda: när markbördigheten förbättras växer grödorna kraftigare, blir mer stresståliga och gynnas av effektivare näringsomsättning. Forskningen visade dock också att dessa fördelar inte är garanterade. När *Desmodium*-biomassa regelbundet skördas som foder eller när gödselmedel appliceras på sätt som leder till markförsurning kan näringsutarmning fortfarande uppstå. PP-systemets långsiktiga hållbarhet beror därför på förvaltningsmetoder som upprätthåller markbördigheten, inklusive balanserade näringstillskott och begränsning av biomassauttag.

PP-systemets effekt på *Striga* visade tydligt sammanhangsberoende mönster, där markförhållanden påverkade effektiviteten i endast Rwanda. I degraderade eller näringsfattiga jordar, där *Striga*-trycket vanligtvis är som störst, framstod PP:s undertryckande mekanismer som starkare. I länder med liten variation i markegenskaper eller mindre *Striga*-fröbank var dessa markrelaterade mönster svårare att påvisa, eftersom avsaknaden av tydliga gradienter begränsade möjligheten att observera interaktioner. Däremot var PP-systemets förmåga att minska skadegörarskador i stort sett oberoende av markförhållanden, även om styrkan i denna effekt varierade mellan länder.

Resultaten från denna avhandling visar att framgången för PP som ekologisk intensifiering är starkt kontextberoende. Biodiversitetsrika landskap ger starkare naturlig skadedjurskontroll. Jordar med specifika näringsbegränsningar svarar olika på PP-systemets ekologiska mekanismer. Säsongsmönster reglerar abundansen av både skadegörare och deras naturliga fiender. Och böndernas förvaltningsbeslut avgör om marken förbättras eller försämras över tid. Ingen enskild faktor styr utfallet; det är samspelet mellan odlingssäsong, mark, landskap och skötsel som avgör hur väl PP fungerar.

Naturen tillhandahåller redan många av de verktyg som behövs för ett hållbart jordbruk. Genom att förstå och främja dessa ekologiska processer kan bönder bygga produktiva system som är mindre beroende av kostsamma insatsmedel och som baseras på biodiversitet, friska jordar och funktionella landskap. Ekologisk intensifiering är inte bara ett alternativ, det är en väg mot ett jordbruk som stärker både ekosystem och försörjningsmöjligheter.

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ORIGINAL RESEARCH ARTICLE

Elevation and grassland cover shape natural enemy communities in the Kenyan maize crops

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Abstract

Natural enemies, including arthropod predators and parasitoids, provide essential pest control services in agricultural systems by reducing pest populations. However, studies examining how natural enemies respond to environmental gradients, such as elevation and grass cover, are limited in sub-Saharan Africa. This study investigates the effect of elevation (1150–1970 m above sea level) and grassland cover in the surrounding landscape (2–30%) on natural enemy communities in maize fields in western Kenya over two consecutive sampling seasons. We selected maize fields along gradients of elevation and percentage of grassland and conducted field surveys using pitfall traps to assess the diversity and composition of natural enemies. Natural enemy diversity, richness, evenness, abundance and community composition were compared across gradients using Generalised Linear Mixed Models and Non-Metric Multidimensional Scaling. Across gradients, ants were the most abundant predator group. Lower elevations supported natural enemy communities with higher evenness, while higher elevations were dominated by *Myrmicaria* ants. Grassland cover had limited overall effects, with a non-significant but positive association with species richness. Notably, community composition shifted along the elevational gradient, with *Myrmicaria* ants being less dominant < 1600 masl. Their dominance at high elevations, where grass cover is lower, may reduce overall pest control resilience, as low evenness and reliance on a single genus diminish functional redundancy. This underscores the need for integrated pest management strategies that consider multiple environmental variables. Overall, our findings highlight the importance of environmental gradients in shaping natural enemy biodiversity in agricultural fields with implications for pest control in western Kenya.

Keywords Ant assemblages · Climate change · Environmental gradients · Myrmicaria · Pest control · Sub-Saharan africa

Introduction

Natural enemies, such as arthropod predators, parasitoids, pathogens (i.e., bacteria, fungi, viruses, and nematodes), birds, reptiles and amphibians, provide essential pest control services in agricultural systems (Cortez-Madrigal and Gutiérrez-Cárdenas 2023; Ratto et al. 2022). Their presence can reduce crop pests by up to 90% (Martin et al. 2013). Studying how natural enemies respond to differences in environmental gradients, such as landscape composition and elevation, can offer valuable insights into the measures needed to ensure their survival. Although invertebrate predators in agricultural systems have been extensively studied in the global North (Daelemans et al. 2023; Karimzadeh and Sciarretta 2022; Klinnert et al. 2024), similar studies

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in sub-Saharan Africa remain scarce, particularly regarding how environmental gradients shape these communities.

The surrounding landscape can play an important, though inconsistent, role in shaping invertebrate predator communities in agricultural fields (Feit et al. 2019; Karp et al. 2018; Klinnert et al. 2024). Landscapes with greater proportions of natural or semi-natural habitats often support higher natural enemy diversity and abundance, which can help suppress pest populations in crops (Alarcon-Segura et al. 2025; Litovska et al. 2025; Mazón et al. 2024). However, these effects are not always consistent (Karp et al. 2018), and seem to be dependent on species functional traits such as dispersal, dietary breadth and overwintering preferences (Alexandridis et al. 2022; Martin et al. 2019). Grasslands, in particular, are important components in the agricultural landscape (Debinski 2023; Nagy et al. 2020). They can act as havens for natural enemies when crops are disturbed, as they share many invertebrate species with annual crops (Nagy et al. 2020; Perrot et al. 2021, 2023). Their structural complexity, plant diversity, and microhabitats provide nesting sites and alternative food sources that support a wide range of invertebrates (Nagy et al. 2020; Silva-Monteiro et al. 2022). Empirical evidence shows that grasslands can enhance natural enemy activity in adjacent crops (Debinski 2023; Perrot et al. 2021, 2023). For example, Perrot et al. (2021), reported that increasing grassland cover from 0 to 50% can increase aphid predation by 20%. Beyond providing habitats, grasslands also enhance landscape connectivity, serving as corridors for the dispersal of natural enemies. This connectivity facilitates movement and colonisation of crop fields, thereby strengthening the suppression of pests (Fartmann 2024; Novaes et al. 2024).

While landscape composition is important, elevation also shapes arthropod diversity and spatial distribution (Smith et al. 2023), physiology (Khaliq et al. 2023), habitat selection (Uhey et al. 2022), and ecological interactions (Sam et al. 2023; Wang et al. 2024). As elevation increases, changes in temperature, humidity, and atmospheric conditions create distinct ecological niches, leading to the zonation of arthropod communities (Uhey et al. 2022). Lower elevations, characterised by warmer climates and longer growing seasons, generally support broader ecological niches, enhancing species coexistence and resource use (Herrera-Alsina et al. 2025; Polato et al. 2018). In contrast, higher elevations are characterised by lower temperatures and reduced habitat area, supporting fewer endemic species adapted to extreme conditions (Hodkinson 2005; Poveda et al. 2019; Rödder et al. 2021). Elevational gradients also affect arthropod phenology by shifting their developmental time, reproduction and activity (Helms 2023), which in turn influences interactions with other organisms, including mutualism (Luna et al. 2023), and predation (Randall 2025). Together, these processes demonstrate how elevation shapes both the spatial and temporal patterns of arthropod diversity, reflecting the interplay between environmental pressures and biological diversity (Bishop et al. 2014). This highlights the need to consider elevational variation in studies of arthropod communities and their ecological roles.

Superimposed on these elevational gradients, climate warming is increasingly becoming a cause for concern (Rumpf et al. 2019). As the temperature increases at lower elevations, species are expected to shift upwards (Jacobsen 2020; McCain and Garfinkel 2021). Inevitably, these changes may bifurcate coevolved interactions between host plants, herbivores, and their natural enemies (Rasmann et al. 2014). Long-term studies have revealed declining diversity of specialised mountain parasitoids at higher elevations, while generalists are expanding their ranges and moving to higher elevations (Di Marco et al. 2023). The loss of specialised natural enemies can leave their functional roles not fully replaced by generalist species and reduce the overall effectiveness of pest suppression. This reduction in diversity also reduces functional redundancy, which is vital in buffering ecosystems against disturbances, thereby increasing the risk of herbivory outbreaks. For example, a seed-feeding moth expanded to higher elevations faster than its parasitoids, creating a mismatch that elevated the pest population (Randall 2025). Such mismatches of pests and their natural enemies, as a result of climate change, weaken agroecosystems' resilience by reducing their capacity to regulate pests, increasing vulnerability, which may have severe consequences on crop production (Eigenbrode and Adhikari 2023; Paudel et al. 2021; Randall 2025).

This study examined how elevation (1150–1970 masl) and grass cover in the surrounding landscape (2–30%) affect natural enemy communities in maize fields in western Kenya. Specifically, we tested whether (i) increasing elevation, and (ii) greater grassland cover affect natural enemy abundance, species richness, Shannon diversity and Pielou's evenness; metrics that capture complementary aspects of community structure. Previous studies have shown that increasing elevation reduces overall species diversity (Dolson and Kharouba 2024; Joseph et al. 2019), while increasing grass cover can positively enhance natural enemies diversity (Alarcon-Segura et al. 2025; Nagy et al. 2020; Perrot et al. 2021), shaping ecological interactions and pest suppression potential. By linking these gradients to multiple facets of diversity, we aim to provide a more mechanistic understanding of how grass cover in the surrounding landscape and elevation shape biocontrol communities, with implications for pest management and biodiversity conservation strategies in sub-Saharan African agriculture. Based on this, we hypothesised that elevation could drive shifts in natural enemies' composition, whereas grassland cover would promote diversity and eventually enhance pest control.

Materials and methods

Study site

This study was conducted in Western Kenya across the six counties, Bungoma, Homabay, Kisumu, Trans-Nzoia, Uasin-Gishu and Vihiga (Fig. 1). The region experiences a bimodal rainfall pattern, with long rains from March to May, and short rains between October and December, averaging rainfall of 1,500 mm annually, and a temperature of 24 °C (Hession and Moore 2011). This region is a major producer of maize, beans and sugarcane due to its favourable climate.

Sampling

We selected 24 smallholder maize fields along an altitudinal gradient ranging from 1000 m above sea level (masl) in Homabay to about 2000 masl in Trans-Nzoia county, and percentage grass cover ranging from 2% to 30% within a 1 km radius. We used high-resolution satellite imagery from Google Earth, referencing the year 2017, to analyse the landscape composition around each field. Circular buffers with a 1 km radius were created around the centre of each field using the 'buffer' tool in ArcGIS (version 10.5.1), representing a scale appropriate for studying population dynamics of arthropod predators in crop fields (Rusch et al. 2016). Within these buffers, polygons representing areas dominated by grassland were manually drawn based on visual observations. The percentage of grass cover within each buffer was then calculated to assess its impact on the natural enemy communities.

Ground-dwelling arthropods were sampled over two planting seasons: the short rains (October to December 2019) and the long rains (March to May 2020). Sixteen fields located between 1150 masl and 1600 masl were sampled during both the short rains (Season 1) and long rains (Season 2). An additional eight fields at higher elevations (>1600 masl), where maize is cultivated only once per year, were sampled only during the long rains (thus, in total 24 fields were sampled in the long rains). Six wet pitfall traps (7 cm diameter, 15 cm height) were placed in each field at least 3 rows from the field edge and at 5–10 m apart from each other. The cups were filled to two-thirds with water and a few drops of unscented detergent to reduce the surface tension (Yi et al. 2012). Sampling was conducted twice during each season, for 24h (±3 h) to account for occasional logistical delays in deactivating pitfall traps. The specimens were conserved in 70% ethanol and stored in a freezer at −35 °C. All arthropods were identified to the genus level by a taxonomist at the International Centre of Insect Physiology and Ecology (*icipe*). For subsequent analysis, we focused on natural enemies, specifically arthropod predators (including carnivores and omnivores) and parasitoids, as these functional groups are directly involved in regulating crop pests (Online material 1).

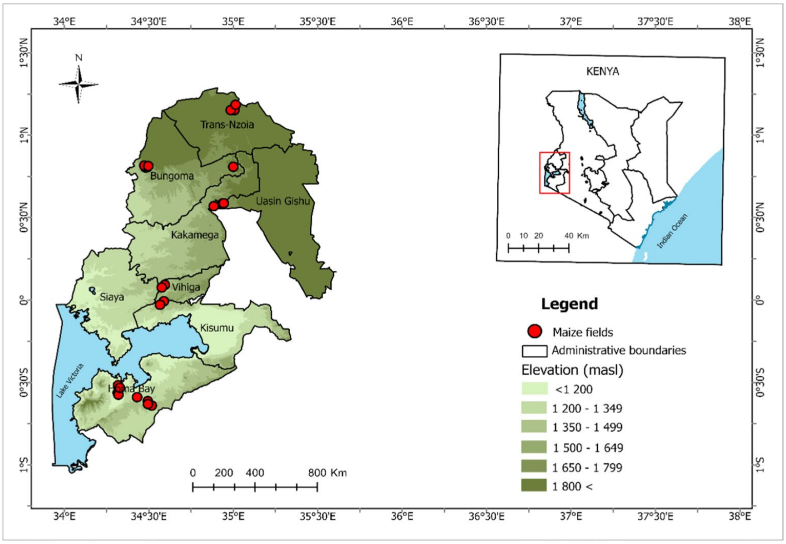

Fig. 1 Map showing the location of the studied smallholder maize fields in western Kenya along altitudinal gradients

Statistical analysis

To assess the effects of elevation and surrounding grassland cover on natural enemy community composition, we used generalised linear mixed models (GLMM) and Non-Metric Multidimensional Scaling (NMDS). All statistical analyses were conducted in R version 4.4.0 (R Core Team 2024).

Data from the two sampling rounds in each season were first pooled, and the normality of the data was tested using the Shapiro-Wilk test. Shannon diversity index, species richness, Pielou's evenness, and overall abundance were calculated for the predator communities in each field using the 'vegan' package (Oksanen et al. 2020). Metrics from both seasons were combined and analysed using GLMMs, richness and abundance were fitted with a negative binomial distribution, evenness with a beta distribution, and Shannon diversity with a Gaussian distribution, with the field included as a random factor.

Grass cover and elevation were negatively correlated ($\rho = -0.705$, $p < 0.001$). To further assess multi-collinearity, we employed Variance Inflation Factors (VIFs) among predictors (percentage grassland cover, elevation and their interaction), using the \`vif′ function in the \`fmsb′ package (Minato 2024). All VIF values were < 3, and therefore, both predictors were included in subsequent analyses despite their negative correlation (Zuur et al. 2010). The models were fitted using the \`lme4′ and \`MASS′ packages, with elevation and grass cover included as fixed effects. Models were selected based on Akaike's Information Criterion (ΔAICc<2) using the 'dredge' function in the MuMIn package (Bartoń 2024), followed by model averaging with the \`model.avg′ function or the selection of the single best model when there were no competing models ($\Delta$AICc$>2$) (Burnham et al. 2011). The goodness of fit for all models was assessed using the 'simulateResiduals' function in the \`DHARMa′ package.

To assess natural enemy community composition across elevations and grassland cover, we applied NMDS using the Bray-Curtis dissimilarity matrix with the function \`metaMDS′ in the package \`vegan′ (Oksanen et al. 2020). For a clearer visualisation, sites were grouped into categorical classes. Elevation was classified into six categories: <1200 m, 1200–1349 m, 1350–1499 m, 1500–1649 m, 1650–1799 m, and >1800masl. Grass cover in the surrounding landscape was grouped into three classes: <10%,10–20%, and >20% cover. We performed a multivariate homogeneity analysis (PERMDISP) using the \`betadisper′ function in the vegan package to assess whether the assumption of homogeneity of group dispersions was met (compositional variance). Then we performed a multivariate permutation analysis of variance (PERMANOVA), using the \`adonis′ function from the vegan package to evaluate the differences in community composition between elevation and grassland cover categories, followed by a pairwise comparison (Anderson 2005).

Results

We collected a total of 1,317 arthropod predators and parasitoids across both seasons ($n = 522$ in the short rains season, $n = 795$ in the long rains season). The specimens represented 60 families and 174 genera (Online Resource 1). Ants (Formicidae) dominated the community, constituting 52% of all individuals, followed by Trigonidiidae (crickets, 10%) and Lycosidae (wolf spiders, 9%). At the genus level, *Myrmicaria* spp. (Hymenoptera: Formicidae) was most abundant (17% of the total natural enemy abundance), followed by *Pachycondyla* spp. (Hymenoptera: Formicidae, 7%), *Lycosa* spp. (Araneae: Lycosidae, 7%), *Aphaenogaster* spp. (Hymenoptera: Formicidae, 6%), and *Allonemobius* spp. (Orthoptera: Gryllidae, 5%) (Fig. 2).

The GLMMs revealed that the effects of elevation and grassland cover on diversity metrics varied. Evenness decreased significantly with increasing elevation (Fig. 3; Table 1). Grassland cover was retained in the final model for species richness, but it was not significant (Fig. 3; Table 1). For Shannon diversity and abundance, neither elevation, grass cover, nor their interaction was retained in the final model (Online Resource 2). The NMDS analysis revealed dissimilarities in natural enemy composition across the elevation and grass cover categories. PERMANOVA confirmed significant differences across elevations in both seasons (short rains : $p = 0.02$, $R^2 = 0.29$; long rains : $p < 0.01$, $R^2 = 0.38$ (Fig. 4; Table 2), with elevation accounting for approximately 29% and 38% of the variation, respectively. Pairwise comparison showed no significant differences during the short rains, but in the long rains, a near-significant difference was observed between the lowest and highest elevation (<1200 m vs.>1800 m: p-value=0.08; Online Resource 3). Grass cover significantly influenced community composition only in the long rains season ($p < 0.01$, $R^2 = 0.15$, Fig. 5; Table 2), explaining approximately 15% of the variation. No effect of grass cover was detected in the short rains season ($p = 0.50$, $R^2 = 0.13$, Online Resource 4). Pairwise PERMANOVA in the long-rain season revealed significant differences in the community composition between < 10% and > 20% grass cover categories ($p = 0.05$), whereas no significant pairwise differences were detected during the short rains (Online Resource 5).

Notably, *Myrmicaria* ants became increasingly dominant at elevations > 1600masl and at landscapes with < 10% grassland cover, whereas *Dolichoderus* and *Aphaenogaster* ants, and *Allonemobius* crickets were more common in fields with > 20% surrounding grass cover.

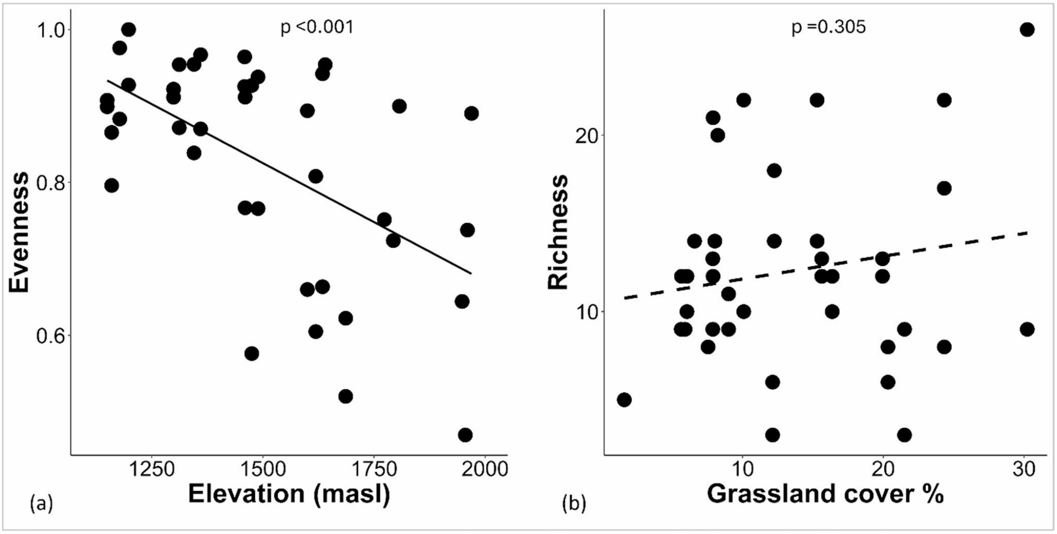

Fig. 2 Scatterplots illustrating the relationship between (**a**) elevation and evenness, and (**b**) grass cover and species richness. Solid line indicates a significant effect, and a dashed line indicates a non-significant effect which were retained in the final model

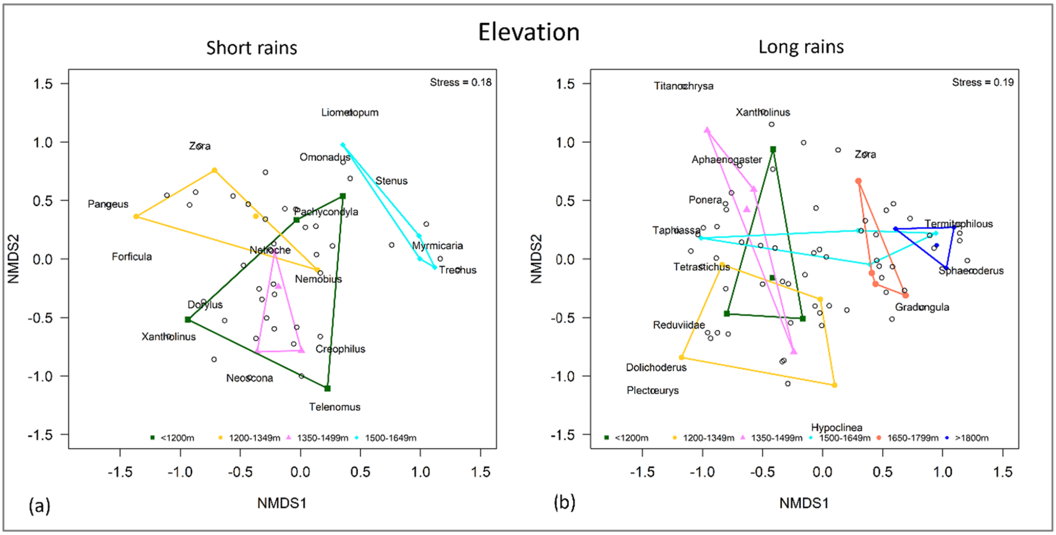

Fig. 3 Non-metric Multidimensional Scaling (NMDS) ordination of natural enemy community composition across elevation categories in (**a**) Short rains and (**b**) Long rains seasons. The community dissimilarity was computed using the Bray-Curtis index

Discussion

This study investigated the effects of elevation (1150–1970 masl) and surrounding grassland cover (2–30%) on natural enemy communities in maize fields in western Kenya across two seasons. We found that species evenness declined significantly with increasing elevation, and that community composition shifted with elevation and grassland cover, with an increasing dominance of *Myrmicaria* ants at higher elevations with lower grassland cover. While grassland cover did not significantly predict key diversity metrics, our findings showed a positive, non-significant trend with

Table 1 Results of the final GLMM for natural enemy evenness and richness in relation to elevation and grass cover. Estimates (Est. ± SE), z values and p values Pr(>|z|) are shown. For evenness, Pseudo-R^2 is provided, while for richness, both marginal R^2m and conditional R^2c coefficients are reported

Response variable	Predictors	Est. ± SE	z value	Pr(>|z|)	Pseudo-R^2
Natural enemy evenness	Intercept	1.55 ± 0.12	12.94	< 0.001	−0.18
	Elevation	−0.40 ± 0.11	−3.64	**< 0.001**	
Response variable	**Predictors**	**Est. ± SE**	**z value**	**Pr(>|z|)**	**R^2m/R^2c**
Natural enemy richness	Intercept	2.50 ± 0.08	31.35	< 0.001	0.08/0.18
	Grass cover	0.07 ± 0.07	1.03	0.305	

Negative Pseudo-R² indicates the full model did not improve fit over the null model.

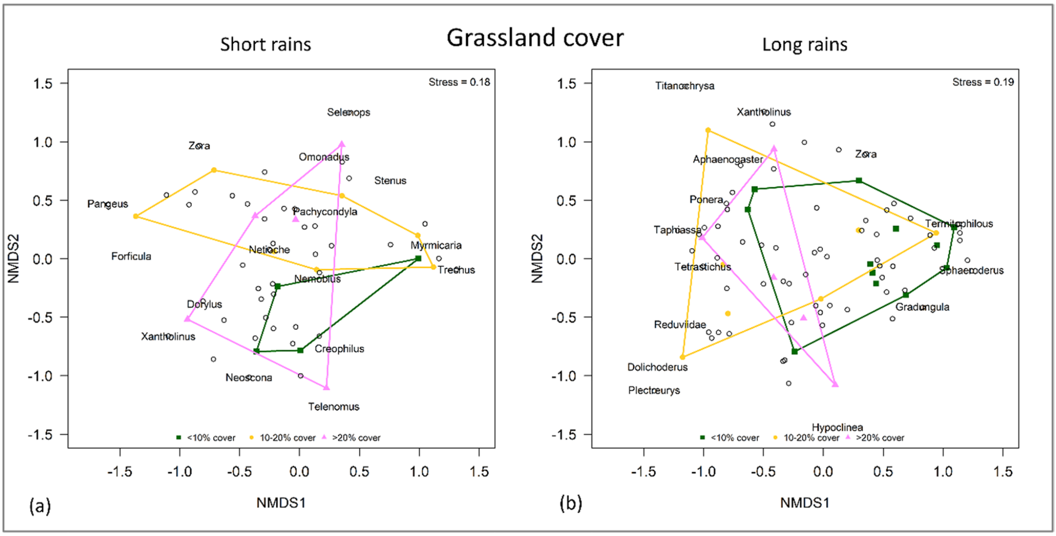

Fig. 4 Non-metric Multidimensional Scaling (NMDS) ordination of natural enemy community composition across grass cover categories in (**a**) Short rain and (**b**) Long rain. The community dissimilarity was computed using the Bray-Curtis index

species richness and a shift in community composition during the long rains season, which may have important implications for pest control.

Our findings demonstrated that an increase in elevation can decrease species evenness, significantly shaping natural enemy communities along an elevational gradient. Although we found no significant decline in species richness, similar studies have reported lower arthropod species richness and abundance with increasing elevation (Costa et al. 2023; Gilgado et al. 2022; Kunene et al. 2022). Lower elevations typically offer more favourable conditions for higher plant and arthropod diversity (Farooq et al. 2022), which in turn, results in more abundant food, breeding, and nesting resources for natural enemies (Farooq et al. 2022; Pilar et al. 2020). These more abundant resources likely contribute to the higher species evenness that we observed at lower elevations.

Higher elevations are often dominated by a few specialised species that tolerate harsh conditions like lower temperatures and limited microhabitats (Jiang et al. 2022). These constraints likely create physiological stress for many natural enemies by reducing resources, thereby lowering evenness, as only a few dominant species can thrive (Ceia-Hasse et al. 2023). While previous studies have consistently shown that higher elevations host fewer species overall (Dolson and Kharouba 2024; Supriya et al. 2019), our results revealed a more nuanced pattern. Our study found no significant effect of elevation on overall natural enemy abundance and richness. Instead, our results indicated that although the total number of species and individuals remained stable, the community structure shifted at higher elevations, dominated by a few species as reflected by the lower evenness. Ants dominated across all elevations, accounting for more than half (52%) of all individuals, with *Myrmicaria* emerging as the most abundant genus. Such strong numerical dominance of ants is consistent with other studies in tropical agroecosystems, where ants often outcompete other insects due to their aggressive foraging strategies and generalist feeding

Table 2 Results of the PERMANOVA assessing the effects of elevation and grass cover on natural enemy community composition across two seasons. Degree of freedom (Df), sum of squares, explained variation (R^2), F-statistic and significance levels are shown in bold

Seasons	Source of variation	Df	Sum of sqs	R^2	F	Pr(>F)
Short rains	**Elevation**	3	1.58	0.29	1.67	**0.02**
	Residual	12	3.79	0.71		
	Total	15	5.37	1.00		
Long rains	**Elevation**	5	3.02	0.38	2.20	**<0.01**
	Residual	18	4.93	0.6		
	Total	23	7.95	1.00		
Long rains	**Grass cover**	2	0.15	0.15	1.83	**<0.01**
	Residual	21	6.77	0.85		
	Total	23	7.95	1.00		

behaviours (Helms 2023; Schultheiss et al. 2022). Lower elevations (<1600masl) were dominated by several ant genera, including *Pachycondyla*, *Odontomachus*, *Crematogaster* and *Aphaenogaster*, alongside *Lycosa* (spiders) and *Allonemobius* (crickets). In contrast, maize fields at higher elevations (>1600masl) were consistently dominated by *Myrmicaria* ants.

Similar changes in the community structure of natural enemies along elevation gradients have been reported in various ecosystems (Gilgado et al. 2022; Kunene et al. 2022; Måsviken et al. 2023; Pilar et al. 2020). In other studies along elevational gradients, *Pachycondyla*, *Odontomachus* and *Crematogaste*r ants were recorded at lower elevations (Kunene et al. 2022; Munyai and Foord 2012). Contrary to our findings, *Myrmicaria* ants were recorded mostly between 800-1400masl; however, these studies were conducted in different ecosystems, where other environmental variables and differing climatic conditions might have influenced the distribution of these ants (Kunene et al. 2022; Munyai and Foord 2012). Our data show a negative correlation between grassland cover and elevation, suggesting that the dominance of *Myrmicaria* ants at high elevations may be driven by low grassland cover, a variable that may have differed in other studies.

The effect of grass cover in the surrounding landscape on natural enemy communities was less pronounced than that of elevation. Although grassland cover was retained in the final model for species richness, its effect was non-significant. Nonetheless, the positive trend with increasing grass cover (Fig. 3) suggests that non-crop habitats may contribute to higher species richness by providing dietary and nesting resources for natural enemies (Farooq et al. 2022; Pilar et al. 2020). Surrounding areas with low grass cover (<10%) were dominated by *Myrmicaria* ants, while those with higher grass cover (>20%) were dominated by *Dolichoderus* or *Aphaenogaster* ants, as well as *Allonemobius* crickets. Previous studies have reported that ant communities are primarily shaped by fine-scale habitat features, such as soil types, leaf litter depth, light penetration, or canopy density (Maravalhas and Vasconcelos 2020; Pérez-Sánchez et al. 2023), with broad-scale vegetation cover having a weak influence (Achury et al. 2022; Pérez-Sánchez et al. 2023). These findings suggest that the potential weak effects of surrounding grassland cover observed in our study may stem from other unaccounted variations in microhabitat complexity, unmeasured climatic gradients or sampling limitations.

Seasonality likely plays a role in shaping natural enemy composition in the region. We observed that the effect of grass cover was more pronounced during the long rainy season, likely due to shifts in climatic conditions, vegetation growth, and resource availability (Bishop et al. 2014). Seasonal increases in rainfall and plant productivity can enhance floral and extrafloral nectar resources, alternative prey, and nesting sites, which in turn support higher natural enemy activity (Achury et al. 2022). This highlights the importance of developing pest management strategies that account for seasonal dynamics in vegetation and climate, ensuring natural enemies are maximised during periods of peak pest pressure.

Implications and limitations

The natural enemy communities in our study were dominated by ants. Although research on the role of ants in pest control is limited in sub-Saharan Africa, evidence suggests that ants may help reduce pest populations in African cropping systems. For example, studies in Benin and Ghana found that *Pheidole* and *Campotonus* ants effectively controlled fall armyworms in maize and banana fields (Dassou et al. 2021; Koffi et al. 2020). In our study region, the dominant ant species included *Myrmicaria*, *Pachycondyla*, *Odontomachus*, and *Crematogaster*. Functional traits of these genera suggest potential roles in pest suppression: *Pachycondyla* and *Odontomachus* ants are medium to large predatory ants that actively hunt lepidopteran caterpillars, such as the fall armyworm larvae, and other arthropods in the soil and leaf litter (Schmidt and Shattuck 2014; Vicente et al. 2016); *Myrmicaria* are small to medium-sized omnivorous ants that scavenge and prey opportunistically on small pests, and they nest in the soil and grass (Ward and Brady 2003); and *Crematogaster* are small to medium-sized aggressive omnivorous ants that prey opportunistically on small pests (Styrsky and Eubanks 2007). Although some taxa of ants, including some species of *Crematogaster*, defend plant-sucking insects, such as aphids, against other natural enemies, potentially worsening pest problems (Styrsky and Eubanks 2007; Wills and Landis 2018), the main pests in our systems are fall armyworms and stem-boring caterpillars (Kansiime et al. 2024). Given the predatory nature of the dominant ants observed, it seems likely that they can protect crops against these pests, making them potential allies in integrated pest management strategies.

The evenness of natural enemies declined at higher elevations and, to a lesser extent, in landscapes with low grassland cover, with communities becoming increasingly dominated by certain ants (especially *Myrmicaria*). Reduced evenness implies that a few taxa disproportionately contribute to the community composition, which is likely to compromise the stability of pest control services if those dominant taxa are negatively affected by environmental stressors (Feit et al. 2021). In the short term, conserving dominant ants such as *Myrmicaria*, which are ground-foraging generalist predators capable of preying on a wide range of insects, could help maintain pest control services in higher elevations and in landscapes with reduced grassland cover (Pilar et al. 2020). However, reliance on a single dominant genus may reduce resilience to pest outbreaks over time as functionally important, less common taxa are underrepresented. Thus, promoting greater evenness in natural enemy communities could be particularly important at higher elevations and in landscapes with low grass cover. Such areas could benefit from additional interventions, such as habitat restoration, that may enhance the stability of pest regulation.

This study's limitations include the relatively low sample size and snapshot character of the sampling regime. Low sample sizes may have limited our ability to infer more subtle differences in natural enemy communities and may have contributed to the lack of differences in species richness and abundance. The use of pitfall traps as the only method to assess natural enemy communities is a further limitation. This method has a reduced likelihood of detecting foliage-dwelling natural enemies, such as lady beetles and mirid bugs, known to be prevalent in this system (Yi et al. 2012). Future research should thus aim to incorporate additional sampling methods, such as sweep netting and a larger sample size, covering longer time periods to capture a broader range of natural enemies.

Conclusion

Our study highlights the importance of elevation and grass cover in shaping natural enemy communities in agricultural landscapes in western Kenya. While elevation had a strong negative effect on evenness, grassland cover exhibited a more subtle influence on richness. For both environmental variables, community composition did change radically, with stronger dominance of *Myrmicaria* ants at higher elevations and with reduced landscape-level grass cover. Considering that climate change is expected to alter species distribution, these findings are critical. As temperature zones shift, the observed dynamics in our study, such as the dominance of specific genus like *Myrmicaria* ants, could be impacted, potentially influencing pest management outcomes in the future (Eigenbrode and Adhikari 2023; Randall 2025). Our findings, therefore, underscore the need to consider multiple landscape variables, alongside climate factors, when designing pest management strategies in sub-Saharan agricultural landscapes.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s42690-025-01670-w.

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Declarations

Conflict of interest The authors declare no conflict of interest.

References

Achury R, Lars C, Anne E, Sebastian M, Winfried V, Wolfgang WW (2022) Plant diversity and functional identity alter ant occurrence and activity in experimental grasslands. Ecosphere 13(10):e4252. https://doi.org/10.1002/ecs2.4252

Alarcon-Segura V, Grass I, Feuerbacher A, Gonzales-Chavez A, Mupepele AC (2025) Semi-natural habitats and their contribution to crop productivity through pollination and pest control: a systematic review. Landscape Ecol 40(7):137. https://doi.org/10.1007/s10980-025-02160-7

Alexandridis N, Marion G, Chaplin-Kramer R, Dainese M, Ekroos J, Grab H, Jonsson M et al (2022) Archetype models upscale understanding of natural pest control response to land-use change. Ecol Appl 32(8):e2696. https://doi.org/10.1002/eap.2696

Anderson MJ (2005) Permutational Multivariate Analysis of Variance

Bartoń K (2024) MuMIn: Multi-Model inference: 1.47.5. https://doi.org/10.32614/CRAN.package.MuMIn

Bishop TR, Robertson MP, Van Rensburg BJ, Parr CL (2014) Elevation diversity patterns through space and time: ant communities of the Maloti-Drakensberg mountains of Southern Africa. J Biogeogr 41(12):2256–2268. https://doi.org/10.1111/jbi.12368

Burnham KP, Anderson DR, Huyvaert KP (2011) AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. Behav Ecol Sociobiol 65(1):23–35. https://doi.org/10.1007/s00265-010-1029-6

Ceia-Hasse A, Boieiro M, Soares A, Antunes S, Figueiredo H, Rego C, Borges PAV, Conde J, Serrano ARM (2023) Drivers of insect community change along the margins of mountain streams in Serra da Estrela natural park (Portugal). Insects 14(3):243. https://doi.org/10.3390/insects14030243

R Core Team (2024) https://www.R-project.org/

Cortez-Madrigal H, Gutiérrez-Cárdenas OG (2023) Enhancing biological control: conservation of alternative hosts of natural enemies. Egypt J Biol Pest Control 33(1):25. https://doi.org/10.1186/s41938-023-00675-2

Costa FVD, Viana-Júnior AB, Aguilar R, Silveira FAO, Cornelissen TG (2023) Biodiversity and elevation gradients: insights on sampling biases across worldwide mountains. J Biogeogr 50(11):1879–1889. https://doi.org/10.1111/jbi.14696

Daelemans R, Hulsmans E, Laenen E, Remy S, Beliën T, Honnay O (2023) Direct and indirect effects of management and landscape on biological pest control and crop pest infestation in Apple orchards. J Appl Ecol 60(1):181–192. https://doi.org/10.1111/1365-2664.14319

Dassou AG, Idohou R, Azandémè-Hounmalon GY, Sabi-Sabi A, Houndété J, Silvie P, Dansi A (2021) Fall armyworm, *Spodoptera frugiperda* (J.E. Smith) in maize cropping systems in Benin: abundance, damage, predatory ants and potential control. Int J Trop Insect Sci 41(4):2627–2636. https://doi.org/10.1007/s42690-021-00443-5

Debinski DM (2023) Insects in grassland ecosystems. Rangeland wildlife ecology and conservation. Springer, Cham, pp 897–929. https://doi.org/10.1007/978-3-031-34037-6_26

Di Marco M, Santini L, Corcos D, Tschorsnig HP, Cerretti P (2023) Elevational homogenization of mountain parasitoids across six decades. Proc Natl Acad Sci U S A 120(46):e2308273120. https://doi.org/10.1073/pnas.2308273120

Dolson SJ, Kharouba HM (2024) 30 years of terrestrial insect richness patterns across elevation: what have we learned? A global meta-analysis. J Anim Ecol 93(12):1819–1829. https://doi.org/10.1111/1365-2656.14193

Eigenbrode SD, Adhikari S (2023) Climate change and managing insect pests and beneficials in agricultural systems. Agron J 115(5):2194–2215. https://doi.org/10.1002/agj2.21399

Farooq MO, Razaq M, Shah FM (2022) Plant diversity promotes species richness and community stability of arthropods in organic farming. Arthropod-Plant Interact 16(6):593–606. https://doi.org/10.1007/s11829-022-09920-1

Fartmann T (2024) Insect conservation in grasslands. In: *R. (eds) Handbook of Insect Conservation 1st* edn. Routledge, pp 263–274. https://doi.org/10.4324/9781003285793

Feit B, Blüthgen N, Traugott M, Jonsson M (2019) Resilience of ecosystem processes: a new approach shows that functional redundancy of biological control services is reduced by landscape simplification. Ecol Lett 22(10):1568–1577. https://doi.org/10.1111/ele.13347

Feit B, Blüthgen N, Daouti E, Straub C, Traugott M, Jonsson M (2021) Landscape complexity promotes resilience of biological pest control to climate change. Proc R Soc Lond B Biol Sci 288(1951):20210547. https://doi.org/10.1098/rspb.2021.0547

Gilgado JD, Rusterholz HP, Braschler B, Zimmermann S, Chittaro Y, Baur B (2022) Six groups of ground-dwelling arthropods show different diversity responses along elevational gradients in the Swiss Alps. PLoS One 17(7):e0271831. https://doi.org/10.1371/journal.pone.0271831

Helms JA (2023) Climate, geography, and the mating phenology of ants. Insectes Soc 70(1):119–125. https://doi.org/10.1007/s00040-022-00888-y

Herrera-Alsina L, Parvanova R, Guirguis J, Bocedi G, Trethowan L, Lancaster LT, Travis JMJ (2025) Disentangling evolutionary, geometric and ecological components of the elevational gradient of diversity. Evol Lett 9(1):51–64. https://doi.org/10.1093/evlett/qrae048

Hession SL, Moore N (2011) A spatial regression analysis of the influence of topography on monthly rainfall in East Africa. Int J Climatol 31(10):1440–1456. https://doi.org/10.1002/joc.2174

Hodkinson ID (2005) Terrestrial insects along elevation gradients: species and community responses to altitude. Biol Rev 80(3):489–513. https://doi.org/10.1017/S1464793105006767

Jacobsen D (2020) The dilemma of altitudinal shifts: caught between high temperature and low oxygen. Front Ecol Environ 18(4):211–218. https://doi.org/10.1002/fee.2161

Jiang K, Dong X, Zhang J, Ye Z, Xue H, Zhu G, Bu W (2022) Diversity and conservation of endemic true bugs for four family groups in China. Divers Distrib 28(12):2824–2837. https://doi.org/10.1111/ddi.13648

Joseph GS, Muluvhahothe MM, Seymour CL, Munyai TC, Bishop TR, Foord SH (2019) Stability of Afromontane ant diversity decreases across an elevation gradient. Glob Ecol Conserv 17:e00596. https://doi.org/10.1016/j.gecco.2019.e00596

Kansiime MK, Makale F, Chacha D, Nunda W, Karanja D, Durocher-Granger L (2024) Area-wide pest management and prospects for fall armyworm control on smallholder farms in africa: A review. Sustainable Environ 10(1):2345464. https://doi.org/10.1080/27658511.2024.2345464

Karimzadeh R, Sciarretta A (2022) Spatial patchiness and association of pests and natural enemies in agro-ecosystems and their application in precision pest management: a review. Precis Agric 23(5):1836–1855. https://doi.org/10.1007/s11119-022-09902-6

Karp DS, Chaplin-Kramer R, Meehan TD, Martin EA, DeClerck F, Grab H, Gratton C et al (2018) Crop pests and predators exhibit inconsistent responses to surrounding landscape composition. *Proceedings of the National Academy of Sciences* 115(33). https://doi.org/10.1073/pnas.1800042115

Khaliq I, Shahid MJ, Kamran H, Sheraz M, Awais M, Shabir M, Asghar M et al (2023) The role of thermal tolerance in determining elevational distributions of four arthropod taxa in mountain ranges of Southern Asia. J Anim Ecol 92(10):2052–2066. https://doi.org/10.1111/1365-2656.13996

Klinnert A, Barbosa AL, Catarino R, Fellmann T, Baldoni E, Beber C, Hristov J et al (2024) Landscape features support natural pest control and farm income when pesticide application is reduced. Nat Commun. https://doi.org/10.1038/s41467-024-48311-3

Koffi D, Kyerematen R, Eziah VY, Agboka K, Adom M, Goergen G, Meagher RL (2020) Natural enemies of the fall armyworm, *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae) in Ghana. Fla Entomol 103(1):85. https://doi.org/10.1653/024.103.0414

Kunene C, Foord SH, Scharff N, Pape T, Malumbres-Olarte J, Munyai TC (2022) Ant diversity declines with increasing elevation along the Udzungwa mountains, Tanzania. Diversity 14(4):260. https://doi.org/10.3390/d14040260

Litovska I, Plas FVD, Kleijn D (2025) Arthropod abundance is most strongly driven by crop and semi-natural habitat type rather than management in an intensive agricultural landscape in the Netherlands. Agric Ecosyst Environ 378:109298. https://doi.org/10.1016/j.agee.2024.109298

Luna P, Villalobos F, Escobar F, Neves F, Castillo-Campos G, Hinojosa-Díaz I, Luciano C et al (2023) Temperature dissimilarity drives flower–visitor interaction turnover across elevation in the Mexican transition zone. J Biogeogr 50(10):1737–1748. https://doi.org/10.1111/jbi.14684

Maravalhas JB, Vasconcelos HL (2020) Ant diversity in Neotropical savannas: hierarchical processes acting at multiple spatial scales. J Anim Ecol 89(2):412–422. https://doi.org/10.1111/1365-2656.13111

Martin EA, Reineking B, Seo B, Steffan-Dewenter I (2013) Natural enemy interactions constrain pest control in complex agricultural landscapes. Proc Natl Acad Sci U S A 110(14):5534–39. https://doi.org/10.1073/pnas.1215725110

Martin EA, Dainese M, Clough Y, Báldi A, Bommarco R, Gagic V, Garratt MPD et al (2019) The interplay of landscape composition and configuration: new pathways to manage functional biodiversity and agroecosystem services across Europe. Ecol Lett 22(7):1083–1094. https://doi.org/10.1111/ele.13265

Måsviken J, Marquina D, Norén K, Dalén L, Dalerum F (2023) Elevational variation of spider and insect communities in the Swedish mountains. Ecosphere 14(6):e4540. https://doi.org/10.1002/ecs2.4540

Mazón M, Bordera S, Rodríguez-Berrío A, Frago E (2024) The relative influence of agricultural abandonment and semi-natural habitats on parasitoid diversity and community composition. PLoS One 19(8):e0303656. https://doi.org/10.1371/journal.pone.0303656

McCain CM, Garfinkel CF (2021) Climate change and elevational range shifts in insects. Curr Opin Insect Sci 47:111–118. https://doi.org/10.1016/j.cois.2021.06.003

Minato N (2024) Fmsb: functions for medical statistics book with some demographic data: 0.7.6. https://doi.org/10.32614/CRAN.package.fmsb

Munyai TC, Foord SH (2012) Ants on a mountain: spatial, environmental and habitat associations along an altitudinal transect in a centre of endemism. J Insect Conserv 16(5):677–695. https://doi.org/10.1007/s10841-011-9449-9

Nagy RK, Bell LW, Schellhorn NA, Zalucki MP (2020) Role of grasslands in pest suppressive landscapes: how green are my pastures? Austral Entomol 59(2):227–237. https://doi.org/10.1111/aen.12464

Novaes DR, Sujii PS, Rodrigues CA, Silva KMNB, Machado AFP, Inoue-Nagata AK, Nakasu EYT, Togni PHB (2024) Natural habitat connectivity and organic management modulate pest dispersal, gene flow, and natural enemy communities. Ecol Appl 34(2):e2938. https://doi.org/10.1002/eap.2938

Oksanen AJ, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR et al (2020) Package Vegan

Paudel S, Kandel P, Bhatta D, Pandit V, Felton GW, Rajotte EG (2021) Insect herbivore populations and plant damage increase at higher elevations. Insects 12(12):1129. https://doi.org/10.3390/insects12121129

Pérez-Sánchez AJ, Schibalski A, Schröder B, Klimek S, Dauber J (2023) Local and landscape environmental heterogeneity drive ant community structure in temperate seminatural upland grasslands. Ecol Evol 13(3):e9889. https://doi.org/10.1002/ece3.9889

Perrot T, Rusch A, Coux C, Gaba S, Bretagnolle V (2021) Proportion of grassland at landscape scale drives natural pest control services in agricultural landscapes. Front Ecol Evol. https://doi.org/10.3389/fevo.2021.607023

Perrot T, Rusch A, Gaba S, Bretagnolle V (2023) Both long-term grasslands and crop diversity are needed to limit pest and weed infestations in agricultural landscapes. Proc Natl Acad Sci U S A 120(49):e2300861120. https://doi.org/10.1073/pnas.2300861120

Pilar FC, Mocellin L, Desfossez E, Rasmann S (2020) Seasonal changes in arthropod diversity patterns along an alpine elevation gradient. Ecol Entomol 45(5):1035–1043. https://doi.org/10.1111/een.12881

Polato NR, Gill BA, Shah AA, Gray MM, Casner KL, Barthelet A, Messer PW et al (2018) Narrow thermal tolerance and low dispersal drive higher speciation in tropical mountains'. Proc Natl Acad Sci U S A 115(49):12471–76. https://doi.org/10.1073/pnas.1809326115

Poveda K, Díaz MF, Espinosa S, Obregon D, Ramirez A (2019) Landscape complexity and elevation affect the effectiveness of a local pest-management practice. Glob Ecol Conserv 20:e00763. https://doi.org/10.1016/j.gecco.2019.e00763

Randall MGM (2025) Tritrophic interactions in a changing climate: a seed-feeding moth and its larval ectoparasitoids along an elevational gradient. J Insect Conserv 29(3):38. https://doi.org/10.1007/s10841-025-00674-8

Rasmann S, Pellissier L, Defossez E, Jactel H, Kunstler G (2014) Climate-driven change in plant–insect interactions along elevation gradients. Funct Ecol 28(1):46–54. https://doi.org/10.1111/1365-2435.12135

Ratto F, Bruce T, Chipabika G, Mwamakamba S, Mkandawire R, Khan Z, Mkindi A et al (2022) Biological control interventions reduce pest abundance and crop damage while maintaining natural enemies in sub-Saharan Africa: a meta-analysis. Proc R Soc Lond B Biol Sci 289(1988):20221695. https://doi.org/10.1098/rspb.2022.1695

Rödder D, Schmitt T, Gros P, Ulrich W, Habel JC (2021) Climate change drives mountain butterflies towards the summits. Sci Rep 11(1):14382. https://doi.org/10.1038/s41598-021-93826-0

Rumpf SB, Hülber K, Zimmermann NE, Dullinger S (2019) Elevational rear edges shifted at least as much as leading edges over the last century. Glob Ecol Biogeogr 28(4):533–543. https://doi.org/10.1111/geb.12865

Rusch A, Chaplin-Kramer R, Gardiner MM, Hawro V, Holland J, Landis D, Thies C et al (2016) Agricultural landscape simplification reduces natural pest control: a quantitative synthesis. Agric Ecosyst Environ 221:198–204. https://doi.org/10.1016/j.agee.2016.01.039

Sam K, Re Jorge L, Koane B, Amick PK, Elise S (2023) Vertebrates, but not ants, protect rainforest from herbivorous insects across elevations in Papua new Guinea. J Biogeogr: Jbi 14686. https://doi.org/10.1111/jbi.14686

Schmidt CA, Shattuck SO (2014) The higher classification of the ant subfamily ponerinae (Hymenoptera: Formicidae), with a review of Ponerine ecology and behavior. Zootaxa 3817(1). https://doi.org/10.11646/zootaxa.3817.1.1

Schultheiss P, Nooten SS, Wang R, Wong MKL, Brassard F, Guénard B (2022) The abundance, biomass, and distribution of ants on earth. Proc Natl Acad Sci U S A 119(40):e2201550119. https://doi.org/10.1073/pnas.2201550119

Silva-Monteiro M, Scheper J, Pehlak H, Kurina O, Timonen S, Pessa J, Pasanen E et al (2022) Invertebrate abundance increases with vegetation productivity across natural and agricultural wader breeding habitats in Europe. Biol Conserv 273:109670. https://doi.org/10.1016/j.biocon.2022.109670

Smith MA, Warne C, Pare K, Dolson S, Loewen E, Jones K, Janzen DH (2023) Communities of small terrestrial arthropods change rapidly along a Costa Rican elevation gradient. In *Neotropical gradients and their analysis*. Springer Int Publishing 255–307. https://doi.org/10.1007/978-3-031-22848-3_10

Styrsky JD, Eubanks MD (2007) Ecological consequences of interactions between ants and honeydew-producing insects. Proc R Soc Lond B Biol Sci 274(1607):151–64. https://doi.org/10.1098/rspb.2006.3701

Supriya K, Moreau CS, Sam K, Price TD (2019) Analysis of tropical and temperate elevational gradients in arthropod abundance. Front Biogeogr 11(2). https://doi.org/10.21425/F5FBG43104

Uhey DA, Bowker MA, Haubensak KA, Auty D, Vissa S, Hofstetter RW (2022) Habitat type affects elevational patterns in ground-dwelling arthropod communities. J Insect Sci 22(4):9. https://doi.org/10.1093/jisesa/ieac046

Vicente RE, Prado LP, Izzo TJ (2016) Amazon rainforest ant-fauna of Parque Estadual do Cristalino: understory and ground-dwelling ants. Sociobiology 63(3):894. https://doi.org/10.13102/sociobiology.v63i3.1043

Wang XP, Ollerton J, Prendergast KS, Cai JC, Tong MY, Shi MM, Zhao ZT, Li SJ, Tu TY (2024) The effect of elevation, latitude, and plant richness on robustness of pollination networks at a global scale. Arthropod-Plant Interact 18(3):389–401. https://doi.org/10.1007/s11829-024-10056-7

Ward PS, Brady SG (2003) Phylogeny and biogeography of the ant subfamily myrmeciinae (Hymenoptera: formicidae). Invertebr Syst 17(3):361. https://doi.org/10.1071/IS02046

Wills BD, Landis DA (2018) The role of ants in North temperate grasslands: a review. Oecologia 186(2):323–338. https://doi.org/10.1007/s00442-017-4007-0

Yi Z, Jinchao F, Dayuan X, Weiguo S, Axmacher JC (2012) A comparison of terrestrial arthropod sampling methods. J Resour Ecol 3(2):174–182. https://doi.org/10.5814/j.issn.1674-764x.2012.02.010

Zuur AF, Ieno EN, Elphick CS (2010) A protocol for data exploration to avoid common statistical problems: *Data exploration*. Methods Ecol Evol 1(1):3–14. https://doi.org/10.1111/j.2041-210X.2009.00001.x

Supplementary materials

Elevation and grassland cover shape natural enemy communities in Kenyan maize crops

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Online Resource 1| Families of natural enemies recorded in maize agroecosystems. All taxa are either carnivorous, omnivorous or parasitoids based on well-established knowledge of their feeding habits

Order	Family	Abundance	Number of genera
Acariformes	Erythraeidae	1	1
	Phytoseiidae	1	1
Araneae	Anapidae	3	1
	Anyphaenidae	5	1
	Araneidae	28	2
	Clubionidae	5	1
	Corinnidae	2	1
	Ctenidae	6	1
	Deinopidae	1	1
	Dictynidae	1	1
	Filistatidae	2	1
	Gnaphosidae	4	3
	Gradungulidae	2	1
	Hahniidae	2	1
	Hypochilidae	1	1
	Lamponidae	13	2
	Lycosidae	117	7
	Miturgidae	3	1
	Orsolobidae	1	1
	Oxyopidae	4	1
	Pholcidae	2	1
	Plectreuridae	2	1
	Salticidae	3	2
	Scytodidae	1	1
	Selenopidae	3	2
	Sicariidae	2	1
	Theridiidae	2	1
	Theridiosomatidae	2	1
	Thomisidae	3	1
	Zoropsidae	2	2

Order	Family	Abundance	Number of genera
Chilopoda	Scolopocryptopidae	3	3
Coleoptera	Anthicidae	3	3
	Carabidae	50	12
	Chrysomelidae	1	1
	Coccinellidae	8	3
	Elateridae	3	2
	Lampyridae	23	2
	Staphylinidae	50	16
Dermaptera	Forficulidae	13	3
Diptera	Dolichopodidae	17	7
	Hybotidae	1	1
Hemiptera	Cydnidae	1	1
	Pentatomidae	1	1
	Reduviidae	4	3
Hymenoptera	Braconidae	7	4
	Bethylidae	4	1
	Chalcididae	3	1
	Eulophidae	1	1
	Figitidae	6	3
	Formicidae	683	46
	Ichneumonidae	3	2
	Platygastridae	1	2
	Platygastrinae	4	1
	Pompilidae	1	1
	Scelionidae	12	1
Mantodea	Mantidae	1	1
Opiliones	Phalangiidae	1	1
	Sclerosomatidae	3	1
Orthoptera	Gryllidae	56	5
	Trigonidiidae	129	3

Online Resource 2 | The results of model selection assessing Shannon diversity, Pielou’s evenness, Richness and Abundance to the elevation gradient and grass cover. AIC (Akaike Information Criterion) values indicate model fits, with lower values representing a better fit. Models are arranged from the lowest to the highest. Models with ΔAIC < 2 are highlighted in bold

a. Model selection results based on AIC for Shannon diversity index

Model	Variables	AIC	Delta AIC
1	Shannon ~ 1	**75.3**	0.00
2	Shannon ~ Elevation	77.5	2.19
3	Shannon ~ Grass cover	78.6	3.33
4	Shannon ~ Elevation+ Grass cover	82.3	6.99
8	Shannon ~ Elevation+ Grass cover+ Elevation: Grass cover	86.7	11.43

b. Model selection results based on AIC for Richness

Model	Variables	AIC	Delta AIC
1	Richness ~ 1	**250.6**	0.00
3	Richness ~ Grass cover	**252.0**	1.38
2	Richness ~ Elevation	252.9	2.31
4	Richness ~Elevation+ Grass cover	254.4	3.75
8	Richness ~Elevation+ Grass cover+ Elevation: Grass cover	256.0	5.40

c. Model selection results based on AIC for Evenness

Model	Variables	AIC	Delta AIC
2	Evenness ~ Elevation	**-66.4**	0.00
4	Evenness ~Elevation+ Grass cover	-63.9	2.49
8	Evenness ~Elevation+ Grass cover+ Elevation: Grass cover	-61.3	5.09
3	Evenness ~ Grass cover	-59.2	7.20
1	Evenness ~ 1	-57.6	8.81

d. Model selection results based on AIC for Abundance

Model	Variables	AIC	Delta AIC
1	Abundance ~ 1	**341.3**	0.00
3	Abundance ~ Grass cover	343.4	2.13
2	Abundance ~ Elevation	343.6	2.33
4	Abundance ~Elevation+ Grass cover	344.5	3.21
8	Abundance ~Elevation+ Grass cover+ Elevation: Grass cover	347.3	5.99

Online Resource 3| Pairwise comparison of natural enemy composition across elevation in two seasons. Values indicate Bray-Curtis's similarity index

Season	Elevation 1 (masl)	Elevation 2 (masl)	Similarity
Short rains	<1200	1200-1349	0.76
Short rains	<1200	1350-1499	0.70
Short rains	<1200	1500-1649	0.25
Short rains	1200-1349	1350-1499	0.51
Short rains	1200-1349	1500-1649	0.17
Short rains	1350-1499	1500-1649	0.17
Long rains	<1200	1200-1349	0.92
Long rains	<1200	1350-1499	0.23
Long rains	<1200	1500-1649	0.12
Long rains	<1200	1650-1799	0.08
Long rains	<1200	>1800	0.08
Long rains	1200-1349	1350-1499	0.12
Long rains	1200-1349	1500-1649	0.08
Long rains	1200-1349	1650-1799	0.08
Long rains	1200-1349	>1800	0.08
Long rains	1350-1499	1500-1649	0.08
Long rains	1350-1499	1650-1799	0.08
Long rains	1350-1499	>1800	0.08
Long rains	1500-1649	1650-1799	0.47
Long rains	1500-1649	>1800	0.11
Long rains	1650-1799	>1800	0.12

Online Resource 4| Results of the PERMANOVA assessing the effects of grass cover on natural enemies' composition in the short rains season. Degree of freedom (Df), sum of squares, explained variation (R^2), F-statistic and significance levels are shown

Seasons	Source of variation	Df	Sum of sqs	R^2	F	Pr(>F)
Short rains	Grass cover	2	0.70	0.13	0.98	0.50
	Residual	13	4.67	0.87		
	Total	15	5.37	1.00		

Online Resource 5| Pairwise comparison of natural enemy composition across grass cover percentage in Season 2. Values indicate Bray-Curtis's similarity index

Season	Grass cover 1 (%)	Grass cover 2 (%)	Similarity
Long rains	<10	10-20	0.17
Long rains	<10	>20	0.05
Long rains	10-20	>20	0.19

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Push-pull (PP) is an important ecological intensification strategy in sub-Saharan Africa, but its ability to suppress *Striga* and reduce pest damage is strongly context-dependent. This thesis shows that PPs' performance varies with local soil conditions, landscape structure, and management practices, which shape the underlying ecological mechanisms. Aligning PP with local agroecological and landscape contexts is therefore essential for maximising its benefits in Fall armyworm, stemborer and *Striga* control.

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