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Ecology and biological control options against *Spodoptera frugiperda* (Lepidoptera: Noctuidae) in South Kivu, Eastern DR Congo

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Abstract

Spodoptera frugiperda (J.E. Smith 1797) known as the fall armyworm (FAW), is a significant agricultural pest originally native to the Americas, that poses a threat to crops worldwide. FAW feed on the leaves, stems, and reproductive parts of plants. It has a broad host range, affecting over 80 plant species including maize, rice, sorghum, cotton, and vegetables. Infestations can lead to significant yield losses and increased costs for pest management. The economic impact is particularly severe in developing countries where farmers have limited access to effective control measures. Eight years after its invasion in Africa, research has been launched in several countries to assess the infestation rates and economic impact of the pest on maize crops, the climatic factors associated with its distribution and damage, genetic studies of the pest population and methods of managing it, through the inventory of its natural enemies for biological control. However, studies on FAW in Democratic Republic of Congo (DRC) are scarce on the abovementioned aspects. This thesis provides the first data on FAW invasion, especially in eastern DRC.

Chapter 1 summarizes the FAW invasions, highlighting their relationship with climatic conditions and farmers' knowledge of its presence in both native and invaded countries. It explores the different control strategies used by farmers to manage this pest and looks at the potential of biological control agents for its sustainable management. The invasion dynamics and response strategies highlight the urgent need for sustainable solutions in agricultural practices.

The objectives are to investigate the habitat range and environmental preferences of FAW, map its distribution, and understand how seasonal variations and environmental factors influence its infestation patterns in South Kivu. The thesis also examines smallholder farmers' knowledge and practices in managing FAW, with the aim of improving integrated pest management strategies adapted to their context. Finally, the thesis explores the dynamics between FAW populations and their natural enemies in maize fields, focusing on the potential of indigenous insects' parasitoids, predators and entomopathogenic fungi (EPFs) as biological control agents (BCAs).

The impact of environmental factors on FAW invasion in South Kivu is analyzed in the **Chapter 2**. Using a MaxEnt species distribution model, the study predicts FAW's potential distribution based on environmental factors such as mean annual temperature, annual rainfall, temperature seasonality, and dry season duration. The model, with an average area under the curve of 0.827, highlights annual rainfall as the most significant variable affecting FAW distribution. The study identifies two corridors of high FAW presence in South Kivu: An eastern corridor encompassing Kalehe, Kabare, Walungu, Uvira, and Fizi territories, and a western corridor covering Kalehe, Kabare, Walungu, and Mwenga. Field surveys conducted across two agro-ecological zones, Kabare and Ruzizi Plain, reveal varying FAW infestation dynamics influenced by local bioclimatic conditions. The Ruzizi Plain experiences higher FAW incidence, leaf damage, and larval density due to its warmer climate, particularly evident in the late 2019 season. Two generations of FAW are likely to be observed in maize agro-systems in South Kivu. Analysis of planting dates further indicates that late plantings correlate with increased FAW larval density, incidence, and severity of damage, emphasizing the need for climate-smart integrated pest management strategies to mitigate FAW's agricultural impact in the region.

FAW management remains a critical issue for smallholder farmers in Africa, as highlighted in **Chapter 3** by a survey in central and west Africa. Almost all farmers were familiar with FAW and reported damage to their fields. Although maize is the main target, farmers identified several alternative host plants such as Napier grass, sorghum, onion and cabbage. While cultural and mechanical methods are used, synthetic pesticides remain popular, particularly in Burkina Faso and Gabon. Conversely, Senegal is less dependent on insecticides. Innovative approaches such as semiochemicals and biological control are emerging in some regions, but are less well known in DR Congo, Gabon and Benin. In the future, the promotion of sustainable practices such as the push-pull approach, the development of biopesticides and resistant cultivars will be crucial to mitigate the impact of FAW while ensuring agricultural and environmental resilience.

In **Chapter 4**, a monitoring system was established to assess natural enemies of the FAW. This system involved trapping, visual observation of predators, and collection of larvae and eggs for parasitoid study in Kamanyola (Low altitude) and Kabare (Mid-altitude). Ten parasitoid species were identified, with *Telenomus remus* achieving high egg parasitism and *Coccygidium luteum* dominating larval parasitism. Predator abundance, such as ants, earwigs, and ladybirds, varied with maize growth stages, with ants particularly abundant among all the predators' groups. Insect predators were more prevalent at the four leaves completely unfolded stage (V4), coinciding with high FAW larval densities. Microbial control, seen as a sustainable alternative to hazardous pesticides to mitigate FAW damage, was investigated by sampling maize fields for FAW larvae infected with entomopathogenic fungi (EPFs). Unexpectedly, earwig cadavers collected with

FAW larvae were also examined. Morphological and phylogenetic analyses confirmed the fungi as *Beauveria bassiana*. Three isolates (P5E, KA14 and PL6) were recovered from both FAW and earwig cadavers and compared with commercial (GHA) and local (BGx) strains in bioassays against FAW larvae. Results showed significant mortality (approximately 70%) with GHA, KA14 and PL6 isolates.

Chapter 5 discusses the results of this research project in the context of FAW monitoring and forecasting, the challenges and opportunities of using biological control agents, and a proposal for an integrated FAW management strategy in South Kivu. An early warning system based on climate forecasts is needed to alert farmers to pest invasions and sowing dates. Training farmers in natural enemy identification, pest knowledge and the effective use of biological control agents is essential for the successful implementation of an integrated approach to FAW control in DRC. Biological control is an essential component of integrated FAW control in South Kivu. The results of this thesis advance knowledge of FAW invasion in Africa and provide the first data on macro- and micro-organism biological control agents in the DRC.

Résumé

Spodoptera frugiperda (J.E. Smith 1797), connue sous le nom de chenille légionnaire d'automne (CLA), est un ravageur important originaire de l’Amérique tropicale et Subtropicale, qui constitue une menace pour les cultures dans le monde. CLA se nourrit des feuilles, des tiges et des parties reproductrices des plantes. Elle possède une large gamme d'hôtes, affectant plus de 80 espèces de plantes, dont le maïs, le riz, le sorgho, le coton et les légumes. Les infestations peuvent entraîner d'importantes pertes de rendement et une augmentation des coûts de lutte. L'impact économique est particulièrement grave dans les pays en développement où les agriculteurs ont un accès limité à des mesures de lutte efficaces. Huit ans après son invasion en Afrique, des recherches ont été lancées dans plusieurs pays pour évaluer les taux d'infestation et l'impact économique du ravageur sur les cultures de maïs, les facteurs climatiques associés à sa distribution et à ses dégâts, les études génétiques de la population du ravageur et les méthodes de lutte, à travers l'inventaire de ses ennemis naturels pour la lutte biologique. Cependant, les études sur CLA en République Démocratique du Congo (RDC) sont rares sur les aspects susmentionnés. Cette thèse fournit les premières données sur l'invasion de CLA, en particulier à l'Est de la RDC.

Le **chapitre 1** présente une littérature sur les invasions de CLA, en soulignant leur relation avec les conditions climatiques et les connaissances qu'ont les agriculteurs de sa présence, tant dans les pays originaires que dans les pays envahis. Il explore les différentes stratégies de contrôle utilisées par les agriculteurs pour lutter contre ce ravageur et examine le potentiel des agents de contrôle biologique pour sa gestion durable. La dynamique d'invasion et les stratégies de réponse soulignent le besoin urgent de solutions durables dans les pratiques agricoles.

Les objectifs de cette thèse sont d'étudier l'aire d'habitat et les préférences environnementales de CLA, de cartographier sa distribution et de comprendre comment les variations saisonnières et les facteurs environnementaux influencent ses schémas d'infestation au Sud-Kivu. La thèse examine également les connaissances et les pratiques des petits exploitants agricoles en matière de gestion de CLA, dans le but d'améliorer les stratégies de lutte intégrée contre les ravageurs adaptées à leur contexte. Enfin, la thèse explore la dynamique entre les populations de FAW et leurs ennemis naturels dans les champs de maïs, en se concentrant sur le potentiel des parasitoïdes, des prédateurs et des champignons entomopathogènes indigènes en tant qu'agents de contrôle biologique.

L'impact des facteurs environnementaux sur l'invasion des FAW dans le Sud-Kivu est analysé dans le **chapitre 2**. En utilisant un modèle de distribution des espèces MaxEnt, l'étude prédit la distribution potentielle de CLA en fonction de facteurs environnementaux tels que la température annuelle moyenne, la pluviométrie annuelle, la saisonnalité de la température et la durée de la saison sèche. Le modèle, avec une aire moyenne sous la courbe (AUC) de 0.827, met en évidence les précipitations annuelles comme étant la variable la plus significative affectant la distribution de CLA. L'étude identifie deux corridors de forte présence de CLA au Sud-Kivu : un corridor oriental englobant les territoires de Kalehe, Kabare, Walungu, Uvira et Fizi, et un corridor occidental couvrant Kalehe, Kabare, Walungu et Mwenga. Les observations de terrain menées dans deux zones agroécologiques, Kabare et la plaine de Ruzizi, révèlent des dynamiques d'infestation de CLA variables, influencées par les conditions climatiques locales. La plaine de Ruzizi connaît une incidence plus élevée de CLA, des dommages aux feuilles et une densité larvaire plus importante en raison de son climat plus chaud, particulièrement en saison B de 2019. Deux générations de CLA sont susceptibles d'être observées dans les agrosystèmes de maïs au Sud-Kivu. L'analyse des dates de plantation indique en outre que les plantations tardives sont corrélées à une augmentation de la densité larvaire de CLA, de l'incidence et de sévérité, soulignant la nécessité de stratégies intelligentes de gestion intégrée des ravageurs sur le plan climatique pour atténuer l'impact agricole de CLA dans la région.

La gestion de CLA reste une question cruciale pour les petits exploitants agricoles en Afrique, comme c’est souligné dans le **chapitre 3** au cours d'une enquête menée en Afrique centrale et occidentale. Presque tous les agriculteurs connaissent CLA et ont signalé des dégâts dans leurs champs. Bien que le maïs soit la cible principale, les agriculteurs ont identifié plusieurs plantes hôtes alternatives telles que le Napier, le sorgho, l'oignon et le chou. Bien que des méthodes culturales et mécaniques soient utilisées, les pesticides synthétiques restent populaires, en particulier au Burkina Faso et au Gabon. A l'inverse, le Sénégal est moins dépendant de ces pesticides. Des approches innovantes telles que la lutte sémiochimique et la lutte biologique émergent dans certaines régions, mais sont moins connues en République démocratique du Congo, au Gabon et au Bénin. A l'avenir, la promotion de pratiques durables telles que l'approche push-pull, le développement de biopesticides et de cultivars résistants sera cruciale pour atténuer l'impact de CLA.

Dans le **chapitre 4**, un système de suivi a été établi pour évaluer les ennemis naturels de CLA. Ce système comprend le piégeage, l'observation visuelle des prédateurs et la collecte de larves et d'œufs pour l'étude des parasitoïdes à

Kamanyola (basse altitude) et à Kabare (moyenne altitude). Dix espèces de parasitoïdes ont été identifiées, *Telenomus remus* ayant un taux élevé de parasitisme des œufs et *Coccygidium luteum* dominant le parasitisme des larves. L'abondance des prédateurs, tels que les fourmis, les perce-oreilles et les coccinelles, a varié en fonction des stades de croissance du maïs, les fourmis étant particulièrement abondantes parmi tous les groupes de prédateurs. Les insectes prédateurs étaient plus nombreux au stade quatre feuilles complètement dépliées (V4), qui coïncide avec les fortes densités de larves de CLA. La lutte microbienne, considérée comme une alternative durable aux pesticides dangereux pour atténuer les dégâts causés par CLA, a été étudiée en échantillonnant des champs de maïs à la recherche de larves de CLA infectées par des champignons entomopathogènes. De manière inattendue, des cadavres de perce-oreilles collectés avec des larves de CLA ont également été examinés. Les analyses morphologiques et phylogénétiques ont confirmé que les champignons étaient des *Beauveria bassiana*. Trois isolats (P5E, KA14 et PL6) ont été obtenus à la fois sur des cadavres de CLA et de perce-oreilles et comparés à une souche commerciale (GHA) et locale (BGx) contre les larves de CLA. Les résultats ont montré une mortalité significative (environ 70%) avec les isolats GHA, KA14 et PL6.

Le **chapitre 5** discute les résultats de ce projet de recherche dans un contexte de surveillance et de prévision de CLA, des défis et des opportunités liés à l'utilisation d'agents de contrôle biologique, et d'une proposition de stratégie de gestion intégrée de CLA au Sud-Kivu. Un système d'alerte précoce basé sur les prévisions climatiques est nécessaire pour avertir les agriculteurs des invasions de ravageurs et des dates de semis. La formation des agriculteurs à l'identification des ennemis naturels, à la connaissance des ravageurs et à l'utilisation efficace des agents de lutte biologique est essentielle pour la réussite de la mise en œuvre d'une approche intégrée de lutte contre CLA en RDC. La lutte biologique est une composante essentielle de la lutte intégrée contre CLA au Sud-Kivu. Les résultats de cette thèse font progresser les connaissances sur l'invasion de CLA en Afrique et fournissent les premières données sur les macro- et micro-organismes agents de contrôle biologique en RDC.

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List of acronyms

ABA: abscisic acid;
AEZ: agro-ecological zone;
AIC: akaike information criterion;
AICc: akaike information criterion for small sample size;
ANOVA: analysis of variance;
AUC: area under the curve;
BCAs: biological control agents;
BOLD: barcode of life data
Bt: *Bacillus thuringiensis;*
BVs: budding viruses;
CABI: Centre for agriculture and bioscience international;
CIAT: international center for tropical agriculture;
CLIMEX: climate and population modeling software;
COI: cytochrome oxidase subunit I;
Cry: crystalline proteins;
DD: degree day;
DNA: desoxyribonucleic acid,
DRC: democratic republic of Congo;
ENM: ecological niche modeling;
EPF: entomopathogenic fungi;
EPFs: entomopathogenic fungi;
EPPO: European and mediterranean plant protection organization;
FAO: food and agriculture organization;
FAW: fall armyworm;
GCMs: general circulation models;
GLMMs: generalized linear mixed-effects models;
GPS: global positioning system;
GVs: granuloviruses;
HCPC: hierarchical clustering on principle components;
HSD: honestly significant difference;
ICTs: information and communication technologies;
IITA: international institute of tropical agriculture;
IJs: infective juveniles;
IPM: integrated pest management;
IQR: interquartile range;

ITS: internal transcribed spacers;
JA: jasmonic acid;
LR: likelihood ratio;
MaxEnt: maximum entropy;
MEGA: molecular evolutionary genetics analysis;
MUSCLE: multiple sequence alignment**;**
NCBI: national center for biotechnology information;
NGOs: non-governmental organizations;
NIL: number of infested leaves per plant;
NIP: number of infested plants;
NLDA: number of larvae per defined area;
NLL: number of lesions per leaf;
NLP: number of larvae per plant;
NOG: number of generation;
NPVs: nucleopolyhedroviruses;
ODVs: occlusion-derived viruses;
PCA: Principal component analysis;
PCR: polymerase chain reaction;
PPT: Push-pull technology;
RA: relative abundance;
RDA: redundancy analysis;
ROC: receiver operating characteristic;
SA: salicylic acid;
SDA: sabouraud dextrose agar;
SDM: species distribution model;
SfMNPV: *Spodoptera frugiperda* multiple nucleopolyhedrovirus;
SNPs: single nucleotide polymorphisms;
SSA: sub-Saharan Africa;
TNP: total number of plants;
Tpi: triosephosphate isomerase;
UEA: université évangélique en Afrique
VOCs: volatile organic compounds;
WGS: world geodetic system;
WHO: world health organization.

Chapter 1

General introduction

Photo by Marcellin C. Cokola

Chapter 1. General introduction

1. The fall armyworm invasion scenario

The fall armyworm (FAW), *Spodoptera frugiperda* (J.E. Smith 1797), is a larval moth considered a highly destructive pest that primarily attacks maize crops (Luginbill, 1928; Baudron et al., 2019). It is native to tropical and subtropical regions of the Americas, particularly the southern United States, Central America and South America (Busato et al., 2005; Day et al., 2017; Tay et al., 2022), and has spread rapidly to different parts of the world (Kenis et al., 2023; Tay et al., 2023b). However, due to its adaptability, high flight capacity, globalization of trade and travel, and climate change (Westbrook et al., 2016; Ramirez-Cabral et al., 2017; Early et al., 2018), FAW has spread rapidly to various parts of the world, causing significant crop damage and posing a significant threat to food security (Mendesil et al., 2023).

FAW was first reported in Africa in 2016 (Goergen et al., 2016) and has since spread rapidly across the continent. It is now present in almost all African countries, causing significant damage to maize and other cereal crops, as well as vegetables (Cokola et al., 2023b; Kenis et al., 2023; Mendesil et al., 2023). FAW was first reported in India in 2018 (Sharanabasappa et al., 2018) and has since spread to several Asian countries, including China, Bangladesh, Myanmar, Thailand and Vietnam (Rane et al., 2023). FAW was reported in Australia in 2020 (Maino et al., 2021) and in several Pacific Island countries, including Papua New Guinea and Fiji (Tay et al., 2023b). In Europe, FAW has been reported in several southern European island’s countries, including Spain and Portugal (EFSA et al., 2020). Although its presence in Europe is currently limited, there are concerns about its potential spread to other parts of the continent (Wang et al., 2023), as FAW is a species that migrates in response to favorable climatic conditions, as reported in the United States (Westbrook et al., 2019). Recent data indicates its presence in Greece, Cyprus and Turkey (EPPO, 2024). Its impact in North America is relatively well managed compared to other parts of the world (Overton et al., 2021). It is important to note that the distribution of the FAW, as shown in Figure 1, may continue to change over time due to factors such as climate change, international trade and the effectiveness of pest management strategies (Early et al., 2018; Ramirez-Cabral et al., 2017; Mendesil et al., 2023).

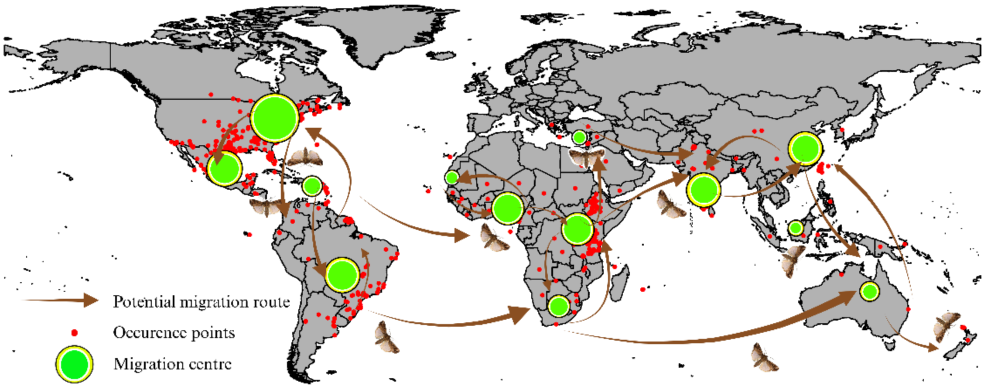

Figure 1. Worldwide distribution, occurrence and potential migration route of the fall armyworms. Occurrence points were obtained from GBIF (https://www.gbif.org/) and updated from EPPO (2024). Potential migratory movements on the map were adapted from Early et al. (2018); Westbrook et al. (2016); Niassy et al. (2021); Maino et al. (2021). The final map was generated by the author using ArcMap 10.8.1 (https://desktop.arcgis.com/en/arcmap/).

The FAW life cycle consists of four main stages: egg, larva, pupa, and adult. The female moth lays clusters of eggs, typically 100-300, on the underside of leaves or other plant surfaces (Luginbill, 1928). Upon hatching, the larvae go through 6 instars (developmental stages). The first instar larvae (L1) are small and feed on the plant surface (Luginbill, 1928; Capinera, 2000). As they grow, they become more destructive, eating large portions of leaves and stems. Fully grown larvae (L6) are the most damaging, as the larvae feed voraciously on crops (Hardke et al., 2015). The larvae are characterized by their striped bodies and a distinct inverted "Y" shape on their head (Sharanabasappa et al., 2018b). The characteristics of each larval stage are presented in Table 1 in the appendixes. After the larval stage, the caterpillar burrows into the soil to pupate. During this stage, the insect undergoes metamorphosis, transitioning from the larval to the adult stage (Luginbill, 1928; Capinera, 2000). The adult moth is nocturnal and primarily active during the night (Sparks, 1979). Moths are excellent travelers and can migrate long distances (Westbrook et al., 2019; Maino et al., 2021), which facilitates their rapid spread. The entire life cycle can be completed in about 30 days under optimal conditions, with multiple generations occurring in a single growing season (Busato et al., 2005). Figure 2 shows a diagram of FAW's development cycle.

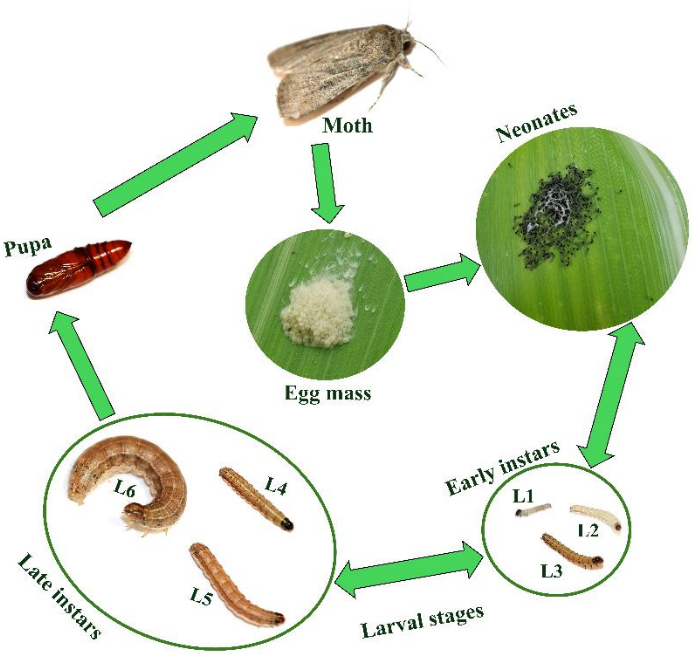

Figure 2. Diagram representing the fall armyworm life cycle.

In maize, FAW infestation evolves according to the age of the plant, with young larval stages found mainly in the early developmental stages of the plant (V3, V4), often with several larvae per plant moving around through silk secretion (McGrath et al., 2018), while older larvae are found in the later stages of the maize plant, with generally only one larva per plant due to cannibalism, predation and parasitism (Peireira and Hellman, 1993). In terms of adaptation, FAW does not diapause (Luginbill, 1928; Sparks, 1979) and adult moths migrate seasonally (Nagoshi and Meagher, 2004; Westbrook et al., 2016). Due to its polyphagous behavior, FAW can attack more than 350 plants, including 80 crops such as maize, rice and cotton, according to literature compiled by Montezano et al. (2018), and this is only in its native range. In invaded regions such as Africa, Asia and Oceania, the literature on alternative host plants is not yet well documented, although some plants have been reported in Africa, such as cabbage, onion, elephant grass, sorghum, ... (Fotso Kuate et al., 2019; Cokola et al., 2021b; Cokola et al., 2023b); and in Asia, such as sugarcane, banana and ginger (Srikanth et al., 2018; Shankar and Adachi, 2019). The host plants on which FAW was found in eastern Democratic Republic of Congo (DRC) are illustrated in Figure 3.

Regarding host plants, FAW consists of two strains (Pashley, 1986), which are morphologically identical (Nagoshi et al., 2015) but can be differentiated using molecular tools. The first strain (C strain) attacks maize (*Zea mays* L.), cotton and sorghum, while the second (R strain) attacks rice (*Oryza sativa* L.) and forage grasses (Nagoshi et al., 2007; Hardke et al., 2015). Mating between strains can occur, although there is variability in mating preferences (Unbehend et al., 2014). R-strain females prefer to accept C-strain males, resulting in hybrid populations, but C-strain females and R-strain males appear to be reproductively incompatible (Quisenberry, 1991). The most commonly used molecular tools to distinguish between them are molecular markers (Nagoshi et al., 2012; Cock et al., 2017; Nagoshi et al., 2022). Genetic variation between these strains is compared using segments of two genes, cytochrome oxidase I (COI) and the Z chromosome-linked gene encoding the homologous enzyme triosephosphate isomerase (*Tpi*) (Nagoshi et al., 2015). Single nucleotide polymorphisms (SNPs) in the COI and *Tpi* genes are commonly used to distinguish the two strains in Western Hemisphere populations, with the two markers generally giving concordant results (Nagoshi, 2012). However, results from Nagoshi et al. (2022); Omuut et al. (2023) indicate that COI is not a reliable marker for strain identification in Africa, and that a significant proportion of the FAW population in this region may result from hybridization between strains (Nagoshi et al., 2019). A recent study (Durand et al., 2024) supports the hypothesis that FAW populations are of the maize C strain. A study in Uganda confirms observations that invasive FAW populations in the rest of Africa and Asia share a common origin (Omuut et al., 2023). The identification of FAW strains is important as research has shown biological, behavioral, toxicological and genotypic differences between strains in their native range and in invaded regions (Nagoshi et al., 2019; Tay et al., 2022; Rane et al., 2023). Genetic differentiation within FAW populations is a topic of considerable interest to researchers as it has implications for pest management, control strategies and understanding the evolutionary dynamics of this species (Tay et al., 2023c).

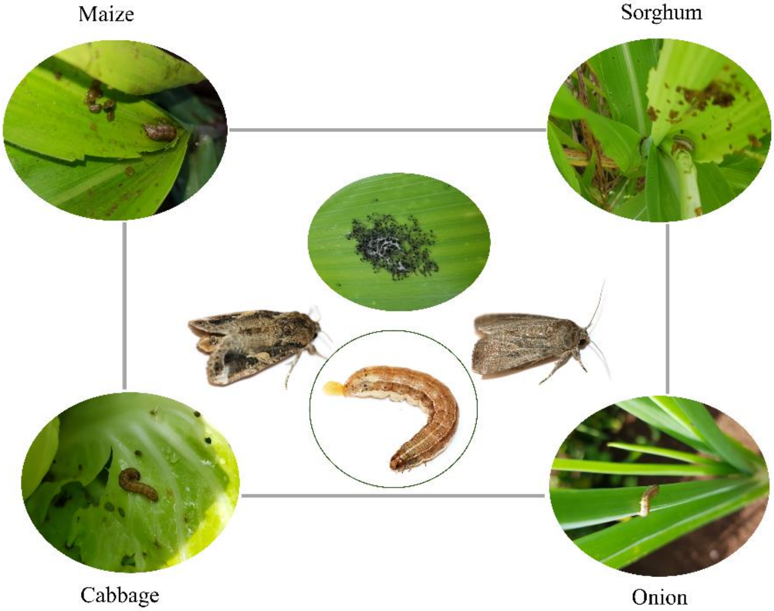

Figure 3. Host plants associated with fall armyworm in eastern DRC. Figure adapted from Cokola et al. (2021b); Cokola et al. (2023b). Plants shown are those from which larvae were collected and identified as those of fall armyworm. ©Marcellin C. Cokola.

The economic impact of FAW infestations is significant, resulting in reduced maize yields, increased production costs due to the need for control measures, and in extreme cases, total crop losses (Abrahams et al., 2017; Eschen et al., 2021). Smallholder farmers, particularly in regions where resources and access to agricultural inputs are limited, such as in sub-Saharan Africa, are disproportionately affected by these infestations, exacerbating food insecurity and poverty (Day et al., 2017; Tambo et al., 2021). FAW causes damage to vegetative parts, which is becoming increasingly alarming for farmers (Hruska, 2019). The presence of leaf damage does not necessarily imply yield loss, as the plant is able to compensate for leaf lesions that occur over a short period of time (Baudron et al., 2019). Maize can compensate for leaf damage when it receives adequate water and mineral nutrition (Hruska, 2019). According to the literature reviewed by Overton et al. (2021), the trend is that the increased defoliation induced by FAW on maize leaves does not necessarily correlate with a reduction in grain yield. Blanco et al. (2022) indicate that severe artificial defoliation of maize at around 66% in the early stages of maize development does not lead to yield reduction. In a study by Chisonga et al. (2023), leaf damage caused by FAW accounted for less than 3% of the variation in yield at plant level. However, the danger of FAW is that it attacks maize cobs, resulting in direct crop losses (Buntin, 2008). In addition, FAW infestations can increase the risk of aflatoxin contamination of maize grain, which poses a risk to human and animal health (Widstrom, 1979).

Yield losses vary depending on the growth stage of the crop at the time of attack, the larval stage of the FAW, the control methods used and the environmental conditions (Overton et al., 2021). Most studies assessing yield losses due to FAW are based on estimates, and results (Harrison et al., 2022) suggest that the impact of FAW may have been overestimated in many locations in sub-Saharan Africa. Day et al. (2017) reported losses of up to 20.6 million tons of maize for 12 maize producers in Africa, representing financial losses of between US$1.08 and US$4.66 million per year (Rwomushana et al., 2018). Eschen et al. (2021) estimate losses in Africa to be in the order of US$ 9.4 billion. Overton et al. (2021) found significant differences in yield loss estimates between experimental data and farmer surveys, with the former showing an average yield loss of 17.31% and the latter 35.57%. In its native range, such as the USA, Hruska and Gould (1997) reported yield losses of 15 to 73% when 55 to 100% of maize plants were infested with FAW, while Sparks (1986) reported total annual losses of around $60 million. In Mexico, Andrews (1988) found an average yield loss of 13%, with a maximum of up to 30%. In Brazil, field studies with artificially infested maize recorded yield losses of up to 57.6% (Cruz et al., 1999). In Africa, results from Baudron et al. (2019) in Zimbabwe reported yield losses of up to 12%. A study by De Groot et al. (2020) reported yield losses of 33% in Kenya, resulting in an estimated loss of 1 million tons of maize. In Ethiopia, Kassie et al. (2020) found an 11.5% maize yield loss due to FAW. In Central Africa, and more specifically in the Democratic Republic of Congo, losses were estimated by Day et al. (2017) to be around 633.000 tons per year.

2. Fall armyworm dynamics in relation to climatic conditions

Several authors have reported on the impact of climate on FAW invasion. Climatic conditions play a key role in FAW population dynamics (Westbrook et al., 2016; Senay et al., 2022). Parameters such as temperature, precipitation, humidity and wind influence many more aspects of FAW biology, behavior, abundance and distribution (Busato et al., 2005; Early et al., 2018; Niassy et al., 2021; Zacarias, 2020; Wang et al., 2023). Understanding these relationships is essential for predicting and managing FAW infestations. The effects of temperature, humidity, soil, rainfall and host plant on FAW survival and development time, as well as field observations of abundance under different conditions and seasons in the Americas, are summarized by Early et al. (2018) in Figure 4.

Temperature

FAW is strongly influenced by temperature, which affects its development, survival, reproduction and geographical distribution (Ali et al., 1990; Busato et al., 2005; Du Plessis et al., 2018; Huang et al., 2021; Adan et al., 2024). Temperature plays an important role in determining the rate of development of eggs, larvae, pupae and adults (Ali et al., 1990; Early et al., 2018). Temperature affects larval development (from L1 to L6) with an increase in feeding rate between 25 and 30°C (Isenhour et al., 1985), a larval stage duration of approximately 35 days at 18°C and 21 days at 32°C (Du Plessis et al., 2020). Temperature also affects the reproductive capacity of FAW. For example, the number of eggs laid per female decreases significantly at temperatures above 30°C (Barfield and Ashley, 1987). Studies by Barfield and Ashley (1987) showed that fecundity (egg-laying capacity) was optimal at 21 and 25°C and decreased at temperatures above the optimal range (30°C). Warmer temperatures generally accelerate the rate of development, leading to faster population growth and higher infestation rates (Barfield et al., 1978; Labatte, 1994). However, extreme temperatures can also affect the survival of FAW (Huang et al., 2021). For example, prolonged exposure to high temperatures can desiccate eggs and larvae (Valdez-Torres et al., 2012), while cold temperatures can slow development and reduce survival (Wood et al., 1979; Foster and Cherry, 1987). The baseline temperature is set at 7.4°C (Valdez-Torres et al., 2012), 10°C (Wood et al., 1979), 12°C (Du Plessis et al., 2018) and 13.8°C (Hogg et al., 1982). Depending on the temperature, it is possible to know the number of generations of FAW that can be observed in each geographical area (Westbrook and Sparks, 1986; Cokola et al., 2021a). The number of generations is determined based on the degree days accumulated by the insect during its development cycle (Early et al., 2018).

Rainfall

Rainfall affects FAW populations by influencing habitat suitability and plant availability (Sims, 2008). Adequate rainfall can promote the growth of host plants, providing abundant food resources for FAW larvae (Nboyine et al., 2020).

However, excessive rainfall can lead to waterlogging and crop damage, which could indirectly reduce FAW populations by damaging their host plants (Simanjuntak et al., 2023). Conversely, drought can reduce the availability of suitable food sources, causing FAW populations to migrate and disperse in search of more favorable conditions (Díaz-Álvarez et al., 2023). The direct impact of rainfall on FAW is unclear. Infestation of maize by FAW was low when rainfall was at its maximum and then increased when rainfall decreased, but this trend was not clear according to Niassy et al. (2021). From the results of Niassy et al. (2021), the correlation between larval density, number of adults caught in traps and rainfall was negative in a study covering several African countries. In contrast, Nboyine et al. (2020) reported positive effects of rainfall on moth abundance. In a study by Silvain and Ti-A-Hing (1985), moth capture in traps and larval abundance one week later were strongly correlated when rainfall was abundant. According to Early et al. (2018), heavy rainfall affects larvae by causing mortality in the field.

Humidity

Humidity affects FAW behavior and is related to temperature and rainfall (Nboyine et al., 2020). High humidity favors the development and survival of FAW eggs and larvae by preventing desiccation (He et al., 2021). Humidity has a much greater effect on pupae, as this stage occurs at ground level. Pupal survival is directly affected by soil moisture. Simmons (1993) observed delays in adult emergence at 20% compared to 50 or 80% relative humidity. In addition, wet conditions can promote the spread of entomopathogenic fungi that affect FAW populations (Ngangambe and Mwatawala, 2020). Furthermore, excessively wet conditions can also create a favorable environment for their natural enemies, such as parasitoids and predators, which can help regulate population levels (Midega et al., 2018; Harrison et al., 2019).

Wind

Understanding wind-assisted dispersal can improve early warning systems for FAW invasions (Westbrook et al., 2016; Wu et al., 2021). Studies have shown that adult FAW undertake nocturnal flights, often ascending to altitudes where wind currents can carry them considerable distances (Wu et al., 2021). Advances in meteorological modelling have allowed researchers to predict FAW dispersal routes based on wind patterns (Wang et al., 2023; Wu et al., 2021). For example, research by Westbrook and Sparks (1986); Westbrook et al. (2019) demonstrated that wind patterns significantly influence the seasonal migration of FAW in North America. Li et al. (2020) developed a model that integrates wind data to predict the potential spread of FAW in Southeast Asia, thereby supporting the timely implementation of control measures. Integrating wind pattern analysis into monitoring programs, as suggested by Wang et al. (2023), will allow policy makers to better anticipate and mitigate infestations.

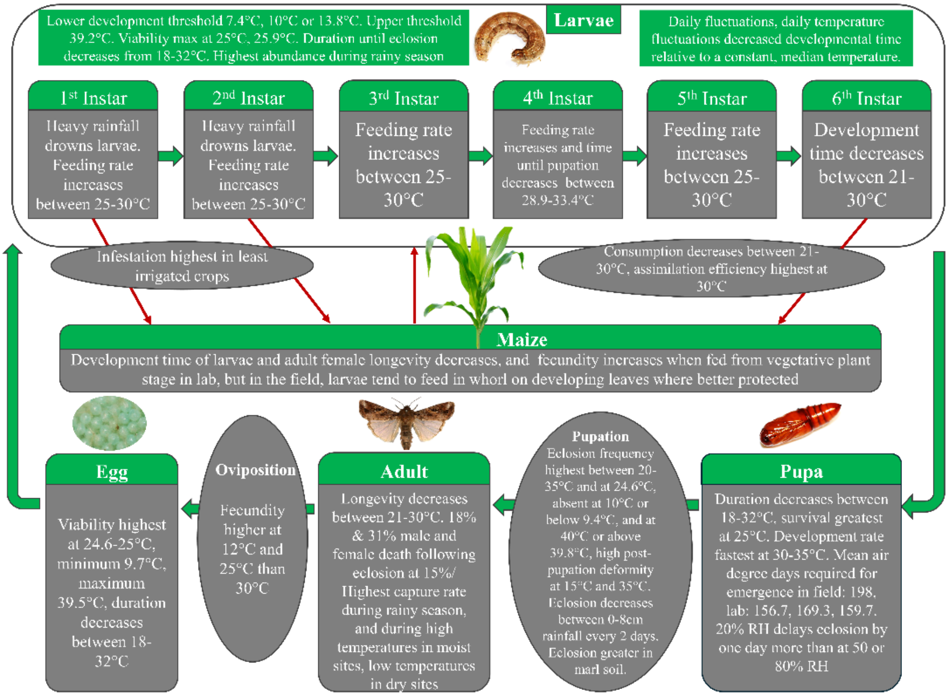

Figure 4. Measured environmental effects on the life cycle of the fall armyworm in the Americas. Figure adapted from Early et al. (2018). Rectangular shapes represent developmental stages, oval shapes represent processes. Red arrows represent effects of fall armyworm on maize and vice versa. RH: relative humidity.

Seasonal variations

FAW populations often exhibit seasonal fluctuations in response to changing climatic conditions (Nagoshi and Meagher, 2004; Westbrook et al., 2019). In temperate regions, populations may decrease during colder winter months and increase during warmer seasons (Ramirez-Cabral et al., 2017; Maino et al., 2021). FAW is a non-diapausing species (Luginbill, 1928; Sparks, 1979), which means that population dynamics are more seasonal in temperate climates (Pair et al., 1986; Westbrook et al., 2016). However, in tropical and subtropical regions, where temperatures are relatively stable throughout the year, FAW populations can persist and reproduce continuously, resulting in year-round infestations (Senay et al., 2022; Adan et al., 2024). Short-term weather events, such as storms and hurricanes, can facilitate long-distance dispersal of moths (Wu et al., 2022). Extreme drought can stress host plants, making them more vulnerable to FAW infestations (Singh et al., 2022).

Climate change and fall armyworm distribution modelling

Species distribution modelling (SDM) is an essential tool for understanding and predicting the geographical distribution of insect pests (Early et al., 2022). Such modelling allows pest spread to be predicted, areas at risk to be identified and effective control strategies to be developed (Du Plessis et al., 2018; Early et al., 2018; Li et al., 2020). Modelling is based on abundance data and environmental variables (Elith and Leathwick, 2009; Fourcade et al., 2014). Researchers are using climate models to predict potential future distributions and outbreak patterns of FAW under different climate change scenarios (Wang et al., 2020; Zacarias, 2020; Timilsena et al., 2022). Climate change could alter the distribution and abundance of FAW populations by affecting temperatures, precipitation patterns and extreme weather conditions (Ramirez-Cabral et al., 2017; Ramasamy et al., 2022). Higher temperatures may expand the range of FAW into previously unaffected areas, while changes in rainfall patterns may affect the availability of suitable habitats and host plants (Senay et al., 2022; Singh et al., 2022). In addition, climate change may alter the planting calendar and phenology of crops (Minoli et al., 2022), which could affect the susceptibility of crops to FAW infestation. Field studies are essential to understand the local dynamics of the pest as a function of microclimate and agricultural practices in order to obtain accurate information on the distribution of the species (Cokola et al., 2020; Abdel-Rahman et al., 2023).

Several methods have been used to model the distribution of FAW in its area of origin as well as in invaded regions (Westbrook et al., 2016; Du Plessis et al., 2018; Early et al., 2018; Li et al., 2020; Zacarias, 2020; Tessnow et al., 2022; Timilsena et al., 2022). Methods based on CLIMEX software and SDMs are the most widely used (Du Plessis et al., 2018; Early et al., 2018; Zacarias, 2020; Wang et al., 2023). The simulations by Zacarias (2020) show that there is a huge climatic potential for the spread of FAW, with potential increases of between 12%

and 44% in the future, mainly affecting border areas between the US and Canada, sub-Saharan Africa and central Europe. However, these simulations did not include data on the occurrence of FAW in Asia (India only) and Oceania. Previously, Early et al. (2018) predicted that South Asia, Southeast Asia and Australia would be potentially favorable areas for FAW, which was the case when FAW invaded them a few years later (Wang et al., 2020; Maino et al., 2021). Overall suitability for FAW is projected to increase by 4.49% under the SSP1-2.6 scenario and by 8.33% under the SSP5-8.5 scenario relative to current climate conditions according to Ramasamy et al. (2022). According to Liu et al. (2020), the most important FAW habitats under current and future conditions are found mainly along the east coast of the United States, including Florida, as well as in Mexico, Central America, southern Brazil, central Africa and southern Asia. Of all continents, Africa is expected to experience the greatest increase in FAW threats in the future (Senay et al., 2022). In contrast to Ramirez-Cabral et al. (2017), the risk of FAW will decrease in the future in regions close to the equator (southern hemisphere) compared to the northern hemisphere, where the risk will increase. According to projections by Timilsena et al. (2022), a large area of eastern and central Africa is likely to retain an ideal climate for the persistence of FAW. These regions will act as 'hotspots' for FAW, from which they will be able to migrate northwards and southwards during favorable seasons. Northwards, the risk of FAW invading Europe has been assessed and expansion towards Spain, Italy and Greece is not negligible in the near future (Wang et al., 2023).

3. Farmers knowledge and control strategies against fall armyworm

Farmers play a crucial role in pest management, as they are often the primary source of pest control and the most vulnerable to pests (Matteson et al., 1984; Van den Berg et al., 2022). Using their experience and knowledge of local conditions, farmers employ a variety of control strategies to mitigate the impact of FAW on their crops (Tambo et al., 2020a; Kasoma et al., 2021). By combining their knowledge and control strategies, farmers can effectively manage FAW infestations and protect their crops from damage, thereby contributing to food security and sustainable livelihoods (Kansiime et al., 2023). Continuous monitoring, adaptation to changing conditions and collaboration between farmers, research institutions and government agencies are essential for successful management of FAW at the farm level (Houngbo et al., 2020; Kansiime et al., 2024). In the Americas, most maize farmers use genetically modified maize (Bt maize) to control FAW (Hruska, 2019; Van den Berg et al., 2021). In Africa and Asia, the vast majority of farmers still use synthetic insecticides (Cokola et al., 2023b; Khan et al., 2023; Tambo et al., 2023). The low incomes of farmers in sub-Saharan Africa after disposing of their production and low productivity mean that they have very few options for managing FAW in their maize fields (Hruska, 2019).

Early detection and monitoring

Since the invasion of FAW in Africa, farmers have been trained to recognize the pest and signs of infestation in their crops, such as leaf damage, presence of larvae and egg masses (FAO, 2018; Chimweta et al., 2020; Tay et al., 2023a). Just over 90% of farmers in Africa know what FAW is and how to detect its damage in maize crops (Kansiime et al., 2019; Houngbo et al., 2020; Caniço et al., 2021; Cokola et al., 2023b). Regular scouting of fields allows farmers to detect infestations early, allowing timely intervention before populations intensify (Prasanna et al., 2018; Kansiime et al., 2024). Some farmers use pheromone traps to monitor adult moth activity and assess the risk of infestation (Ullah et al., 2023; Sisay et al., 2024); others use surveillance to look for eggs, larvae and destroy them manually (Hruska, 2019; Tambo et al., 2020b). As FAW is a pest affecting several countries in Africa, Asia and Oceania, this information is not accessible to some farmers in some countries who do not receive funding from their government or international organizations to respond to the FAW threat (Cokola et al., 2023b).

Cultural practices

To reduce pest pressure and minimize crop damage, farmers adopt certain cultural practices (Abate et al., 2000). These practices include timely planting to avoid peak FAW activity (Nyabanga et al., 2021), crop rotation to disrupt pest life cycles and intercropping of non-host plants to create an environment less conducive to FAW development (Midega et al., 2018; Harrison et al., 2019), and permanent weeding (Tambo et al., 2020b; Cokola et al., 2023b). In some areas of Africa, the planting date is a real challenge for farmers because it is directly linked to global warming (Ansah et al., 2021; Minoli et al., 2023). For example, farmers in eastern DRC sow at different times, which exacerbates FAW infestations (Cokola et al., 2024 in press). Determining the sowing date is a critical factor for farmers, as early or late sowing can lead to crop losses (Tsimba et al., 2013). Sowing date also affects the abundance of natural enemy parasitoids of FAW (Durocher-Granger et al., 2024). Push-pull technology (PPT) is considered one of the promising intercropping methods for pest management in sub-Saharan Africa (Pickett et al., 2014; Midega et al., 2018). The adoption of this technology in FAW-infested regions of sub-Saharan Africa is essential for smallholder farmers who depend solely on agriculture for their livelihoods (Gebreziher et al., 2020).

Use of plant extracts and other local farming practices

In Africa, sustainable pest control is largely dependent on agroecological approaches due to the economic constraints of smallholder farmers (Harrison et al., 2019; Hruska, 2019). The use of plant extracts for pest control is an ancient practice that is gaining renewed interest as an ecological and sustainable approach in modern agriculture (Abate et al., 2000). Plant extracts contain a variety of bioactive compounds that can repel, deter or kill pests while minimizing environmental impact and reducing reliance on synthetic chemical pesticides (Stevenson et al., 2017). Results from Chawanda et al. (2023) showed that botanical powders of *Azadirachta indica*, *Nicotiana tabacum*, *Cymbopogon citratus* and *Lippia javanica* applied to the whorls of maize leaves were effective against FAW. Of the extracts tested by Sisay et al. (2019b), *Azadirachta indica*, *Schinnus molle* and *Phytolacca dodecandra* resulted in high larval mortality. A high percentage of larval mortality (66%) was recorded when *Nicotiana tabacum* and *Lippia javanica* were applied (Phambala et al., 2020). Farmers use other local management practices to control FAW. For example, a study by Kushwaha (2022) found no damage to plants treated with grease. The use of ash, soil and detergents has been reported in several studies in Africa (Hruska, 2019; Tambo et al., 2020a; Cokola et al., 2023b). The mechanism by which soil and ash could control FAW is that they act as abrasives and desiccants when in contact with the insect cuticle (Hruska, 2019; Ahissou et al., 2021a). In addition, direct application of soil could allow entomopathogenic microorganisms present in the soil, such as bacteria, fungi, viruses and nematodes, to directly infect FAW on the maize plant (Chawanda et al., 2023). Regardless of soil type, the results of Chawanda et al. (2023) and Maphumulo et al. (2023) showed that this material was effective when applied directly to FAW. Another method is the use of fish soup and sugar solution. Irrespective of the dose, the results of Niassy et al. (2024) showed that fish soup and sugar solutions attracted a wide range of insects, including potential natural enemies (predators and parasitoids) of FAW.

Biological control

Farmers indirectly encourage the presence of natural enemies of FAW by maintaining natural habitats, such as hedgerows and refuges, which provide shelter and food sources for beneficial insects that prey on FAW larvae (Hruska, 2019), but also by diversifying crops and systems in an agroecological approach (Harrison et al., 2019; Midega et al., 2018). Some use, for example, cooking fat, fish soup or sugar solution to attract ants to the field (Niassy et al., 2024). However, the concept of biological control is still new to many farmers in Africa (Cokola et al., 2023b). In Kenya and Uganda, farmers have an advantage in terms of knowledge of the concept of biopesticides, as products are already on the market (Nyangau et al., 2022). However, there is little readily available, centralized information on the availability and accessibility of biopesticides in most African countries (Bateman et al., 2018; Tepa-Yotto et al., 2022b). There is a need to increase farmers' knowledge of the concept of biological control through integrated media campaigns, extension visits, field days and farmer field schools (Ahissou et al., 2021a; Tambo et al., 2022; Cokola et al., 2023b; Kansiime et al., 2023).

Use of resistant varieties

Farmers in the Americas are selecting and planting maize varieties with resistance or tolerance to FAW infestation (Buntin, 2010; Tabashnik and Carrière, 2017). Resistant varieties contain genetic traits that prevent or reduce FAW feeding and reproduction, thereby reducing crop damage (Singh et al., 2022). Planting a variety of maize varieties with different levels of resistance can improve integrated management of FAW in Africa (Prasanna et al., 2022). In the Americas, farmers are using resistant *Bacillus thuringiensis* (Bt)-based varieties to control FAW (Hruska, 2019), although cases of FAW resistance to these varieties have been reported (Huang et al., 2014; Huang, 2021). This technology has not yet been implemented in Africa, and Van den Berg et al. (2021) suggest that Bt maize, which produces four different Bt toxins, should be developed and made available to smallholder farmers to prevent cases of FAW resistance. However, some countries in Africa have imposed policy restrictions on the use of genetic modified maize varieties (Matova et al., 2020; Tepa-Yotto et al., 2022b), and constraints to farmer adoption of these varieties have been reported in many African countries (Wightman, 2018; Mmbando, 2024). Varietal breeding efforts to address FAW in Africa are expanding rapidly (Kasoma et al., 2020; Kasoma et al., 2021b; Kasoma et al., 2022).

Chemical control

Since the invasion of FAW in Africa, there has been an increase in the market for insecticides and their use in maize crops (Rwomushana et al., 2018). Synthetic insecticides are used to target FAW larvae and reduce their populations (Pitre, 1986; Fiaboe et al., 2024). Farmers are encouraged to use these insecticides judiciously in an integrated approach, following recommended application rates and safety precautions to minimize environmental impact and avoid harming beneficial organisms (Ahissou et al., 2021a; Sharanabasappa et al., 2020; Harrison et al., 2019). Unfortunately, the phenomenon of FAW resistance and the ineffectiveness of certain active molecules have led farmers in Africa to increase their use of insecticides, sometimes at doses and with products that are dangerous for the environment and non-target organisms (Togola et al., 2018; Matova et al., 2020). In several studies on farmers' perceptions of the presence of FAW in Africa, the majority of farmers use insecticides to control FAW more than other existing methods (Chimweta et al., 2020; Ahissou et al., 2022; Cokola et al., 2023b). Some active ingredients in certain products are considered hazardous by the WHO regulations and have been withdrawn from the market, but farmers continue to use them (Kansiime et al., 2019; Kumela et al., 2019; Tambo et al., 2020b; Cokola et al., 2023b). There is an increasing need to help farmers make informed decisions about pesticide choice, timing and dose rates, as well as to promote safe handling practices and minimize risks (Tepa-Yotto et al., 2022b; Kansiime et al., 2023). In a recent study by Tambo et al. (2023), results showed evidence of a reduction in the intensity of pesticide use by farmers to control FAW through the adoption of cultural practices and biopesticides. By integrating pesticides with other pest management practices, farmers can effectively control FAW while minimizing the risks associated with pesticide use (Kansiime et al., 2024).

Community involvement and knowledge-sharing

FAW management among farmers in Africa has been shown to require collective action for innovative control strategies such as biological control

(Durocher-Granger et al., 2023). Farmers need to work with agricultural extension services, research institutions and other farmers to share information, experiences and best practices in FAW management (Tambo et al., 2020a). Extension workers provide training, workshops and demonstrations on FAW integrated pest management (IPM) strategies (Caniço et al., 2021), enabling farmers to acquire the knowledge and skills needed to effectively control FAW infestations while promoting sustainable farming practices (Kalyebi et al., 2023). The use of information and communication technologies (ICTs) enables farmers to manage crop pests and diseases (Panda, 2020). Tambo et al. (2022) found positive effects of the use of information channels on the adoption of environmentally friendly management practices against FAW. Among ICTs, radio and videos sharing had a significant impact on improving farmers' knowledge on monitoring and sustainable management of FAW in a study by Tambo et al (2019).

4. Biological control opportunities of the fall armyworm

Biological control offers promising opportunities to manage FAW populations in an ecologically sustainable manner (Harrison et al., 2019; Wyckhuys et al., 2024a). By exploiting natural enemies and ecological processes, biological control methods can help reduce FAW infestations while minimizing the use of chemical pesticides (Guo et al., 2020). Integrating these biological control options into integrated pest management (IPM) programs can improve the sustainability and effectiveness of FAW control strategies (Tepa-Yotto et al., 2022b). Two options have been explored for the biological control of FAW: macro- and micro-organisms (Luginbill, 1928; Kenis et al., 2023; Koffi et al., 2023; Wyckhuys et al., 2024a). Macroorganisms are a group of arthropods and vertebrates that naturally attack FAW eggs, larvae, pupae and adult moths (Ashley, 1979; Hoballah et al., 2004; Wyckhuys and O'Neil, 2006; Clarkson et al., 2022). Microorganisms include fungi, bacteria, viruses and nematodes found in the soil and in the plant that infect FAW larvae (Guo et al., 2020, Bateman et al., 2018; Patil et al., 2022). Plants emit volatile organic compounds that act as indirect defenses by attracting natural enemies in response to insect attack (Carroll et al., 2006). Plant responses to insect and disease attacks are mainly regulated by phytohormones, including jasmonic acid (JA), salicylic acid (SA) and abscisic acid (ABA) (Pineda et al., 2013; Beck et al., 2018). While most research on plant responses to FAW damage has focused on interactions with parasitoids (Turlings et al., 1989; Ortiz-Carreon et al., 2019; De Lange et al., 2016; Sobhy et al., 2022), there is increasing evidence that herbivorous insect attacks can also affect the plant-entomopathogen symbiosis (Cory and Ericsson, 2010; Shikano et al., 2017). Plant volatiles generally accompany most plant-insect interactions, induced by the insect herbivore, microbial activity, or both (Beck et al., 2018).

Symbiotic relationships between plants and beneficial microbes (e.g. endophytes, mycorrhizal fungi and plant growth promoting rhizobacteria) are mainly mutualistic (Singh, 2003; Shikano et al., 2017). While most beneficial microbes inhabit the rhizosphere, there are also fungal and bacterial endophytes that colonize the aerial parts of the plant (Shikano et al., 2017; Vega, 2018). There is evidence that endophytic entomopathogenic fungi modify the kairomones emitted by the plant to confuse their perception by insect pests (Vega, 2018). Furthermore, it has been reported that microorganisms in the soil (belowground), in this case nematodes, increase the plant's resistance to herbivores at the aerial (aboveground) level (Papadopoulou and van Dam, 2017; Beck et al., 2018). For example, studies have shown that FAW infections by entomopathogenic microorganisms occur in two ways: on the plant itself and at the soil level (Cruz-Avalos et al., 2019; Cokola et al., 2023a); and are influenced by climatic conditions (Pineda et al., 2013; Guo et al., 2020). Climatic parameters, such as rainfall, act by causing FAW larvae to fall to the ground (Early et al., 2018; Cokola et al., 2021a), and here the hypothesis is made of possible contact with entomopathogens (Mascarin and Jaronski, 2016) and predatory insects at ground level (generally ants and ground beetles), as shown in Figure 5. The literature by Wyckhuys et al. (2024a) provides a broad overview of the natural enemies of FAW worldwide, along with the limitations of studies and ways to improve biological control.

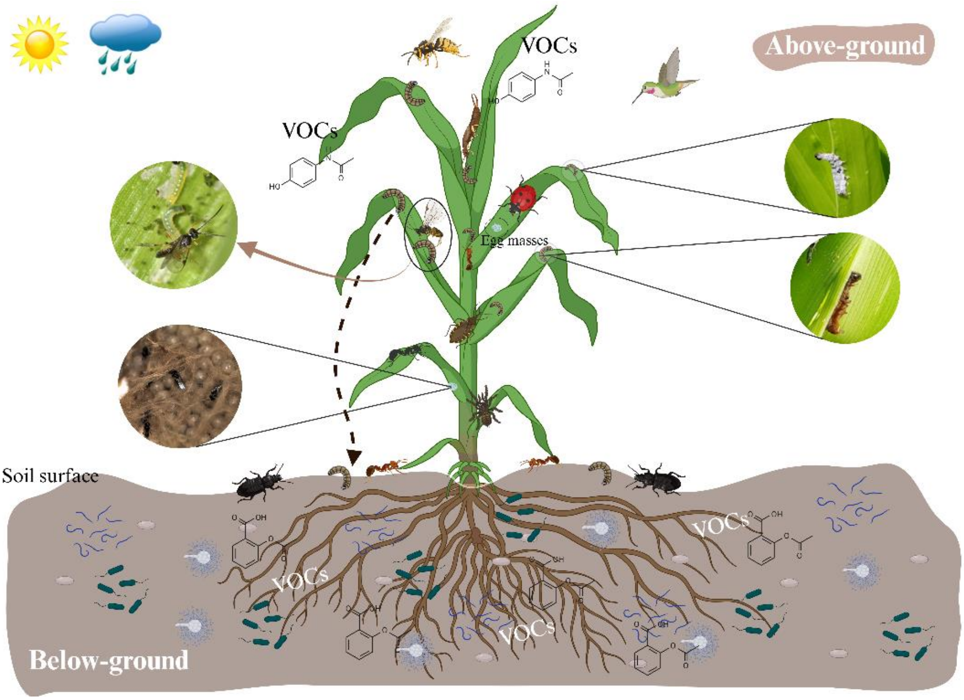

Figure 5. Illustration of the fall armyworm natural enemy complex in the maize system. Macro- and micro-organisms and their interactions with the plant and the climatic conditions above and below ground are shown. Created by the author using BioRender.com.

Parasitoids

Parasitoids are natural enemy insects whose females lay their eggs inside the larvae or eggs of other insects, and the developing parasitoid larvae eventually kill the host (Eggleton and Belshaw, 1992; Waage and Hassell, 1982). They include species that target different stages of the pest's life cycle (Quicke, 2015; Abram et al., 2019). They can be classified as egg parasitoids, larval parasitoids, egg-larval parasitoids and larval-pupal parasitoids (Waage and Hassell, 1982; Quicke, 2015). Commonly studied parasitoids of FAW are *Telenomus remus* and *Trichogramma spp.* (egg parasitoids) and *Campoletis sonorensis*, *Chelonus spp.* and *Cotesia spp.* (larval parasitoids) (Kenis et al., 2023; Wyckhuys et al., 2024a). Studies in different regions of the Americas, Africa and Asia have shown significant parasitism rates (Wyckhuys et al., 2024a). For example, studies in Ghana, Benin, Zambia, Kenya, Ethiopia, etc. have identified several parasitoid species depending on the location (Sisay et al., 2018; Agboyi et al., 2019; Agboyi et al., 2020; Koffi et al., 2020; Durocher-Granger et al., 2021), indicating a significant presence of natural enemies that can be used for biological control.

The effectiveness of these parasitoids can vary. For example, in the West African region, the egg parasitoid *T. remus*, the egg larval parasitoid *Chelonus bifoveolatus* and the larval parasitoid *Coccygidium luteum* were the most widespread and showed promising potential for biological control programs (Agboyi et al., 2019; Kenis et al., 2019; Agboyi et al., 2021). These parasitoids can significantly reduce FAW populations when integrated into pest management systems (Hruska, 2019; Kenis et al., 2023). There is potential in Africa and other infested continents for the release of native parasitoids and for classical biological control involving the introduction of exotic parasitoids from the native range of the pest (Abang et al., 2021; Kenis, 2023). Releases of *T. remus*, *Trichogramma spp.* and *Eiphosoma laphygmae* are planned to enhance control efforts in affected regions (Kenis, 2023).

Predators

The literature on natural predators of FAW highlights the importance of a diverse predator community in controlling this pest in maize crops (Wyckhuys et al., 2024a). A wide variety of predators feed on FAW eggs, larvae or pupae, providing natural biological control (Luginbill, 1928; Hoballah et al., 2004; Wyckhuys and O'Neil, 2006). Predatory beetles such as ladybirds, ground beetles (Carabidae) and staphylinids (Staphylinidae) are known to prey on FAW larvae and eggs (Sharanabasappa et al., 2019; Maruthadurai et al., 2022; Meagher et al., 2023). In addition, spiders, earwig, wasps, ants, bugs and certain insectivorous insects such as lacewings contribute to the suppression of FAW by consuming the larvae and eggs (Isenhour et al., 1990; Fuller et al., 1997; Hoballah et al., 2004; Sueldo et al., 2008; Firake and Behere, 2020; Keerthi et al., 2020; Dassou et al., 2021). Birds and small mammals also contribute to predation by feeding on FAW larvae and adult moths (Luginbill, 1950; Capinera, 2002). Birds are particularly effective during the day when they can detect caterpillars (Clarkson et al., 2022; Kumar et al., 2022). Some rodent species can dig FAW pupae out of the ground and feed on them as a source of protein (Pair and Gross Jr, 1984). Preserving natural habitats and reducing pesticide use can increase predator populations and their effectiveness in controlling FAW (Harrison et al., 2019; Clarkson et al., 2022; Jordon et al., 2022; Dassou et al., 2023).

Entomopathogenic fungi (EPFs)

Some species of EPFs naturally infect and kill FAW larvae (Cruz-Avalos et al., 2019; Visalakshi et al., 2020; Cokola et al., 2023a). These fungi produce spores that adhere to the insect's cuticle, penetrate its body and eventually kill it (Inglis et al., 2012; Vega and Kaya, 2012). Several species of EPFs are known to infect and control FAW populations (Wyckhuys et al., 2024a). *Beauveria bassiana*, the most common and ubiquitous EPF, infects a wide variety of insects (Meyling and Eilenberg, 2007; Mascarin and Jaronski, 2016). *B. bassiana* has been reported to cause significant mortality in FAW larvae (Akutse et al., 2019; Cruz-Avalos et al., 2019). The insecticidal activity of *B. bassiana* is because the fungus secretes a variety of secondary metabolites (Singh et al., 2015; Wang et al., 2021). Field and laboratory studies have demonstrated its potential to reduce FAW populations (Guo et al., 2020). Commercial formulations of *B. bassiana* are available and are applied to FAW-infested crops by spraying (Bateman et al., 2018).

Like *B. bassiana*, *Metarhizium rileyi*, formerly known as *Nomuraea rileyi*, another Hypocreales EPFs, also infects lepidopteran insects (Ingle et al., 2004; Fronza et al., 2017). It is the most abundant EPF in the maize system in newly invaded areas and is promising for biological control of FAW (Withers et al., 2022; Wyckhuys et al., 2024a). Studies have shown that *M. rileyi* is effective against different developmental stages of FAW, resulting in high mortality and reduced pest pressure (Grijalba et al., 2018; Visalakshi et al., 2020; Yan-li et al., 2022; Ramos et al., 2024). *M. rileyi* can be applied in a variety of formulations, including wettable powders and oily suspensions, making it versatile for use in the field (Grijalba et al., 2018). Both *B. bassiana* and *M. rileyi* are endophytes and indirectly affect insect development (Russo et al., 2021; Kinyungu et al., 2023; Zhang et al., 2024).

For more than three decades, the EPFs *Isaria farinosa* and *Isaria fumosorosea* have been referred to as *Paecilomyces farinosus* and *Paecilomyces fumosoroseus*, respectively (Khan and Ahmad, 2015). These fungi are found worldwide and have a wide host range (Weng et al., 2019). *I. farinosa* has lost its importance in research and as a biological control agent, while *I. fumosorosea* is known to be effective with different strains to control several pests (Zimmermann, 2008). Freed et al. (2012) reported that crude proteins produced by *I. fumosorosea* have insecticidal and antifeedant effects on the diamondback moth, *Plutella xylostella*.

I. fumosorosea has been shown to be pathogenic to *Spodoptera* larvae (Hussein et al., 2013).

Environmental conditions such as temperature, humidity and UV radiation affect the germination and virulence of EPF (Jaronski, 2010; Mascarin and Jaronski, 2016). High humidity and moderate temperatures are generally favorable for fungal activity (Jaronski, 2010). Different developmental stages of FAW vary in their susceptibility to fungal infection, with young larvae often being more susceptible (Akutse et al., 2019). Inoculative or flood applications of EPFs, either through biopesticide formulations or as part of conservation biological control strategies, can help reduce FAW populations while minimizing environmental impacts (Bateman et al., 2018).

Viruses

Viruses used as biological control agents (BCAs) in pest management are generally nucleopolyhedroviruses (NPVs) and granuloviruses (GVs), which belong to the baculovirus family (Rao et al., 2015; Sharma and Gaur, 2021). Baculoviruses undergo a two-phase infection cycle involving two forms of rod-shaped enveloped virions (Inceoglu et al., 2006). Occlusion-derived viruses (ODVs) initiate the infection process in the midgut, while budding viruses (BVs) are responsible for spreading infection throughout the insect (Hussain et al., 2021). SfMNPV is the first candidate virus for biological control of FAW (Escribano et al., 1999; Cisneros et al., 2002). These viruses are commercially available as biopesticides and can be applied to crops to control FAW infestations (Barrera et al., 2011; Valicente, 2019). Baculoviruses are selective and generally pose minimal risk to non-target organisms and the environment (Moscardi et al., 2011).

Nematodes

Entomopathogenic nematodes enter the host insect through natural openings such as the mouth, anus or spiracles (Sharma and Gaur, 2021). Once inside, infective juveniles (IJs) release symbiotic bacteria (*Xenorhabdus spp.* or *Photorhabdus spp.*) from their gut into the host haemocoel, where they multiply and kill the host by septicemia or toxaemia (Abd-Elgawad, 2022; Tarasco et al., 2023). There are two main groups, *Steinernema* and *Heterorabditis* (Kaya and Gaugler, 1993). Several species of *Steinernema*, such as *S. carpocapsae* and *S. abbasi*, have been shown to be very effective against FAW larvae, resulting in significant mortality in the laboratory and in the field (Acharya et al., 2020; Fallet et al., 2022a; 2022b; Fallet et al., 2024). Up to 100% mortality on FAW has been achieved in studies by Andaló et al. (2010); Fallet et al. (2022a). These nematodes can be applied to soil or foliage using conventional spraying equipment (Lacey and Georgis, 2012). They are often formulated as aqueous solutions, gels or granules (Sharma and Gaur, 2021; Fallet et al., 2022a). *Heterorhabditis* nematodes are generally applied to soil (Koppenhöfer and Fuzy, 2006). Species such as *H. bacteriophora* and *H. indica* have shown high pathogenicity to FAW (Acharya et al., 2020; Fallet et al., 2022b; Shinde et al., 2022).

Entomopathogenic bacteria

Bacillus thuringiensis (Bt) is a bacterium commonly used as a biological pesticide to control various agricultural pests, including FAW (Bravo et al., 2011; Van den Berg et al., 2021). Bt produces crystalline proteins (Cry proteins) that are toxic to certain insect larvae (Tabashnik, 1992). When the larva ingests these proteins, the Cry proteins are activated in the alkaline environment of the larval gut (Höfte and Whiteley, 1989). The activated toxins bind to specific receptors in the intestinal mucosa, creating pores that disrupt intestinal cells, ultimately leading to larval death (Badran et al., 2016). Commercially available Bt biopesticides come in a variety of forms, including wettable powders, granules and liquid concentrates (Vimala Devi et al., 2020). Cases of resistance of FAW larvae to Bt have been reported in the literature (Tabashnik, 1994; Huang, 2021).

5. Thesis objectives

Since the invasion of FAW on the African continent in 2016, and particularly in the DR Congo, very few studies have been initiated to investigate its presence and the economic losses it causes to maize crops, with a view to develop sustainable strategies for its management as part of an integrated pest management system. The dissertation consists of three parts:

The first investigates the habitat range and environmental preferences of FAW including mapping its geographical distribution, identifying the specific environmental conditions and ecological factors that support its presence and spread. It also investigates and elucidates the influence of seasonal variations and environmental conditions on the patterns and severity of FAW infestations: by identifying specific factors that contribute to the fluctuation in infestation levels, thereby enhancing the understanding of pest dynamics and supporting the development of more effective pest management strategies. The first part also examines the relationship between maize planting dates and the abundance of FAW populations. The research aims to determine how different planting schedules influence the infestation levels of this pest, with the goal of identifying optimal planting times that minimize pest impact.

The second aim of the thesis was to collect and analyze smallholder farmers' knowledge and strategies for managing FAW. This includes understanding their perceptions, experiences and practices in managing FAW infestations, as well as identifying the challenges they face and the effectiveness of the strategies they employ. The goal is to inform the development of improved management practices and support systems tailored to smallholder farmers' needs and contexts.

The last part of the thesis investigates and understand the dynamics of the FAW population and its natural enemies within maize fields. The aim is to analyze the trends in population abundance of both the pest and its natural enemies over time; to provide insights that could inform integrated pest management strategies for controlling the pest in maize crops. The last part also explores the potential of using native EPFs as a biological control method. It’s to identify and isolate indigenous EPFs that are naturally present in the environment and capable of infecting FAW; to evaluate the effectiveness of these fungi in controlling the population of FAW under laboratory conditions.

Thesis outline

In chapter 2, the impacts of environmental factors on the occurrence of FAW in South Kivu were discussed. MaxEnt SDM was used with bioclimatic variables to predict the potential distribution of FAW, which was influenced mainly by mean annual temperature, annual rainfall, temperature seasonality and the length of the longest dry season. The model was highly accurate, with annual rainfall being the most important factor. I divided areas suitable for FAW into eastern and western corridors in South Kivu. Field surveys data were coupled with environmental variables to understand how FAW infestation varies with seasons in Kabare and Ruzizi Plain. The results showed that FAW infestation was more severe under conditions of high temperature and moderate rainfall, particularly in the Ruzizi Plain and in the late season of 2019. In addition, I was interested in understanding the seasonal abundance of FAW by considering the planting dates at Kabare. Late planting periods were found to have higher density, incidence and severity of FAW larvae, with varying distributions of larval stages according to cropping system. The results of this chapter highlighted the need for climate-smart integrated pest management strategies against FAW to mitigate the impact of the pest in the region.

FAW is a major challenge for smallholder maize farmers in Africa who do not have sufficient information about the pest. **In Chapter 3**, a survey on 420 farmers in Central and West Africa, represented by DR Congo, Gabon, Benin, Burkina Faso and Senegal was performed. The pest was not new to farmers in these countries, as its presence has been reported long before it was officially declared. Through these surveys, FAW was found to also attack crops such as Napier grass, sorghum, onion and cabbage. Farmers use a variety of control methods, with almost half preferring synthetic pesticides. The insecticides used vary widely depending on the country. Farmers in the Democratic Republic of Congo, Gabon and Benin are less familiar with newer methods such as semiochemical controls and biological controls using natural enemies. To promote sustainable control of FAW, alternative strategies such as the push-pull method, biopesticides and resistant crop varieties should be included in farmer training programs and widely disseminated in all African countries affected by FAW.

In **Chapter 4,** a monitoring system across two agroecological zones (low and mid-altitude) was developed involving trapping, visual observation of predatory insects, and collection of larvae and eggs for parasitoid study. It was found that the abundance and diversity of natural enemies increase with agroecological zones and maize growth stages. Key findings include the identification of ten parasitoid species and thirty-one predator's species. These findings suggest the need for conservation biological control in smallholder farms, integrating minimal use of plant protection products and crop diversification to support natural enemies. Additionally, microbial control was explored by targeting insects infested with EPFs, identifying *Beauveria bassiana* from FAW and earwig cadavers. Three new *B. bassiana* isolates were isolated and tested against FAW larvae, with isolates KA14 and PL6 showing significant mortality rates. This study was the first to report *B. bassiana* infecting insects in DR Congo and highlights the potential of isolates KA14 and PL6 for ecofriendly pest management in South Kivu.

Chapter 2

Environmental factors and fall armyworm infestation

Photo by Marcellin C. Cokola

Chapter 2. Environmental factors and fall armyworm infestation

1. Exploring the habitat range and environmental preferences of *Spodoptera frugiperda*

This section was adapted from original published article: **Cokola, M.C.,** Mugumaarhahama, Y., Noël, G., Bisimwa, E.B., Bugeme, D.M., Chuma, G.B., Ndeko, A.B., Francis, F., 2020. Bioclimatic zonation and potential distribution of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) in South Kivu Province, DR Congo. BMC Ecology 20, 1–13. https://doi.org/10.1186/s12898-020-00335-1.

Abstract

The fall armyworm (FAW) *Spodoptera frugiperda* (JE Smith), is currently a devastating pest throughout the world due to its dispersal capacity and voracious feeding behavior on several crops. A MaxEnt species distributions model (SDM) was developed based on collected FAW occurrence and environmental data. Bioclimatic zones were identified and the potential distribution of FAW in South Kivu, eastern DR Congo, was predicted. Mean annual temperature (bio1), annual rainfall (bio12), temperature seasonality (bio4) and longest dry season duration (llds) mainly affected the FAW potential distribution. The average area under the curve value of the model was 0.827 demonstrating the model efficient accuracy. According to Jackknife test of variable importance, the annual rainfall was found to correspond to the highest gain when used in isolation. FAWs' suitable areas where this pest is likely to be present in South Kivu province are divided into two corridors. The Eastern corridor covering the Eastern areas of Kalehe, Kabare, Walungu, Uvira and Fizi territories and the Western corridor covering the Western areas of Kalehe, Kabare, Walungu and Mwenga. This research provides important information on the distribution of FAW and bioclimatic zones in South Kivu. Given the rapid spread of the insect and the climatic variability observed in the region that favor its development and dispersal, it would be planned in the future to develop a monitoring system and effective management strategies to limit it spread and crop damage.

Keywords: Bioclimatic zone, Potential distribution, *Spodoptera frugiperda*, MaxEnt model, Environmental variables.

Introduction

The Fall Armyworm (FAW) *Spodoptera frugiperda* (J.E Smith 1797) is native to tropical and subtropical Americas (Goergen et al., 2016; Early et al., 2018) and a major corn pest (Labatte, 1994). Its presence was first reported on the African continent in 2016 (Goergen et al., 2016) and in Asia later on in 2018 (Sharanabasappa et al., 2018a; Shylesha et al., 2018). Whether FAW larvae can infest more than 80 crop species (FAO, 2018; Prasanna et al., 2018), main damages were observed on grasses family (Poaceae) including corn, rice and sorghum (Montezano et al., 2018). Yield losses can reach up to 73% when 100% of the plants are infested with FAW (Hruska and Gould, 1997). According to Baudron et al. (2019), maize infestation of 54.9% might have an impact on yield of approximately 12%. Due to its polyphagous feeding behavior and recent introduction in the African continent, FAW is expected to constitute a lasting threat to several important crops in African (Goergen et al., 2016). Studies on the behavioral characteristics of FAW strains in the Western Hemisphere indicated that two main strains, namely on rice and on maize, can mate with each other despite the existence of hybridization barriers (Pashley and Martin, 1987; Prowell et al., 2004; Schöfl et al., 2009; Nagoshi, 2010). Both rice and maize strains can be found and collected from a single host plant species (Nagoshi and Meagher, 2004; Prowell et al., 2004; Juárez et al., 2014). Given these characteristics, Nagoshi et al. (2019) have even reported that the African infestation may represent a new hybrid population with potentially uncertain behavioral feeding characteristics to become a serious problem for Africa, including Democratic Republic of Congo (DRC).

The fall armyworm has only invaded areas that have a climate pattern similar to the native distribution, justifying the use of climatic Species Distribution Models (SDMs) for further predictive spreading (Early et al., 2018). In recent years, an increasing number of tools for spatial analysis of species distribution at different spatial scales have emerged (Guisan and Thuiller, 2005; Jiménez-Valverde et al., 2008). These tools have become increasingly popular in ecology. Particularly, niche distribution models were widely used in many ecological applications (Peterson, 2006). In fact, several methods of SDMs, also known as ecological niche modeling (ENM) have been developed (Fourcade et al., 2014). To estimate the functional response related to various environmental variables (Austin et al., 2006), SDMs relate known locations of a species with their environmental characteristics, and then predict the potential geographical range of that species (Elith and Leathwick, 2009). According to Westbrook et al. (2019), the initiation and displacement patterns of insect migrations are dependent on these environmental factors.

Distribution of FAW has been investigated by Liu et al. (2020) and Wang et al. (2020) using SDM MaxEnt (Maximum Entropy). Also, the FAW distribution was modeled on a large scale using CLIMEX software integrating the species model “Wet tropical” (Du Plessis et al., 2018). Using similar software and two general circulation models (GCMs), Ramirez-Cabral et al. (2017) assessed the climate change impact on future suitability for FAW expansion. Furthermore, Early et al. (2018) used Species distribution models (SDMs) to forecast FAW global extent. However, FAW occurrence in South Kivu (Eastern DR Congo) has been reported by Cokola (2019) but its distribution remains unknown. Several areas in South Kivu are favorable to FAW development according to suitable temperature, day length and precipitation during warm/wet season as provided by Abraham et al. (2017).

Modeling potential distribution of species in relation to climatic conditions is an important tool to apply such as in South Kivu where FAW geographical distribution is still unknown. A FAW modeled proposal will be useful for further FAW monitoring and management in case of high scale infestations. Therefore, this study aims to determine bioclimatic zones and establish potential distribution of FAW in South Kivu, eastern Democratic Republic of Congo (DRC).

Materials and methods

Study area and occurrence data collection

This study focused on South Kivu in Eastern DRC, between 1º36’ and 5º South Latitude; 26º47’ and 29º20’ East Longitude. Biological data related to FAW occurrence were associated to locations with geo-referenced coordinates. Occurrence data of FAW were collected in Kalehe, Kabare, Walungu, Uvira, Fizi, Mwenga and Idjwi territories in collaboration with local farmers who observed FAW larvae and reported every related field in their localities. All suspected cases of FAW attacks were checked for confirmation through field surveys. To confirm that the larvae observed were indeed those of FAW, we had considered the morphological characteristics of FAW larvae as described by EPPO (2015) and Sharanabasappa et al. (2018b). Geographic coordinates of infested areas were selected only after positive FAW confirmation. Presence records were collected between February 2018 and September 2019 in 156 fields where FAW has been reported. Geographic coordinates on latitude and longitude in the WGS84 system were recorded using GPS Garmin 64s. The map representing the points of occurrence is illustrated in Figure 6.

Figure 6. Occurrence records of fall armyworm (*Spodoptera frugiperda*) in South Kivu, DRC. Each point represents a maize field in which fall armyworm larvae were detected and collected. The figure was created by the authors using ArcMap version 10.6 (https://desktop.arcgis.com/fr/arcmap/).

Environmental variables

In this study, we used elevation and potential evapotranspiration data combined with 19 bioclimatic variables. Altitude (Digital Elevation Model ASTERDEM) with 30m spatial resolution was obtained from USGS database (https://earthexplorer.usgs.gov) and the bioclimatic data's were collected from the Africlim database (https://www.york.ac.uk/environment/research/kite/resources/). They were used to build the species distribution model in order to find the FAW suitable areas. Africlim provides high-resolution climate data for Africa. Bioclimatic data consisted of 21 environmental variables (Table 1) that were obtained from interpolations of monthly averages of precipitation and temperature taking into account climate data collected over long periods of time (1950 - 2000) (Hijmans et al., 2005). The Africlim spatial database includes monthly grids of temperature and rainfall, deriving from bioclimatic summary variables such as moisture indices and dry season length. All environmental variables were in raster format with a 30 arc seconds resolution (0.93 km x 0.93 km ≈ 0.86 km^2 at the equator). Both ArcGIS Desktop 10.6 and QGIS 3.10 were used to process the spatial data: data extraction to the South Kivu province extent, data management in geographic coordinates (datum: WGS84) and resampling all the raster layers to the same resolution for preparing the maps.

Table 1. Environmental variables used to model fall armyworm distribution in South Kivu.

Environmental and bioclimatic parameters	Code	Units
Mean annual temperature (* 10)	bio1	°C
Mean daytime temperature range (monthly average) (* 10)	bio2	°C
Isothermality (bio1/bio7) * 100	bio3	-
Temperature seasonality (standard deviation * 100)	bio4	°C
Maximum temperature of the hottest month (* 10)	bio5	°C
Minimum temperature of the coolest month (* 10)	bio6	°C
Annual temperature range (bio5-bio6) (* 10)	bio7	°C
Mean temperature of the warmest quarter (* 10)	bio10	°C
Mean temperature of the coldest quarter (* 10)	bio11	°C
Annual rainfall	bio12	mm
Rainfall during the wettest month	bio13	mm
Rainfall during the driest month	bio14	mm
Rainfall seasonality	bio15	mm
Rainfall in the wettest quarter	bio16	mm
Rainfall in the driest quarter	bio17	mm
Longest dry season duration	llds	-
Annual moisture index	mi	-
Moisture index of the dry quarter	miaq	-
Moisture index of the wet quarter	mimq	-
Potential evapotranspiration	pet	mm
Elevation	dem	m

Bioclimatic zonation

Initially, all the environmental variables (n = 21) were clipped to have only spatial data corresponding to the extent of the South Kivu province. Then, geographic coordinates of the raster pixels centroids were used to extract the values for each variable corresponding to each pixel in order to produce a dataset to be used to delineate the bioclimatic zones. The generated bioclimatic dataset was used by processing the Principal Component Analysis (PCA) procedure of the *FactoMineR* (Lê et al., 2008) package of the R software version 3.5.3 (R Core Team, 2018). Based on Kaiser's criterion, only the first 5 principal components were selected for further analysis. The loadings of pixels centroids on the first 5 principal components were then used to perform a hierarchical ascending clustering through the HCPC (Hierarchical Clustering on Principle Components) procedure of the *FactoMineR* package. Hierarchical clustering was realised using the Euclidean distance as the metric and Ward's aggregation method to determine the optimal number of clusters to be formed. The Kmeans procedure was then used to consolidate the obtained clusters. Clustering results were then imported into QGis 3.10 to produce a bioclimatic zone map of the South Kivu province.

Selection of environmental predictors

Prior to distribution modeling, all the environmental variables were subjected to a correlation test (Appendixes Table 3) to select those susceptible to be used as predictors of the FAW distribution. Consequently, only variables with pairwise Pearson correlation coefficients falling under the interval of]-0.75, 0.75[were selected for modeling in order to control for multicollinearity problem in environmental predicators (Elith et al., 2010).

Species distribution modelling

MaxEnt (Maximum Entropy) program 3.3.3 (Phillips et al., 2006; 2017) was used to establish current climate envelope for FAW natural occurrence in South Kivu. MaxEnt is a common species distribution modeling (SDM) tool used for predicting the distribution of a species from a set of records and environmental predictors (Fourcade et al., 2014). The MaxEnt technique uses known occurrence locations (presence only data) and a set of gridded environmental layers to produce an output map of the predicted ecological niche of the species on a scale of 0 (lowest suitability) to 1 (highest suitability). MaxEnt is a modeling technique that measures entropy, a measure of ‘how much choice’ is involved in the selection of an event

(Phillips et al., 2004; 2006). MaxEnt is a general-purpose method for characterizing probability distributions from incomplete information. In estimating the probability distribution defining a species distribution across a study area, MaxEnt formalizes the principle that the estimated distribution must agree with everything that is known (or inferred from the environmental conditions where the species has been observed) but should avoid making any assumptions that are not supported by the data (Phillips et al., 2006). The approach corresponded to find the probability distribution of maximum entropy (a distribution that is most spread-out, or closest to uniform) subject to constraints imposed by the information available regarding the species observed distribution and related environmental conditions across the study area (Phillips et al., 2006). MaxEnt was presented as one of the highest performing SDM methods (Bradie and Leung, 2017). We ran 100 models, each trained to a randomly selected bootstrap process of the occurrence dataset. Prediction map from each model has been generated in order to calculate the mean prediction and standard deviation of each pixel. Model predictions were imported into ArcGis 10.6 to generate maps of the FAW occurrence probability in South Kivu.

Model evaluation

In this study, the Receiver Operating Characteristic (ROC) curve method was used to assess the model's performance (Pearce et al., 2001; Cumming, 2002; Peterson et al., 2006). One of the parameters used to evaluate predictive capacity of a model generated by MaxEnt is the area under the curve (AUC) or under the ROC curve. AUC can then be interpreted as the likelihood that a randomly selected point of presence is located in a raster cell with a higher probability of species occurrence than a randomly generated point (Phillips et al., 2006). The AUC is an effective threshold-independent index that can evaluate a model's ability to discriminate presence from absence (or background) occurrence. Also, the AUC is not affected by collinearity and spatiotemporal autocorrelation (Cumming, 2002). The closer AUC is to 1, the more predictive is the model. Random distribution has an AUC of 0.5. Overall value of AUC can be considered in evaluating the final model. AUC values of 0.5 - 0.7 indicate low accuracy, 0.7-0.9 useful applications and > 0.9 high accuracy (Manel et al., 2002).

Assessment of variable contribution

The Jackknife procedure was performed on climate variables to determine the major contributors to the prediction model. The model evaluation was completed by an assessment of the contribution of each variable used in the model based on Jackknife test. However, more detailed evaluation can be carried out during construction of the model by analyzing AUC obtained in different Jackknife test scenario. Then, AUC values obtained from a single variable or with the global models (from which a variable had been removed purposively) can be compared. The main goal in such situation is to identify which variable, when added or removed from the model, mainly modify the AUC value. In this study, the jackknife method was used to analyze the effects of environmental variables on model results to select dominant factors. Specifically, the process involves 3 independent steps: calculating the training gain for the model with only one variable. Higher training gain indicates that the variable has high prediction power and contributes greatly to species distribution, calculating the training gain for the model without a specific variable and analyzing the correlation between the removed variable and the omission error. If the removal of an environmental variable leads to a significant increase in the omission error, it indicates that the variable has a significant effect on the model's prediction, calculating the training gain for the model with all variables.

Results

Bioclimatic zones of the South Kivu province

Three bioclimatic zones obtained by clustering using bioclimatic data were presented (Figure 7). The respective characteristics (mean ± standard error) of each zone are given in Table 2 and distribution probability of occurrence of FAW in the bioclimatic zones (Appendixes Figure 1). Zone 1 is mainly characterized by very high mean daytime temperature range and rainfall parameters (seasonality, duration for the wettest period, in the wettest quarter and annual values). Furthermore, it has very low temperature means (annual, for warmest and coldest quarters, for hottest month and potential evapotranspiration). Also, zone 2 is characterized by very high isothermal and specific rainfall conditions (during driest period, annually, for wettest quarter and moisture index for dry quarter). In addition, it is characterized by very short duration of dry season, very low temperature seasonality and annually, annual moisture index, mean daytime temperature range. Finally, zone 3 was characterized by very high annual temperature and for warmest quarter, longest dry season, very high annual moisture index. However, it was also characterized by very low annual rainfall and for wettest quarter, isothermality and moisture index of the dry quarter. Zones 1, 2 and 3 represented high, low and medium altitude areas respectively.

Table 2. Description of bioclimatic zones of South Kivu.

Variables	**Zone 1**	**Zone 2**	**Zone 3**	**Global**
bio1	160.82 ± 19.96	227.28 ± 16.12	220.09 ± 18.06	210.53 ± 30.83
bio2	95.55 ± 4.53	106.89 ± 2.10	105.46 ± 4.75	103.93 ± 5.85
bio3	792.26 ± 39.18	857.40 ± 17.18	790.86 ± 35.53	812.91 ± 44.31
bio4	3.931 ± 0.80	2.99 ± 0.09	3.63 ± 0.80	3.48 ± 0.75
bio5	219.70 ± 23.05	288.97 ± 16.19	285.48 ± 18.98	273.40 ± 33.02
bio6	98.69 ± 16.75	164.26 ± 16.41	152.09 ± 17.09	145.34 ± 29.30
bio7	121.00 ± 9.754	124.70 ± 4.00	133.39 ± 4.15	128.06 ± 7.72
bio10	164.05 ± 20.37	229.63 ± 16.14	224.03 ± 18.06	213.81 ± 30.84
bio11	155.27 ± 20.02	223.59 ± 16.35	215.82 ± 18.31	206.19 ± 31.47
bio12	1893.89 ± 149.49	1940.80 ± 147.15	1563.16 ± 167.94	1753.17 ± 239.61
bio13	248.36 ± 27.76	235.78 ± 24.11	198.67 ± 16.41	220.80 ± 30.48
bio14	17.38 ± 8.03	55.42 ± 13.17	21.59 ± 10.16	31.81 ± 19.79
bio15	80.28 ± 11.02	61.72 ± 6.24	63.03 ± 6.53	66.07 ± 10.41
bio16	668.48 ± 65.06	668.73 ± 62.81	549.53 ± 50.97	612.44 ± 83.07
bio17	89.43 ± 35.89	198.67 ± 34.19	93.86 ± 38.22	127.25 ± 61.75
dem	2197.31 ± 348.68	847.65 ± 283.62	1145.35 ± 326.32	1259.45 ± 582.61
llds	2.69 ± 0.81	1.26 ± 1.13	3.29 ± 0.59	2.51 ± 1.23
mi	147.95 ± 23.30	118.39 ± 8.86	98.43 ± 12.58	114.91 ± 23.68
miaq	29.30 ± 13.16	50.70 ± 8.95	24.02 ± 9.79	33.81 ± 15.77
mimq	212.43 ± 35.75	160.83 ± 13.39	140.35 ± 15.53	161.54 ± 34.09
pet	1295.55 ± 100.38	1640.62 ± 65.71	1595.30 ± 92.60	1549.86 ± 155.42
Total area (km^2)	11411.20	17293.40	30389.80	59094.40

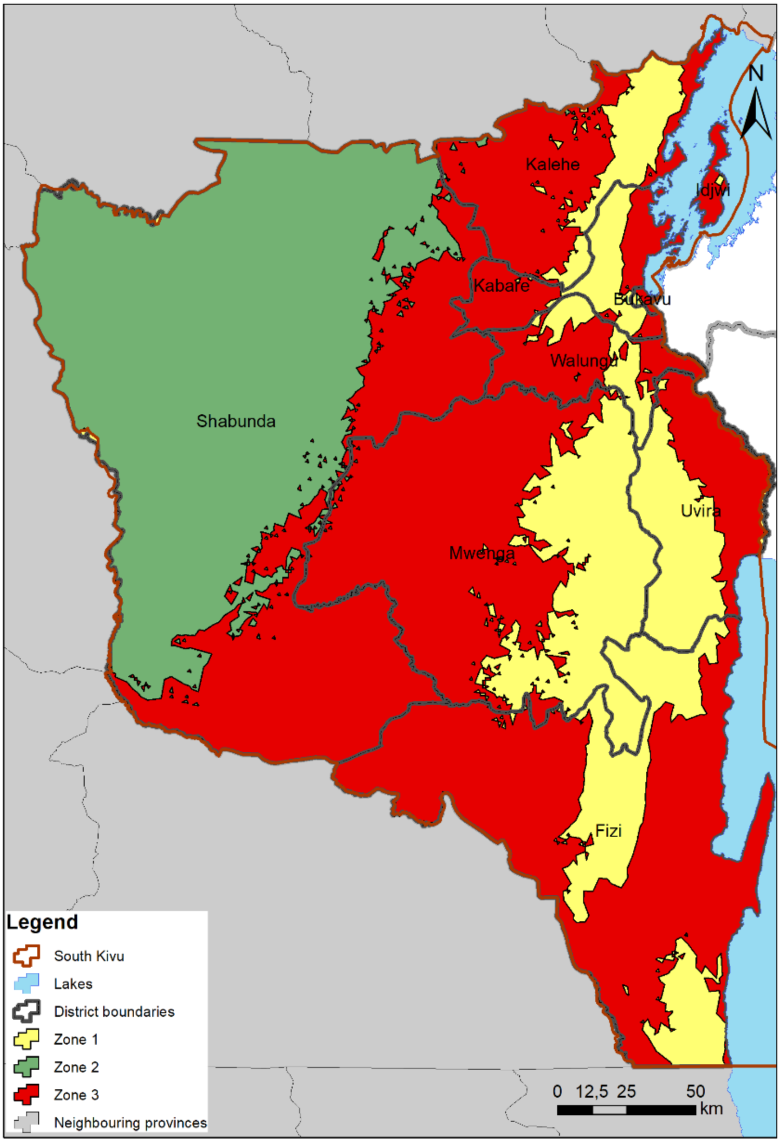

Figure 7. Bioclimatic zones of South Kivu. The zones are indicated in different colors on the map. The first zone appears on the map in yellow, the second in green and the third in red. This figure was created by the authors using ArcMap version 10.6 (https://desktop.arcgis.com/fr/arcmap/).

Model performance

In this study, from the ROC curves, AUC values were used to evaluate the performance of the MaxEnt model. Many studies showed that an AUC of high values leads to better results that significantly differed from the random predictions.

The next picture is the receiver operating characteristic (ROC) curve showing the performance of the FAW MaxEnt model. The prediction accuracy of FAW MaxEnt model was found to be acceptable (AUC mean of 0.827 ± 0.033, Figure 8) according to the identified evaluation criteria.

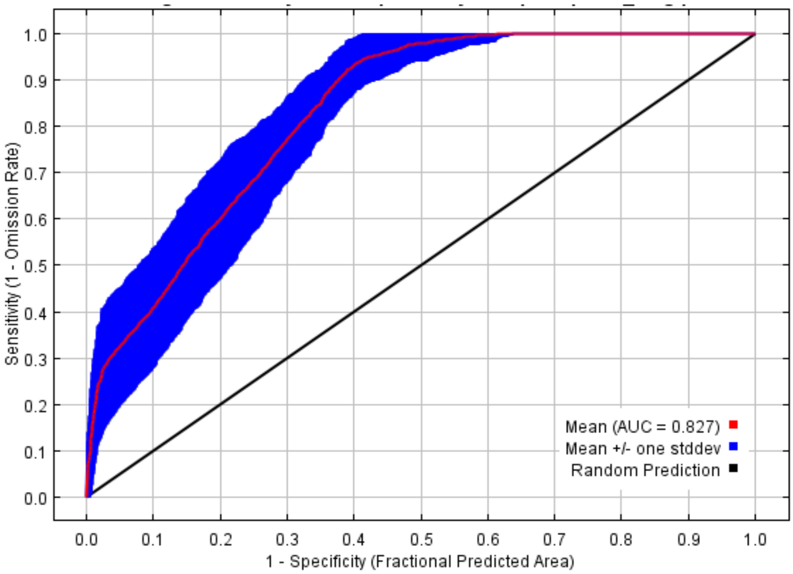

Figure 8. Receiver Operating Characteristic (ROC) curve and Area Under the Curve (AUC) value of MaxEnt modeling (100 runs).

The suitable areas of FAW in South Kivu province are divided into two corridors (Figure 9): one covering eastern Kalehe, Kabare, Walungu, Uvira and Fizi territories and another the western areas of Kalehe, Kabare, Walungu and Mwenga territories, southern Shabunda and north-western Fizi territories. The most suitable areas for FAW in South Kivu are mostly located in bioclimatic zone 3. In bioclimatic zones 1 and 2, the probabilities of FAW occurrence are very low (medians below 0.063). As for bioclimatic zone 3, the probabilities of occurrence are relatively higher, with a median of 0.29. In South Kivu, FAW are most likely to be found in areas characterized by very high annual temperature range, longest dry season, very high annual moisture index. Furthermore, these zones are also characterized by very low rainfall (annually, in the wettest quarter, during the wettest month).

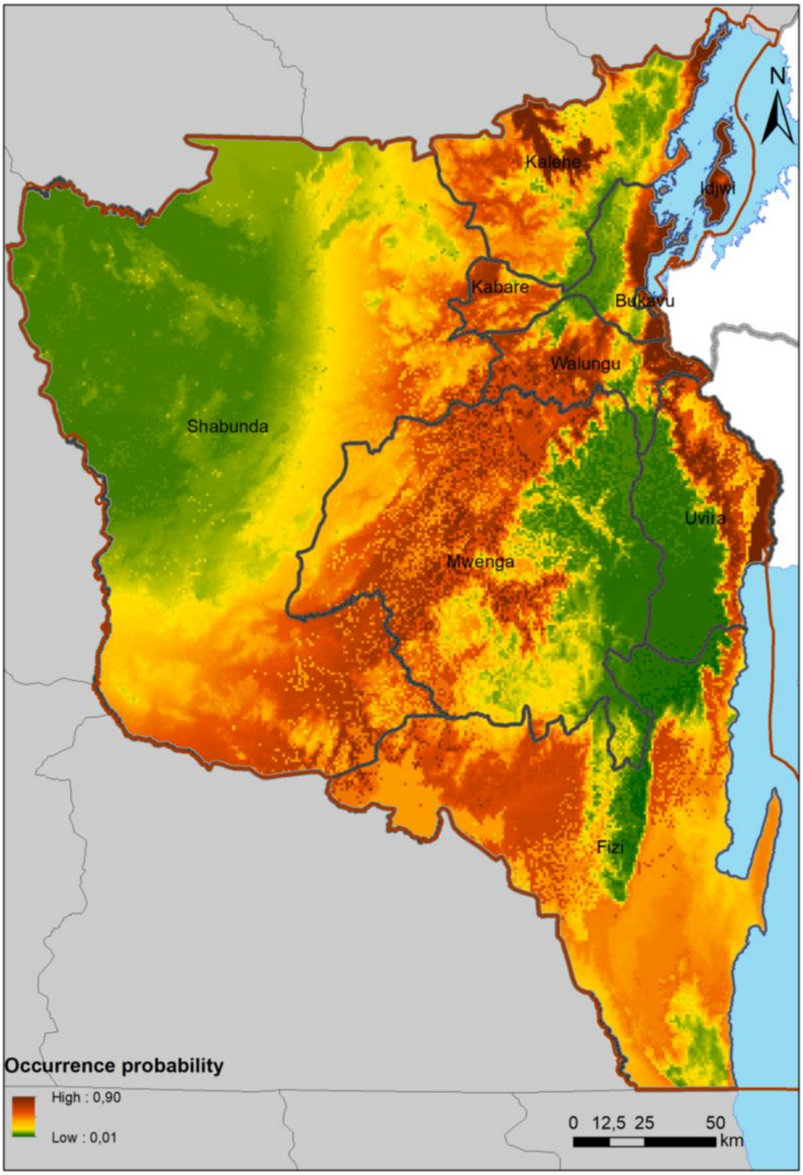

Figure 9. Distribution of suitable areas of fall armyworm (*Spodoptera frugiperda*) in South Kivu, DRC. This figure was created by the authors using ArcMap version 10.6 (https://desktop.arcgis.com/fr/arcmap/).

Analysis of variable contributions

The estimates of relative contributions of the environmental variables to the FAW MaxEnt model are presented **(**Figures 10 and 11) showing that bio12 (Annual rainfall) played a major role in the FAW spread. Furthermore, the environmental variable with highest gain when used in isolation was bio12 (Annual rainfall) according to the Jackknife test of variable importance (Figure 11). This environmental variable also decreases the most the gain while omitted, but also having the most useful information by itself and much more that is not available in the other variables. The bio12 variable was highly correlated with bio7 (Annual temperature range), bio13 (Rainfall of wettest month), bio16 (Rainfall of wettest quarter) and mi (Annual moisture index). Thus, it appears that these four variables also play a major role in the speed of FAW in South Kivu.

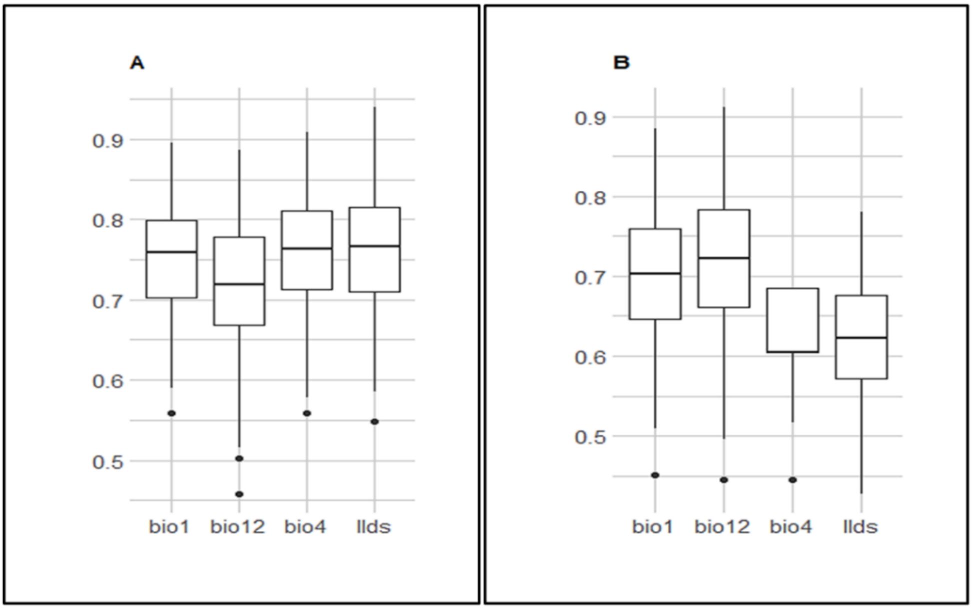

Figure 10. Contribution and permutation importance of variables used as predictors in the fall armyworm (*Spodoptera frugiperda*) MaxEnt model. bio1: mean annual temperature; bio12: annual rainfall; bio4: temperature seasonality; llds: longest dry season duration.

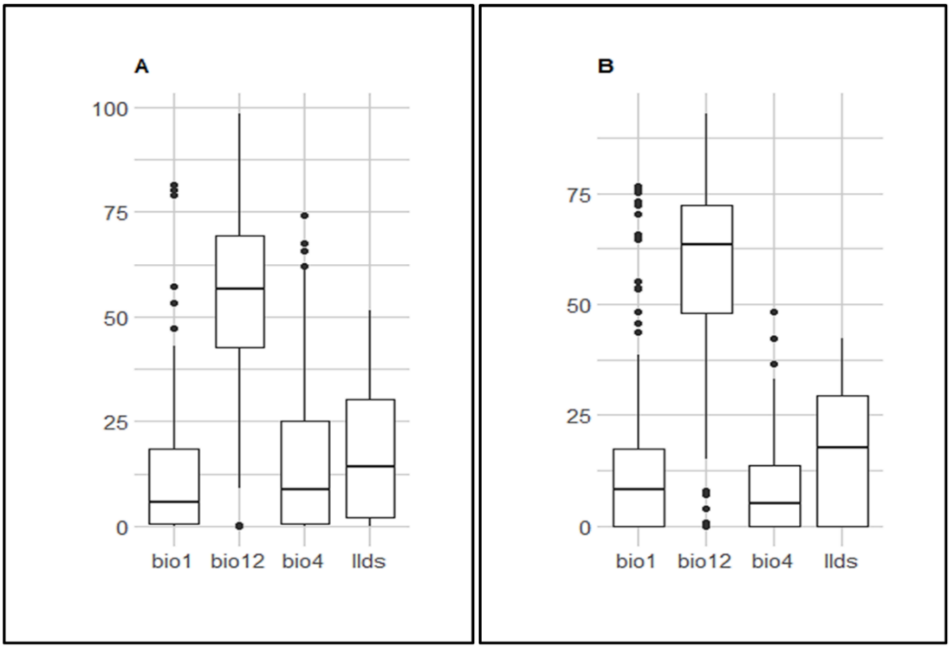

Figure 11. Jackknife test of variables' contribution in modeling *Spodoptera frugiperda* habitat suitability distribution in South Kivu: (**A**) without variable (**B**) with the variable only. bio1: mean annual temperature; bio12: annual rainfall; bio4: temperature seasonality; llds: longest dry season duration.

Response of variables to suitability

The mean responses of variables to FAW habitat suitability over 100 replicate MaxEnt runs (red) and the mean +/- one standard deviation (blue, two shades for categorical variables) are presented. The bio12 (annual rainfall with less than 1600 mm) variable plays a major role in the FAW distribution according to the Jackknife test (Figure 11). Furthermore, with a strong negative correlation with bio7 (annual temperature range), FAW also favours locations with high annual temperature. The probability of FAW occurrence is high in environments where (1) mean annual temperature (bio1) is comprised between 19°C and 23°C; (2) temperature seasonality (bio4) is less than 2.5 and (3) length of the longest dry season (llds) comprised between 2.5 and 4.5 (Figure 12).

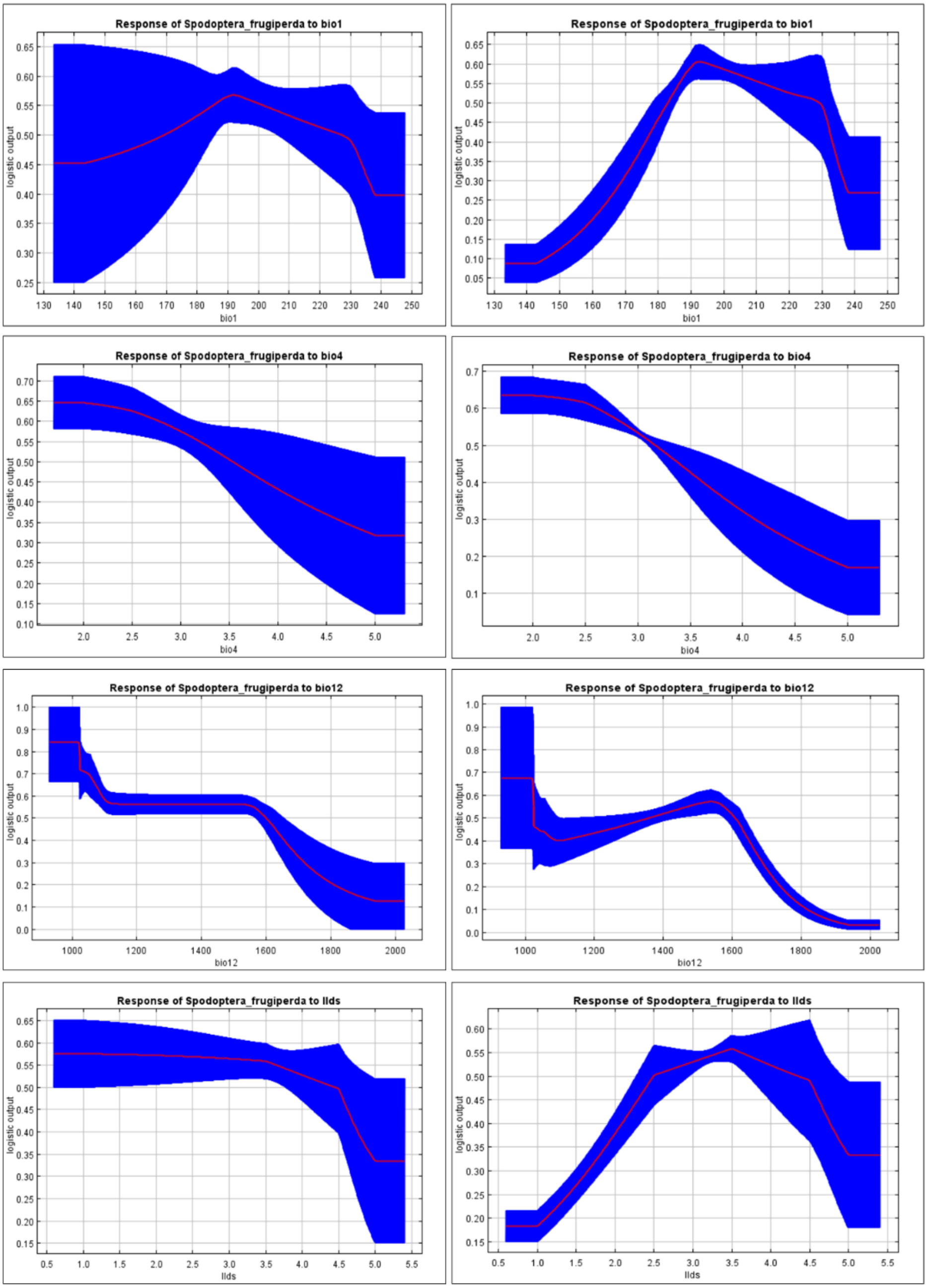

Figure 12. Responses of variables to fall armyworm habitat suitability. These curves show how each environmental variable affects the MaxEnt prediction. They also show how the predicted probability of presence changes as each environmental variable is varied, keeping all other environmental variables at their average sample value (Left side) or a MaxEnt model created using only the corresponding variable (Right side).

Discussion

The FAW is a tropical species mostly adapted to warmer parts of the New World (CABI, 2020). In the current study, we modeled its distribution under tropical conditions in Eastern DR Congo. The existence of 3 bioclimatic zones for FAW was determined in South Kivu. One (zone 3) was found to correspond to the highest probability of FAW occurrence. Climate change has been reported to have different effects on insects, directly impacting their life cycles or indirectly their hosts and/or predators (Patterson et al., 1999; Bale et al., 2002). However, the FAW may benefit from the climate change due to its polyphagous feeding behaviour, its phenotypic and genotypic plasticity (Ramirez-Cabral et al., 2017). Also, the adult migratory ability is one more adaptative trait to allow moving across regions to several miles (300 miles/generation in some years) (Sparks, 1979; Westbrook et al., 2016). In an area such as South Kivu with an approximate surface area of 69,130 km^2, the FAW migration would take place very quickly. Outbreaks of FAW are closely related to climate conditions and with good winter and spring conditions (Ramirez-Cabral et al., 2017). Cokola (2019) noted that FAW incidence in South Kivu has been associated by temperature and rainfall. Moreover, study conducted by Liu et al. (2020) founded that land-use was more important than climate factors, with larger potential distributions. In this study, among the 21 used bioclimatic variables, four of them influenced the potential distribution of FAW in the region. It is therefore seen that these four variables also play a major role in the spread of FAW in South Kivu. Wang et al. (2020) modelled the distribution of FAW through MaxEnt with 19 bioclimatic variables related to temperature and humidity of which 10 influenced the FAW distribution. However, the FAW distribution may be influenced by other several non-climatic factors, such as host, natural enemy, management level and human activities (Hill et al., 2012), soil properties, land cover and agricultural management interventions (such as use of pesticides or fertilizers) (Biber-Freudenberger et al., 2016). This aspect needs to be then incorporated into the model. Furthermore, it would also be important to model the FAW distribution by integrating local bioclimatic data into the model to minimize errors related to imported bioclimatic data. Soria-Auza et al. (2010) reported that one of the least studied sources of uncertainty in species distribution modeling comes from the environmental data used to run the models, particularly the climate data, especially in the tropics, where comparatively few climatic stations are available. In the case of South Kivu province, however, it is difficult to obtain sufficient local bioclimatic data given the limited number of meteorological stations found in this region.

The accuracy of prediction of FAW MaxEnt model showed high values of AUC (Figure 3) confirming a good model performance (Manel et al., 2002). Comparing our results with other studies, including Wang et al. (2020), an excellent AUC was found. For instance, AUC often increases with the size of the study area because it contributes to include background points that have environmental characteristics greatly distant from the species requirement, resulting in artificial increase of SDM validation (Barve et al., 2011). The suitable areas of FAW in South Kivu province are divided into two corridors (Figure 9). The Eastern corridor covering the Eastern areas of Kalehe, Kabare, Walungu, Uvira and Fizi territories and the Western corridor covering the Western areas of Kalehe, Kabare, Walungu and Mwenga territories, southern Shabunda and north-western Fizi territories. Infestations are most prevalent in the first corridor. Differences in the FAW infestations within the said corridor, between the Ruzizi plain (low altitude) and Kabare (mid altitude) have been demonstrated (Cokola, 2019). According to the modeling realized by Early et al. (2018), Sub-Saharan Africa, especially DR Congo, Gabon and Cameroon, appeared to have low suitability for FAW. Early et al. (2018) explain that low suitability in these countries was more likely because of extensive forest cover. This is the case for example, here for Shabunda territory. However, this does not mean that pockets of the suitable habitats in the cited countries will not be severely affected, given the ability of the FAW to travel long distances (Early et al., 2018).

Among the four environmental variables used as predictors in the FAW MaxEnt model, bio12 (annual rainfall) played a major role in the spread of FAW and contributed more to run the MaxEnt model (Figures 11 and 12). With the Jackknife test for variable importance, the environmental variable exhibited highest gain when used in isolation with bio12 (annual rainfall). Day et al. (2017) found that rainfall in the wettest periods and the coldest annual temperatures were important variables in FAW migration. The effects of rainfall on the distribution of FAW have been documented. For example, Early et al. (2018) reported that rainfall have a negative impact on FAW larvae. Furthermore, a suitability map provided by Du Plessis et al. (2018) demonstrated that natural rainfall and irrigation scenario were important variables in FAW distribution. The coldest annual temperature and the rainfall during the wettest three months were consistently identified by Early et al. (2018) as the environmental variables that most affected FAW distribution. In this work, most suitable habitat for FAW was found in places where annual rainfall was less than 1600mm. According to Nagoshi et al. (2012) and Early et al. (2018), FAW was most commonly found in areas with very little forest cover, a minimum annual temperature of 18-26°C and with 500-700 mm rainfall in the three wettest months.

Furthermore, given that variable bio12 is strongly negatively correlated with bio7 (annual temperature range), it seems clear that FAW also favours locations with high annual temperature. Temperature was the main environmental factor affecting the growth and reproduction of the FAW (Hogg et al., 1982; Busato et al., 2005). FAW was most likely to be found in areas characterized by very high annual temperature range, very long duration of the longest dry season, very high annual moisture index, high maximum temperature of the hottest month and very high mean temperature of the warmest quarter. The probability of FAW occurrence is high in environments where mean annual temperature (bio1) is comprised between 19°C and 23°C. Du Plessis et al. (2020) found that the development rate of FAW increased linearly with increasing temperatures between 18 and 30°C. Additionally, Wang et al. (2020) found that when the Mean Temperature of the Warmest Quarter varies between 19.15-29.73°C, the existence probability of the FAW is higher.

Conclusion

In areas where investigations on FAW invasions remain limited, such as in the DR Congo, it is important to model its distribution and to detect areas with high infestation potential. Based on the obtained results, the South Kivu province is a favorable habitat for the development of FAW. However, given the rapid spread of the insect and the climatic variability observed in the region that favor its development and dispersal, it is necessary to pay particular attention to the management of this species now, to take effective measures and prevent its further spread. At the same time, effective and efficient monitoring systems should be set up in its range to collect field data's and improve further control of this pest.

2. Unravelling the impact of seasonal and environmental factors on *Spodoptera frugiperda* infestations

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Abstract

The fall armyworm (FAW) *Spodoptera frugiperda* (J. E. Smith) has become a global devastating pest because of its broad dispersal capacity and the high crop damages. At present, research on FAW infestations of crops in the DR Congo remains undocumented. Here, FAW infestations in two agro-ecological zones (Kabare and Ruzizi Plain) were compared in South-Kivu Province. Surveys were carried out during the early 2018 and late 2019 crop seasons to assess the impact of FAW on maize crops. In each agro-ecological zone, 50 fields were selected for investigation. A total of hundred (100) fields were assessed in the 2018 crop season. During the 2019 crop season, the same fields were investigated. The two zones had very different bioclimatic characteristics. FAW attacks were more pronounced under conditions of relatively high temperatures with high evapotranspiration, which occurred in the Ruzizi Plain and late 2019 season. In comparison, Kabare territory and the early 2018 season were characterized by heavy rainfall. The incidence, level of leaf damage, and density of FAW larvae varied significantly with season and agro-ecological zone. The Ruzizi Plain had the highest incidence (60 ± 30%), level of leaf damage and larval density (28.5 ± 19.3). The late 2019 season had the highest incidence (70 ± 20%) as well as the larval density (27.8 ± 19.2). Total annual number of FAW generations was 5.64 and 3.36 in the Ruzizi Plain and Kabare territory, respectively. In conclusion, FAW infestation represents a major problem for agricultural production due to the climatic conditions in the study region.

Key words: *Spodoptera frugiperda*, infestations, season, agro-ecological zone, degree day.

Introduction

The fall armyworm (FAW) *Spodoptera frugiperda* (J. E. Smith) is one of the most important pests in the world due to its polyphagous behavior and high damages on major crops (*e.g.* maize, rice, sorghum,) (CABI, 2020) and to its extreme potential of expansion (Early et al., 2018). A recent study conducted by Montezano et al. (2018) reported 353 plant species attacked by FAW, which are distributed in 76 families whose the main plant families are Poaceae, Asteraceae and Fabaceae. The FAW was first reported in the Americas as its place of origin (Luginbill, 1928; Ayala et al., 2013; Early et al., 2018). At the present day, FAW has become one of the most important pests at the global stage (Zacarias, 2020) since it first invaded Africa in 2016 (Goergen et al., 2016), and also infested Asia in 2018 (Sharanabasappa et al., 2018; Shylesha et al., 2018). FAW exists in two morphologically indistinguishable strains, the corn strain (CS) and the rice strain (RS) (Pashley, 1986; Vélez-Arango et al., 2008; Cano-Calle et al., 2015; Nagoshi et al., 2015).

Maize is grown across diverse agro-ecological zones in Sub-Saharan Africa, where over 208 million people depend on this crop to meet their nutritional needs (Day et al., 2017). While maize is the most important staple cereal crop grown by smallholder farmers in Sub-Saharan Africa (Macauley, 2015; Ekpa et al., 2018), the susceptibility of this crop to FAW infestation is high due to physiological differences between strains, which affect the ability of FAW to consume maize efficiently (Veenstra et al., 1995). FAW often infests maize at the whorl stage, causing leaf damage (Capinera, 2000). This direct foliar damage is alarming to many farmers, who have never experienced this type of damage before (Hruska, 2019). FAW also infests the ears, especially during large infestation causing the direct loss of grain (Buntin, 2008). Estimates provided by Day et al. (2017) indicate that FAW impacts between 8.3 and 20.6 million tons maize yield per year out of the total expected production of 39 million tons per year in Africa. Yield losses of 15-73% were predicted by Hruska and Gould (1997) when 55-100% of corn plants were infested with FAW.

It is important to understand how pests, hosts and the environment interact, with environment being primarily represented by weather conditions (López et al., 2019). Climatic conditions appear to be the most cited factor driving the presence of FAW, including temperature, length of exposure and precipitation during the warm/wet season (Du Plessis et al., 2018; Early et al., 2018). Recent studies (Koffi et al., 2020;

Nboyine et al., 2020) reported that maize infestation of FAW in Africa varied over time within seasons and agro-ecological zones (AEZ). The degree-day (DD) is also an important parameter for forecasting pest phenology and voltinism (Tu et al., 2014), as well as identifying key biological events for the FAW, such as egg hatching adult dispersal and to determine when to respond by setting traps, assessing damage, and collecting samples (Labatte, 1994; Westbrook et al., 2016; Du Plessis et al., 2020).

Since its invasion of the African continent, several countries (e.g. Benin, Ghana, Togo, Cameroun, Kenya…) have carried out infestation assessment studies (Goergen et al., 2016; Fotso Kuate et al., 2019; Baudron et al., 2019; Nboyine et al., 2020; Koffi et al., 2020). However, studies and data on FAW infestation in DR Congo remain limited and poorly documented. This study aimed to evaluate FAW infestations regarding season and the agro-ecological zones (AEZ) of selected maize growing areas in the eastern DR Congo. Within this framework, accumulated degree DD by FAW were evaluated from a starting date in each season and agro-ecological zone. The results are expected to provide baseline information to update FAW pest status and develop effective strategies to manage it in the Eastern DR Congo.

Materials and Methods

Study area description

To assess FAW infestations, a survey was conducted in South-Kivu Province, DR Congo. Investigations were set up in two agro-ecological zones (Figure 13): Kabare (2°27'26.94"S, 28°49'12.75"E, 1563m), and Ruzizi Plain (2°47’14.54’’S, 28°59’54.1’’E, 899m). Kabare is located in the extreme East of DR Congo (mid-altitude zone), on the western shores of Lake Kivu. It has a humid tropical type of climate. This territory has two seasons: a dry season that lasts three months (June to August) and a rainy season that lasts nine months (September to May). The rainy season is divided into two crop seasons: September to January (season A) and February to June (season B). The Ruzizi Plain is divided between three countries: namely DR Congo, Rwanda, and Burundi. The name Ruzizi Plain derives from its relief, which is a large plain (lowland area) located along the Ruzizi River. Ruzizi Plain has a semi-arid climate with a bimodal rainfall regime: from October to January and from February to May (Vancoppenolle et al., 1984).

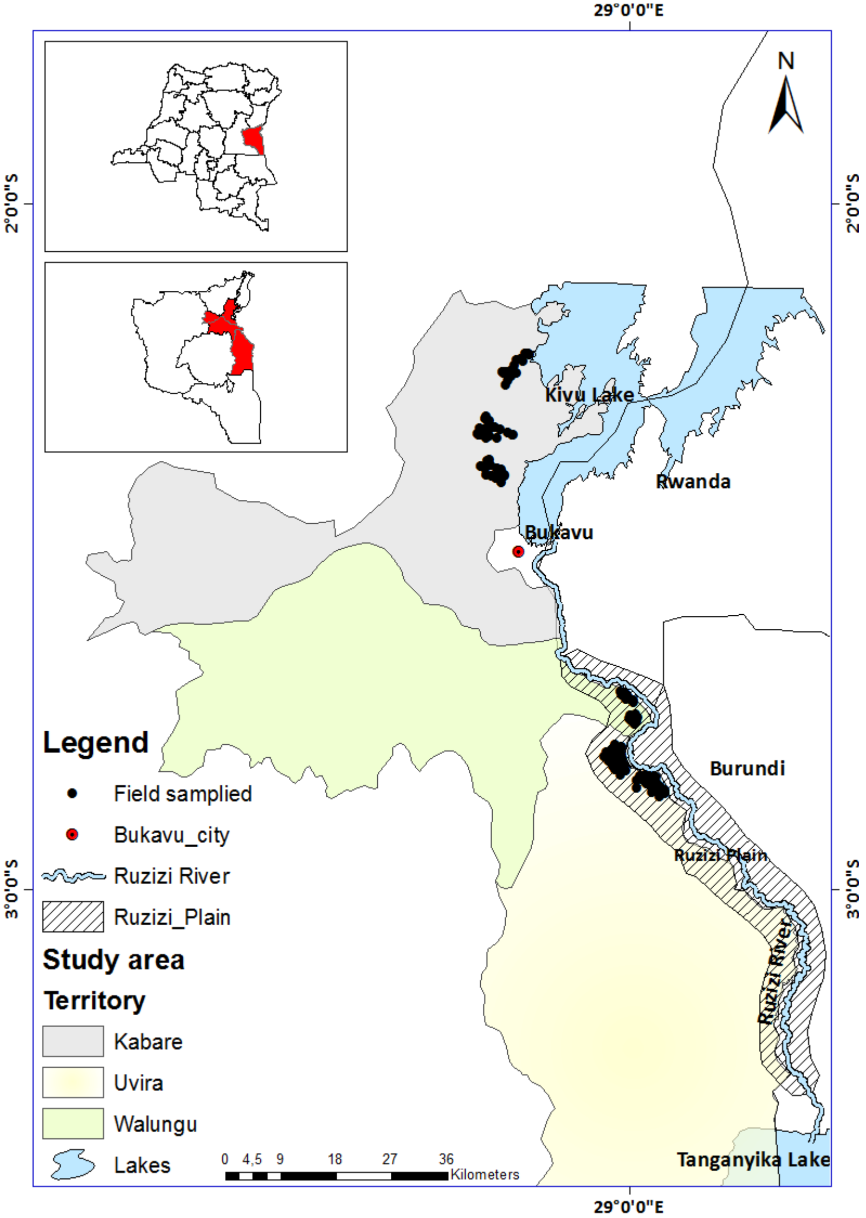


Figure 13. Map show the study area. Fields sampled are indicated.

Evaluation of the seasonal infestation of FAW

Incidence surveys of damaged plants by FAW were conducted at Kabare in November 2018 and at Ruzizi Plain in December 2018, when maize was at the 8-leaf stage. The same surveys were conducted at Kabare in March 2019 and Ruzizi

Plain in April 2019, when all maize crops were at the 8-leaf stage. The assessment consisted of analyzing the incidence and severity of infestation on maize leaves. A transect method was used on maize farms in each agro-ecological zone. Fifty (50) fields were selected for the investigation in each agro-ecological zone. A total of hundred (100) fields were assessed in the 2018 crop season. During the 2019 crop season, the same fields were investigated using a tracking system. The tracking system, GPSMAP (GARMIN GPS devices) allowed the same geographical coordinates to be evaluated in 2019 as in 2018. This approach allowed us to determine seasonal variability in FAW infestation. Seven quadrats, each 20 m^2 in size, were randomly formed in each field using the W sampling method proposed by McGrath et al. (2018). Maize plants were considered infested when larvae, fresh sawdust-like frass, or fresh larval feeding plant injury were found (Koffi et al., 2020).

To assess incidence, several parameters were considered in each quadrat. These parameters included the number of infested plants (NIP), total number of plants (TNP), number of larvae per plant (NLP), and number of larvae per defined area (20 m^2) (NLDA). The number of damaged leaves per plant (NIL) and the number of lesions per leaf (NLL) were determined by considering the whorled and furled leaves. These variables were determined on 10 plants randomly selected from the quadrat. In each quadrat, the number of larvae per plant (NLP) was assessed by counting the larvae on each infested plant. The detection of larvae was carried out by opening the whorled leaves on each infested plant (Koffi et al., 2020). Next, the number of larvae per quadrat (NLDA) was assessed by summing the NLP for all plants infested in the quadrat. To ascertain that the damages observed was indeed those of FAW, samples of FAW larvae in each agro-ecological zone were taken for subsequent morphological identification in the laboratory. Severity was determined based on the number and size of lesions for each leaf based on the scale of the evaluation proposed by Davis et al. (1992) (Table 2 in Appendixes). The percentage of infested plants per field was also determined.

Climatic data collection and calculation of FAW Degree days

The climatic data included environmental and bioclimatic parameters were measured during the 2018 and 2019 seasons. Particularly, the information on the bioclimatic characteristics of the study areas was obtained from images of bioclimatic variables that were downloaded from the Africlim site (https://www.york.ac.uk/environment/research/kite/resources/) over long periods of time (1950 - 2000) using the geographical coordinates of the investigated maize fields. The bioclimatic variables of the study areas are presented in Table 3. These variables were then used as additional variables in the principal component analysis that provided a better understanding of the variation in FAW infestation and the factors that are likely to influence them.

Table 3. Environmental and bioclimatic parameters.

Environmental and bioclimatic parameters	Code	Units
Mean annual temperature (* 10)	BIO1	°C
Mean daytime temperature range (monthly average) (* 10)	BIO2	°C
Isothermality (bio1/bio7) * 100	BIO3	-
Temperature seasonality (Standard deviation * 100)	BIO4	°C
Maximum temperature of the hottest month (* 10)	BIO5	°C
Minimum temperature of the coolest month (* 10)	BIO6	°C
Annual temperature range (bio5-bio6) (* 10)	BIO7	°C
Mean temperature of the warmest quarter (* 10)	BIO10	°C
Mean temperature of the coldest quarter (* 10)	BIO11	°C
Annual rainfall	BIO12	mm
Rainfall during the wettest month	BIO13	mm
Rainfall during the driest month	BIO14	mm
Rainfall seasonality	BIO15	mm
Rainfall in the wettest quarter	BIO16	mm
Rainfall in the driest quarter	BIO17	mm
Longest dry season duration	LLDS	-
Annual moisture index	MI	-
Moisture index of the dry quarter	MIAQ	-
Moisture index of the wet quarter	MIMQ	-
Potential evapotranspiration	PET	mm
Elevation	DEM	m

To determine the number of FAW generations (NOG) in each season and agro-ecological zone, degree days (DD) were estimated. This measure was used because each species requires a defined number of DD to complete its development (Zalom et al., 1983). According to Day and Karayiannis (1998), DD may be calculated using four main methods. In our case, mean daily temperature (from daily maxima and minima) was used. DD was calculated using the following formula (Snyder, 1985; Michaud and Moreau, 2011):

$$DD = [(T_{min}+T_{max})/2] - T_{HR}$$

where T_{min} and T_{max} represent the minimum and maximum air temperatures reached per day and T_{HR} is the minimum threshold temperature. For estimated T_{HR}, we accounted for the variation reported in published literature (Hogg et al., 1982; Ali et al., 1990; Valdez-Torres et al., 2012; Early et al., 2018; López et al., 2019). We considered a T_{HR} of 12 °C based on Du Plessis et al. (2018), which reflected the tropical distribution of FAW. The number of FAW generations (NOG) was calculated as follow:

$$\text{NOG} = \frac{\sum_{n=1}^{\infty} DD}{PDD}$$

where NOG is the number of FAW generations, PDD is the minimum degree day sum needed to complete a generation (600-degree days) according to Du Plessis et al. (2018); and DD is the mean daily degree day.

Data analysis

R version 3.5.1 was used for statistical analysis (R development Core Team, 2018). Wilcoxon rank test was applied at the 5% significance level ($P < 0.05$) to compare FAW infestations parameters (incidence, NIP, TNP, NIL, NLL, NLP and NLDA) from season and AEZ. The multivariate statistical analyses allow to summarize principal data structure or to reveal particular correlations between original variables. We used principal component analysis (PCA) to describe our dataset using package FactoMineR (Lê et al., 2008). Eight variables were used to characterize FAW infestation: NIP, TNP, NIL, NLP, NLL, NLDA, Severity, and incidence. Bioclimatic variables, season and AEZ were considered as additional variables in the PCA. The PCA produced eight main axes, of which four were used to interpret the relationships between the variables characterizing FAW infestation. The Kaiser criterion was used to select the main components for factor analysis, the eigenvalues of which were above unity, since they generated components with relevant amounts of the original information.

Results

Bioclimatic characterization of maize fields in Kabare territory and Ruzizi Plain

The fields investigated here were located at different altitudes, and so had very different bioclimatic characteristics (Table 4). For instance, in Kabare, the environment was characterised by low values for almost all characteristic variables related to temperature, but exhibited high values for all rainfall variables. The opposite trend in bioclimatic characteristics was obtained for Ruzizi Plain. The Ruzizi Plain was characterized by high temperatures and low rainfall, whereas Kabare was characterized by high rainfall and low temperatures.

Table 4. Description (Mean ± SD) of bioclimatic characteristics of sampled field locations in Kabare and Ruzizi plain.

Variables	Kabare	Ruzizi Plain	Total
BIO1	186.2 ± 5.3	231.3 ± 3.8	209 ± 23.1
BIO2	106.7 ± 2	122.8 ± 1.3	114.8 ± 8.2
BIO3	839.9 ± 9.1	800.1 ± 4.6	819.8 ± 21.2
BIO4	3 ± 0	3.5 ± 0.5	3.3 ± 0.4
BIO5	250.4 ± 5.7	310.2 ± 3.7	280.6 ± 30.4
BIO6	123.5 ± 5.8	156.8 ± 4.4	140.3 ± 17.5
BIO7	126.9 ± 2.8	153.3 ± 2	140.2 ± 13.5
BIO10	189.5 ± 5.5	236.6 ± 3.7	213.3 ± 24
BIO11	183 ± 5.9	227.7 ± 3.9	205.6 ± 23
BIO12	1579.4 ± 41.3	1063.7 ± 30.4	1318.9 ± 261
BIO13	184.6 ± 5	142.8 ± 4.9	163.5 ± 21.5
BIO14	22.2 ± 1.4	7.7 ± 0.6	14.9 ± 7.4
BIO15	54.4 ± 2.1	46 ± 1	50.2 ± 4.5
BIO16	508 ± 14.6	389.4 ± 8.4	448.1 ± 60.6
BIO17	118.7 ± 4.8	50 ± 4.1	84 ± 34.8
DEM	1609.2 ± 87.5	917.3 ± 45.1	1259.6 ± 353.7
LLDS	3 ± 0	4.4 ± 0.5	3.7 ± 0.8
MI	107.1 ± 3.9	59.8 ± 2	83.2 ± 23.9
MIAQ	33.4 ± 1.8	12 ± 0.9	22.5 ± 10.8
MIMQ	138.6 ± 4.9	91.1 ± 2.4	114.6 ± 24.1
PET	1474 ± 16.9	1775.6 ± 14.5	1626.4 ± 152

Characterization of FAW seasonal infestation in the maize fields of Kabare and Ruzizi Plain

Table 5 shows the differences in FAW infestation in Kabare and the Ruzizi Plain. FAW infestation appeared to be more severe in Ruzizi Plain compared to Kabare. Ruzizi Plain had the highest values for NIP, TNP, NLP, NLL, NLDA, Severity, and incidence. However, the range of variation in the observed infestation parameters noticeably differed. Data from Ruzizi Plain showed high statistically differences, highlighting some variability in FAW infestation. In comparison, in Kabare, the ranges of variation seemed to be smaller, reflecting lower heterogeneity in infestation compared to Ruzizi Plain. Thus, FAW infestation was more pronounced in the warmer environment with lower rainfall, and was less pronounced in environments with higher rainfall and cooler temperatures. Seasonal infestations of FAW were more pronounced in the B2019 season compared to the A2018 season. Season B2019 had the highest NIP, NIL, NLDA, and incidence. The severity of infestation was similar for both seasons.

Table 5. Effect of season and agro-ecological zone (AEZ) on the parameters of fall armyworm infestations.

Variables	**Agro-ecological zones (AEZ)**		**Seasons**	
	Kabare	**Ruzizi Plain**	**A2018**	**B2019**
NIP	13.1 ± 8 b	20.6 ± 10.1 a	14.2 ± 7.9 b	19.5 ± 10.8 a
TNP	31.4 ± 11.1 b	35.4 ± 9.3 a	38.7 ± 10.4 a	28.2 ± 7.3 b
NIL	5.1 ± 1.9 a	5.4 ± 1.8 a	4.6 ± 1.6 b	5.9 ± 1.8 a
NLP	1.5 ± 0.5 b	1.7 ± 0.6 a	1.5 ± 0.6 a	1.6 ± 0.6 a
NLL	13.3 ± 6.2 b	16.6 ± 7.8 a	14.1 ± 6.4 a	15.8 ± 7.9 a
NLDA	16.1 ± 11.9 b	28.5 ± 19.3 a	16.9 ± 12.9 b	27.8 ± 19.2 a
Severity	5.4 ± 1.2 b	6.2 ± 1.5 a	5.8 ± 1.3 a	5.8 ± 1.5 a
Incidence	0.4 ± 0.2 b	0.6 ± 0.3 a	0.4 ± 0.2 b	0.7 ± 0.2 a

Means ± SD followed by the same lowercase letter within rows are not significantly different according Wilcoxon rank test at 5% significance level (P <0.05). NIP, number of infested plants; TNP, total number of plants; NIL, number of infested leaves per plant; NLP, number of larvae per plant; NLL, number of lesions per leaf; NLDA, number of larvae per defined area (20 m^2). A2018: early season from september 2018 to january 2019; B2019: late season from february to june 2019.

Principal Component analysis of FAW infestations in Kabare and Ruzizi Plain

The principal component analysis of the two study areas is presented in Figure 14 and Appendixes Table 4. Four (4) principal components with eigenvalues greater than 1 were retained for interpretation. All bioclimatic variables, Season, and Area of study were used as supplementary variables, and did not contribute to the principal components. The four principal components represented more than 78% of total variance of the entire data set, with the first two components representing more than 52% of total inertia.

The first axis (Dim.1) captured more than 35% of total variance. It was highly correlated with NLDA, Severity, and incidence. This axis made it possible to characterize FAW infestation better. It provided information on the relationship between the incidence and severity of FAW infestation at the two study areas as a function of season and bioclimatic factors. FAW infestation was more pronounced under relatively higher temperatures (BIO1, BIO2, BIO5, BIO6, BIO7, BIO10 and BIO11) with high evapotranspiration (PET) over relatively long periods (LLDS). These conditions were characteristic of the Ruzizi Plain and/or B2019 season. In comparison, FAW infestation was less pronounced in conditions with heavy rainfall (BIO12, BIO13, BIO14, BIO15, BIO16, and BIO17). These characteristics were encountered at Kabare and/or A2018 season.

The second axis (Dim.2) described the relationships between the number of infested leaves (NIL), total number of plants (TNP), and seasonal FAW infestation. It described the distribution of FAW in fields with respect to field characteristics. Fields with high numbers of plants (TNP) tended to have low numbers of infested leaves per plant (NIL). During the A2018 season, NIL was lower in maize. FAW infestation was less pronounced during the A2018 season, and was mostly characterized by heavy rains and low temperatures. These conditions represent unfavorable periods (low temperatures) for FAW, which, while present, caused less damage, with almost no incidence. In other words, larvae were present, but were not yet at the stage where they would cause damage to plants, with almost nil incidence in the A2018 season.

The third axis (Dim.3) provided information on the relationships between the number of infested plants (NIP), number of larvae per plant (NLP), and total number of plants in the field (TNP). FAW tended to infest all plants in a field, with the highest numbers of infested plants being observed in fields with the highest numbers of maize plants. However, when infestation was spread across a larger number of maize plants, larval numbers per plant were low. Unexpectedly, the fourth axis (Dim.4) showed that cases existed where the incidence was low, because maize fields contain large numbers of plants (TNP). Consequently, plants containing large numbers of larvae (NLP) infected a large number of leaves (NIL), causing a large number of lesions on leaves (NLL); however, the degree of damage was very low.

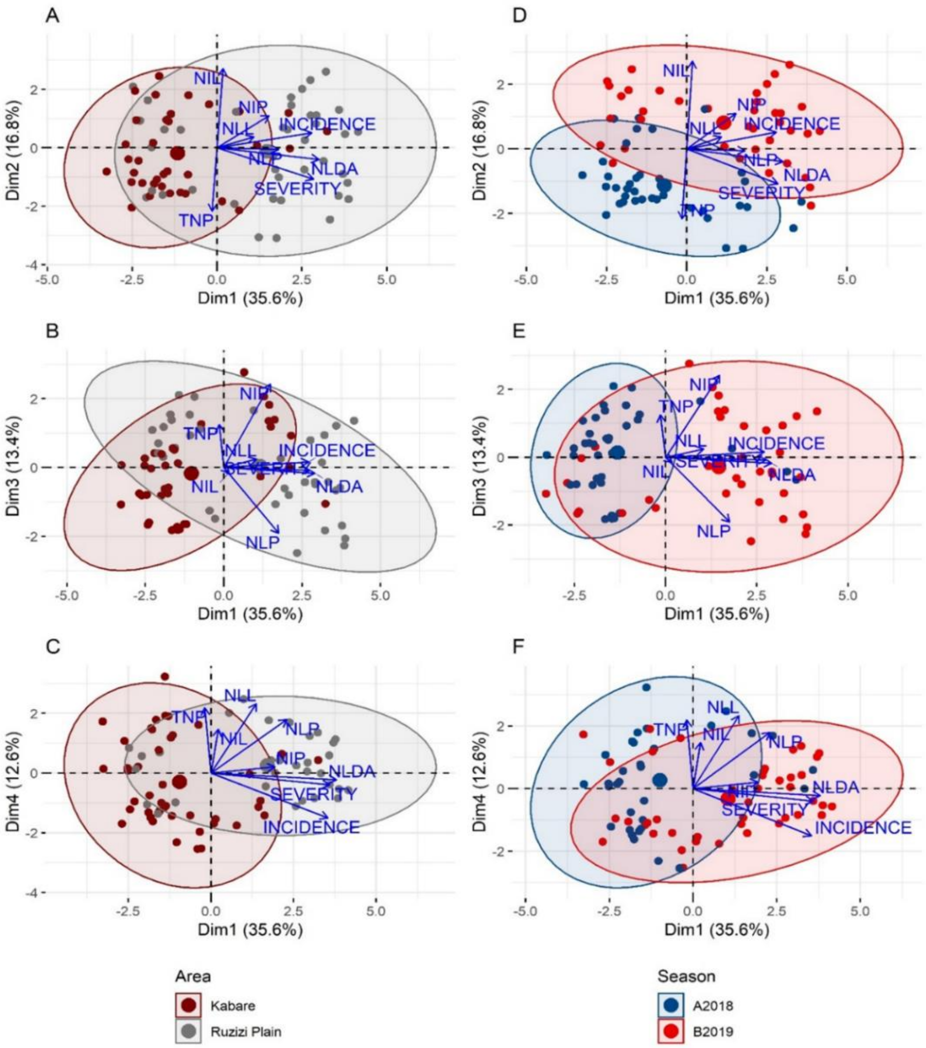


Figure 14. Output of the Principal Component Analysis: characterization of fall armyworm infestation in the study areas (A – C) and seasons (D – F) in the planes Dim.1-Dim.2, Dim.1-Dim.3 and Dim.1-Dim.4.

Variation of degree day, precipitation, and number of FAW generations across seasons and agro-ecological zones

Table 6 shows the difference in terms of infestation between the two seasons and the two agro-ecological zones. The Ruzizi Plain was more favorable to FAW based on the sum of accumulated degree days. Mean NOG was 1.68 (~2) and 2.82 (~3) in Kabare territory and Ruzizi Plain, respectively. Across the two seasons, about two and three generations were observed in Kabare territory and the Ruzizi Plain, respectively. The total annual number of generations was 5.64 (~6) and 3.36 (~3) in the Ruzizi Plain and Kabare territory, respectively. Precipitations were higher in the A2018 season in Kabare territory compared to Ruzizi Plain. Of note, higher rainfall was recorded during the B2019 season compared to the A2018 season in the Ruzizi Plain compared to Kabare territory.

Table 6. Sum of degree day (DD), number of FAW generations (NOG), and precipitations (P^{mm}) during the seasons in the agro-ecological zones.

Season	**Month**	**DD**		**P^{mm} (mm)**		**NOG**	
		Ruzizi plain	**Kabare**	**Ruzizi plain**	**Kabare**	**Ruzizi plain**	**Kabare**
A2018	September	357	215.8	50	129.7	2.89	1.72
	October	359.9	210.2	83.3	167.3		
	November	331.5	195.2	103	178.1		
	December	343	202.8	121.5	169.6		
	January	344.9	209.8	120.2	148.2		
	∑	**1736.6**	**1034.1**	**478.2**	**793.1**		
B2019	February	312.5	188.5	109.8	147.3	2.75	1.64
	March	345.5	210.1	136.3	178.8		
	April	333.3	200.7	141.6	180.2		
	May	343.6	206.3	96.8	124.7		
	June	319.3	183.7	24.3	44.1		
	∑	**1654.4**	**989.3**	**509**	**675.4**		

Discussion

FAW infestations on maize have been observed since 2016 in South-Kivu Province (personal observations), the year it was first introduced to the African continent. However, preliminary research has been limited, due to the negligible extent of damage observed during this time. Over the last three years, this pest has started to devastate maize crops in the region. Koffi et al. (2020) reported that infestation levels of FAW vary from one agro-ecological zone to another. López et al. (2019), and Koffi et al. (2020) reported that damage to crops (such as corn) by FAW varies across years. The incidence, level of leaf damage, and larval density of FAW varied significantly depending on the season and agro-ecological zone. The incidence of FAW was higher in the Ruzizi Plain and B2019 season (Table 3). Baudron et al. (2019) showed that the incidence of plants with FAW damage symptoms varied depending on the estimate used for determining the parameter. Around 48.3% of plants were estimated to have leaf damage, while 31.6% of plants had frass in the whorl (Baudron et al., 2019). FAW infestation varied considerably among farms in three countries surveyed by Sisay et al. (2019), with mean percent FAW infestation ranging from 5.3% to 100%. When 100% of the irrigated maize plants were infested by FAW under experimental conditions, yield declines by 45% (Hruska and Gladstone, 1988). Under natural rainfall, where 100% of infestation occurs, yield declines by 15–30% (Van Huis, 1981) and up to 73% (Hruska and Gould, 1997). The Davis damage score was intermediate for each season and each agro-ecological zone of the current study, dominated by score 5. In comparison, low to moderate leaf damage scores were reported by Sisay et al. (2019). A lower Davis damage score of 3.78 was recorded by Baudron et al. (2019). Baudron et al. (2019) suggested that FAW damage does not necessarily significantly impact crop yield. Beserra et al. (2002) showed that the distribution of FAW larvae and eggs varied with the phenological stage of corn. At the 8-leaf stage (V8), the larval density of FAW per plant varied with respect to agro-ecological zone in our study, with 1.7 larvae per plant being recorded in the Ruzizi Plain and 1.5 in Kabare. Only one larva was recovered per plant in a study by Murúa et al. (2006), and Fotso Kuate et al. (2019). This decrease in NLP was due to cannibalism, dispersal, and predation (Peireira and Hellman, 1993; Chapman et al., 1999; Capinera, 2000), because larval density per plant is higher at the start of infestation. Marenco et al. (1992) documented that a mean density of 0.2 to 0.8 larvae per plant during the late whorl stage could reduce yield by 5 to 20%.

Differences recorded in the parameters of FAW infestations during this study were directly related to climatic conditions. Indeed, Hruska and Gladstone (1988) stated that damage caused by FAW is strongly associated to environmental conditions. The study areas had totally different bioclimatic characteristics. Nboyine et al. (2020) reported that the abundance of FAW in maize is influenced by the growth stage of the crop, rainfall and relative humidity. Murúa et al. (2006) suggested that temperature and rainfall are the climatologic factors that significantly impact FAW density. FAW infestation was pronounced at relatively higher temperatures with high evapotranspiration, which were conditions characteristic of the Ruzizi Plain and B2019 season. In comparison, Kabare territory and A2018 season were characterized by heavy rainfall conditions. One factor that might have contributed to the high severity and incidence of FAW infestation during the B2019 season was a short period of drought between the end of the A2018 season and the beginning of the B2019 season. However, Fotso Kuate et al. (2019) observed that areas with bimodal rainfall have a higher accumulation of FAW populations during the first planting season. Indeed, rainfall enhances larval mortality state of FAW (Early et al., 2018; Cokola, 2019) with the first season (A2018) characterized by huge amounts of rain.

Barfield and Ashley (1987) reported that the developmental times of FAW are temperature-dependent, being modified by the stage of maize consumed. Hogg et al. (1982); Barfield and Ashley (1987); and Busato et al. (2005) reported that the development time of eggs, larvae, and pupae decreases with temperature up to 35 °C. Accumulated DD by FAW was important in the Ruzizi Plain compared to Kabare, because the Ruzizi Plain is dominated by a semi-arid climate. Fatoretto et al. (2017) documented that FAW is highly reproductively efficient in tropical areas. In warmer temperature conditions (such as the Ruzizi Plain), there may be several generations per year versus two or less generations in temperate areas. The development of FAW and other insects is favored by warm temperatures, which increase the number of generations in a given region (Westbrook and Sparks, 1986). Up to three generations of FAW were reported in this study during the B2019 season in the Ruzizi Plain and Kabare territory and two during A2018 in both areas. The total annual number of generations is about six in the Ruzizi Plain and three in Kabare territory. Busato et al. (2005) reported up to eight generations per year in the maize fields of tropical areas. Du Plessis et al. (2018) reported that the NOG of FAW occurring in an area varies with the appearance of the dispersing adults. However, outside the growing season, FAW populations can be maintained by infesting other crops (Montezano et al., 2018). During the dry season, the annual NOG of FAW likely increases, because FAW infest crops other than maize and sorghum in the study area (personal communication). Vegetable crops, such as onion, have been reported as alternate hosts during the dry season. Rapid generation turnover in FAW is facilitated by the presence of intercropping, where different crops grow at the same time and successively throughout the year, maintaining a high density of FAW (Fatoretto et al., 2017).

FAW is an important pest in the Eastern DRC, with infestation varying with the cropping seasons and agro-ecological zone. The late season (B2019) and the Ruzizi Plain were the most favorable for FAW development. Rainfall seemed to be a factor limiting FAW infestation in the region, whereas warm temperatures accelerated development and increased the number of generations per year. Because of its polyphagous feeding behavior, FAW threaten agriculture in Eastern DRC. In the context of monitoring and developing effective control strategies against FAW, it is necessary to be vigilant for dry season populations by identifying alternative host plants.

3. Maize planting date and *Spodoptera frugiperda* abundance

This section was adapted from manuscript: **Cokola, M.C.,** Noël, G., Mugumaarhahama, Y., Caparros Megido, R., Bisimwa, E.B., Francis, F., 2024. Planting date in South Kivu, Eastern DR Congo: a real challenge in the sustainable management of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) by smallholder farmers. Under review in PLoS ONE.

Abstract

There is growing research interest in the fall armyworm *Spodoptera frugiperda,* a polyphagous insect that is a major pest of maize crops worldwide. We investigated the relationship between planting date and FAW infestation in South Kivu, eastern DR Congo, in two sampling periods (September to October 2020 and February to March 2021). Five planting dates were considered for 45 fields in each period. The incidence, severity of attack and larval density of FAW were assessed at the 8-leaf stage (V8) of maize development in monoculture and intercropping systems. Planting period, classified as late or early, had a strong influence on FAW larval density, incidence and severity. The results showed that the late planting period had the highest larval density, incidence and severity of attack compared to the early planting period. During the first period (early season), five larval stages were found in the same field, whereas all larval stages were present in second period (late season), regardless of planting period. High densities of L4, L5 and L6 larvae were much more associated with late planting and incidence appeared to be highest when these larvae were present. The presence of L2 and L3 larval stages was observed in maize cropping systems intercropped with soybean and peanuts, while maize in monoculture and intercropped with cassava and beans was colonized by L4, L5 and L6 larvae. This study highlights the dynamics of FAW in relation to the existence of multiple planting dates. It provides a basis for developing climate-smart integrated pest management in South Kivu.

Keywords: fall armyworm, planting time, infestation, maize, pest management.

Introduction

Since 2016, Africa has been invaded by the fall armyworm (FAW), *Spodoptera frugiperda* (J. E. Smith, 1797) (Goergen et al., 2016). This species from tropical and subtropical America (Early et al., 2018; De Groote et al., 2020) is a highly mobile insect pest with a wide range of host plants (Montezano et al., 2018; Cokola et al., 2023a), preferentially cereals including maize crop (Harrison et al., 2019). Currently, only the European continent has not yet undergone an invasion of the FAW (Early et al., 2018). FAW is a prolific species that does not undergo a diapause (Luginbill, 1928; Sparks, 1979) and whose adult moths can migrate from one region to another when conditions are no longer optimal (Westbrook et al., 2019; Maino et al., 2021). Because of its polyphagous feeding behavior, FAW can maintain its population throughout the year by infesting other crops (Montezano et al., 2018; Cokola et al., 2021b). In the Americas, approximately 353 species have been identified as alternate hosts of FAW based on the literature compiled by Montezano et al. (2018). On the African continent, sorghum, cabbage, Napier grass and onion have been officially reported as alternative hosts (Cokola et al., 2021b; Cokola et al., 2023b) while in Asia, sugarcane and ginger was recorded (Srikanth et al., 2018; Shankar and Adachi, 2019).

The fall armyworm is known to have the ability to cause huge infestations up to 100% in maize plantations (Hruska and Gould, 1997). Considering the phenological stages of maize, FAW attacks start once the first leaves unfold, precisely at early whorls (VE to V6 stages) and the infestation is intense at the vegetative growth stage, usually at the late whorl (stages V7, V8 to VT) (McGrath et al., 2018). Day et al. (2017) estimated losses caused by FAW in the range of 8.3 to 20.6 million tons of maize each year in the absence of effective control methods in Africa. For the case of the DRC, losses may be as high as 633,000 tons/year (Day et al., 2017). Recent studies in Africa by Eschen et al. (2021) report average losses caused by FAW on maize crops in monetary value of 9.4 billion USD. According to Overton et al. (2021), there is a positive relationship between the density/infestation rate of FAW and yield reduction in maize while Harrison et al. (2022) found the opposite. Due to the extent of damage on maize leaves, most farmers in Sub-Saharan Africa use synthetic chemicals (Kansiime et al., 2019; Cokola et al., 2023b). The use of insecticides to control FAW in maize crops is often considered ineffective due to incorrect application methods and the larvae's feeding behavior, which gives them a degree of resistance to certain active molecules (Van den Berg et al., 2021).

Sustainable management of FAW depends on knowledge of its bioecology rather than the use of synthetic insecticides (Harrison et al., 2019; Niassy et al., 2021). Sustainable management methods include agricultural practices grouped in an agroecological approach (Harrison et al., 2019); semiochemical based methods that combine the use of pheromones and cropping systems in a push-pull arrangement (Midega et al., 2018). In plant protection, manipulation of crop planting date is one of six categories of preventive actions against crop pests (Barfield and Stimac, 1980). For example, Slosser (1993) measured the influence of planting date on cotton pests and showed that early planting reduces damage caused by thrips, cotton aphids, and boll weevils in the northern Texas Plains. Planting time was tested by Mitchell (1978) to prevent insects damage on corn in Florida who showed that corn cobs in late planting, approximately two weeks after the ideal planting date, were severely damaged by earworm and FAW.

In the African context, the planting season depends on the effective rainfall (Asante et al., 2017). However, in several countries in sub-Saharan Africa, farmers do not know how to plant at the ideal time. Several factors may explain this, including climatic variability expressed in terms of rainfall, input availability, weeds and pests, labor, etc. (Bussmann et al., 2016). Alternatively, farmers may try to maximize crops with abundant rainfall during a cropping season by shifting planting times (Mugiyo et al., 2021), which gives pests the opportunity to become well established (Litsinger et al., 2007). Early planting means waiting for the effective onset of rains during the growing season to escape pest pressure (Mugiyo et al., 2021). This is when the plant benefits from the maximum amount of water and heat units. It grows rapidly and is more resistant to insect attack (Nyabanga et al., 2021). Niassy et al. (2021) found that FAW infestations are usually low during periods with high rainfall. A late planting date does not often mean that the crop will be exposed to pests as late planting is also a strategy to prevent the recurrence of certain pests that could affect the crop at the beginning of the season (Slosser, 1993). Rodríguez-del-Bosque et al. (2010) found that FAW damage to maize cobs was highest in early planting, then decreased in mid-planting and increased further in late planting.

Since the invasion of the FAW in Africa, few studies have been conducted (Nyabanga et al., 2021) to assess the effect of planting date on the incidence of the pest. The studies by Nyabanga et al. (2021) demonstrate that early planting reduces FAW infestations in maize crop in Zimbabwe, but Baudron et al. (2019) did not find any effect of planting date on FAW infestations to maize in a farming survey in the same country. According to Baudron et al. (2019), further research is needed to determine the effect of planting date on FAW outbreaks, which could be a cost-effective method of controlling the pest in African farmer context. Planting at the ideal moment is currently a challenge for most farmers in eastern Democratic Republic of Congo (DRC). The objective of this study is to evaluate the existence of multiple planting dates on the infestation of FAW under the conditions of smallholder maize farmers of South Kivu in eastern DRC.

Materials and Methods

Study sites

The study was conducted in Kabare territory in eastern DRC, located in the South Kivu province. This territory has an area of approximately 1.690 km^2 and its population, spread over two chiefdoms, Kabare and Nindja, is estimated at 535.114 inhabitants, with a density of 288 inhabitants per km^2 (Chuma et al., 2021). The altitude is between 1000 and 3250 m above sea level. The average annual precipitation and temperature are 1601 ± 154 mm and 19.67 ± 2.3°C respectively. Three sites were considered for investigation in this territory: Miti-Murhesa, Katana and Mudaka. These sites were selected based on their accessibility and are part of the corridor potentially suitable for FAW in South Kivu (Cokola et al., 2020).

Fields monitoring

Field monitoring was conducted in farmer fields of Kabare territory in March 2020 with a focus on the planting date and the degree of FAW infestation in the above-mentioned sites. It should be noted that two cropping seasons exist in South Kivu each year: early season, which starts from September to January, and late season, from February to June. Based on information collected on the planting period and observations of farmers' fields infested by the FAW during this period (March-May 2020), a study was carried out during the crop seasons from September to October 2020 and from February to March 2021.

Based on the differences in maize development stages from field to field and observations of the level of FAW infestation in the study area during the field monitoring period from March to May 2020, five planting dates separated by approximately two weeks were considered for each season. To identify the fields according to the planting dates, the transect method (Eberhardt, 1978) was used in each selected site to track the fields. After identifying the first sowing date for each season (01 September and 01 February), the remaining dates were identified each after approximately 2 weeks depending on the period considered. The geographical coordinates of the various fields were registered using a Global Positioning System (GPSMAP® 64s, GARMIN, United States) and allowed for the recognition of the fields during data collection of FAW infestation parameters. The dates of September 1, September 15, October 1, October 15 and October 30, 2020, were considered for early season, while the dates of February 1, February 15, March 1, March 15 and March 30, 2021, were selected for late season. In South Kivu, the ideal planting date for early season is September 15 and February 15 late season. We qualified the date of September 1, September 15, October 1, February 1, February 15 and March 1 as early planting and October 15, October 30, March 15 and March 30 as late planting.

Information on field characteristics was collected during field identification and survey and including field type (farmer or exploitation, farm), cropping system (monoculture or intercropping), variety of planted maize, fertilization plan, and the surface area of each field (in square meters). Most of the fields planted after October 15 and March 15 were found in water-logged soils (usually marshlands). For early season, 45 fields were surveyed and distributed among the five planting dates with nine fields for each planting date. For late season, 45 new fields were selected based on the planting dates considered in that period. Overall, 90 fields were surveyed for the entire study period. The field allocation by planting date, site and season is presented in Appendixes Table 5.

Assessment of fall armyworm infestation parameters

Three important parameters for assessing FAW infestation in the maize crop were considered: the percentage of plants infested by FAW, the damage severity determined using a Davis rating scale (Appendixes Table 2) updated by Toepfer et al. (2021) and the larval density obtained by counting larvae. To complete the three parameters, the type of FAW larval stage was determined in each field according to the planting dates. All the parameters were surveyed in each field when maize was at the V8 growth stage (8 leaves fully emerged) using the absolute (quadrat) count method (Cokola et al., 2021a). The incidence and severity of FAW are high at the vegetative growth stage, which justifies the choice of the V8 stage for investigations. The stage corresponds to the 30th and 28th day after sowing for the early and late seasons respectively.

To determine the larval stage of FAW, 50 larvae were randomly collected from maize plants in each field surveyed following Wyckhuys and O'Neil (2006) methods. Larvae were kept in rearing boxes (25cm × 17cm × 10cm) at a rate of 25 larvae per box and were fed with fresh maize leaves to avoid cannibalism in a rearing room of the Faculty of Agriculture and Environmental Sciences of the Université Evangélique en Afrique (UEA/Bukavu). Larvae from each field were soaked in 70% ethanol solution for approximately one minute on the same day of collection (3 hours after field investigation). The size of the larva in length was measured using a millimeter paper. A SOLOMARK stereomicroscope - Science Lab 3D with an ocular micrometer was used to confirm insect identification and determine the width of the head capsule. The head capsule width and larval size (in length) values were compared to existing literature values (Luginbill, 1928; Capinera, 2001) to determine the identity of the larval stages collected in each field.

Statistical analysis

All the statistical analysis was performed on R version 4.1.3 (R core Team, 2021). The percentage of infested plants, the severity of the damages and the number of larvae were tested to compare the early and late planting group by student t-test for each planting season. These variables of both seasons are significantly and positively correlated with a correlation coefficient > 0.85 (p-value < 0.05). Therefore, the number of larvae as function of the independent explicative variables (i.e., fixed effects) was arbitrarily selected: the maize planting date (numerically converted in number of Julian day), the type of field, the parcel surface (m^2), the cropping system, the maize cultivar and the type of fertilizer. Given the unbalanced data gathering and the presence of pseudo-replication, generalized linear mixed-effects models (GLMMs) were performed using *lme4* R package (Harrison et al., 2018). The sampling sites were considered as factor effects (1|Sites). As counting data, Poisson distribution was selected to explain the distribution error. For the model selection, the second order Akaike Information Criterion (AICc) was assessed to classify the relative support given by the data to each model.

Redundancy analysis (RDA) was performed to assess (after removing colinear variable) the influence of latitude, maize planting date, incidence, type of field, parcel surface (m^2), cropping system, maize cultivar, and type of fertilizer on the larval stage composition from L1 to L6. All the explicative variables were previously standardized with *decostand* function from *vegan* R package (Oksanen et al., 2022). The Hellinger's transformation was applied on the larval stage composition because it contains many zeros (Legendre and Gallagher, 2001). The model using *ordistep* function (Oksanen et al., 2022) (automatic stepwise model) was simplified by performing forward selection with 1000 permutations to select variables that are statistically important. Then, analysis of variance (ANOVA) was performed to analyze the significance of our RDA on the model and each selected variable of the model with 1000 permutations. All the graphics were generated with ggplot2 R package (Wickham, 2016).

Results

Fall armyworm infestation varies with the planting period in South Kivu

In general, the number of larvae was great during the later planting dates in both season (October 15th, October 30th, March 15th and March 30th), and decreased at earlier planting dates (September 01st, September 15th, October 01st, February 01st, February 15th and March 01st) as shown in Figure 15. In the context of early season, the mean number of larvae reached 30.44 ± 6.90 in the late planting group against 17.78 ± 7.01 in the early planting group ($t_{Welch} = -6.38$, df = 40.55, p-value < 0.001). A similar trend was observed in late season, where late planting resulted in a higher larval population (33.27 ± 6.90) compared to early planting (19.00 ± 7.01) ($t_{Welch} = -6.75$, df = 37.01, p-value < 0.001).

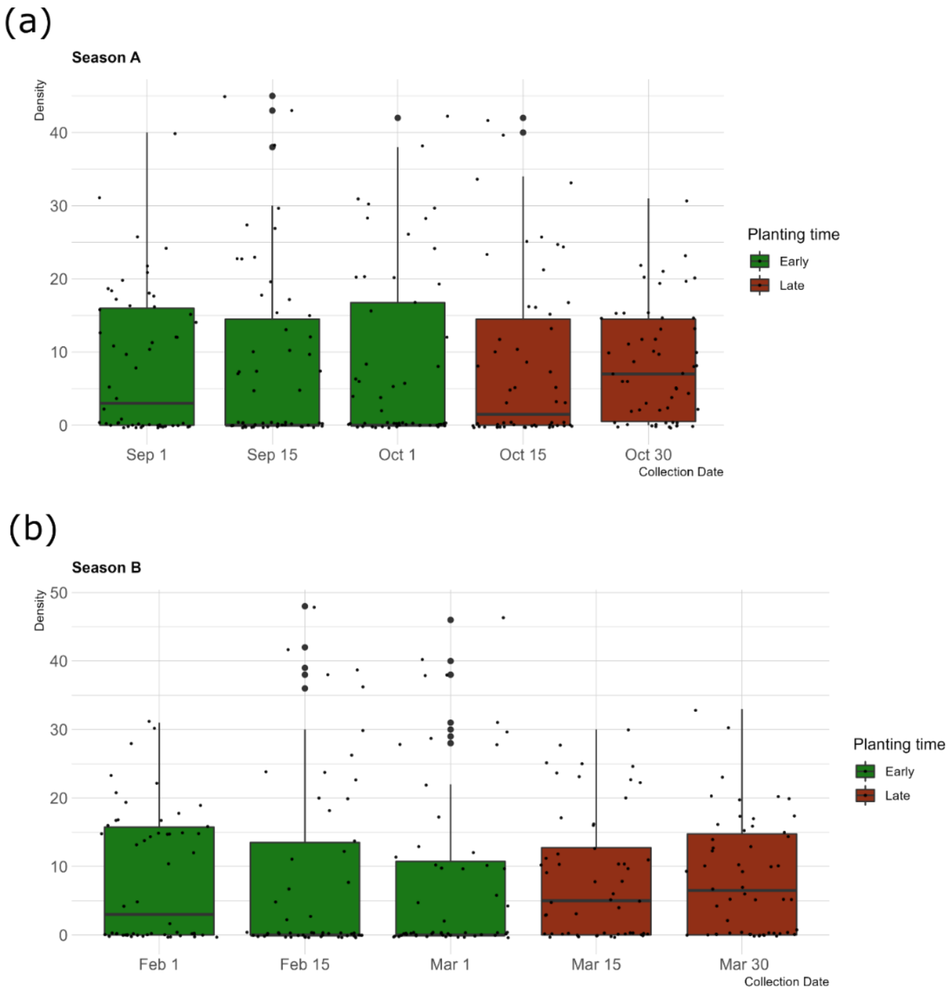


Figure 15. Variation in larval density of *Spodoptera frugiperda* measured as the number of larvae per quadrat at different planting dates. (**a**)**:** number of larvae for early season; (**b**)**:** number of larvae for late season.

The incidence, which represents the proportion of plants with leaf damage by FAW, varied significantly based on the planting period in both early season and late season (Figure 16). The incidence reached its highest mean values in both seasons when planting was delayed, with rates of 57.89 ± 12.23% for early season (t_{Welch} = -10.55, df = 25.34, p-value < 0.001) and 62.58 ± 8.41% for late season (t_{Welch} = -14.54, df = 29.24, p-value < 0.001), as compared to early planting (23.79 ± 7.44% for early season and 28.86 ± 6.25% for late season). This indicates an approximate 35% mean difference in incidence between late and early planting. In early Season, the mean damage score for late planting was 6.94 ± 0.99, whereas for early planting, it averaged at 4.37 ± 0.88 (t_{Welch} = -8.87, df = 33.43, p-value < 0.001). Likewise, during late Season, a similar statistical pattern was observed, with mean values of 7.44 ± 0.78 for late planting and 5.19 ± 1.11 for early planting (t_{Welch} = -7.99, df = 42.81, p-value < 0.001). On the Davis scale, a damage score of 7 indicates the presence of numerous elongated lesions of varying sizes on multiple whorl and furl leaves accompanied by several large holes with uniform to irregular shapes resulting from FAW feeding. Conversely, scores 4 and 5, denoting the severity of FAW attack in early planting, indicate the presence of several small to mid-sized elongated lesions on a limited number of whorl and furl leaves.

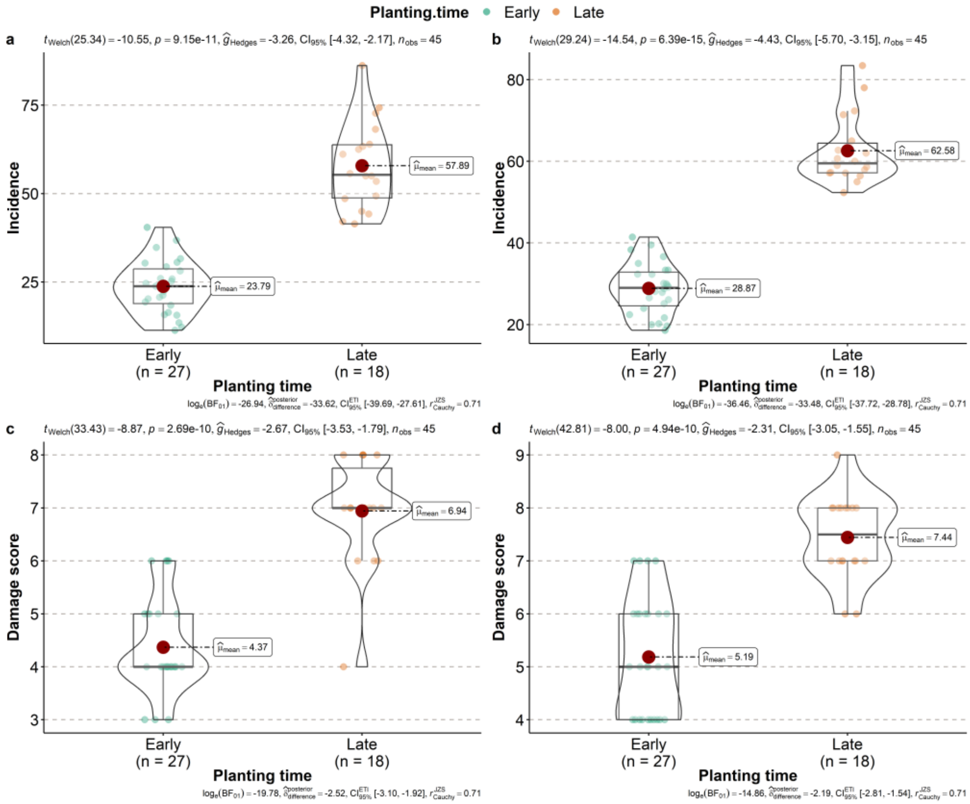


Figure 16. Violin plot of incidence and severity per quadrat of *Spodoptera frugiperda* in relation to planting time. Overall statistical test with p-value and effect size with confidence intervals are shown on each plot. **a-b** represents the incidence for early season and late season respectively; **c-d** represents the severity for early season and late season respectively.

Population variation of *Spodoptera frugiperda* larvae

In both seasons, a total of five models were constructed, as detailed in Appendixes Tables 6 and 7. Using the Akaike Information Criterion corrected for small sample size (AICc) as a selection criterion, the Julian calendar model, presented as model 5 in Table 7, emerged as the most appropriate explanatory variable for elucidating the effect of planting period on larval density during the early season. In contrast, for the late season, the model 1 with all the explicative variables (also detailed in Table 7) was retained as the optimal model. Furthermore, it is noteworthy that, in the context of late season, the classification of planting periods, distinguishing between late and early planting, had a substantial and consistent influence on larval density across all study sites.

Table 7. Summary of the results of the Generalized linear mixed models (GLMMs) fitted by maximum likelihood (Laplace approximation) for explaining the variability of the larval density of FAW with planting time.

Fixed effects	**Early season**				
	Estimate	**Std. Error**	**Z value**	**P value**	**AICc**
Intercept	-1.21	0.43	-2.76	**0.005**	282.00
Julian calendar	0.01	0.00	10.04	**< 0.001**	
	Late season				
Intercept	3.38	0.46	7.22	**< 0.001**	335.50
Type of field (Exploitation)	-0.27	0.33	-0.81	0.416	
Type of field (Farmer)	-0.54	0.33	-1.62	0.105	
Surface (m^2)	-0.04	0.06	-0.68	0.4913	
Planting time (Late)	0.56	0.14	3.76	**< 0.001**	
Maize variety (M'Roma)	0.00	0.12	0.03	0.971	
Maize variety (SAM4 Vita)	0.13	0.19	0.69	0.484	
Maize variety (Z-M)	-0.01	0.08	-0.18	0.855	
Fertilizers (None)	-0.06	0.16	-0.40	0.686	
Fertilizers (NPK)	-0.27	0.16	-1.73	0.082	
Fertilizers (NPK+Manure)	-0.40	0.23	-1.70	0.088	
Fertilizers (Urea+Manure)	-0.32	0.41	-0.78	0.434	
Julian calendar	0.00	0.00	0.18	0.855	

Larval density exhibits significant variation with planting period (Figure 17). Late planting is consistently correlated with increased larval density, indicating a robust association between late planting and increased FAW infestation, regardless of season. This association is statistically supported in both early season ($R^2 = 0.670$, p-value < 0.001) and late season ($R^2 = 0.375$, p-value < 0.001).

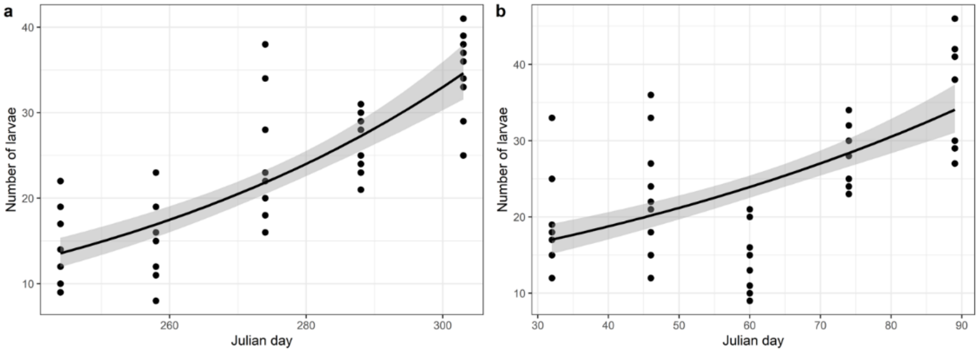


Figure 17. Poisson prediction model of larval density per quadrat with planting time. Trend lines indicate model predictions, while dots represent observations. The grey area indicates the confidence interval set for the model at 95% level. **a** and **b** represent larval density prediction model for early season and late season respectively.

Various larval stages in relation to planting time

Statistical differences were observed in density of each larval stages depending on the planting period as shown in Figure 18. In early season, five larval stages were found in the same field at the V8 growth stage of maize. Only the L1 FAW larval stage was missing in the batch of collected larvae. In late season, all larval stages were present in the same field. The tendency of results shows that later planting period has the highest density of each larval stage compared to early planting period. Considering the L1 larval stage, the density was recorded at late planting compared to early planting for late season ($t = -4.20$; $df = 43$; p-value < 0.001). In the case of L2 larval stage, the density was high for late planting compared to early planting at early season ($t = -5.29$, $df = 43$; p-value < 0.001) and late season ($t = -3.73$, $df = 43$; p-value < 0.001). Furthermore, for the L4 larval stages, the density was high for late planting compared to early planting at late season ($t = -3.44$, $df = 43$, p-value < 0.01). No significant difference between early and late planting was observed for L3, L5, L6 at both seasons and L4 at early season. These results indicate that, in addition to density, the presence of FAW is related to the category of larval stages found in the same field, regardless of the planting period. Consequently, the species is more frequent throughout the growing season.

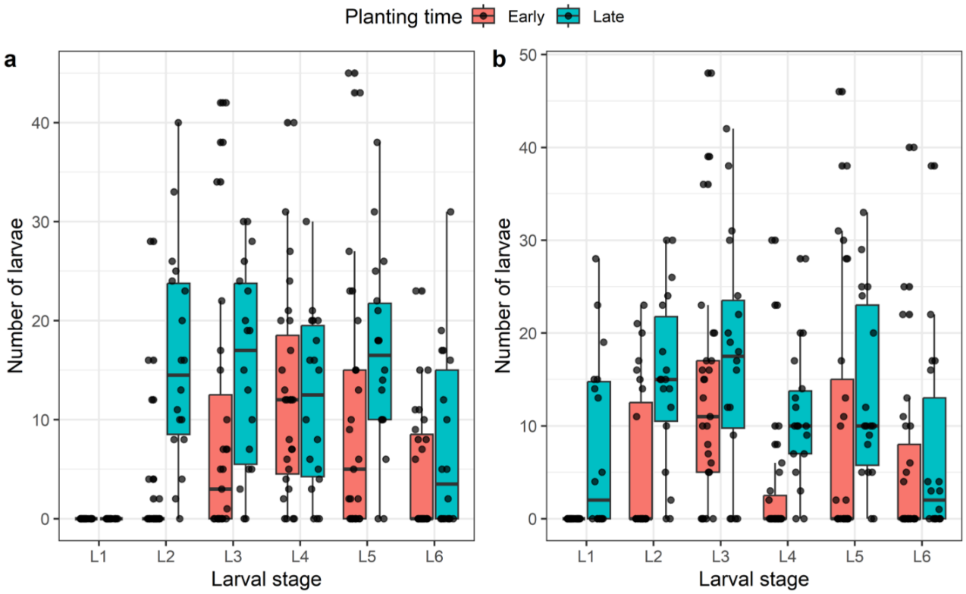


Figure 18. Differences in larval density expressed as the number of individuals of each larval stage of *Spodoptera frugiperda* in relation to the planting time. **a** and **b** represent larval stage density for early season and late season respectively.

The summary results of the RDA analysis of variance (Table 8) show the variables that had the most significant influence on the composition of larval stage of FAW in both seasons.

Table 8. Output analysis of variance (ANOVA) explaining the redundancy analysis (RDA) of *Spodoptera frugiperda* larval stage composition for early and late seasons.

Early season					**Late season**				
Variables	**df**	**Variance**	**F**	**P value**	**Variables**	**df**	**Variance**	**F**	**P value**
Type of field	2	0.22	1.62	0.149	Type of field	2	0.09	0.7	0.631
Cropping system	4	0.89	3.23	0.000 ***	Cropping system	3	0.11	0.54	0.833
Maize variety	3	0.19	0.93	0.475	Maize variety	3	0.40	1.91	0.064
Fertilizers	5	0.33	0.97	0.500	Fertilizers	4	0.14	0.51	0.943
Julian calendar	1	0.41	6.03	0.002 **	Julian calendar	1	2.02	28.46	0.000 ***
Incidence	1	0.07	1.12	0.312	Incidence	1	0.94	13.21	0.000 ***
Latitude	1	0.26	3.78	0.025 *	Longitude	1	0.05	0.75	0.499
Surface (m^2)	1	0.04	0.67	0.607	Latitude	1	0.05	0.71	0.529
Residual	26	1.79			Surface (m^2)	1	0.06	0.94	0.408
					Residual	27	1.92		

The projection fields of the three sites considered in this study on the main planes formed by RDA1 and RDA2 do not show any differences between the sites in the two seasons (Figure 19). In early season, three variables including cropping system, planting date (numerically expressed as Julian calendar) and latitude influenced the larval stage at the three sites considered. High densities of L2 and L3 larvae are much more associated with late planting in early season. Considering the cropping system, maize monoculture, maize intercropping with cassava and maize intercropping with bean systems had a significantly greater influence on the presence of FAW L4, L5 and L6 larvae, whereas maize intercropping with groundnut and maize intercropping with soybean systems seemed to influence FAW L2 and L3 larvae. L1 larvae of FAW were found in all cropping systems. In late season, two variables had an influence on the larval stage composition of FAW. These were the planting date and incidence. High densities of L4, L5 and L6 larvae are much more associated with late planting. The highest incidence occurs when L4, L5 and L6 larvae are present, typically associated with late planting, whereas the incidence is low when L1, L2, L3 larvae are found in early sown fields.

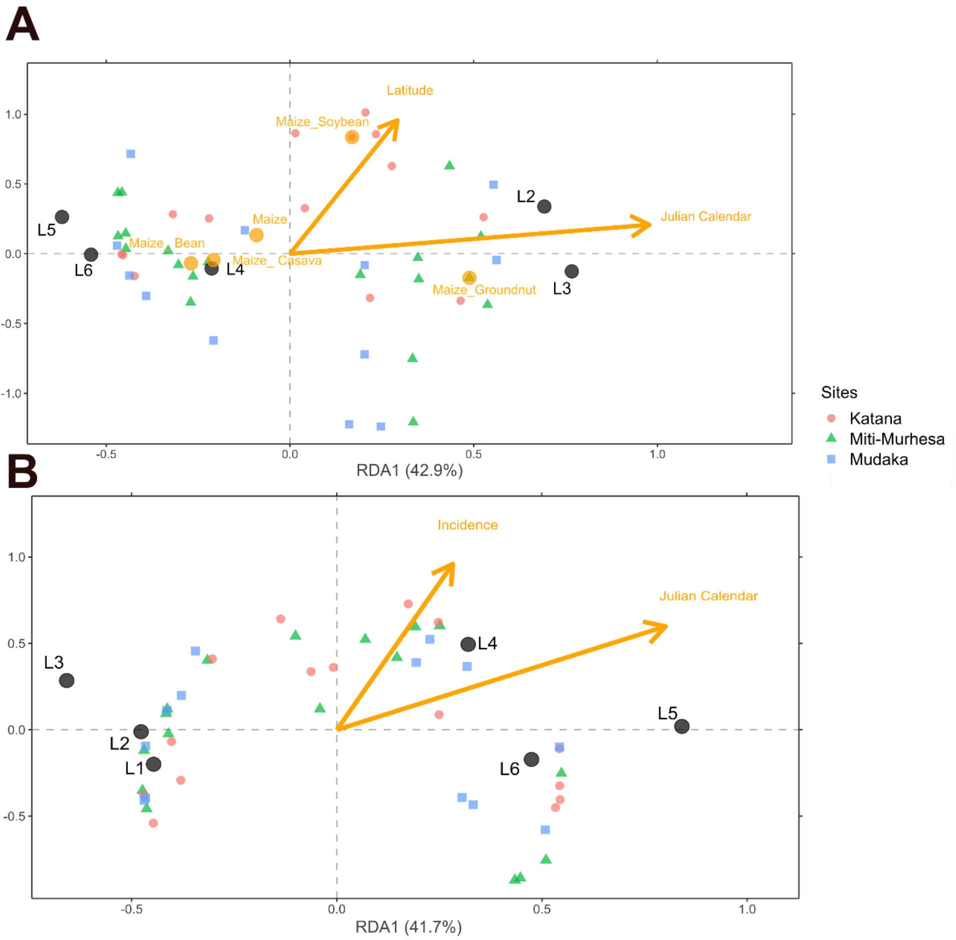


Figure 19. Redundancy analysis triplot of larval stage composition for early season (A) and late season (B)**.** Sites scores are grouped by collection sites: red dot for Katana; green triangle for Miti-Murhesa; blue square for Mudaka. Black dots represent the larval stage of *Spodoptera frugiperda*. Orange solid line vectors represent significant quantitative environmental variables. Orange dots represent significant centroid of qualitative environmental variable only for early season.

Discussion

The fall armyworm is already well established in eastern DRC (Cokola et al., 2020). Its damage to maize crops varies according to season and agroecological zones (Nboyine et al., 2020; Cokola et al., 2021a). In general, considering the phenological stages of maize, FAW attacks start once the first leaves unfold, precisely at early whorls (McGrath et al., 2018) depending on the planting period. Results from this study show that late-sown fields were much more severely infested by FAW than early sown fields. The populations of pests in the early or late-sown fields resulted from a temporal separation of pest and crop (Boiteau, 1984). Incidence and severity had the highest mean values in both seasons when planting was delayed compared to early planting. The mean difference in incidence between late and early planting is approximately 35%. Results from Nyabanga et al. (2021) showed that planting date had a significant effect on both FAW incidence and severity, with higher values for late planting. In contrast, Baudron et al. (2019) found no effect of planting date on FAW infestation. However, both authors conducted their research in the same country. FAW incidence may vary between agroecological zones, depending on the seasonal cropping systems in each zone (Kansiime et al., 2023). In the absence of a continuous supply of host plants to attack, FAW may be present in some areas at different times (Niassy et al., 2021).

In this study, FAW larval density was higher in late than in early plantations. According to Nyabanga et al. (2021), early planted crops escape pest pressure because the phenology of the crop does not coincide with the period of pest abundance. Hruska and Gould's (1997) results showed that early maize growth stages are more tolerant to lepidopteran attack than later stages. It is known that maize yield is not always affected when FAW infestation occurs at the vegetative growth stage (Chisonga et al., 2023), as the plant is able to compensate for damage when in optimal soil and climatic conditions (Harrison et al., 2019; Van den berg et al., 2021). In general, early planting is linked to effective rainfall. In South Kivu, FAW infestation is less severe during the early season, a season characterized mainly by heavy rainfall and low temperatures, conditions that are unfavorable for FAW (Cokola et al., 2021a). According to Niassy et al. (2021), rainfall affects the dynamics of FAW, but the impact of this parameter on FAW populations in Africa has not been fully investigated. Nboyine et al. (2020) found a correlation between rainfall and FAW moth capture, suggesting that rainfall and relative humidity contribute positively to moth abundance. Furthermore, early planting after optimal rainfall allows the maize crop to be in optimal conditions by efficiently using water and heat units early in the growing season (Harrison et al., 2019; Mugiyo et al., 2021). In a study by Rodríguez-del-Bosque et al. (2010), FAW damage was highest at the earliest planting dates, decreased at intermediate dates and increased at the latest dates. Considering that the FAW is a polyphagous species with multiple generations that can be observed from 4 to 6 per year, depending on optimal climatic conditions expressed in degree-days (Luginbill, 1928; Hardke et al., 2015), it is obvious that late plantations will have more attacks during the seasons. In Africa, studies show that the number of generations varies according to the seasons and climatic conditions throughout the year (Niassy et al., 2021), compared to conditions in the Americas, where the species migrates when conditions are no longer optimal (Westbrook et al., 2019). Late planting is not always disadvantageous for the crop in terms of pests, as Slosser (1993) found that delaying planting predicted the infestation of certain pests, in this case boll weevil, and did not systematically increase the pest problem.

Looking at the developmental cycle of FAW, the presence of larvae, regardless of stage, should be uniform in the same field, with small variations depending on the feeding ability of each larva (Hardke et al., 2015). However, in some situations there may be differences in size due to delayed oviposition and female longevity (Luginbill, 1928; Capinera, 2001). According to the results of this study, five larval stages of FAW were found in the same maize field in the early season and all larval stages in the late season at V8 maize stage, regardless of the planting period. This situation is surprising because under normal conditions, the first generation of FAW that emerges at the V3 stage can complete its development from early larval stages (L1) to adult, mate and re-infest the maize crop at the reproductive stage during the same cropping season (McGrath et al., 2018). This is generally the case in eastern Congo, where temperatures easily reach 25°C, ideal for the development of FAW (Cokola et al. (2021a). In many regions where FAW is already endemic, multiple overlapping generations can be observed on the same maize plant (McGrath et al., 2018), demonstrating the potential for continuous infestation throughout the growing season. Behaviorally, when population densities of FAW in a field are high, females lay eggs indiscriminately on all maize plants (Sparks, 1979). At this point, differences in larval size can be observed. The indiscriminate egg-laying behavior observed in females may be due to their desire to give the larvae at least some chance of development, given their highly adaptable, almost omnivorous nature (Luginbill, 1928). This behavior may allow the larvae to eventually find a suitable host plant for further growth. In this study, we did not trap FAW moths to understand the results related to the presence of different larval stages in the same field. However, studies by Nboyine et al. (2020) show that there is a positive correlation between the trapping of adults and the abundance of larvae.

The trend in the results shows that the late planting period has the highest density of each larval stage compared to the early planting period. The L1 stage was not found in the batch of FAW larvae in early season and only in late season when sowing was late. As the sampling was random, the probability of not finding a stage was not negligible, especially if the larva is small. The L1 larval stage of FAW is small and difficult to find in the whorled leaves of maize (McGrath et al., 2018).

High densities of L2 and L3 larvae are much more associated with late planting in early season, while high densities of L4, L5 and L6 larva, more voracious (Luginbill, 1928; Hardke et al., 2015), are much more associated with late planting in late season. The presence of these larval stages in large numbers during the late season explains why late planting during this period is dangerous, not only in the Kabare area where the study was conducted, but also throughout the Great Lakes sub-region (Cokola et al., 2021a). The results of this study show that the incidence is highest when L4, L5 and L6 larvae are present at the V8 stage, often associated with late planting, and decreases when L1, L2, L3 larvae are present in early sown fields. This contradicts the results of Cokola et al. (2021a), who found that the presence of young larvae, generally L1, L2 and L3, cause numerous lesions resulting in high incidence.

The maize monoculture, maize-cassava intercropping and maize-bean intercropping systems had a significantly greater influence on the presence of FAW L4, L5 and L6 larvae, whereas the maize-groundnut and maize-soybean intercropping systems appeared to have an influence on FAW L2 and L3 juvenile larvae. Understanding the relationship between cropping systems and pests is crucial for sustainable agricultural production. Crop diversification influence pest dynamics in general (Smith and McSorley, 2000) and FAW specifically (Harrison et al., 2019; Midega et al., 2018). Maize-legume intercropping has been studied as an alternative FAW management method in two different models. The first model is a conventional maize-legume system (soybean, bean, groundnut, ...) (Udayakumar et al., 2021; Hailu et al., 2021) and the second is a push-pull system (Khan et al., 2010; Midega et al., 2018). Maize-legume intercropping improves soil health while promoting plant vigor, especially through nitrogen fixation, which improves local atmospheric conditions at the plot level (Fu et al., 2023). In addition, intercropping limits larval movement between plants and prevents females from laying eggs on maize by emitting semiochemicals (Smith and McSorley, 2000; Khan et al., 2010). The abundance, diversity and activity of natural enemy arthropods also increase in this system, helping to reduce pest populations (Smith and McSorley, 2000; Harrison et al., 2019). In a study by Udayakumar et al. (2021), maize intercropping with faba bean, *Desmodium sp.* and groundnut recorded significantly higher rates of egg parasitism and FAW predation. The young larval stages (L1, L2, L3) found in intercropping systems in this study are the ones most likely to be parasitized by insects, according to Durocher-Granger et al. (2021) results, which explains the low incidence associated with their presence in maize intercropped with soybean and groundnut. Considering the push-pull system, results from Sobhy et al. (2022)

showed that companion crop volatiles repel FAW while attracting its natural enemy parasitoids, explaining why the system has fewer larvae and lower infestations than monoculture maize.

Conclusions

Management of FAW requires knowledge of its bioecology. In situations where farmers are unable to recognize the level of threat posed by a pest such as FAW, agricultural production - particularly maize, the main staple food in sub-Saharan Africa - will always be affected. The results show that early plantings have lower levels of FAW infestation than late plantings in all seasons. The density of larvae in late planting, coupled with the presence of all larval stages in each maize growing season in the same field, demonstrates the threat posed by FAW to maize production in South Kivu. The moths occur frequently throughout the growing season and at all phenological stages of maize, with overlapping generations. Under normal conditions, their presence may only be reported twice during maize V4 and flowering development (i.e. two generations in one season). This complicates pest management for smallholder farmers, who sometimes must apply large quantities of pesticides at frequent intervals. The planting season has an impact on the sustainable management of this pest, which is increasingly complicated by the existence of several planting dates in a season. In addition, the presence of maize crops during the dry season in the marshlands, as was the case in this study, further complicates the situation. Knowing the ideal planting time in South Kivu is challenging because there are practically no weather stations or forecasting systems that can establish a direct relation between FAW infestation rates and climatic variables such as rainfall and temperature. The existence of weather stations and forecasting systems would enable farmers to choose the ideal planting time to effectively manage FAW and maximize maize production in the region.

Chapter 3

Insights on fall armyworm knowledge and management strategies from smallholder farmers

Photo by Marcellin C. Cokola

Chapter 3. Insights on fall armyworm knowledge and management strategies from smallholder farmers

This chapter was adapted from original published article: **Cokola, M.C.,** Van Den Bussche, R., Noël, G., Kouanda, N., Sèye, F., Yarou, B.B., Caparros Megido, R., Bayendi Loudit, S.M., Lonpi Tipi, E., Michel, B., Francis, F., 2023. Managing fall armyworm *Spodoptera frugiperda* (Lepidoptera: Noctuidae): experience from smallholder farmers in central and western Africa. Food and energy security 12, e491. https://doi.org/10.1002/fes3.491.

Abstract

The fall armyworm *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae) is currently an important pest of maize crops worldwide not only because of its dispersal ability but also because of its polyphagous feeding behavior. Lack of sufficient information on the management of the fall armyworm attacks remains a crucial problem for maize smallholder farmers in Africa. In this study, 420 farmers were surveyed in central and west Africa using individual interviews to assess farmers' knowledges and perceptions of the fall armyworm damages and the management practices used. Most farmers (99.4%) were shown to recognize the fall armyworm and 92.5% claimed to already have damages in their fields. The fall armyworm seems not to be a new pest as most farmers identified it in different countries from 2015 to 2019. Apart from maize as the preferred crop of *S. frugiperda*, several alternative host plants including Napier grass, sorghum, onion, and cabbage were identified by the farmers. Although cultural and mechanical control methods are used by several farmers, the synthetic pesticide market is still preferred by almost half of the farmers (44.28%) who still use them. To control fall armyworm, 96.4% in Burkina Faso, 85.3% in Gabon, 65.2% in Benin and 25% in Democratic Republic of Congo (DRC) reported using insecticides, against 5.9% in Senegal. Semiochemical-based method and biological control by promoting natural enemies of the fall armyworm are new concepts for farmers in DRC, Gabon and Benin. To avoid additional problems regarding health and resilience of agricultural systems, alternative methods such as push-pull approach, the development of biopesticides and resistant cultivars should form the basis of training given to farmers and should be popularized for sustainable control of the fall armyworm in central and west Africa.

Keywords: fall armyworm, maize, pest management, farmer's perception, pesticide.

Introduction

The fall armyworm (FAW), *Spodoptera frugiperda* (J. E. Smith), is a lepidopteran species in the Noctuidae family native to tropical and subtropical America (Early et al., 2018; Cokola et al., 2020). Since its arrival in West and Central Africa in early 2016 (Goergen et al., 2016), this pest has spread rapidly throughout sub-Saharan Africa (SSA) and is causing significant damages to a wide range of crop plants (Baudron et al., 2019). In almost 4 years, this devastating pest has invaded 3 continents, starting in Africa and extending to Oceania (CABI, 2021). With a preference for Poaceae, this caterpillar pest mainly attacks maize (Rwomushana et al., 2018; Cokola et al., 2021a). Nevertheless, in its native region, it can establish more than 350 plant species, of which 80 are commonly cultivated plants such as maize, sorghum, rice, or cotton (Montezano et al., 2018). Because of this polyphagous nature, FAW can establish and adapt well in a newly invaded area by attacking other crops, usually vegetable crops (Cokola et al., 2021b). Its rapid spread across the African continent is causing significant yield losses to maize crops for tens of millions of smallholder farmers who depend on this crop for their food security (Day et al., 2017). Estimates report annual yield losses to agriculture in Africa, especially maize, in monetary values of 9.4 billion USD (Eschen et al., 2021). Considering the rate of infestation, analyses by Tambo et al. (2021) indicate that households that reported severe FAW infestations experienced a significant 44% decline in income per capita.

Given the level of infestation, the presence of the FAW in Africa is irreversible, and therefore, the smallholder farmers must learn how to manage this insect pest (Hruska, 2019). In response to this threat, one of the first reactions of farmers is the use of neurotoxic insecticides that are often not efficient and pose environmental hazard (Togola et al., 2018). The increased incidence of FAW has potentially intensified smallholder reliance on pesticides (Kansiime et al., 2019). In the purely African context, there is no registered synthetic insecticide for FAW control, except for emergency label-authorized applications, suggesting an urgent need for synthetic insecticide screening (Sisay et al., 2019b). To help farmers find sustainable solutions to limit the damage caused by this caterpillar, non-governmental organizations (NGOs) and producers' associations are implementing training through schemes such as demonstration fields or farmer field schools that allow farmers to share their experiences to control this pest (Prasanna et al., 2018; FAO, 2018).

Since its invasion in all tropical and subtropical regions of the world, the FAW has attracted increasing research interest to find sustainable management options through agroecological practices and the use of biopesticides (Midega et al., 2018; Bateman et al., 2018; Harrison et al., 2019). In the Americas, producers and researchers have long studied FAW and their experiences are being used to develop sustainable management options appropriate for large-scale farmer systems (Sparks, 1986; Meagher et al., 2022). For example, in the United States, Brazil and Argentina, FAW was commonly controlled by the application of effective pesticides and the use of genetically modified corn (Bt corn), which incorporated genes to produce lethal toxins against FAW (Hruska, 2019). Farming systems as well as agroecological and socio-economic conditions (such as farm size, yields, and access to institutional support services) did not allow African farmers to explore these options (Tambo et al., 2019). In the African context, training programs through village meetings, farmer field schools and communication campaigns have been launched to teach farmers basic concepts on the biology and ecology of this pest and to allow them to exchange experiences and techniques for its management (Rwomushana et al., 2018). Unfortunately, these meetings are limited only in some regions and no action has yet been taken in other parts of Africa.

In parallel, a number of literatures explore the control strategies used by farmers in some parts of Africa and their perception towards such management practices against FAW (Kumela et al., 2019; Hruska, 2019; Kansiime et al., 2019; Tambo et al., 2019, 2020a, 2020b, 2021, 2022; Chimweta et al, 2020; Houngbo et al., 2020; Kassie et al., 2020; Ansah et al., 2021; Caniço et al., 2021; Kasoma et al., 2021a; Ahissou et al., 2022). Although research has already been undertaken in Africa, information on indigenous practices is lacking in some African countries, especially in French-speaking countries, such as DRC, Gabon, Senegal, etc., yet farmers in these countries have been facing the FAW invasion since 2016 and indigenous knowledge, perceptions and management practices might be different depending on the situation in each country. Farmers in these countries undoubtedly have different farming practices in relation to soil and climate conditions. In addition, local data on FAW management methods used by farmers after the training programs remain poorly available. The objective of this study is to contribute to the data on farmers' local practices and their perception of the presence of FAW in 5 African countries: DRC, Gabon, Benin, Burkina Faso and Senegal. This study constitutes a source of information in the development of an integrated management strategy for FAW in Africa through the integration of indigenous methods of smallholder farmers.

Materials and Methods

Study area

The survey was conducted in two countries in Central Africa and three in West Africa. First, the study focused on Gabon and the DRC. In Gabon, interviewed farmers were primarily from the Estuary province near the township of Ntoum (0º22'46" N, 9º46'26" E). In DRC, surveys were conducted in two provinces. In the southwest, in Kongo Central Province around the Luki Biosphere Reserve, specifically in the townships of Lukula (5º37'19" S, 13º05'55" E), Muanda (5º38'22" S, 13º3'44" E) and Banza Seke (5º29'55" S, 13º17'28" E). In eastern DRC, farmers interviewed were from South Kivu province in three territories: Kabare (2º18'56" S, 28º47'40" E), Walungu (2º37'51" S, 28º45'41" E) and Uvira (2º50'55" S, 29º1'30" E). Secondly, in West Africa, the survey was conducted in three countries: Benin, Burkina Faso and Senegal. In Benin, the surveys were distributed in the provinces of Ouémé and Zou, specifically in the townships of Djidja (7º23'20" N, 2º4'31" E), Bonou (6º54'25" N, 2º27'19" E) and Adjohoun (6º43'15" N, 2º28'40" E). In Burkina Faso, the farmers surveyed came from two agro-climatic zones (Sudanian and Sahelian). The Sudano-Sahelian zone included the township of Bama in Houet province, the towns of Tiéfora (10º39'4" N, 4º38'42" W) and Banfora (10º40'33" N, 4º49'2" W) in Comoé province, and the township of Léo (11º11'36" N, 2º0'44" W) in Sissili province. In the Sudan-Sahelian zone, farmers were from the township of Sapouy (11º40'34" N, 1º39'13" W) located in Ziro province. In Senegal, the farmers who were interviewed were located in the Kaffrine region around the Boulel township (14º17'10" N, 15º32'7" W) and Saint Louis (15º55'9" N, 16º22'48" W). An overview map of the study area with a repartition of the respondents in the regions where the study was conducted is presented (Figure 20).

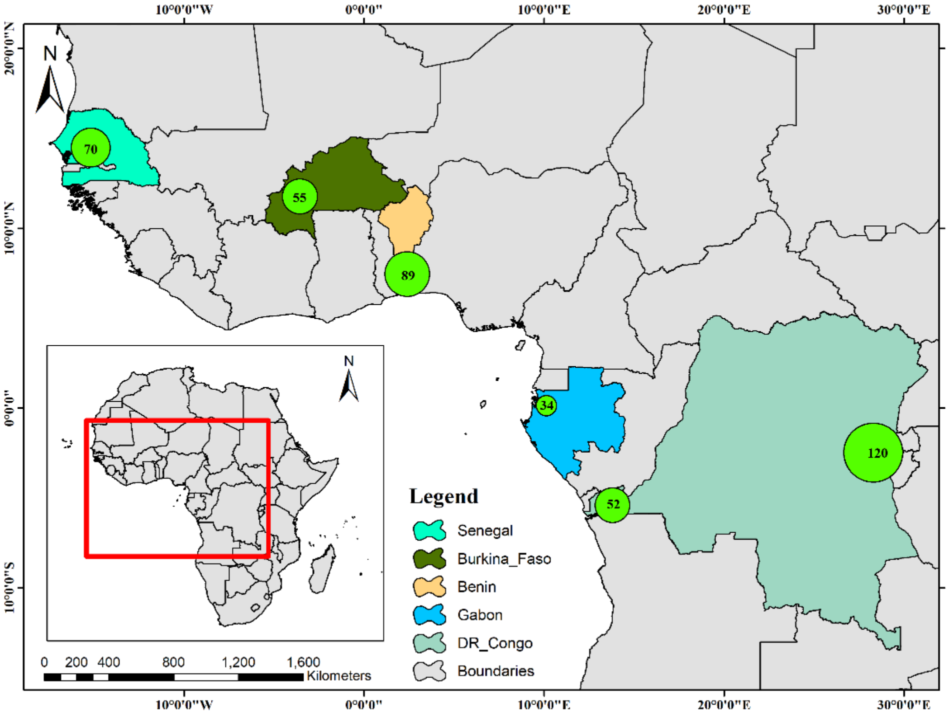


Figure 20. Map showing the study area with the countries and investigated zones in each country. The size of green circle corresponds to the number of survey respondent in the considered area. DR Congo is colored in pale blue, Gabon is colored in blue, Benin is colored in light orange, Burkina-Faso is colored in dark green and Senegal in turquoise. The map was generated by the author using ArcMap 10.8.1 (https://desktop.arcgis.com/en/arcmap/).

Survey design

The survey form was developed based on existing information and data sources on FAW in Africa (Rwomushana, 2018). This questionnaire was created to collect basic information about the respondent such as gender, age, education level, household characteristics, farm structure, farmers' knowledge and perception of FAW damage and management practices implemented. The questionnaire was sent in electronic format to the different partners involved in the study. To facilitate the survey, the questionnaire was encoded in the KoBoToolbox online data collection software (https://www.kobotoolbox.org/), and smartphones such as the Samsung Galaxy were used to conduct the survey, each time with the geographical coordinates of the locations and fields observed.

Data collection

In the survey phase, a questionnaire was administered to farmers face-to-face with interviewers. In total, 420 farmers were randomly selected and interviewed, of which 172 were in the Democratic Republic of Congo, 89 in Benin, 55 in Burkina Faso, 34 in Gabon and 70 in Senegal (Figure 20). The sampling design of this study is appropriate to understand the actions taken by regional/local farmers from 5 distinct countries to control FAW 7 years after the first invasion in Africa. The surveys were conducted during the period from August to October 2020 in the fields and households of farmers. The period of the surveys coincided with different agricultural phases across countries: at the end of the growing season, into the dry season or the starting of the maize cultivation.

The concepts of knowledge, perceptions and management practices were used to analyze farmers' management decisions against FAW. These concepts have been widely used in previous studies (Kumela et al., 2019; Kansiime et al., 2019; Houngbo et al., 2020; Tambo et al., 2020a; Caniço et al., 2021; Kasoma et al., 2021a; Ahissou et al., 2022) and were used as a basis in conducting this study. The knowledge referred to what the farmers know about the FAW: identification, year of observation of the pest and its damage on crops mainly maize. Questions related to trainings conducted by non-governmental organizations (NGOs), research institutions and international organizations such as International Institute of Tropical Agriculture (IITA), International Center for Tropical Agriculture (CIAT), food and agriculture organization (FAO) were asked to find out the level of knowledge of some farmers who received trainings on FAW and those who did not. To facilitate this, pictures of the FAW (different instars usually larval instar 4, 5 and 6) including damages/symptoms on the maize plant were printed on A4 size paper. Perceptions refer to how farmers assess the intensity of FAW damages on maize crop and the effectiveness of management practices (Kansiime et al., 2019). During the surveys, farmers were asked questions related to the year of FAW observation in own maize and other crop fields. Farmers gave a list of wild and cultivated plants. To confirm the presence of FAW, surveys were conducted on dry season crops (usually vegetables and fodder grasses) such as cabbage, onion, tomato, eggplant and grasses. The presence of FAW was confirmed in these crops by some experts participating in the survey.

Regarding management practices, farmers were given the possibility to provide more than one response to a proposed list of practices (Tambo et al., 2019, 2020b).

To document pesticide usage, the trade names of the products were noted. Furthermore, in certain instances, additional details regarding the pesticides used, such as dosage, active ingredient, spraying regime and application method, were gathered from the product packaging discovered in or near the fields. The electronic survey form was improved during the data entry process in order to provide additional information's given by the farmers (e.g. crops not initially referenced or other reasons given by the farmers for not applying FAW management practices...).

Data analysis

Data summary and descriptive statistics (frequencies, means, and standard deviations) were performed using the data processing and statistical analysis software Rstudio 4.0.2 (R Core Team, 2021). Analysis of variance (ANOVA) was performed using the "rstatix" package (Kassambara, 2021) to estimate differences between countries not only on quantitative data of farmers' households such as their age, household size and labor force (number of assets in the household) but also on characteristics such as farm size and maize area cultivated in the year. In the case of rejecting the null hypothesis, a multiple comparison of means between each country was performed by a Tukey HSD (Honestly Significant Difference) test using the "multicompView" package (Graves et al., 2019). For the remaining questions, the frequency of response to the question was assessed and a chi-square test was performed to analyze relationships between countries and gender; between countries and farm size; between countries and variables related to the use of plant protection products; and between countries, kinds and sources of information received by farmers, and pest management practices. Excepting for the phytosanitary products where the percentages were calculated on the total number of farmers in the 5 countries, the other rates were calculated for each country. The significance level was set at 5% for all tests.

Results

Socio-economic characteristics

Among all farmers surveyed in the five countries, 76.1% were men (Table 9). In Gabon, all smallholder farmers surveyed were men while rates of 94.4%, 96.4% and 97.1% were found in Benin, Burkina Faso and Senegal respectively. The female majority was only found in the Democratic Republic of Congo. Global average age of the survey population was 44.4 years. Farmers in Senegal were the oldest with an average age of ~ 50 years while the ones in Benin were the youngest around 40 years. In Burkina Faso and Senegal, household size was found to be above average with ~ 9 and 10 persons respectively. Smallest households were found in Gabon with approximately four persons. Senegal is the country with the largest number of active members by household, with an average of ~ 10 persons, unlike Gabon, where fewest active members were observed with an average of approximately two persons. Regarding the maize planted area during the year 2020, no significant difference between all countries was found as farmers planted an average of 1.99 ha of maize. There were differences between countries in the distribution of farm sizes. Then, farms of 1-5 ha were the most numerous in Benin, Burkina Faso and Gabon. In Senegal, most farmers had larger than 10 ha, while it was mainly between 0.5 and 5 ha in DR Congo.

Farmers' knowledge and perception of FAW infestation

In general, farmers correctly identified the FAW (Table 10). Farmers reported recognizing the FAW caterpillar in 99.4% of the cases and 70.6% of them claimed to have already had damages to their crops due to this pest. Among farmers who received information's on FAW from NGO or other organizations, they were a majority in Burkina Faso (52.7%), while they represented only 2.3% in Benin, 4.3% in Senegal and 13.4% in DRC. In Gabon, no information was collected as farmers were concerned only by monitoring and control methods including the use of pesticides against FAW. The information sources came mainly from the FAO for farmers in Benin and from the farmers' field schools and demonstration fields set up by the farmers' communities in Burkina Faso. In DRC, fewer farmers received training, but it was more likely to come from several different sources. These included farmer associations that collaborate with NGOs and research institutions, university students, and the NGOs Mercy Corps and Food for the Hungry, or international institutions such as IITA and CIAT. In Senegal, the information was provided by the television and/or radio.

Table 9. Socio-economic profiles of surveyed farmers and associated data of their farms.

	Countries							
Variable	**Benin n=89**	**Burkina Faso n=55**	**Gabon n=34**	**DRC n=172**	**Senegal n=70**	**Mean n=420**	χ^2	**F-Test**
Gender (%):								
Male	94.4	96.4	100.0	47.1	97.1	76.13	135.88 ***	
Female	5.6	3.6	0.0	52.9	2.9	23.87		
Age	39.5 ± 11.1c	44.8 ± 9.5ab	41.9 ± 10.3bc	46.6 ± 10.0ab	49.6 ± 11.7a	44.5 ± 10.5		11.29 ***
Household size	7.5 ± 4.2bc	8.9 ± 4.7b	3.5 ± 3.3d	6.8 ± 2.3c	14.1 ± 7.6a	8.2 ± 4.4		45.98 ***
Household active members	3.9 ± 2.6c	4.9 ± 2.8bc	1.7 ± 1.4d	5.6 ± 2.1b	9.7 ± 6.5a	5.2 ± 3.1		42.42 ***
Average maize area (ha)	2.19 ± 1.48a	1.63 ± 1.36a	1.85 ± 1.40a	1.23 ± 4.85a	3.05 ± 1.14a	1.99 ± 2.04		1.99 ns
Farm size (%):								
< 0.5ha	0.0	0.0	2.9	19.2	0.0	4.4	275.06 ***	
0.5-1ha	12.4	1.8	20.6	39.0	0.0	14.7		
1-5ha	65.2	63.6	58.8	39.5	23.1	54.4		
5-10ha	21.4	30.9	14.7	1.7	36.9	21.1		
≥ 10ha	1.1	3.6	2.9	0.6	40.0	9.6		

Note: Means ± standard deviations of countries followed by identical letters are not statistically different at the 5% significance level according to the HSD Tukey test. Statistically significant at ***$P < 0.001$; ns = not significant.

Table 10. Knowledge, types and sources of information on fall armyworm.

Variables	Countries					Mean n=420	χ^2
	Benin n=89	Burkina Faso n=55	Gabon n=34	DRC n=172	Senegal n=70		
Familiar with FAW (%Yes)	98.9	100.0	100.0	99.4	98.6	99.4	1.39 na
FAW infestation (%Yes)	100.0	100.0	100.0	91.8	70.6	92.5	56.62***
Informed about FAW (%Yes)	2.3	52.7	0.0	13.4	4.3	14.5	92.11***
Types of information:							
Monitoring	0.0	1.8	0.0	5.3	3.5	2.7	49.36 na (a)
Monitoring & control methods	0.0	12.3	0.0	0.0	0.0	3.1	
Control methods	0.0	22.8	0.0	14.0	0.0	9.2	
Pesticides application	0.0	14.0	0.0	1.8	1.8	4.4	
Indigenous control methods	3.5	0.0	0.0	10.5	0.0	3.5	
Information sources:							
FAO	50.0	0.0	0.0	19.0	0.0	17.3	67.04 na (a)
NGO, Mercy Corp & FH	50.0	4.2	0.0	14.3	0.0	17.1	
Farmer field school	0.0	50.0	0.0	33.3	0.0	20.8	
Demonstration fields	0.0	45.8	0.0	4.8	0.0	12.7	
Television and/or radio	0.0	0.0	0.0	0.0	66.7	16.7	
IITA	0.0	0.0	0.0	9.5	0.0	2.4	
CIAT	0.0	0.0	0.0	9.5	0.0	2.4	
Other sources	0.0	0.0	0.0	23.8	33.3	14.3	

Note: (a) Gabon was not included in the calculation of the χ^2. Statistically significant at ***$P < 0.001$; na = not applicable. IPM: integrated pest management; FAO: food and agriculture organization; NGO: Non-governmental organization; FH: Food for the hungry; IITA: International Institute of Tropical Agriculture; CIAT: International Center for Tropical Agriculture.

In total, 5 years (2015-2019) were listed by farmers as years of first observation of FAW in their fields (Figure 21). This information was collected in DRC and Gabon. In other countries such as Burkina Faso and Benin, 4 years were recorded (2016-2019). In Senegal, only 3 years were identified (2015-2017). In most cases and in every country except Gabon, farmers claimed to have seen the FAW for the first time in 2017. This represented 44.7% in DRC, 62.9% in Benin, 69% in Burkina Faso and 55% in Senegal. A very small minority of farmers claimed to have observed armyworm in 2015 (<0.05% in DRC, <0.05% in Senegal and <0.5% in Gabon) and 2019 (<0.05% in DRC, <0.05% in Gabon, <0.05% in Burkina Faso and <0.05% in Benin). Nevertheless, the year 2016 was listed by farmers in all 5 countries as the year of the first observation of FAW with considerable percentages.

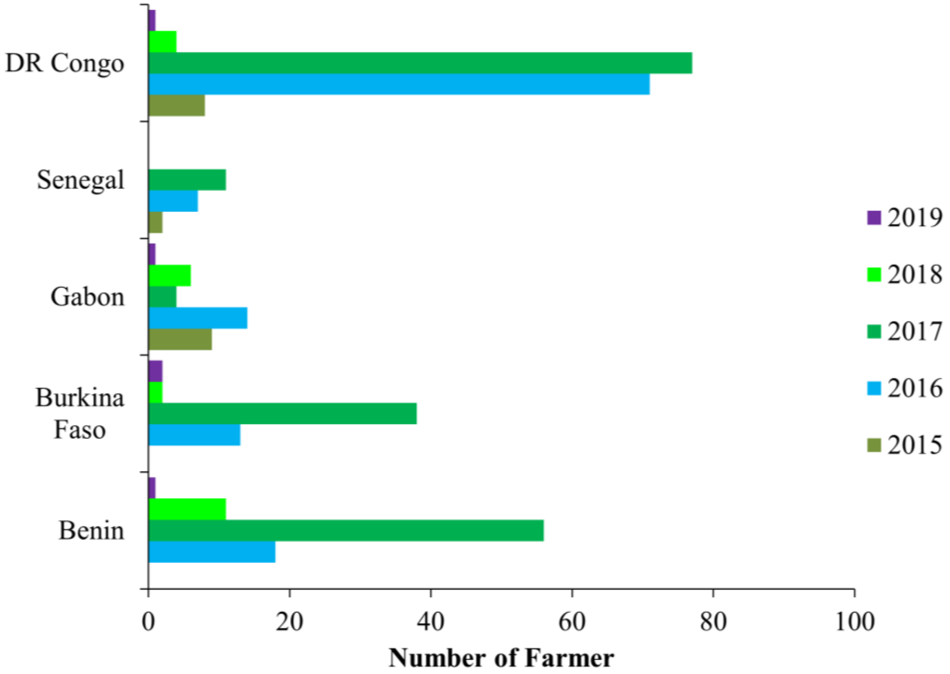


Figure 21. Observation years of fall armyworm by farmers in five central and west African countries.

From farmer observations and confirmations by some experts participating in the surveys in the concerned countries, four plant species constituting alternative hosts of the FAW were recorded (Table 11). These included a forage grass (*Pennisetum purpureum*), a cultivated grass (*Sorghum bicolor*) and two vegetable species, namely *Allium cepa* (onion) and *Brassica oleracea* (cabbage). These taxa are belonging to three botanical families. This information was collected in four of the five countries that participated in the survey. All alternative host plants of FAW were recorded in DRC. In Gabon and Burkina Faso, only one species (Napier grass) was recognized by farmers as an alternative host for FAW. No information on alternative hosts was collected in Senegal and Benin.

Table 11. List of plants identified as alternate hosts for fall armyworm.

Scientific name	Common name	Familly	Observation country
Pennisetum purpureum Schumach	Napier grass	Poaceae	Burkina Faso, Gabon, DRC
Sorghum bicolor L.	Sorghum	Poaceae	DRC
Allium cepa L.	Onion	Amaryllidaceae	DRC
Brassica oleracea L.	Cabbage	Brassicaceae	DRC

Management methods to control fall armyworm

A total of 14 methods were identified by farmers in West and Central Africa as indigenous management against FAW (Table 12), grouped into three categories including physical, cultural and chemical approaches. Chemical methods involve the use of synthetic pesticides and the application of certain plant extracts such as tobacco powder, *Tithonia diversifolia* extract, aqueous extract of garlic and Neem. All of them varied according to the reality of each country participating in the surveys. Farmers in Benin opted for cultural (frequent weeding, early planting) and physical methods (hand picking of larvae and egg masses). In Burkina Faso, cultural methods were dominant (early planting, use of resistant cultivars and crop rotation), with the addition of physical methods such as the application of ash. In DRC, cultural methods (frequent weeding) and physical methods were dominant (application of ash, hand picking of larvae and egg masses). In some cases, notably in Benin, hand picking contributed to feed livestock, while in DRC and Burkina Faso, caterpillars and eggs were destroyed on site without being recovered to feed livestock. In Gabon, no method was reported and farmers opted for no action. However, to manage FAW in this country, farmers have opted for chemical control. In general, during the surveys, several farmers responded that they were using no control methods, representing 14.6% in Benin, 10.9% in Burkina Faso and 16.3% in DRC. Two methods of FAW management were not recognized by farmers: the use of trap plants such as Napier grass or maize as a false seedling technique and biological control. The push-pull technology was only recognized in Burkina Faso and Senegal. Several other cultural methods were mentioned, including the application of both chemical and organic fertilizers, replanting areas attacked by FAW, destruction of crop residues, uproot and burn-infested plants and association of maize with both non-legume and legume crops.

Table 12. Indigenous methods of managing fall armyworm in Central and West Africa.

Management methods	**Countries**					**Mean n=420**	χ^2
	Benin n=89	**Burkina Faso n=55**	**Gabon n=34**	**DRC n=172**	**Senegal n=70**		
Early planting	44.94	41.82	0.00	3.49	5.00	18.92	95.2***
Resistant/tolerant cultivars	1.12	41.82	0.00	1.16	5.00	7.30	114.3***
Crop rotation	5.62	41.82	0.00	1.16	10.00	8.65	93.0***
Regular weeding	48.31	16.36	0.00	48.84	20.00	37.84	47.1***
Fertilization	12.36	18.18	0.00	6.98	0.00	8.92	13.1***
Application of ash	2.25	38.18	0.00	37.21	0.00	23.51	63.5***
Use of plant extracts	7.87	16.36	0.00	4.65	10.00	7.03	11.76***
Intercropping with non-legumes crop	1.12	7.27	0.00	17.44	10.00	10.00	22.60***
Intercropping with legumes crop	2.20	0.00	0.00	30.20	0.00	14.60	63.25***
Trap cropping	na	na	na	na	na	na	na
Push Pull	0.00	3.64	0.00	0.00	5.00	0.81	na
Destruction of crop residues	0.00	0.00	0.00	16.3	35.0	9.50	43.17***
Uproot and burn infested plants	5.62	3.64	0.00	3.49	0.00	3.51	na
Hand picking of larvae and egg masses	23.60	0.00	0.00	48.30	0.00	28.10	78.06***
Replanting of attacked areas	3.37	7.27	0.00	0.00	0.00	1.89	na
Biological control	na	na	na	na	na	na	na
No action	14.61	10.91	100.00	16.28	0.00	23.14	125.74***

Note: Statistically significant at ****P < 0.001;* na = not applicable.

To control FAW, 96.4% of farmers in Burkina Faso, 85.3% in Gabon, 65.2% in Benin and 25.0% in DRC reported the use of insecticides, compared to 5.9% of farmers in Senegal (Table 13). Paradoxically, farmers using mostly insecticides were also those who knew people having health problems due to pesticides with 42.7%, 41.8% and 29.4% for Benin, Burkina Faso and Gabon respectively. This situation did not seem to discourage their use. Among farmers using pesticides, those wearing personal protective equipment (PPE) represented 93.1% of cases in Benin, 90.6% of cases in Gabon, 30.2% in Burkina Faso and 31.4% in DRC. Masks and Ruber boots were the most common PPE in all countries, with 35.5% of farmers using masks and 36.0% using Ruber boots. Coveralls were the least frequently encountered equipment, with 8.9% of farmers using them. Also, some farmers used equipment that did not provide effective protection against pesticides. For example, some farmers indicated that they used a hat or a motorcycle helmet when applying pesticides. Regarding their perception of the effectiveness of synthetic insecticides against FAW, the largest number of farmers perceived chemical treatments to be very (47.3%) or moderately effective (45.8%) on average in the five countries. Burkina Faso and Benin were the countries where farmers were most likely to use synthetic pesticides and to be convinced of their effectiveness against FAW. Senegal was the country where insecticide treatment was reported by farmers with a small percentage.

Table 13. Perception on the use of insecticides against fall armyworm.

	Countries					Mean n=420	χ^2
Variables	**Benin n=89**	**Burkina Faso n=55**	**Gabon n=34**	**DRC n=172**	**Senegal n=70**		
Application of pesticides (%Yes)	65.2	96.4	85.3	25.0	5.9	55.5	165.56 ***
Health problems related to pesticide use (%Yes)	42.7	41.8	29.4	28.5	75.0	43.5	9.95*
Uses PPE (%Yes)	93.1	30.2	90.6	31.4	80.0	65.1	90.66 ***
Types of PPE used:							
Mask	36.6	51.7	24.5	34.1	30.8	35.5	51.25 ***
Glove	6.1	20.7	20.8	27.5	23.1	19.6	
Ruber boot	40.5	24.1	54.7	37.4	23.1	36.0	
Coveralls	16.8	3.5	0.0	1.1	23.1	8.9	
Perception of pesticide efficacy:							
Low effective	10.3	7.5	0.0	9.3	0.0	6.8	13.68 *(a)
Moderately effective	39.6	28.3	62.1	53.5	0.0	45.9	
Very effective	50.0	64.2	37.9	37.2	0.0	47.3	

Note: Senegal was not included in the calculation of the χ^2. Statistically significant at $*P > 0.05$, $***P < 0.001$; PPE: personal protective equipment.

In this survey, a good number of farmers representing 44.3% of the respondents used pesticides for FAW control (Table 14). A total of 18 commercial pesticides with 13 active molecules were recorded during the surveys. The most commonly used products were COTONIX 328 EC, EMACOT 050 WG, LAMBDA SUPER 2.5 EC and ROCKET. COTONIX 328 EC was used mainly in Benin and was generally supplied by the government. EMACOT 050 WG is a product that has been used mainly for maize crops in Gabon and Burkina Faso. Generally, this product was supplied by traders in Burkina Faso and by the Gabonese chemical company. LAMBDA SUPER 2.5 EC is a product that was most often purchased on the market by Beninese farmers and was mainly used on maize crops. Finally, the insecticide ROCKET was used by Congolese farmers. Among the products used, the first family of insecticides found is highly toxic organophosphates. This is particularly the case for ROCKET, COTONIX 328 EC, Pyro FTE 472 EC, LAVA 100 EC and TAFGOR 40 EC. After organophosphates, the second most common pesticide family found is pyrethroids in slightly more than 10% of cases. Another very toxic product that was found is THIODAN composed of endosulfan which belongs to the organochlorine family.

Table 14. Trade names, active molecules and frequencies of pesticides found in the community of farmers interviewed.

Trade products	Active molecules	Number of farmers	% of farmers [a]	WHO classes [b]
Insecticide treatments		186	44.28	
ACARIUS 018 EC	Abamectin 18 g/L	4	0.95	Ib
CAÏMA B19	Emamectin benzoate 19,2 g/L	1	0.23	II
COTONIX 328 EC	Deltamethrin 12g/L + Chlorpyriphos-ethyl 300g/L + Acetamiprid 16g/L	10	2.38	II
CYPER LACER 5 EC	Cypermethrin 5%	1	0.23	II
DECIS 25 EC	Deltamethrin 25g/L	3	0.71	II
DIMETHOATE 40 EC	Dimethoate 400g/L	7	1.66	II
EMACOT 019 EC	Emamectin benzoate 19 g/L	9	2.14	II
EMACOT 050 WG	Emamectin benzoate 50g/kg	49	11.66	II
K-OPTIMAL EC	Acetamiprid 20 g/L + Lambda-cyhalothrin 25g/L)	3	0.71	II
LaraFORCE	Lambda-cyhalothrin 2,5%	6	1.42	II
LAMBDA SUPER 2,5 EC	Lambda-cyhalothrin 25g/L	27	6.42	II
LAVA 100 EC	Dichlorvos 1000 g/L	8	1.90	Ib
PACHA 25 EC	Acetamiprid 10 g/L + Lambda-cyhalothrin 15 g/L	13	3.09	II
Pyro FTE 472 EC	Cypermethrin 72 g/L + Chlorpyriphos-ethyl 400 g/L	11	2.61	II
ROCKET	Chlorpyrifos 20% EC	24	5.71	II
TAFGOR 40 EC	Dimethoate 40%	3	0.71	II
THALIS 56 EC	Acetamiprid (32 g/L) + Emamectin benzoate (24 g/L)	6	1.42	II
THIODAN 50WP	Endosulfan 50%	1	0.23	II

Note: [a] Percentage based on total number of farmers surveyed; [b] Classification WHO (world health organization): Ib = highly hazardous; II = moderately hazardous.

Reasons for non-application of management methods against FAW are presented (Table 15). Also, a number of farmers generally used cultural, physical and chemical methods in managing FAW in the affected areas in Africa (Table 12). However, other farmers preferred not to deal with the observed damages or limited the use of a management method. Several reasons for non-application associated with the management methods are mentioned. For example, farmers in Benin, Burkina Faso and DRC often practiced early planting as a preventive method, but this method was limited when there was a delay in rainfall due to climatic variability that favored

FAW outbreaks. Farmers would like to use resistant cultivars to FAW but information on these was not available in some parts of Africa and in others, inputs were inaccessible. Methods such as fertilization and pesticide use appeared to be expensive and often not accessible. Information on the trap crop used in false seeding technique was not available and farmers were not aware of this method. The concepts of semiochemical based and biological control by promoting natural enemies of FAW were new to farmers in DRC, Gabon and Benin with respect to the push-pull method, and to all respondents with respect to biological control. Replanting was not favored by farmers because of the time required for that and input accessibility. The use of plant extracts should allow farmers to manage FAW at first sight but some of them did not understand how to apply the recommendation in the presence of several categories of plant extracts.

Table 15. Reasons for not applying fall armyworm management methods.

Management methods	**Reasons for not applying**						
	Expensive	**Time required**	**Data not available**	**Inputs not accessible**	**Not understood the recommendation**	**Delayed rainfall**	**Don't know the method**
Early planting						+	
Resistant/tolerant cultivars			+	+			
Fertilization	+			+			
Use of plant extracts					+		
Trapping crop			+				+
Push pull			+	+			+
Replanting of areas attacked		+		+			
Biological control			+		+		+
Application of pesticides	+			+			

Note: + indicates the reason for not using fall armyworm management methods.

Discussion

The dominance of men in farms was reported in four of the five countries (Burkina Faso, Benin, Gabon and Senegal). The same trend was observed by Chimweta et al. (2020) in Zimbabwe; by Caniço et al. (2021) in Mozambique; and by Kasoma et al. (2021a) in Zambia. In Africa, agricultural activities involved men and women differently (Palacios-Lopez et al., 2017). Men often dominate agricultural activities in Africa due to their status as household heads, landowners, and ultimate decision makers in resource use (Kasoma et al., 2021a; Chuma et al., 2022). From another perspective, women are active in agricultural activities in Africa as in DRC where more than half of the farmers were women. According to Mugumaarhahama et al. (2021), the agriculture practiced by women in most cases is of the "subsistence" type, unlike men ensure cash crops. In terms of maize area cultivated, no difference was reported between countries. This reflects the reality of agriculture in SSA, which is still practiced in small areas (Jayne et al., 2010; Hruska, 2019) between 0.5 and 5 ha for this study.

Six years after its introduction on the African continent, several programs have been initiated in some countries invaded by the FAW to educate farmers on the pest and how to manage it (Tambo et al., 2019; Chimweta et al., 2020). Unfortunately, these programs are present in some African countries to the exclusion of others. This is the case, for example, in Gabon where NGOs and other organizations were not reported. According to Houngbo et al (2020), belonging to a farmers' organization and being in contact with research or extension services is an advantage in the knowledge and perception of FAW damage. For effective deployment of control methods against a given pest, farmers must be able to morphologically identify the target pest and distinguish it from non-target ones (Caniço et al., 2021). Although methods and technologies are rapidly developing scientifically to find sustainable solutions against FAW, there is still human action that must be considered in the African context (Kansiime et al., 2019). FAW is not a new pest to farmers in Central and West Africa, who have observed it from the year 2015 for some and later in 2019 for others. Studies by Houngbo et al. (2021); Ahissou et al. (2022) also indicated that some farmers in Benin and Burkina Faso reported the presence of FAW in 2015. In this study, the vast majority of farmers reported 2016 and 2017 as the years they observed FAW in their fields. The year of introduction of FAW on the African continent remains an open question although first reported in 2016 (Goergen et al., 2016). Similar to the studies by Kumela et al. (2019); Houngbo et al. (2020); Caniço et al. (2021), this study indicated that farmers recognize FAW well and the majority of them already had damage in their maize crops. Furthermore, four plant species were recorded as alternative hosts of FAW including onion which was previously reported by Cokola et al. (2021b). The other crops reported, namely cabbage, sorghum and Napier grass, constitute new information that could help researchers and governments in the development of an integrated approach against FAW on the African continent.

Almost half of the farmers surveyed in this study used pesticides against FAW. Chimweta et al. (2020) and Tambo et al. (2020a) indicated higher values. Several molecules found in this survey were also found by Kansiime et al. (2019) and Tambo et al. (2020b). Most of the active molecules found are not registered in Africa and are prohibited by Regulation (EC) 1107/2009. Most farmers perceived insecticide treatments to be very effective against FAW. This trend was very pronounced in Benin and Burkina Faso, where nearly two-thirds of farmers reported using insecticides. The same results were noted by Kumela et al. (2019). However, the use of PPE was far from widespread there. In Burkina Faso, half of the farmers who used insecticides did not wear PPE. Given the molecules used and the level of exposure, farmers in this part who did not wear PPE, while spraying products exposed themselves to high health risks for themselves and their relatives (Jepson et al., 2014; Togola et al., 2018). The progressive banning of molecules that are toxic to the environment and human health in industrialized countries continues to fuel the pesticide market in Africa. While farmers struggle to find organic fertilizer for their crops, pesticides are more accessible (e.g., at the market, at the corner shop, at the neighbor's house or provided by the state). In the global context of climate change and biodiversity loss, insects have important roles to play for ecosystems. However, pesticides are partly responsible for the disappearance of many species, which leads to the instability of agricultural ecosystems and makes them more vulnerable to the emergence of invasive species (Cardoso et al., 2020).

Despite the "farmer school field" programs undertaken in West Africa to find alternative methods, the pesticide use is not decreasing. Several factors may be responsible for the higher proportion of users. The land area is larger and the number of household members is smaller than the size of the household. The results of Tambo et al. (2020b) indicated a positive relationship between maize area and pesticide use. In contrast, farmers in central Africa have smaller landholdings than in Benin and Burkina Faso. The ratio of assets in households is higher there, which makes it possible to favor mechanical methods such as hand picking, which are more labor-intensive (Ansah et al., 2021; Tambo et al., 2020b). Nevertheless, this method is still applicable at the farmer scale in SSA due to the relatively small areas of production (Hruska, 2019). In DRC and Benin, about one-third of the farmers interviewed used the hand-picking method, which showed their interest in finding alternatives to chemicals. Agroecological practices and the use of biopesticides as proposed by Midega et al. (2015, 2018); Bateman et al. (2018); Harrison et al. (2019), should form the basis of alternatives to be implemented in the training programs given to farmers and should not be limited in some countries as is the case for example in Ghana (Tambo et al., 2020b) or Ethiopia (Gebreziher et al., 2020). As Yarou et al. (2017) pointed out, to encourage farmers to adopt new practices, we need to be able to convince them that the long-term benefits of agroecological practices will be more attractive than the immediate benefits provided by synthetic pesticides. Generally, farmers use a variety of inexpensive and locally available agroecological practices in pest management (Abate et al., 2000). Some farmers in this study opted for cultural methods such as frequent weeding, early planting and crop rotation. Similar results were noted by Tambo et al. (2020a, 2020b) in studies involving 5 other countries in Africa (Ghana, Rwanda, Uganda, Zambia, Zimbabwe). The push-pull method was only recognized in this study in Burkina Faso and Senegal with very low application frequencies. Similar results were obtained by Tambo et al. (2020a) in Ghana and Zambia where only two households in a sample of 465 farm households applied the push-pull method. The concept of biological control appears to be new among the farmers interviewed in this study compared to Houngbo et al. (2020) who reported birds (francolin and the village weaver) and the common wasp as natural enemies of FAW identified by farmers in Benin.

Several reasons for not applying FAW management methods were mentioned by farmers. The early planting method is limited by climatic variability. At any given time, farmers do not know the ideal planting time in the presence or absence of rain (Ansah et al., 2021). The cost associated with pesticide application and fertilization has been cited for farmers who do not apply these methods. In Zimbabwe, for example, farmers reported lack of financial resources as the main constraint (Chimweta et al., 2020). Availability and accessibility of resistant cultivars to FAW, etc. is also a major constraint. The use of Bt maize cultivars is discussed as an alternative in the sustainable management of FAW in Africa but its use is not approved so far (Van den Berg et al., 2021). The availability of information and the lack of knowledge of certain methods by farmers (push pull, biological control...) constitute a real challenge in this study. Education campaigns on identification and the above-mentioned methods should be the priority in the control of FAW in countries where the level of knowledge of the pest remains low as proposed by Caniço et al. (2021).

Conclusions

Currently, the training programs provided to African farmers for FAW control predominantly emphasize the utilization of synthetic insecticides. However, alternative methods employed by farmers were also mentioned, with their implementation based on the specific circumstances within each country. The limited adoption or absence of these alternative methods was attributed to several factors, including insufficient knowledge about certain techniques like push-pull and biological control, as well as limited availability of FAW-resistant crop varieties. This study identified four plants as alternative hosts of FAW, including fodder grass (*Pennisetum purpureum*), cultivated grass (*Sorghum bicolor*) and two plant species, namely *Allium cepa* (onion) and *Brassica oleracea* (cabbage). This information is one of the approaches to be used in the development of an integrated management strategy (IPM) for FAW in Africa. In the future, the data collection system set up should make it possible to monitor the progress of FAW control programs and to target regions in SSA where farmers still need advice. This survey is a preliminary analysis of the management methods used by farmers against FAW in Central and West Africa. Continuation of the study and future analyses could provide a useful source of information for researchers and governments to monitor the evolution of farmers' practices and disseminate innovative methods of sustainable pest management that would have been implemented through farmers' organizations, research institutions and NGOs.

Chapter 4

Biological control of the fall armyworm

Photo by Marcellin C. Cokola

Chapter 4. Biological control of the fall armyworm

1. Fall armyworm biological control based on beneficial insects

This section was adapted from manuscript: **Cokola, M.C.,** Kenis, M., Noël, G., Caparros Megido, R., Durocher-Granger, L., Francis, F., 2024. *Spodoptera frugiperda* and associated insect natural enemies in eastern DR Congo: community trends and diversity in relation to the pest abundance in maize. Scientific Reports (submitted).

Abstract

The fall armyworm (FAW), *Spodoptera frugiperda* (J. E. Smith) has become a global maize crop pest because of its polyphagous feeding behavior, resistance to certain active chemical molecules and the dispersal ability of moths. A monitoring system based on the trapping, visual active observation of predatory insects and the collection of larvae and eggs for studying parasitoids was developed in two agro-ecological zones (Low and mid-altitude) in eastern DR Congo. The percentage of parasitism was determined for parasitoid species and the abundance of predatory insects was associated to the plant phenology, the larval density, damage score and incidence of FAW. The insect natural enemies collected were identified morphologically and molecularly using DNA barcoding. Ten parasitoid species were collected, including 2 parasitizing eggs and 8 parasitizing larvae. *Telenomus remus* exhibited the highest parasitism rate among egg parasitoids, achieving 91.7%, whereas *Coccygidium luteum* had the highest parasitism rate among larval parasitoids, with 19.5%. The abundance and the diversity of insect natural enemies vary with agro-ecological zones and maize growth stages. Three groups of predators (ants, earwig and ladybirds) were more abundant in maize fields in both agro-ecological zones. Ants were most abundant at green mealie maize stage (R1) and were the only group with significant densities at all maize growth stages. Three groups of insect predators, including ladybirds, earwigs and wasps, were more abundant at four leaves completely unfolded V4 maize stage when FAW larval densities were high. Based on these findings, conservation biological control should be developed on smallholder farms in DRC through an integrated approach that minimizes plant protection products and diversifies crops to encourage natural enemies of FAW.

Keywords: fall armyworm, predators, parasitoids, incidence, maize, biological control.

Introduction

In recent years, agricultural ecosystems have been severely affected by relentless pest attacks, with maize crops being particularly vulnerable (Singh et al., 2022). Among the many pests that threaten agriculture, *Spodoptera frugiperda* (J. E. Smith), commonly known as the fall armyworm (FAW), has emerged as a devastating pest (Luginbill, 1928; Abrahams et al., 2017). Native to tropical and subtropical America (Day et al., 2017; Early et al., 2018), this voracious lepidopteran pest has spread rapidly throughout the world, except for Europe, in less than a decade (Kenis et al., 2023). It is a prime example of a highly adaptable and invasive species. Initially restricted to its native habitat in the Americas, this pest has crossed geographical boundaries, facilitated by global trade and climate change (Early et al., 2018; Singh et al., 2022). First in Africa (Goergen et al., 2016), then in Asia (Sharanabasappa et al., 2018) and finally in Oceania (Maino et al., 2021). The presence of FAW in newly invaded countries poses a major challenge to agricultural productivity, especially in maize cultivation (Kansiime et al., 2023; Cokola et al., 2023b). This voracious pest is known for its polyphagous nature, rapid migration and devastating impact on crops worldwide (Tay et al., 2023). With a wide host range that includes more than 80 plant species (Montezano et al., 2018), maize is its preferred target, making it a major concern for maize-dependent regions of the world, especially sub-Saharan Africa and Asia (Overton et al., 2021).

FAW larvae exhibit a voracious appetite, consuming leaves until only the veins are left, causing severe damage at all phenological stages of maize (Luginbill, 1928; McGrath et al., 2018). Severe attacks are observed at early stages of plant development, causing extensive defoliation (McGrath et al., 2018). However, when attacks occur at later stages of crop development, FAW larvae tend to cause less damage to grain yield than when attacks occur at early stages (Anyanda et al., 2022; Cokola et al., 2024 in press). The migratory behavior of FAW, coupled with rapid reproductive rates, increases the challenge of controlling this pest (Harrison et al., 2019). In the Americas, FAW is increasingly controlled through the use of resistant varieties (Bt maize) and entomopathogenic microorganisms (Guo et al., 2020), while in newly invaded regions, farmers have no other choice in control methods and resort to the use of synthetic pesticides (Hruska, 2019; Cokola et al., 2023b), which often prove inadequate, prompting the adoption of sustainable pest management strategies focused on biological control. Biological control of FAW involves both micro- and macro-organisms in their native range as well as in newly invaded areas (Kenis et al., 2023). Introducing natural enemies from their native regions, is regarded as a potential management strategy against FAW (Kenis, 2023). The predatory and parasitoid macro-organisms that comprise the natural enemy community influence FAW infestation dynamics (Hoballah et al., 2004; Wyckhuys and O’Neil, 2006; Maruthadurai et al., 2022). According to recent literature (Wyckhuys et al., 2024a), FAW is attacked by 304 genera of parasitoids and 215 genera of predators in its native range and in newly invaded areas. A large number of these natural enemies are found in the Americas with parasitoids being the focus of most studies (Ashley et al., 1979; Molina-Ochoa et al., 2003; Hoballah et al., 2004). Predators such as spiders, ground beetles, social wasps, earwig, ants and predatory bugs actively attack FAW eggs and larvae in the Americas (Luginbill, 1928; Fuller et al., 1997; Hoballah et al., 2004; Wyckhuys and O'Neil, 2007). The use of natural enemies in the biological control of FAW in Africa has not been fully investigated, with only 17 countries reporting the presence of parasitoid species attacking FAW out of around 40 countries invaded (Kenis et al., 2023). As in the Americas, most studies of the natural enemies of FAW in Africa examine the presence of parasitoids by assessing their parasitism rates (Sisay et al., 2018; Agboyi et al., 2019; Koffi et al., 2020; Agboyi et al., 2021; Caniço et al., 2021; Durocher-Granger et al., 2021) and their presence as a function of planting dates and maize growth stages (Durocher-Granger et al., 2024). However, information on predators is scarce, although some authors have already reported their presence (Koffi et al., 2020; Ahissou et al., 2021b; Dassou et al., 2021; Chipabika et al., 2023). Furthermore, very few studies in Africa have shown a link between predator presence and their impact on FAW in the field (Jordon et al., 2022) but also their abundance related to maize phenology. Predators’ importance and dynamics in relation to maize development and FAW populations deserve further study to assess their potential for biological control in Africa (Kenis et al., 2023). For example, studies in Americas (Wyckhuys and O’Neil, 2006) have shown that the high abundance of ground beetles (Carabid) and earwigs was associated with low density of FAW populations during maize vegetative growth.

A thorough understanding of the abundance, diversity and impact of locally available natural enemies is essential to effectively promote conservation biological control in specific cropping systems (Wyckhuys and O’Neil, 2006). Conservation biological control of the FAW involves enhancing the existing natural enemies of this pest to manage its population in an environmentally sustainable way (Harrison et al., 2019). The complex interactions within the natural enemy community show dynamic patterns shaped by a wide range of factors (Welch and Harwood, 2014). Habitat diversity, agricultural practices and climatic conditions have a profound influence on the composition and abundance of natural enemies in maize agroecosystems (Wyckhuys and O'Neil, 2007; Clarkson et al., 2022; Jordon et al., 2022). Studies have revealed interesting patterns of community structure, with some natural enemy taxa showing preferences for specific microhabitats and crop management practices (Wyckhuys and O'Neil, 2006; Jordon et al., 2022). Agroecological approaches emphasizing habitat diversification and conservation practices have shown promise in promoting natural enemy dispersal and enhancing their effectiveness in controlling FAW (Harrison et al., 2019). FAW is not a relatively new pest in the Democratic Republic of Congo (DRC). No studies have been carried out on its natural enemies since its invasion in the DRC, particularly in South Kivu. This study records the potential predators and parasitoids which are associated with FAW impact in different climate and altitude landscape according to maize growth stages. In the context of eastern DRC, where maize is a major staple crop, understanding the complex relationship between FAW and their natural enemies is crucial to designing effective control strategies. By elucidating the population dynamics of FAW and their natural enemies, this research aims to contribute to the development of context-specific integrated pest management to safeguard maize production and food security in the region.

Materials and Methods

Study location

The study was conducted in South Kivu, eastern Democratic Republic of Congo (DRC), in two agroecological zones namely Kashusha in Kabare territory and Ruzizi plain represented by Kamanyola. The two agro-ecological zones were selected based on their altitude and climate profiles (Cokola et al., 2020). The Kashusha area is located at 2° 30' south latitude and 28° 48' east longitude, in the far east of the DRC, on the western shore of Kivu Lake. Kashusha has a humid tropical climate, with temperatures varying between 19 and 21°C and extremes of 15 and 25°C. The annual rainfall is about 1500 mm. Its altitude varies between 1400 and 1800 m at the top of the high mountains along the Kahuzi Biega National Park. Kamanyola is a district of the Ngweshe chiefdom in the Walungu territory, located at 2°44' south latitude and 29°00' east longitude, close to the Rwandan border on National Road 5, 45 km south of the city of Bukavu. Kamanyola is characterized by warm temperatures with mean annual range between 25 and 27°C and an average altitude of 973m. It is an area with characteristics of semi-arid regions. Rainfall is bimodal, from October to January and from February to May, with an average annual rainfall of around 800 to 1000 mm in 130 to 150 rainy days. The map of the study area is presented in Figure 22 with mean temperature data (period 1950-2000) downloaded from Africlim (https://www.york.ac.uk/environment/research/kite/resources/) at a spatial resolution of 30 arc seconds.

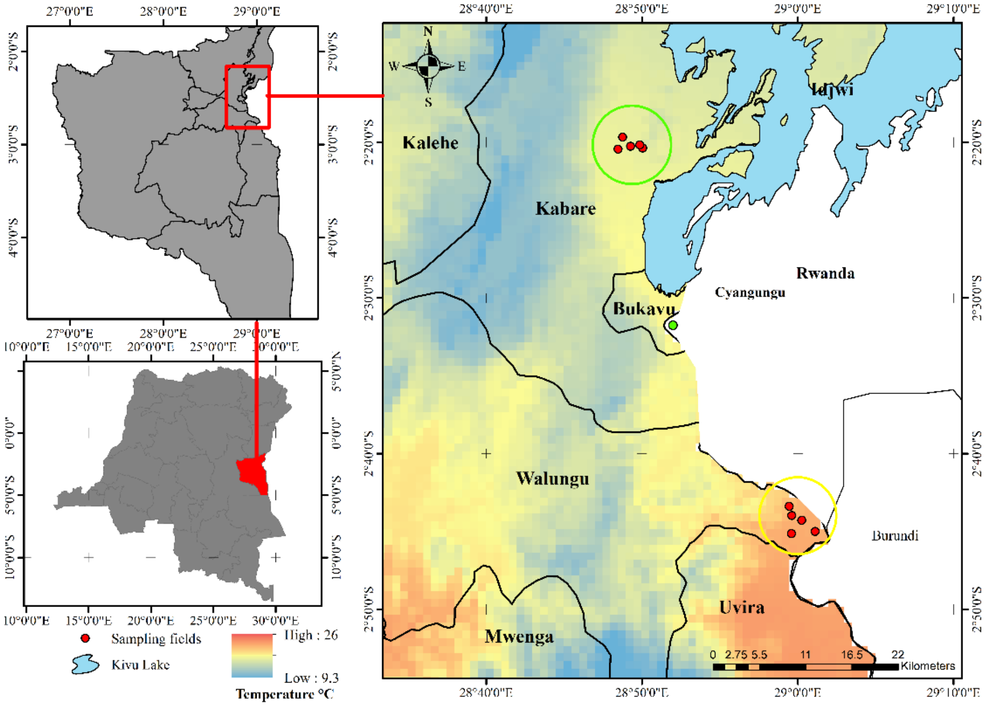


Figure 22. Map showing the geographical location of the study area, based on mean annual temperature data for South Kivu. The map was created using ArcMap 10.8.1 software (https://desktop.arcgis.com/en/arcmap/).

Fields characteristics and determination of fall armyworm infestation

Given the characteristics of the study sites at low altitude (Kamanyola) and mid-altitude (Kashusha), a study was conducted during the cropping season from March to May in 2021 and 2023. This period is part of the short cropping season of the year, which extends from February to June. At each site, 5 fields were randomly selected to study the infestation of FAW in maize crops. The distance between fields was 0.7 ± 0.2 km (mean ± SD) in Kashusha and 0.9 ± 0.1 km in Kamanyola. The coordinates of each field were previously recorded using a global positioning system (GPSMAP® 64s, GARMIN, United States) during the 2021 season, allowing the same fields to be surveyed during the 2023 season. The mean size of each field was 6500 ± 1000 m^2 in Kashusha and 9100 ± 1400 m^2 in Kamanyola. All the fields belonged to smallholders and were cultivated as maize monocultures, using all the cultivation practices designed to improve production (in this case organic and mineral fertilizers, 75×50 cm spacing, regular weeding, etc.), except for the use of insecticides. The maize varieties used were Z-M and ECAVEL in Kashusha and HIMBO in Kamanyola. The selected fields were visited periodically during March-May 2021 and 2023, corresponding to the phenological stages of maize chosen for the study of natural enemy populations and FAW infestation. In each field, 4 quadrats of 20 m^2 (4×5 m) were formed using wire and stakes, and the W-sampling technique was used to allocate the quadrats in each field (McGrath et al., 2018; Cokola et al., 2021). Field visits were made at approximately 1-week intervals in early morning (11 AM), from the completely unfold four-leaf stage (V4) to green mealie stage (R1). Growth stages were determined by counting the number of fully expanded leaves and the duration of each stage (McGrath et al., 2018). The stages considered were 4 leaves completely unfolded (V4), 6 leaves completely unfolded (V6), 8 leaves completely unfolded (V8), 10 leaves completely unfolded (V10), 12 leaves completely unfolded (V12), silk appearance and pollen shedding (VT) and green mealie (R1). The parameters measured for each growth stage and in each quadrat included incidence, severity, larval density and predator density. Incidence was assessed as a percentage in each quadrat by the ratio of the number of plants attacked to the total number of plants in the quadrat. The number of larvae was determined by counting larvae inside the whorled leaves of maize and on the surface of the leaves in each quadrat. Severity was determined by comparing leaf damage to the existing leaf damage scale (Toepfer et al., 2021) on a total of 10 randomly selected plants in each quadrat.

Sampling natural enemies of the fall armyworm

During the fields visits to collect information on FAW infestation rates, predatory insects and FAW larvae were monitored and collected. The quadrats previously established for the study of FAW infestation parameters were also used for the study of predatory natural enemies. In each quadrat, predators were observed according to their known status as natural enemies of FAW. The focus was on ladybirds, ants, earwigs, wasps, bugs and carabids. Two methods were considered for studying the abundance of these natural enemies, the use of yellow pan traps (Flora®, 27 cm diameter and 10 cm depth) and active visual observation (Montgomery et al., 2021; Sunderland et al., 2023). Four yellow pan traps were placed in each field just after maize germination (at V2 stage) in the middle of each quadrat. The height of each trap was adjusted according to the height of the maize plants at each growth stage. Then, 350 ml of 10% concentrated soapy water was regularly added to each trap to prevent escape of the captured insects. Insects were collected at three-day intervals and the captured insects were immediately preserved in 50 ml polystyrene vials containing 70% alcohol to prevent deterioration of the specimens and to facilitate their subsequent handling in the laboratory. As with the determination of the infestation rate, collections were recorded at maize growth stages V4, V6, V8, V10, V12, VT and R1. For the active visual observation method, two observers counted insects in each quadrat. The first observer counted the insects of each group and a few minutes later the second observer counted insects of each group in the same quadrat (Lapchin et al., 1987). The method assumes no emigration or immigration and equal capture efficiency for both counts (Sunderland et al., 2023). Insects in flight, such as wasps, were captured with the sweep net and transferred to vials (Montgomery et al., 2021). In situations where it was difficult to observe the insect directly on the maize plants but present, such as earwigs and other arthropods living in maize whorls, the plants were gently shaken to force the insects to leave the whorl (Wyckhuys and O'Neil, 2007).

FAW eggs and larvae found at maize stages V4, V6, V8 and R1 were collected and taken to the laboratory of the Faculty of Agriculture and Environmental Sciences of the Université Evangélique en Afrique (UEA/Bukavu) for parasitoid studies. Larvae were individually reared in plastic Petri dishes (90 mm diameter) (Durocher-Granger et al., 2021) under ambient laboratory conditions (22 ± 3°C, L:D 12:12) and fed on maize leaves freshly collected from the field. Leaves were surface sterilized in 70% ethanol for 2 min, then in 1.5% sodium hypochlorite for 3 min, followed by three rinses with sterile distilled water. Maize leaves were changed every 2 days until parasitoids emerged or pupation (Agboyi et al., 2020). Egg masses were collected with cut pieces of maize on which they were found and placed individually in plastic vials (250 ml) containing dry paper tissue and pieces of previously disinfected maize leaves. Parasitoids emerging from larvae and egg masses were preserved in 50 ml vials containing a 70% alcohol solution for morphological and molecular identification.

Predator’s and parasitoids abundance evaluation

To study the abundance of predatory and parasitoid natural enemies, two parameters were determined: relative abundance for predator groups and percentage of parasitism for parasitoid species. Predators were grouped according to their status as recognized predators of FAW based on the literature and 6 groups were obtained, represented by ladybirds, wasps, carabid, bugs, ants and earwigs. The abundance of each group of predators was determined by considering the insects caught in the yellow pan traps and those recorded by active visual observation according to the growth stages of the maize. The density of the predators recorded by active visual observation was calculated using the following equation:

$$P = \frac{C_1 + C_2}{2}$$

Where P is population density for each predator group, C_1 is the number of predators of each group collected by the first observer and C_2 the number collected by the second. The total density of each predator group was determined using the following equation:

$$N = \sum_{i=1}^{n} C_p + P$$

Where N is the total density of each predator group; C_p is the number of individuals of each group caught in yellow pan traps; P is the number of individuals of each group obtained by active visual observation. The relative abundance of predatory natural enemies was then determined as a function of the number of individuals in each predator group compared to the total number in all other groups, using the following equation:

$$RA = \frac{N_i}{N} \times 100$$

Where RA is the relative abundance converted to a percentage value, N_i is the total number of individuals for a predator group; N is the total density of all the predator groups. The percentage of parasitism was calculated as the ratio of the number of parasitoid species emerging from the larvae to the total number of larvae collected (Firake and Behere, 2020; Koffi et al., 2020; Durocher-Granger et al., 2021; Otim et al., 2021). For egg parasitism, the parasitism rate was calculated considering the number of parasitized eggs out of the total number of eggs constituting an egg mass of FAW (Abang et al., 2021).

Assessment of fall armyworm population and associated insect predators' dynamics in maize

The quadrats previously established for the study of FAW infestation parameters were also used for the study of predatory natural enemies. In each quadrat, the six groups of FAW predators were observed according to their known status as natural enemies. Data on the total density of each predator group (N) were compared with FAW infestation data collected in each zone, including incidence, damage score and larval density per quadrat, to understand the influence of predator presence on FAW. Analyses were conducted on predator groups with potential of affecting FAW population dynamics and have been found in the field predating FAW. We first estimated the trends in FAW population growth over approximately one week to establish the relationship between the abundance of specific predators and the infestation of the FAW. This estimate was based on the developmental stages of the maize, from stage A to stage B, up to ear formation. Then, using Spearman's rank correlation analysis, we assessed the correlation between the calculated field-specific FAW infestation parameters after each sampling event according to the selected growth stages and the abundance of each selected predator at these sampling events (Wyckhuys and O'Neil, 2006). Infestation variables strongly correlated with the total density of each predator group (correlation coefficient > 0.7) were selected to assess their relationship with each predator group according to maize growth stage, year of collection or agro-ecological zone. Finally, the generalized linear mixed effect model (GLMMs) was applied to explain this relationship.

Insects' identification

Predatory insects collected with yellow pan traps and by active visual observation in each maize plot were brought to the laboratory. They were sorted to include only those insects known to be FAW predators in the literature (Wyckhuys et al., 2024a), spread out and identified to order level based on visible morphological traits. Individuals of each order were identified to family level using a binocular and identification key (Aberlenc, 2020). Identification to species level involved morphological comparison of species in each family using collection data and online images, with the assistance of expert entomologists from the functional and evolutionary entomology laboratory in Gembloux and the Royal Museum for

Central Africa in Tervuren. The collected parasitoids were also identified to order, family and species level. The parasitoid species obtained were compared morphologically with species already identified on the African continent (Durocher-Granger et al., 2021; Kenis et al. 2023). Parasitoids specimens that were difficult to identify or for which there was doubt about genus or species identification were analyzed by DNA barcoding of the COI gene. DNA extraction was performed according to the manufacturer's protocol (Qiagen DNeasy® Blood and Tissue). PCR amplification was performed using the universal primers forward LCO1490 (5'-GGTCAACAAATCATAAAGATTGG-3') and reverse HCO2198 (5'-TAAACTTCAGGGTGACCAAAAAATCA-3') (Folmer et al., 1994). PCR amplification reactions were performed in a total volume of 50 µl consisting of a mixture of 25 µl of Q5® High Fidelity PCR Kit, 2.5 µl of forward LCO1490 primer, 2.5 µl of reverse HCO2198 primer, 10 µl of Nuclease free H_2O (New England BioLabs®) and 10 µl of genomic DNA. PCRs were performed as follow: an initial step at 98 °C for 30 sec, followed by 35 cycles of 98 °C for 30 sec, 55 °C for 30 sec, and 72 °C for 30 sec; a step at 72 °C for 2 min; and a final step at 4 °C infinitely. Amplicons were visualized by agarose gel electrophoresis (1%) in a Bio Rad gel documentation system (Gel Doc EZ Imager). Amplicons were purified using NucleoSpin® Gel and PCR Clean-up kit (MACHEREY-NAGEL GmbH, Germany) according to directions of the manufacturer. The purified amplicons were sequenced by Sanger sequencing Eurofins Genomics (Anzinger STR. 7A/D-85560 Ebersberg, Germany). The resulting sequences were compared with online sequences in NCBI GenBank (http://www.ncbi.nlm.nih.gov/genbank/) and BOLD Barcode of Life Data System (http://www.boldsystems.org/) to determine the species identity. Specimens of predators and parasitoids have been deposited in the insect collections of the Functional and Evolutionary Entomology laboratory in Gembloux, Belgium and at the Centre for Agriculture and Bioscience International (CABI) in Delémont, Switzerland.

Statistical analysis

All the statistical analysis was performed on R version 4.1.3 (R core Team, 2021). The Kruskal-Wallis’s test was used to compare the relative abundance of predator groups. This relative abundance was compared by agro-ecological zones for each predator group using the Mann-Whitney U test. The density of each predator group was also compared by maize growth stages using the Kruskal-Wallis’s test. All tests were performed at the 5% significance level. The severity of the damages and the number of larvae were tested to compare the agroecological zones (low and mid-altitude). The severity and the number of larvae were tested as function of the independent explicative variables (i.e., fixed effects): the density of insect predator groups, the maize growth stages, the year of sampling and the agroecological zones (low and mid-altitude). Generalized linear mixed-effects models (GLMMs) were performed using *lme4* R package (Harrison et al., 2018). The fields sampling crossed with quadrat sampling considered as factor effects (1|Field) + (1|Quadrat). As counting data, Poisson distribution was selected to explain the distribution error. To check the influence of fixed effects, we performed ANOVA after GLMMs with type II likelihood ratio tests obeying the principle of marginality. All the graphics were generated with ggplot2 R package (Wickham, 2016).

Results

Identity and diversity of the fall armyworm natural enemies

The collections of FAW parasitoids highlight the presence of effective natural enemies that can be leveraged for biological control. A total of 10 parasitoid species belonging to 2 orders and 6 families were collected (Table 16). The orders Braconidae and Ichneumonidae were the most represented with 3 and 2 species respectively. 2 parasitoids attack eggs, one species attack both egg and larval stages and 7 species attack larvae only. In terms of species richness, one more species was recorded in the mid altitude than in the low altitude. *Trichogramma chilonis* was found only at the low altitude and was collected at the maize green mealie stage (R1). Common species included *Telenomus remus*, *Coccygidium luteum*, *Chelonus bifoveolatus*, *Charops diversipes* and *Drino quadrizonula*. Egg parasitoids were collected at stages V4 and R1, while the other groups (egg-larvae and larvae) were collected at stages V4, V6, V8 and V10. Most of the parasitoid species were collected at stages V4, V6 and V8. The species *Diadegma sp.* and *Drino sp.*, collected at medium and low altitudes, respectively, seem to be new parasitoid species that should be studied in detail for their morphological descriptions.

The predator groups selected for this study represent a total of 31 species in 4 major orders and 8 families (Table 17). Most of these predators were observed in the field feeding on FAW larvae and eggs, and others were reported in the literature as predators of FAW and were present in traps. The majority are predators of larvae (a limit at the L4 stage), with only two families (Coccinelidae and Forficulidae) observed as predators of FAW eggs. The order Hymenoptera contains a larger number of species (18 species) divided into 3 families (Formicidae, Vespidae and

Sphecidae). The families Reduviidae and Pentatomidae were the second in terms of species diversity in Hemiptera group each with four species. In terms of specific diversity, the Sphecidae contains a greater number of predatory species (7 species). Species richness was higher at low altitude than at mid altitude even if there are several species in common in these agroecological zones.

Table 16. Fall armyworm parasitoids species collected from eastern DRC during 2021 and 2023 collections.

Order	**Family**	**Species**	**Host stages parasitized**	**Zones**		**Maize stage**
				Mid-altitude	**Low altitude**	
Hymenoptera	Trichogrammatidae	*Trichogramma chilonis* (Ishii 1941) *	Egg		+	R1
	Scelionidae	*Telenomus remus* (Nixon 1937)	Egg	+	+	V4, R1
	Braconidae	*Coccygidium luteum* (Brullé 1846)	Larvae	+	+	V4, V6, V8
		Chelonus bifoveolatus (Szepligeti 1914)	Egg-Larvae	+	+	V4, V6
		Parapanteles sp.	Larvae	+		V4
	Ichneumonidae	*Diadegma sp.* **	Larvae	+		V4, V6
		Charops diversipes (Roman 1910)	Larvae	+	+	V4, V6, V8
	Chalcididae	*Brachymeria sp.* ***	Larvae	+		V6, V8
Diptera	Tachinidae	*Drino quadrizonula* (Thomson 1869)	Larvae	+	+	V8, V10
		Drino sp. ****	Larvae		+	V6, V8, V10

+ indicate the presence of the species in each location site, * Genbank accession number: ; ** Genbank accession number: ; *** Genbank accession number: ; **** GenBank accession number: ; V4, V6, V8, V10 and V12 represent the completely unfold four, six, eight, ten and twelve leaves stages respectively; VT is silk appearance and pollen shedding stage and R1 the green mealie stage.

Table 17. Complex of insect predators attacking fall armyworm in two agroecological zones of South Kivu.

Order	Family	Species	Predatory stages	Zones	
				Mid-altitude	Low altitude
Coleoptera	Coccinelidae	*Cheilomenes lunata*	Eggs and L1	+	+
		Cheilomenes sulfurea	Eggs and L1	+	+
	Carabidae	*Unidentified*	L1, L2, L3	+	+
Dermaptera	Forficulidae	*Doru sp.*	Eggs and L1	+	+
		Unidentified	Eggs and L1	+	
Hemiptera	Reduviidae	*Unidentified*	L2, L3, L4	+	+
		Unidentified	L2, L3, L4		+
		Unidentified	L2, L3, L4	+	
		Unidentified	L2, L3, L4	+	
	Pentatomidae	*Unidentified*	L2, L3, L4	+	+
		Un identified	L2, L3, L4		+
		Un identified	L2, L3, L4		
		Unidentified	L2, L3, L4		+
Hymenoptera	Formicidae	*Unidentified*	L1, L2, L3, L4	+	+
		Unidentified	L1, L2, L3, L4	+	+
		Unidentified	L1, L2, L3, L4	+	+
		Unidentified	L1, L2, L3, L4		+
		Unidentified	L1, L2, L3, L4		+
	Vespidae	*Polistes sp.*	L1, L2, L3	+	+
		Unidentified	L1, L2, L3	+	+
		Un identified	L1, L2, L3	+	+
		Unidentified	L1, L2, L3		+
		Unidentified	L1, L2, L3		+
		Unidentified	L1, L2, L3	+	+
	Sphecidae	*Unidentified*	L1, L2, L3, L4		+
		Unidentified	L1, L2, L3	+	+
		Unidentified	L1, L2, L3, L4		+
		Unidentified	L1, L2, L3	+	+
		Unidentified	L1, L2, L3, L4	+	+
		Unidentified	L1, L2, L3	+	
		Unidentified	L1, L2, L3	+	+

+ indicate the presence of the species in each location site

Fall armyworm natural enemies' abundance

Telenomus remus had the highest percentage of parasitism (91.7%) among egg parasitoids at mid altitude, while *C. luteum* had the highest percentage of parasitism (19.5%) among larval parasitoids in both zones (Figure 23). The common species (*Chelonus bifoveolatus*) parasitizing FAW eggs and larvae had a percentage of 12.3 and 9.9 at low and mid altitude, respectively. The species *Drino sp.* and *Brachymeria sp.* were collected occasionally with a parasitism rate of 0.5%.

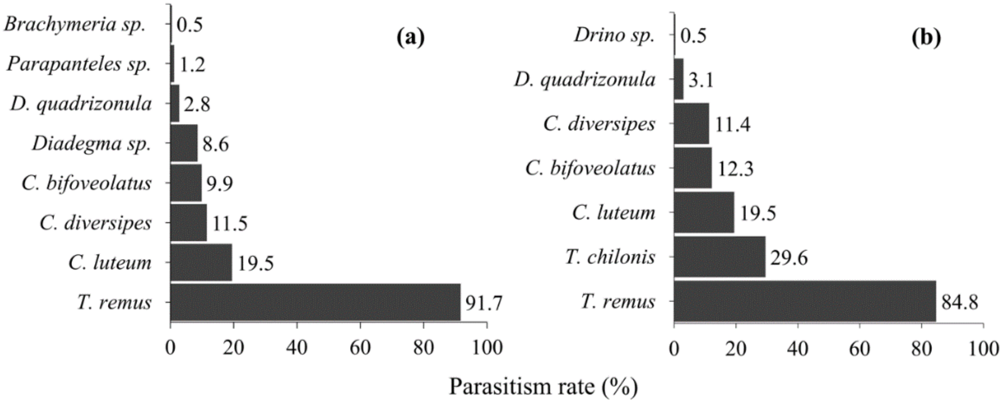


Figure 23. Parasitism rate of parasitoids species recorded on fall armyworm egg masses and larvae. **a:** species recorded in Kabare (Mid-altitude); **b:** species recorded in Kamanyola (Low altitude).

The results present descriptive statistical measures of the relative abundance of FAW insect predators by agro-ecological zones (Figure 24). The results of the Kruskal-Wallis's rank sum test showed that there were significant differences ($p < 0.001$; df = 5; Kruskal-Wallis Chi^2 = 1269.4) in relative abundance between the six groups of FAW predators. Ants were highly abundant with a median of 23.8%, an IQR of 32.3% and a wide range of data points up to 100%. Carabid beetles were the least abundant group, with a median of 0% and an IQR of 1.90%. When comparing agro-ecological zones for each predator group, the Mann-Whitney U-test indicated significant differences between low and mid altitudes in the relative abundance of ants ($p < 0.001$; W = 61984). Ants had a high relative abundance at low altitude, with a median of 37.4% and an IQR of 34.8% compared to mid-altitude. Bugs generally had a relatively low abundance, but the median and IQR were slightly higher at low altitude than at mid altitude ($p < 0.01$; W = 45401). Statistical differences were observed for carabid beetles ($p < 0.001$; W = 31562), with a median of 0% in both agro-ecological zones and a higher IQR at mid altitude.

Earwig had a higher relative abundance at low altitude than at mid altitude ($p < 0.001$; W = 47796), with a median of 14.3% and an IQR of 23.9%. The relative abundance of ladybirds was higher at mid altitude than at low altitude ($p < 0.001$; W = 25348), with a median of 14.3% and an IQR of 27.4%. Wasps were more abundant at mid altitude than at low altitude ($p < 0.001$; W = 25363).

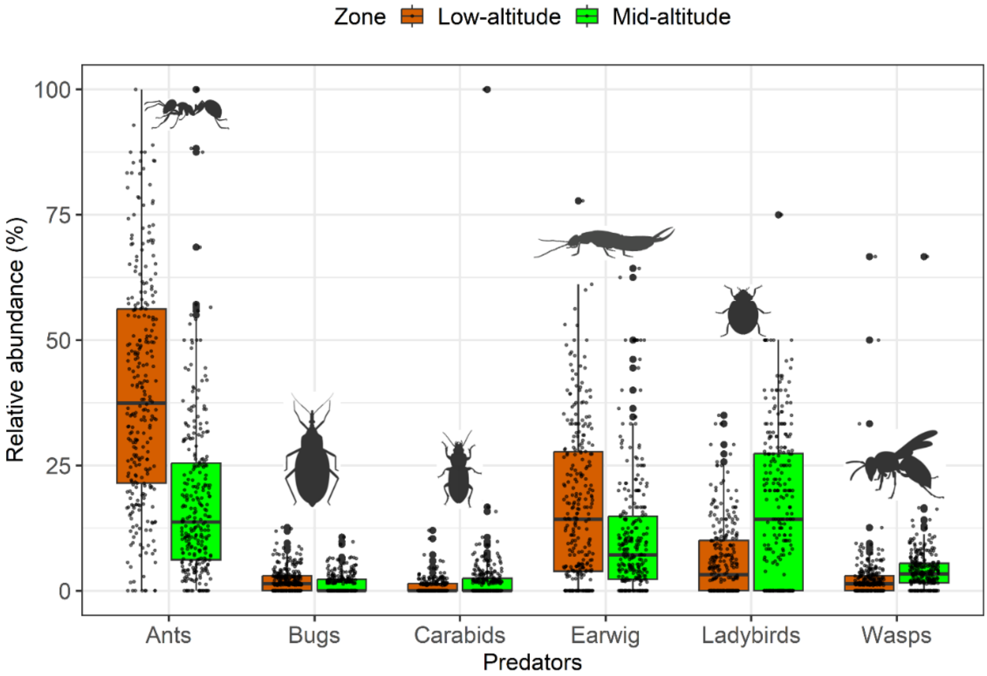


Figure 24. Insect predators' natural enemies' relative abundance in relation to agroecological zones. Data shown are from 2021 and 2023 surveys. The boxes show the interquartile range (IQR), with the median line inside the boxes. The distribution of the data is represented by the small dots inside the boxes.

The box plots in Figure 25 show the density distribution of FAW insect predator groups at different maize growth stages, highlighting trends and variations. The Kruskal-Wallis's test showed a significant difference in predator density between maize growth stages ($p < 0.001$; df = 6; Kruskal-Wallis $Chi^2 = 84.74$). Results in Figure 24 show that three groups of predators (ants, earwig and ladybirds) were more abundant in maize fields in both agro-ecological zones, with ants much more abundant. At different maize growth stages, the same trend was observed. Ant density at different maize growth stages showed some variability ($p = 0.015$; df = 6; Kruskal-Wallis $Chi^2 = 15.73$). The highest median ant density was recorded at stage V6 (9.5), while the lowest (5) was recorded at stage V12. The IQR of the VT stage was higher (17.2), which indicates a higher variability of the ant's density at this stage. Conversely, stages V8 and V10 had a lower IQR (7), indicating more uniform density. As maize progressed from V4 to V10, ant density values generally decreased, with a slight increase from V12 to R1. Earwig density varied significantly between maize stages ($p < 0.001$; df=6; Kruskal-Wallis $Chi^2 = 39.06$). Stages V4 and R1 had high earwig densities compared to the other stages, with an IQR of 10 and 8 individuals respectively. At stage V4, the number of ladybirds was high compared to the other maize growth stages ($p < 0.001$; df = 6; Kruskal-Wallis $Chi^2 = 117.03$) and decreased as the plant developed. The same trend was observed for wasps ($p < 0.001$; df = 6; Kruskal-Wallis $Chi^2 = 22.96$). Differences in density between maize growth stages were observed for bugs ($p < 0.01$; df = 6; Kruskal-Wallis $Chi^2 = 20.54$) and carabids ($p = 0.018$; df = 6; Kruskal-Wallis $Chi^2 = 15.23$), although their densities were low.

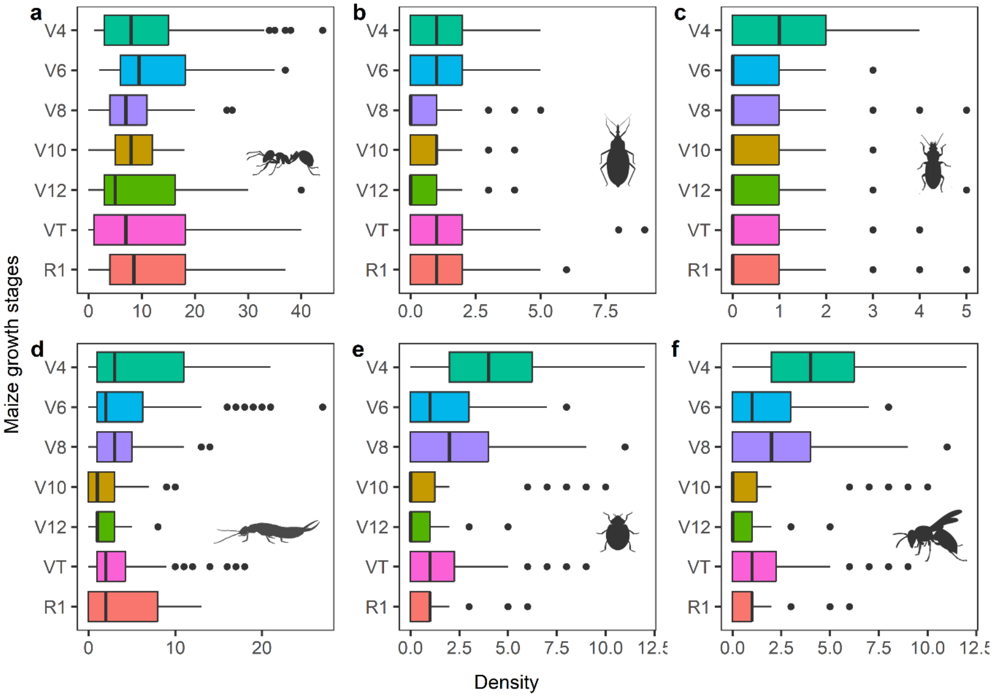


Figure 25. variation of fall armyworm insect natural enemies' predators associated with maize growth stages. **a:** ants' density; **b:** bugs density; **c:** carabids density; **d:** earwig density; **e:** ladybirds' density; **f:** wasps' density. Data shown are from 2021 and 2023 surveys. The height of the boxes indicates the range where the central 50% of the predator's density values lie, representing the interquartile range (IQR); the lines inside the boxes represented as the median. The points outside the whiskers are outliers, indicating unusually high or low predators' density values for maize growth stages. V4, V6, V8, V10 and V12 represent the completely unfold four, six, eight, ten and twelve leaves stages respectively; VT is silk appearance and pollen shedding stage and R1 the green mealie stage.

Population dynamics of fall armyworm and associated insect predators' natural enemies

The results in Figure 2 in the Appendix show that the FAW infestation parameters vary according to the maize growth stage, with differences between the two agro-ecological zones. The incidence is low at the beginning (V4 stage) and increases as the plant grows, reaching a maximum at R1 stage. The severity score is lower at stage V4 than at the other growth stages. As the plant progresses in stage, the degree of infestation increases, with a higher score recorded at stage V12. However, the larval density is highest at stage V4, decreases until stage VT and increases again at stage R1. This trend in larval density indicates the possible existence of a second generation of FAW at stage R1. To compare these results with those of the density of predatory insects, a correlation test was carried out and variables that were highly correlated were included in the model. Two infestation parameters, namely severity and larval density, were arbitrarily selected to explain the relationship with the density of each predator group (Table 18).

Differences between the characteristics of the different maize stages and agro-ecological zones were observed as a function of severity, but predator groups did not positively influence the severity. However, according to the model, predator groups influenced the FAW larval density. The trends observed at the early growth stage of the maize (V4) are such that at this stage there is high larval density, low incidence and low severity (Figure 2 Appendix). It is also at this stage that we see a high abundance of ladybirds, earwigs and wasps (Figure 25). This means that these groups of predators are more likely to attack the young larval stages of FAW (neonates, L1, L2). The results in Table 18 show that ladybirds, ants, carabid beetles, bugs, year of collection and growth stage of maize have a significant effect on FAW larval density. Ladybirds and carabid beetles probably attack the L1, L2, L3 and L4 stages of FAW (Table 17), but their densities were low and sometimes zero at certain growth stages. This suggests occasional predation in the maize system. Ants were most abundant at R1 stage and were the only group with significant densities at all growth stages. No significant effect of wasps, earwigs and agro-ecological zones on FAW larval density according to the model.

Table 18. General linear mixed models assessing the effects of predator community, the year, the agroecological zones and the maize growth stages on the severity and number of fall armyworm larvae. Model statistics are reported after ANOVA and likelihood ratio (LR) tests.

Response variable	Fixed variable	LR	df	p-value (>Chisq)
Severity	Ladybirds	0.24	1	0.623
	Earwig	1.1	1	0.294
	Ants	0.77	1	0.380
	Wasps	0.02	1	0.871
	Carabids	0.01	1	0.896
	Bugs	0.23	1	0.627
	Year	2.24	1	0.134
	Zones	**10.70**	**1**	**0.001**
	Maize stages	**260.15**	**6**	**<0.001**
Number of FAW larvae	**Ladybirds**	**17.37**	**1**	**<0.001**
	Earwig	0.05	1	0.820
	Ants	**99.12**	**1**	**<0.001**
	Wasps	0.48	1	0.486
	Carabids	**30.97**	**1**	**<0.001**
	Bugs	**49.99**	**1**	**<0.001**
	Year	**23.75**	**1**	**<0.001**
	Zones	1.07	1	0.299
	Maize stages	**7661.20**	**6**	**<0.001**

Discussion

In a community, all animals feed on plants, either directly or indirectly. Herbivores eat plants directly, and other animals are eaten by predators and parasitoids. Some predators prey on herbivores, while others prey on other predators or parasitoids (Sunderland et al., 2023). The complex network of interactions within the FAW natural enemy community shows dynamic patterns according to agro-ecological zones and maize growth stages (Murúa et al., 2006; Wyckhuys and O'Neil, 2006; Durocher-Granger et al., 2024). The natural enemies of FAW, such as parasitoids and predators, play an essential role in integrated pest management (IPM) strategies for FAW (Tepa-Yotto et al., 2022b). This study highlights the diversity of natural enemies of FAW, their abundance in different agro-ecological zones and their impact on FAW population dynamics in the maize system. The study identified 10 species parasitizing FAW in six families, of which Braconidae and

Ichneumonidae were the most abundant. These results are consistent with previous studies highlighting the importance of these families in FAW-targeting parasitoid communities (Meagher et al., 2016; Kenis et al., 2023). Notable species include *Te. remus*, *Ch. bifoveolatus*, *Charops diversipes* and *C. luteum*, which are known for their effectiveness in parasitizing FAW eggs, both eggs and larvae, and larvae (Agboyi et al., 2020; Durocher-Granger et al., 2021). Parasitoid species were more abundant in the early stages of maize growth (V4, V6 and V8) and in the late stage R1. Similar results were obtained by Durocher-Granger et al. (2024) showing the abundance and diversity of parasitoid species at early and late stages, highlighting the effect of planting dates.

The diversity of parasitoid species was much higher at mid-altitude than at low altitude. One reason for this difference is that sampling of larvae was greater at mid-altitude than at low altitude. This difference could also be explained by the composition of the landscape as reported by Mailafiya et al. (2010). The mid-altitude is characterized by a mountainous landscape with a high plant diversity, while the low altitude is a plain. The discovery of *Tr. chilonis* at low altitude and its specific collection at the R1 stage suggest a possible niche adaptation, confirming studies highlighting the habitat specificity of parasitoid species (Hoballah et al., 2004). The likely presence of new species (*Diadegma sp.* and *Drino sp.*) requires detailed morphological and molecular studies to confirm their taxonomy and assess their biocontrol potential, as suggested by Fagan-Jeffries et al. (2024). Among the parasitoid species reported in the literature from Africa and Asia (Kenis et al., 2023), *Brachymeria sp.* is not included. This study is the first to report its presence on FAW in Africa. In the literature by Wyckhuys et al. (2024a), *Brachymeria ovata* was reported in laboratory performance tests against FAW pupae. *Te. remus* showed the highest parasitism rate among egg parasitoids at mid-altitude, reinforcing its status as a primary biocontrol agent against FAW (Kenis et al, 2019; Kenis, 2023). The parasitism rate of *Te. remus* was low at low altitude compared to mid-altitude, but the opposite was observed for predators and even the infestation rate of FAW. This can be explained by the fact that *Te. remus* and *Tr. Chilonis* were sometimes found colonizing the same egg masses at low altitude. Under conditions where *Te. remus* alone parasitized the egg masses, 100% parasitism was observed at low altitudes. In Cameroon, 100% parasitism by *Te. remus* was also reported by Abang et al. (2021). The relatively high parasitism rates of larval parasitoids such as *C. luteum*, *Charops diversipes* and *Ch. bifoveolatus* highlight the potential of multi-stage parasitoid species in the management of FAW populations (Durocher-Granger et al., 2021). *C. luteum* is a species that parasitizes several lepidopteran species and is common in several studies of FAW parasitoids in Africa. Like *Te. remus*, it is a candidate for augmentative biological control of FAW in Africa (Agboyi et al., 2019; Agboyi et al., 2021; Otim et al., 2021).

Predator diversity was significantly higher, with 31 species in four orders and eight families. Hymenoptera were well represented, in line with literature indicating their role as generalist predators in agroecosystems (van Huis, 1981; Perfecto et al., 1991; Held et al., 2008). Predator species richness was higher at low altitude than at mid-altitude. The high predator species richness at low altitude suggests that environmental factors such as temperature and humidity play a critical role in the formation of predator communities (DeBach and Rosen, 1991). Habitat diversity influences the abundance of insects in an ecosystem in general and the natural enemies of FAW in particular (Wyckhuys et al., 2024b). According to Corcos et al. (2018), habitat diversity did not affect species richness, but it modulated the regularity of most groups of predatory and parasitoid insects along an altitudinal gradient. In a study by Wyckhuys and O'Neil (2007), the abundance of social wasps was associated with floral cover, while earwigs were associated with herbaceous cover in habitats beyond the field boundary. After correcting for altitudinal effects, many associations between predator abundance and FAW dynamics remained valid according to Wyckhuys and O'Neil (2006). The relative abundance of ants, particularly at low altitude, highlights their potential as key predators in the control of FAW, consistent with Way and Khoo (1992) on the effectiveness of ants in pest control. Analyses of predator abundance revealed significant differences between agro-ecological zones and maize growth stages. Ants were particularly abundant in all maize growth stages, suggesting their role as primary predators of FAW (Perfecto, 1991). Dassou et al. (2021) found ants to be the most abundant and diverse in maize-based systems. Wyckhuys et al. (2024a) also suggest that although they are the most abundant group of predators in tropical and subtropical agrosystems, their role as natural enemies is overlooked.

Differences in predator abundance were recorded in this study, with ants and earwigs showing higher densities at low altitude and at specific maize stages (V6 and R1), and ladybirds at mid-altitude. Chipabika et al. (2023) recorded significant densities of two groups of predators (wasps and bugs) in different agro-ecological zones. Taking altitude into account, Wyckhuys and O'Neil (2006) found no variation between altitude and FAW predator abundance. Earwigs were the most abundant in Wyckhuys and O'Neil's (2006) studies and their numbers increased gradually during the whorl stage of maize. Sharanabasappa et al. (2019) reported a density of 1 to 2 individuals per plant compared to ladybirds, which represented 0.5 to 1 individual per plant. The presence of earwigs at the V6 and R1 stages is justified by the fact that they consume eggs and young larvae (Hoballah et al., 2004; Ahissou et al., 2021). These maize stages correspond to the period of oviposition and emergence of young larvae in both zones. As for the ladybirds, their presence was mostly observed at the V4 stage. Ladybirds are known as large aphid predators (Lapchin et al., 1987; Weber and Lundgren, 2009), but their role as predators of other insects has been reviewed by Evans (2009), who points to numerous studies showing that their impact on non-hemipteran or homopteran prey (such as juvenile Lepidoptera and Coleoptera) varies considerably. This impact can be low or high depending on the prey species and the different environments. Hoballah et al. (2004) reported predation on FAW eggs, which corroborates our observations of egg and L1 stage predation. Predators such as stink bugs were found at lower densities but were observed parasitizing advanced larval stages of FAW. The same observations were reported by Hoballah et al. (2004); Firake and Behere (2020). Regarding the diversity of arthropod natural enemies of FAW, the groups considered in this study are not the only known predators, as Wyckhuys and O'Neil (2006); Hoballah et al. (2004); Firake and Behere (2020); Maruthadurai et al. (2022); Riaz et al. (2024) have also reported spiders, lacewings and staphylinid larvae as predators of FAW.

FAW infestation levels were lower at mid-altitude than at low altitude. This corroborates the results of Cokola et al. (2021a). FAW infestation parameters varied according to the growth stage of maize. Beserra et al. (2002) found that the distribution of FAW larvae and eggs varied according to the phenological stage of maize. During the early stages of the plant (V1-V3), the first and second instars are predominant and approximately one to six larvae per plant are observed (Murúa et al., 2006). In this study, larval densities peaked at stages V4 and R1, indicating two potential generations of FAW. Correlation analyses revealed significant relationships between predator densities and FAW larval densities, particularly in the early maize stages (V4) where ladybirds, earwigs and wasps were more abundant. Mathematical modelling by Reuben et al. (2023) supports our findings by suggesting that during early maize growth, integrating natural enemies with best agricultural practices is a sustainable method of FAW management, as predator effects are predictable during this time. The statistical model indicates that ladybirds, ants, ground beetles and stink bugs significantly influence FAW larval density, highlighting the importance of predator diversity in reducing pest populations (Finke and Denno, 2005). However, the lack of a significant effect of wasps and earwigs on larval density suggests that their role may be more context specific or complementary to other natural enemies (Symondson et al., 2002).

Sporadic low densities of wasps were reported by Wyckhuys and O'Neil (2006). The high abundance of ants, ladybirds and earwigs during the early stages of maize development was associated with high larval abundance and low incidence and severity of FAW in maize. A similar trend was observed by Wyckhuys and O'Neil (2006). At this point, it is difficult to conclude that the presence of these predators significantly reduces the incidence and severity of FAW, as larval densities are usually high initially with young larvae that cannot feed sufficiently on maize leaves (Beserra et al., 2002). Given the egg-laying capacity of moths, it is expected that the density of FAW in a maize field would be explosive at advanced stages of the crop. This density is sufficiently reduced as the crop grows to only one larva per plant (Murúa et al., 2006). This reduction could be due to predation and parasitism or cannibalism between FAW larvae. Studies on FAW predation in Africa are scarce and it is difficult to compare the results of this study with those reported in the literature from Africa. At least some authors, such as Koffi et al. (2020); Ahissou et al. (2021); Dassou et al. (2021); Chipabika et al. (2023), report on a particular group without specifying the exact relationship with FAW infestation. To better understand the impact of the predator groups on FAW, experimental field trials and laboratory studies could be conducted as recommended by Wyckhuys and O'Neil (2006).

Conclusions

The study provides a comprehensive understanding of the identity, diversity, and dynamics of FAW infestations and its natural enemies in eastern DRC. The identification of potentially new parasitoid species and predators specific to the eastern DRC region offers opportunities to expand biocontrol programs. The escalating threat posed by FAW underlines the urgency of understanding the interactions between this damaging pest and its natural enemies in maize ecosystems. The results highlight the importance of maintaining and increasing natural enemy populations for the sustainable management of FAW. By leveraging the strengths of various natural enemies and considering environmental factors, effective IPM strategies can be developed to manage FAW populations. By elucidating community trends, diversity patterns, and ecological interactions, researchers can unveil novel avenues for enhancing biological control measures and mitigating the impact of FAW infestations on maize production. Future research should focus on the ecological interactions between FAW and its natural enemies, the impact of environmental variables on these interactions, and the potential for integrating biocontrol agents into broader pest management programs.

2. Microbial based biocontrol of *Spodoptera frugiperda* by indigenous entomopathogenic fungi

This section was adapted from original published article: **Cokola, M.C.,** Ben Fekih, I., Bisimwa, E.B., Caparros Megido, R., Delvigne, F., Francis, F., 2023. Natural occurrence of *Beauveria bassiana* (Ascomycota: Hypocreales) infecting *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae) and earwig in eastern DR Congo. Egyptian Journal of Biological Pest Control 33, 54. https://doi.org/10.1186/s41938-023-00702-2; and a manuscript in preparation: Endemic isolates of *Beauveria bassiana* from eastern DR Congo: assessing direct and indirect potential against *Spodoptera frugiperda.*

Abstract

The fall armyworm (FAW), *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae), poses a threat to the food security of populations in Sub-Saharan Africa because of its damage to maize crops. As alternative to the use of hazardous pesticides, microbial control is one of the most promising sustainable approaches adopted to limit the damages caused by FAW. The sampling was conducted in maize fields and targeted mainly larvae of FAW infested with entomopathogenic fungi, however during the survey; cadavers of earwig found on the same sampling sites were also collected and involved in the study. Morphological study of fungal features and molecular characterization by phylogenetic analysis confirmed that isolates belong to *Beauveria bassiana*. 3 isolates of *B. bassiana* P5E (OP419735.1), KA14 (OP419734.1) and PL6 (OR687721.1) were isolated from cadavers of FAW and earwig. These three isolates were compared with the commercial strain GHA and a Gembloux isolate (BGx) against the L2 and L4 larval stages of FAW. The bioassay results show that when applied to L4 larvae, isolates GHA, KA14 and PL6 showed higher mortality rates with 72.68 ± 8.82%, 68.52 ± 16.03% and 65.28 ± 2.40% respectively. By approximately the seventh day, 50% of the L2 and L4 larval stages treated with the GHA, KA14 and PL6 isolates had died. To our knowledge, this is the first study reporting the occurrence of *B. bassiana* infecting insects in DR Congo. Isolates KA14 and PL6 are of interest for the development of ecofriendly integrated pest management against FAW in South Kivu.

Keywords: *Spodoptera frugiperda*, *Beauveria bassiana*, epizooty, earwig, molecular characterization, pathogenicity.

Introduction

Agriculture, food, fisheries, and forestry resources have been increasingly affected by invasive species such as the fall armyworm (FAW) *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae) throughout the world (Teem et al., 2020). The invasive behavior of a species depends on the characteristics related to its biology and the climatic conditions where it is introduced (Early et al., 2018). The FAW, *S. frugiperda* a lepidopteran insect pest, well-known as a devastating pest in North and South America where it originated and has become a major invasive pest at a global scale in the past decade (Tay et al., 2023c). This pest was first reported in Africa in 2016 (Goergen et al., 2016) and has spread rapidly over the rest of the world excluding Europe. The polyphagous nature of FAW enables it to successfully establish in newly invaded areas with suitable climatic conditions for its survival (Cokola et al., 2021b).

Management of FAW is mainly based on the excessive use of pesticides to face with alarming damages observed among smallholder farmers in Africa (Hruska, 2019). Studies reported losses of 26.5-58.8% when non-chemical applications are made to control FAW (Van den Berg et al., 2021). In the Democratic Republic of Congo, FAW losses in maize production are approximately 633.000 metric tons per year, with an estimated monetary value of US$ 74.5 to 185.5 million (Day et al., 2017). The environmental risks associated with pest-control measures have always urged scientists towards biological-based alternatives. Ecofriendly pest management approaches are nowadays of utmost importance to ensure a sustainable agriculture (Hruska, 2019).

The FAW is naturally attacked by several microorganisms including entomopathogenic fungi (EPFs), nematodes, viruses and bacteria and larval mortalities were often found in infested corn fields (Visalakshi et al., 2020; Withers et al., 2022). In its native area, e.g. Mexico, FAW has been found infected naturally by EPFs (Cruz-Avalos et al., 2019). In agroecosystems, EPFs, especially the anamorphic taxa *Beauveria bassiana* and *Metarhizium anisopliae* (Ascomycota: Hypocreales), are among the natural enemies of several insect pests that have been potential candidates for conservation biological control (Meyling and Eilenberg, 2007). Laboratory tests generally target second-instar larvae (Akutse et al., 2019;

Guo et al., 2020) and results have shown larval mortality of up to 95% (Wraight et al., 2010).

Beauveria bassiana is widely distributed in nature and is the most common and ubiquitous EPF with the ability to infect a variety of insects belonging to various orders (Guo et al., 2020). In America, *B. bassiana* has been isolated from both FAW cadavers and from soil (Cruz-Avalos et al., 2019). However, *B. bassiana* has not been officially recorded in Africa on FAW cadavers. Most bioassays of *B. bassiana* to control FAW in Africa used existing strains from collections obtained either from soil or from other insects (Akutse et al., 2020). Although, the fungal infections with *M. rileyi* have been reported in field populations at Africa (Withers et al., 2022) and Asia (Acharya et al., 2022). Data on the characterizations of EPFs to control insect pests of crops in Democratic Republic of Congo (DRC) are scarce. Therefore, no study has been conducted on FAW using *B. bassiana* in DRC. Existing information's on EPF's were provided by Akutse et al. (2020) from tests performed with *M. anisopliae* isolated from soil to determine their virulence against FAW. This study provides the first occurrence, characterization and pathogenicity of a *B. bassiana* new isolates obtained from FAW and earwig cadavers under maize growing conditions in eastern DRC.

Materials and methods

Sampling sites and collection of cadavers

A monitoring system has been developed in South Kivu province, Eastern DRC during the period from December 2019 to June 2021. South Kivu is one of 26 provinces of the DRC with an area of approximately 65.070 Km^2. Three sites named Ruzizi plain (Kamanyola), Kabare and Kalehe were investigated, and characteristics are presented in Table 19. These sites are part of the corridor considered suitable for the FAW according to the existing bio-climatic zones in South Kivu (Cokola et al., 2020). Fields infested with FAW and in which the application of insecticides was not reported were targeted. Transect method was applied to select the studied fields. Accordingly, 14 fields were investigated in Kamanyola during the period between February and June 2021 versus 17 in Kabare during the period between December 2019 and May 2021 and 8 in Kalehe in December 2019. The W-sampling technique was used in each field to identify and collect cadavers from maize plants (Cokola et al., 2021a). Sampling was targeting FAW cadavers with and without symptoms of fungal infection. A total of 78 cadavers including 71 of FAW and 7 of earwig were collected. 54 cadavers were collected in Kamanyola of which 46 were mycosed against 8 non-mycosed; 22 in Kabare of which 7 were from earwigs. Among the 15 cadavers from FAW, 9 were mycosed versus 6 non-mycosed and 2 mycosed cadavers in Kalehe. All collected specimens were placed in sterile 1.5 ml eppendorf tubes and stored at 4ºC on the day of collection until isolation.

Table 19. Characteristics of the study sites.

Characteristics	Sites		
	Kabare	**Kalehe**	**Ruzizi plain (Kamanyola)**
Latitude	2º18'57" S	2º04'37" S	2º46'21" S
Longitude	28º47'20" E	28º53'31" E	29º00'5" E
Elevation (m)	1637	1725	889
Mean annual temperature (ºC)	22.06	24.01	25.06
Annual precipitations (mm)	1601	1527.3	1063.7

Fungal isolation

Collected samples were allocated into three groups: (1) freshly looking mycosed cadavers, (2) cadavers without visible mycelium, and (3) cadavers with very old state of mycosis. The latter group was excluded from the study. Same protocol of grouping was adopted for earwig's cadavers. Sabouraud Dextrose Agar (SDA) medium (Sigma-Aldrich®) supplemented Streptomycin (0.5 ml of 0.6 g ml-1), Tetracycline (0.5 ml of 0.05 g ml-1) and Cyclohexamide (1 ml of 0.05 g ml-1) was used as media for fungal growth. Fungal isolation procedure from the collected cadavers was performed following two methods. From the first group, each cadaver was examined under binocular and a sterile inoculation needle was used to pick up a mycelia fragment and to inoculate the SDA media following a zigzag pattern. From the second group, the cadavers were surface sterilized with 70% ethanol for a period of 10 seconds to be washed three times with demineralized sterile water and placed on filter paper to absorb the remaining water. Afterward, each cadaver was incubated in SDA. All the plates were incubated at 25±1ºC in darkness. Plate with cadavers was checked for fungal growth up to 5-8 days. Cadavers showing a fungal outgrowth were subject to the protocol for fungal isolation as adopted for the first group. Plates inoculated with mycelia were checked up to 15 days for fungal growth.

Morphological identification

Beside the aspect and color of fungal colonies, morphological studies of the isolated fungi were mainly based on the shape and size of conidia. Fungal structures were mounted in lactophenol blue solution (Sigma-Aldrich®) and characterized using an Olympus microscope at 400× magnification. The fungi were identified using the key by Humber (2012). Microphotographs were taken with a DS-Qi2 camera (Nikon camera DSQi2, Nikon France, France). Intermediate internal magnification dial was set up to switch the magnification of the entire microscope between 1.0x and 1.5x with an exposure time of 300 ms and dial-illuminator's intensity of 30%. To determine the microscopic measurements of the conidia, the mean and standard deviation values were calculated from 50 randomly selected conidia using Fiji ImageJ 1.53t (National institute of health, USA). Parameters measured were length representing the diameter along major axis of conidia and width representing the diameter along minor axis of conidia (Talaei-Hassanloui et al., 2006). To characterize the *Beauveria* isolate, these parameters were compared to another *B. bassiana* isolate KA14 obtained in the same region (eastern DRC) on earwig cadaver.

DNA extraction, PCR amplification and purification

Pure culture of mycelial was harvested with a sterile scalpel blade from the SDA plate and placed in sterile 2 ml Eppendorf tubes containing two sterile 3 mm diameter Tungsten Carbide Beads (QIAGEN, Germany). The Eppendorf tubes were cooled in liquid nitrogen for 30 sec, before being crushed using a Retsch Mixer Mill MM 400 for 1 min at 30 Hz. The freshly crushed material was used for ribosomal DNA extraction, using the Qiagen DNeasy® Plant Mini Kit following the manufacturer's protocol. The rDNA concentration was measured with the Nanodrop (Nanodrop One ISOGEN) and diluted to 10 ng/µl. Extracted genomic DNA was amplified by internal transcribed spacers (ITS-5.8S rDNA). Forward ITS5 (5'-TCCTCCGCTTATTGATATGC-3') and Reverse ITS4 (5'-GGAAGTAAAAGTCGTAACAAGG-3') primers were used to amplify the region (White et al., 1990). Amplification reactions were performed in a total volume of 50 µl consisting of a mixture of 25 µl of Q5® High-Fidelity PCR Kit (E0555L), 2.5 µl of Reverse ITS4 primer, 2.5 µl of Forward ITS5 primer, 15µl of molecular grade H_2O and 5 µl of genomic DNA. PCR reactions were performed under the following conditions: an initial step at 98°C for 3 min., followed by 35 cycles of 98°C for 1 min, 55°C for 1 min, and 72°C for 1 min 30 sec; a step at 72°C for 10 min; and a final step at 4°C infinitely. Amplicons were visualized by agarose gel electrophoresis (1%) in 100 ml of 1 × Tris-Boric Acid-EDTA (TBE) and added 5 µl of ethidium bromide (EtBr 50 mg/ml). Electrophoresis was performed in 1 × TBE buffer at 100 V for 45 min and recorded in a Bio Rad gel documentation system (Gel Doc EZ Imager).

Sequencing analysis

The purified amplicons were sequenced by Sanger sequencing Eurofins Genomics (Anzinger STR. 7A/D-85560 Ebersberg, Germany). The sequences were assembled and edited using BioEdit sequence alignment editor 7.2.5 (Hall, 1999). The resulting contigs were processed through BLASTn analysis using the GenBank database (https://blast.ncbi.nlm.nih.gov/). The sequences of *B. bassiana* isolates were submitted to GenBank data base and compared to those of the type strains previously reported in the literature to construct phylograms. The sequences of the *B. bassiana* isolate were grouped with other *Beauveria* sequences deposited in the GenBank and were aligned by multiple sequence alignment (MUSCLE) using MEGA 11 software (Tamura et al., 2021). The ITS sequence of *Penicillium chrysogenum* was used as out-group. The evolutionary history was inferred using the Neighbor-Joining method (Saitou and Nei, 1987). The percentage of replicate trees in which the associated taxa were clustered together in the bootstrap test with 1000 replicates (Felsenstein, 1985). The evolutionary distances were computed using the p-distance method (Nei and Kumar, 2000). This analysis involved 17 nucleotide sequences and conducted using MEGA11.

Bioassay

The FAW strain from CABI (Delémont, Switzerland) was reared in the quarantine laboratory (L2Q) of the laboratory of Functional and Evolutionary Entomology in Gembloux, Belgium. The larvae were fed on an artificial diet consisting mainly of maize flour, brewer's yeast and wheat germaline. The larvae were reared at a temperature of 24 ± 1°C, a relative humidity of 60 ± 5% and a photoperiod of 16/8h (L:D). Five isolates of *B. bassiana* (GHA, KA14, P5E, BGx and PL6) were studied. The commercial strain GHA and the BGx isolates were obtained from the collections of the Laboratory of Functional and Evolutionary Entomology. The commercial strain GHA was obtained from CERTIS Biologicals (BOTANIGARD® 22WP). The BGx isolate was obtained from sugarbeet soil using the bait method. Isolate P5E was obtained from FAW cadavers brought back from South Kivu. The other two isolates (KA14 and PL6) were isolated from earwig cadavers. All isolates were grown on SDA medium and incubated in the dark at 23 ± 1°C.

Fungal conidia were harvested from 2 to 3weeks old sporulated cultures (Akutse et al., 2019) and suspended in a solution containing distilled water with 0.03% Tween 80. Conidia were filtered and quantified under a light microscope using a hemocytometer, and the concentration for each isolate was reduced to 1×10^8

conidia/ml by the dilution method. Prior to the experiments, the viability test was performed with a concentration of 10^5 conidia/ml plated on SDA medium. Conidial germination was assessed after 24 hours by counting 100 randomly selected conidia under a light microscope. Conidia were considered germinated if the length of the germ tube was at least twice the diameter of the conidium (Inglis et al., 2012).

The following *B. bassiana* isolates and a control (sterile distilled water + Tween 80 0.03%) were tested against two larval stages of FAW (L2 and L4). For each larval stage, 30 larvae were placed in a Petri dish with filter paper and 1 ml of solution from each treatment was sprayed with a Burgerjon's sprayer. Treated larvae were individually placed in petri dishes containing a piece of artificial food as a food source and incubated at 24 ± 1°C. Larval mortality was recorded daily for 10 days of the experiment. All treatments were arranged in a completely randomized design with three replicates. A mycosis test was performed to confirm mortality due to infection by the treated fungus. Dead larvae were surface sterilized with 70% alcohol and then rinsed three times in sterile distilled water. Surface sterilized dead larvae were kept separately in petri dishes lined with sterile filter paper moistened for fungal growth to test whether larval mortality was due to the treatments applied (Akutse et al., 2019). Mortality was assessed using the Abbott formula (Abbott, 1925).

Statistical analysis

All statistical tests were performed in R 4.1.3 (R Core Team, 2021). Conidial size differences between isolates were analyzed by Mann Whitney U test. A two-factor analysis of variance (ANOVA) was performed using the 'rstatix' package (Kassambara, 2021) to estimate differences between treatments. In the case of a significant difference, a multiple comparison of means between treatments was performed using a Tukey HSD (Honestly Significant Difference) test using the "multicompView" package (Graves et al., 2019). Using the Kaplan-Meier method, we estimate survival probabilities at each event time using "survival" and "survminer" packages, considering the number of FAW larvae exposed to entomopathogenic fungi and the number of events, to construct the survival curve. The log-rank test was used to assess for any differences in survivals between treatments. The significance level was set at 5% for all tests. The ggplot2 R package (Wickham, 2016) was used to generate all graphs.

Results

Morphology of *Beauveria bassiana* isolates

Based on the morphological characteristics of the conidia of isolates P5E and KA14, preliminary results indicated that it was indeed *B. bassiana*. The morphological characteristics of the isolates are presented in (Figures 26 and 27). Isolates exhibited a cottony, powdery white mycelium without exudate drops on SDA medium. P5E refers to the location "Plaine de la Ruzizi" where the cadaver was collected, the number of the cadaver's sample in the batch collected, and the letter assigned to the replicate Petri dish according to the isolation method used. As with P5E, the name KA14 refers to the isolate obtained in Kabare territory from the 14 cadaver samples collected. The conidia of isolate P5E were generally ovoid to cylindrical and were white, gray to black in transparency compared to isolate KA14 whose conidia were cylindrical and white in transparency.

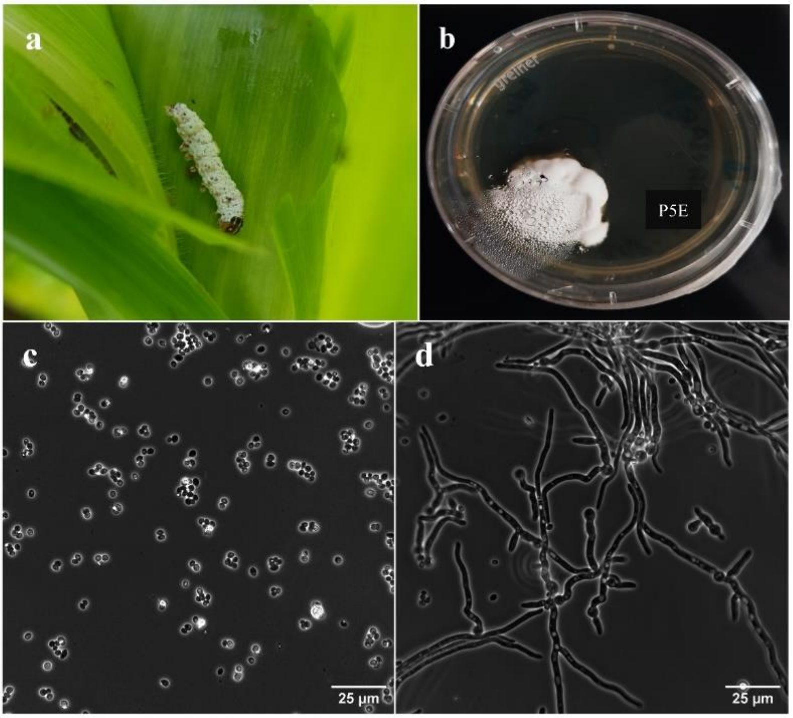


Figure 26. Morphological characteristics of *Beauveria bassiana* infecting the fall armyworm in natural conditions of South Kivu, eastern DR Congo. **a:** mycosed fall armyworm cadaver found on maize leaves. ©Marcellin C. Cokola; **b:** colony growth of *B. bassiana* isolate on SDA medium; **c:** conidia; **d:** conidiogenous cells. Pictures of conidia and conidiogenous

cells were taken by Nikon Eclipse Ti2-E inverted automated microscope with a Nikon camera DSQi2.

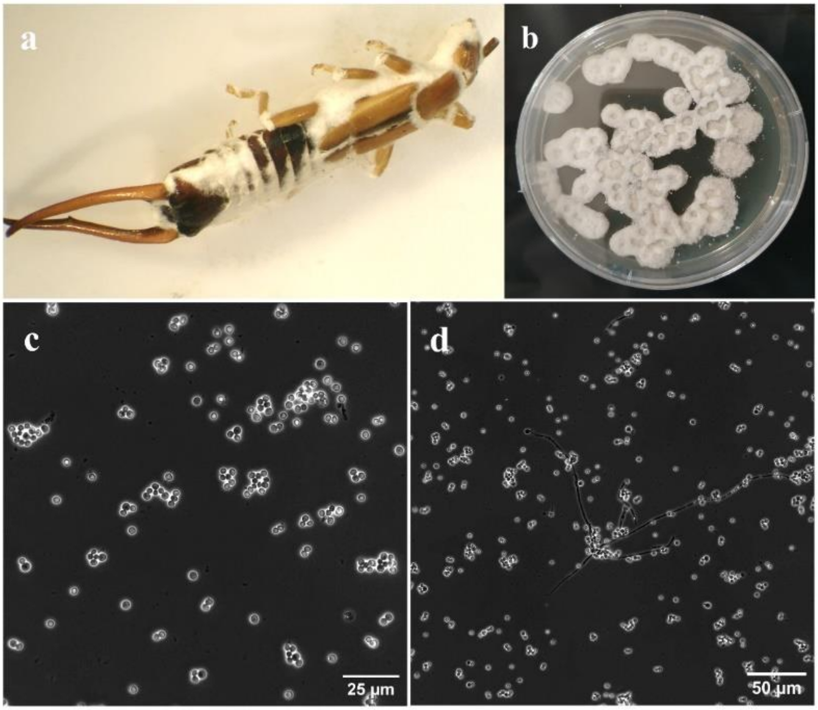


Figure 27. Morphological characteristics of *Beauveria bassiana* infecting the earwig in natural conditions of South Kivu, eastern DR Congo. **a:** mycosed earwig cadaver © Stereomicroscope Euromex DZ Serie; **b:** colony growth of *B. bassiana* isolate KA14 on SDA medium; **c:** conidia; **d:** conidiogenous cells. Pictures of conidia and conidiogenous cells were taken by Nikon Eclipse Ti2-E inverted automated microscope with a Nikon camera DSQi2.

Conidia from *B. bassiana* isolate P5E were slightly larger than those from KA14 in size, on average. Conidial measurements were highly variable and ranged from 2.4 to 3.6 µm in length and from 1.75 to 3.0 µm in width. Conidial size between *B. bassiana* isolate P5E and KA14 was compared in terms of length and width using the Mann Whitney U test (Figure 28). Conidial length varied significantly between the two isolates ($W = 257$; $p < 0.001$). The mean conidial length was 3.17 ± 0.32 µm for isolate P5E versus 2.69 ± 0.21 µm for isolate KA14. For conidial width, a significant difference was also obtained between the two isolates ($W = 965$; $p = 0.049$). The largest value of conidial width was recorded in isolate P5E (2.45 ± 0.27 µm) compared to isolate KA14 (2.34 ± 0.17 µm).

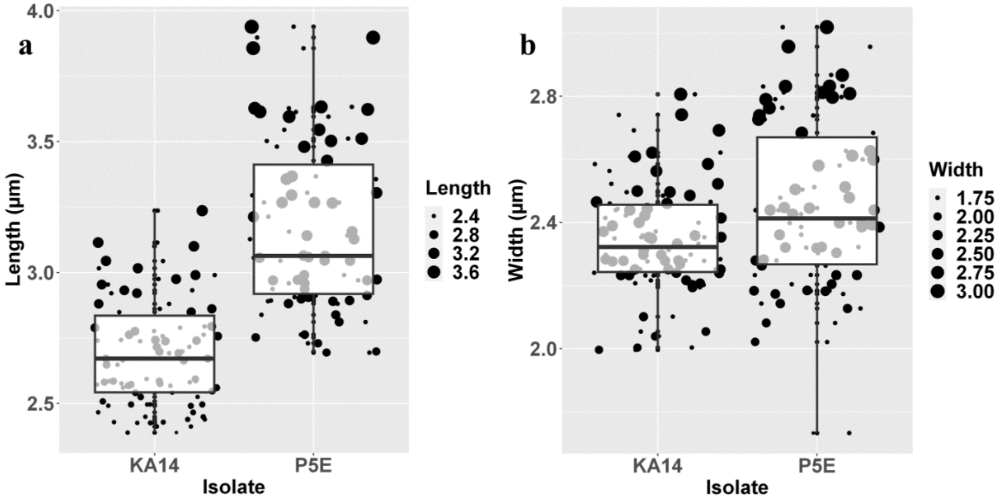


Figure 28. Comparison of conidial size (n = 50) of *Beauveria bassiana* isolate P5E obtained from fall armyworm cadavers to isolate KA14. **a:** conidial length; **b:** conidial width.

Molecular identification of *Beauveria bassiana* isolates

Sequencing of *B. bassiana* isolate ITS5-5.8S rDNA-ITS4 confirmed the identity of the species and corroborate with the morphological identification presented previously. Similarity of ITS amplicon of *B. bassiana* isolate P5E was checked with other sequences available in GenBank NCBI (Blastn). Furthermore, to illustrate differences between the amplicon sequences, phylograms were constructed. In this study, 17 sequences including the P5E isolate were used to build phylogenetic trees that were inferred from sequences of 10 isolates of *B. bassiana* and 6 other species belonging to the *Beauveria* genus. The sequence from *P. chrysogenum* was used as an out-group. The evolutionary history was inferred using the Neighbor-Joining method. The optimal tree was shown (Figure 29). The percentage of replicate trees in which the associated taxa clustered together in the bootstrap test (1000 replicates) was shown above the branches. The analyses clustered the *Beauveria* species into two major groups. The first cluster consisted of all *B. bassiana* isolates except for 1969 one. The P5E (OP419735.1) and KA14 (OP419734.1) isolates branched separately in this group. The P5E isolate was classified in the same clade as TS8 (KY515356.1) isolate from Iran and A30 (KC461101.1) from Mexico. Isolate KA14 was classified in the same clade as isolate 693 ICIPE (KM463112.1) from Kenya and isolate SY192 (OK482896.1) from China. The second group consisted of *B. bassiana* isolate 1969 (AY531998.1) and other *Beauveria* species namely *B.*

brongniartii, *B. pseudobassiana*, *B. varroae*, *B. australis*, *B. amorpha* and *B. caledonica*.

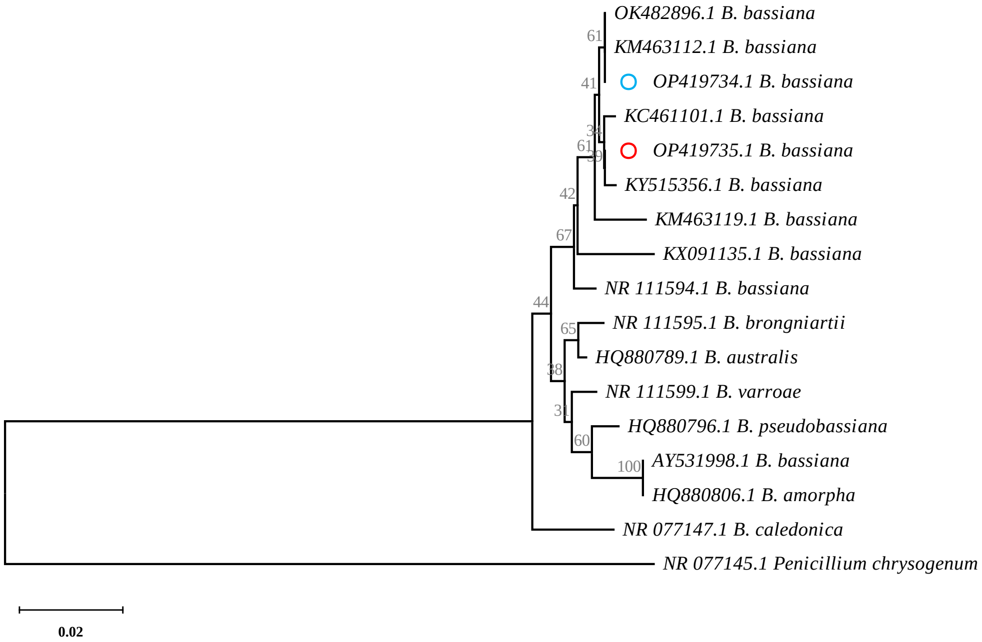


Figure 29. Phylogenetic tree of *Beauveria bassiana* isolated from Eastern DR Congo based on ITS sequences by using the Neighbor-Joining method. The percentage of replicate trees in which the associated taxa were clustered together was shown next to the branches. The tree was drawn to scale, with branch lengths in the same units as those of the evolutionary distances used to infer the phylogenetic tree. The red mark represents *B. bassiana* isolate P5E whereas the blue mark represents isolate KA14.

Pathogenicity of *Beauveria bassiana* isolates against fall armyworm

Figure 30 shows the mortality of FAW larvae exposed to fungal entomopathogenic isolates. All isolates caused mortality of FAW larvae. No significant differences were found when comparing mortality at the larval stage level ($p = 0.984$; df = 1; F = 0.00) and the combination of larval stages and entomopathogenic fungal isolates ($p = 0.429$; df = 5; F = 1.01). When applied to L4 larvae, isolates GHA, KA14 and PL6 showed higher mortality rates than isolates P5E and BGx ($p < 0.001$; df = 5; F = 30.59) with 72.68 ± 8.82%, 68.52 ± 16.03% and 65.28 ± 2.40% respectively. For L2 larvae, isolate KA14 was the most effective with a mortality rate of 72.68 ± 14.18%. No mortality was observed in the control. The p-values in Figure 31 indicate, with a confidence level of 0.95, that there is a statistically significant variance in survival probabilities over time between treatments for both L2 and L4 larvae. The Kaplan-Meier survival curve shows that only 12 to 25% of the larvae survive after 10 days. By approximately the seventh day, 50% of the L2 stage larvae treated with the GHA, KA14 and PL6 isolates had died. It took 7.5 days to kill these larvae with the P5E and BGx isolates. On L4 larvae, isolates GHA, KA14 and PL6 caused the death of 50% of the larvae after 6 days. Isolates BGx and P5E had LT50 of around 8 days at this larval stage.

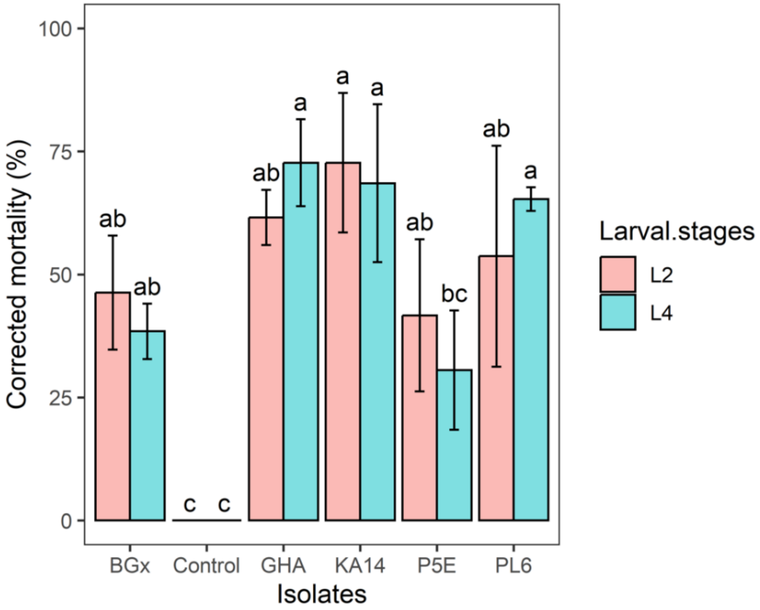


Figure 30. Corrected mortality of entomopathogenic fungal isolates against fall armyworm larvae. Same letters on histograms for each larval stage are not statistically different at 5% significance level according to Tukey's HSD test.

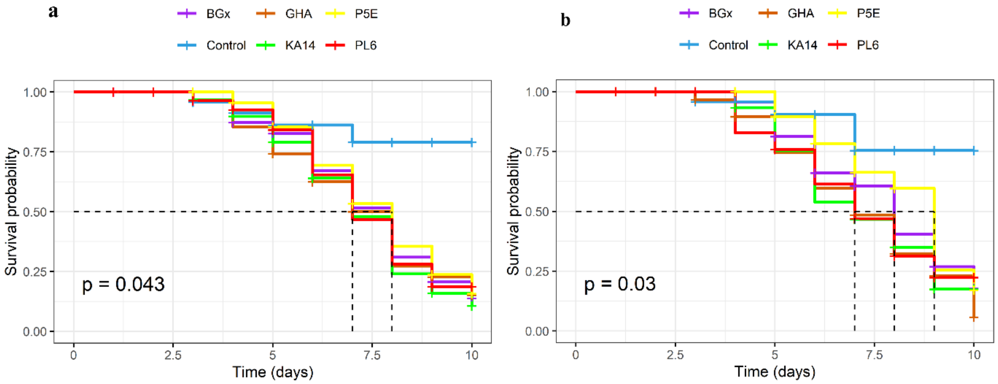


Figure 31. Kaplan Meier survival probability of fall armyworm larval stages infected by entomopathogenic fungi *B. bassiana*. The log-rank test was performed to test for significant differences between treatments. The survival rates were calculated based on tree replicates for each treatment. **a:** Survival probability of L2 larvae; **b:** Survival probability of L4 larvae.

Discussion

Insecticide applications against FAW in maize crop are not more as effective due to the cryptic feeding behavior of FAW larvae (Hardke et al., 2011a) and the application of insecticides when the larvae are too large and no longer susceptible, as well as incorrect application methods and timing (Van den Berg et al., 2021). In addition, pesticide application to control FAW poses a danger to natural enemies' predators and parasitoids that regulate FAW populations in newly invaded areas (Abang et al., 2021). For the first-time, this study describes 2 isolates of EPF *B. bassiana* from the DR Congo obtained from infecting FAW and earwig in maize crop as alternative biological control agents. In its native range, an invasive species such as FAW, has been found to be infected with entomopathogenic microorganisms (Cruz-Avalos et al., 2019). However, in newly invaded areas, new entomopathogenic agents have been reported and their presence indicated genotypes that potentially interact with FAW host populations, each other and their environment and are ideal candidates in the development of sustainable biological control (Withers et al., 2022). Since its invasion in Africa in 2016, no study has been reported about the presence of *B. bassiana* EPFs on FAW cadavers and beneficial insects such as earwig. At least, one study in Africa (Withers et al., 2022) and some others in Asia (Acharya et al., 2022) presented instead the occurrence of *M. rileyi* on FAW populations under natural conditions. However, this information remained unknown in DR Congo, where FAW was reported as a maize pest before being officially reported in Africa in 2016 (Cokola et al., 2021a).

Currently, it is relevant to analyze the multi-trophic interactions involving EPF, insect pest, maize plant and beneficial natural enemies. In this study, earwig known to be a predatory natural enemy of fall armyworm (Firake and Behere, 2020; Ahissou et al., 2021b), was found to be infected by EPF *B. bassiana* under natural maize growing conditions. This observation is not the first elucidated case where an entomopathogen infects a beneficial insect. Goettel et al. (1990) presented the effects or risk associated with the infection of beneficial insects by an entomopathogen and especially predators by giving some examples of mycosed insects under natural conditions. In the literature, infection of earwig by *B. bassiana* is rarely reported under natural conditions. This would have implications for biological control and understanding the epizootiology of this beneficial mycotic insect and the resulting effects in controlling FAW.

In the identification of *Beauveria* species, conidia are the primary morphological feature used, but they are not always sufficiently critical for classification and identification due to similarity with others (Zhang et al., 2022). The conidia of isolate P5E were generally ovoid to cylindrical and were white, gray to black in transparency. This corroborated the description of Rehner and Buckley (2005). Isolate P5E showed different morphological characteristics in terms of conidial size and shape compared to isolate KA14. Conidial measurements (length and width) were highly variable between the two isolates and fell within the range found by other authors (Talaei-Hassanloui et al., 2006). Although pathogenicity has not yet been determined for the P5E isolate, the morphological characteristics (conidial size) and the fungus isolation from FAW cadaver allowed to hypothesize the potentiality of this isolate as candidate for FAW biological control. Previous studies linked conidial size to virulence of EPF (Talaei-Hassanloui et al., 2006). For example, Talaei-Hassanloui et al. (2006) did not find a correlation between virulence and conidial size in *B. bassiana*. In contrast, Liu et al. (2003) found a positive correlation between conidial length and virulence of *B. bassiana* isolates. Additionally, a recent study (Ramírez-Ordorica et al., 2022) demonstrated a different chemical signature and higher virulence of *B. bassiana* isolates from mycosed insect cadavers than those obtained from soil.

The sequencing of the ITS5-5.8S rDNA-ITS4 of selected *B. bassiana* isolate confirmed the identity of the species and corroborated with the morphological identification. None of the sequences was 100% identical to each other, demonstrating the uniqueness and difference between the species considered. In most studies on the genetic diversity of *B. bassiana*, isolates from collections obtained either from infected insects or from soil were considered to build phylograms (Rehner et al., 2011). Phylogenetic analysis performed by Rehner and Buckley (2005) on *Beauveria* taxa showed that morphological species were paraphyletic and were classified into two unrelated clades, one of which was more related to *B. brongniartii* and the other to *B. bassiana*. This was observed in this study when building phylograms where the 1969 isolate of *B. bassiana* was found in the same group as the other species of the genus *Beauveria*. According to Meyling and Eilenberg (2007), the existence of two unrelated clades may partly explain the high genetic diversity within *B. bassiana*. This entomopathogenic species is not a specific host but an opportunist one capable of attacking a wide range of insects belonging to diverse taxa (Rehner and Buckley, 2005). The minor genetic distances (as in this study) between *B. bassiana* isolates according to Fernandes et al. (2009) indicated a considerable correlation with their geographical origin. In this study, isolate P5E was classified in the same clade as isolates from Iran and Mexico, although the latter were isolated from soil. *B. bassiana* EPFs from infected insects are mostly classified in the same clade (Rehner and Buckley, 2005).

FAW mortality was observed for all isolates tested. These results are consistent with previous studies showing efficacy of *B. bassiana* on FAW larvae (Idrees et al., 2022), but also on other pests of the same genus like *S. litura* (Dhar et al., 2019). Mortality on L2 larvae ranges from 42 to 73%, compared to 30 to 73% for L4. Under laboratory conditions, Ramanujam et al. (2020) reported that a concentration of 10^7 conidia caused over 60% mortality of L2 FAW larvae. The same mortality rates under laboratory conditions have been demonstrated by other authors (Cruz-avalos et al., 2019; Ullah et al., 2022). In the field, *B. bassiana* reduced infection rates by 69-76% and increased yields by 55-62% (Ramanujam et al., 2020). The GHA, KA14 and PL6 isolates were more effective against older larvae than younger larvae. These results contradict those of Bahar et al. (2011) where entomopathogenic fungi were more effective on young larval stages than older larvae. However, the result of Akutse et al. (2019) indicate that second instar larvae of FAW are less susceptible to EPFs. Several authors report the presence of mycosed FAW larvae in fields, generally older larvae (Firake and Behere, 2020; Visalakshi et al., 2020; Withers et al., 2022). The P5E isolate was found naturally in an older larva. The results show a LT_{50} of L2 and L4 larvae of 6 to 7 days, confirming the results of Ullah et al. (2022) who found a LT50 of 7 days for *B. bassiana* isolates. Isolates BGx and P5E applied at the same concentration (1×10^8) showed low efficacy against both larval stages of FAW. This could be explained by the viability, virulence or action time of the fungi (Castrillo et al., 2010; Sabbahi et al., 2008). In addition, the action of certain enzymes, such as proteases, chitinases and hydrolases, is crucial for cuticle penetration (Fang et al., 2005; Holder and Keyhani, 2005) and thus influences their virulence. Slow action of these enzymes could delay conidial germination until the next moult, thereby reducing the virulence of the fungus. Based on the results of this experiment, isolates KA14 and PL6 are of interest for the development of alternative methods to chemical control of FAW from an integrated pest management perspective.

Conclusions

This study provides the first information on the presence of EPF *B. bassiana* infecting FAW and earwig in the conditions of South Kivu, eastern DRC. Morphological and molecular characterization of the isolates confirmed the identity of the species and represents a starting point in the development of alternative management methods against FAW in Africa. As data on EPFs are scarce in DR Congo, this study provides insight into the existence of a diversity of entomopathogenic microorganisms that have not yet been exploited and that could be ideal a biocontrol agent for sustainable management of FAW and other pests. However, other EPF species such as *M. rileyi* have been reported to infect FAW larvae in newly invaded areas and it would be important to consider them in further investigations. The isolates reported in this study will be tested in fields for their effectiveness in the management of FAW in DRC. Furthermore, this study has implications in understanding the interactions between entomopathogenic microorganisms' especially *B. bassiana*, FAW, earwig, and climatic conditions of the invaded region.

Chapter 5

General discussion

Photo by Marcellin C. Cokola

Chapter 5. General discussion

1. Monitoring and forecasting of the fall armyworm in South Kivu

Fall armyworm is a highly adaptive and migratory pest that has become a significant threat to maize and other crops in various regions (Day et al., 2017; Mendesil et al., 2023), including eastern DRC. Understanding the habitat extent, environmental preferences and impacts of FAW infestations is essential for developing effective management strategies (Kenis et al., 2023). This discussion explores these aspects by integrating the results of several studies conducted in South Kivu Province, focusing on bioclimatic factors, seasonal variations and farmers' agricultural practices that influence FAW dynamics. The adaptability of FAW is further enhanced by its polyphagous feeding behavior, phenotypic and genotypic plasticity and high migratory capacity, which allows it to rapidly traverse large areas (Westbrook et al., 2016; Montezano et al., 2018). In South Kivu, FAW has colonized new areas by migrating several kilometers per generation (Sparks, 1979).

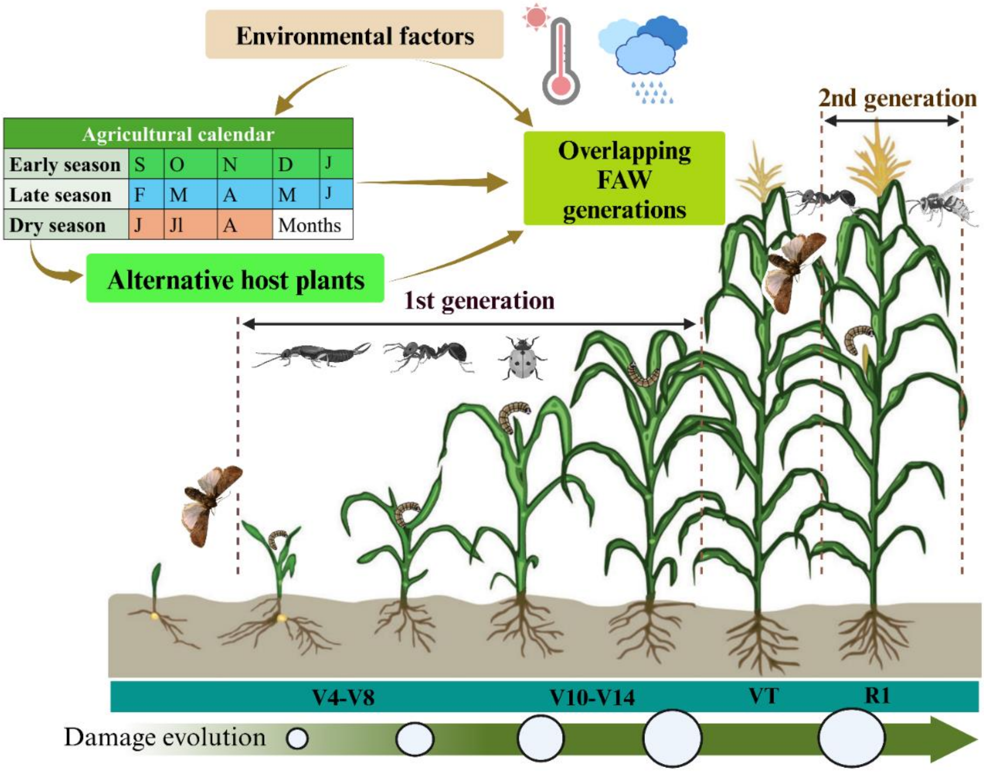
The distribution of FAW, as described in Section 1 of Chapter 2, highlights the existence of three bioclimatic zones, with zone 3 corresponding to the highest probability of its presence. Four bioclimatic variables were crucial in predicting the distribution of FAW. Precipitation and temperature were particularly influential, with high annual temperatures and moderate precipitation being the conditions that influence FAW infestations (Chapter 2, Section 2). It has been observed that FAW infestations in maize crops vary significantly with seasonal and environmental conditions (Koffi et al., 2020; Nboyine et al., 2020; Niassy et al., 2021; Senay et al., 2022). Studies using MaxEnt modelling have shown that rainfall during the wettest periods and annual temperatures are key determinants of FAW occurrence (Wang et al., 2020; Zacarias, 2020). In addition, planting dates are linked to these two climatic parameters and have a significant effect on FAW infestation, as shown in Section 3 of Chapter 2. Late-planted crops show higher larval densities and damage than early planted crops (Nyabanga et al., 2021) because early planting is associated with effective rainfall and lower temperatures, conditions that are less favorable for pest proliferation (Mugiyo et al., 2021). Conversely, late planting is often associated with higher temperatures and drier conditions, which favor higher densities of FAW larvae and more severe infestations (Hruska and Gould, 1997; Rodríguez-del-

Bosque et al., 2010). In addition, the results of this work indicate the presence of all FAW larval stages in the same field during late planting periods, further exacerbating infestation levels.

Studies have shown that infestation levels vary between agro-ecological zones and seasons (Koffi et al., 2020; López et al., 2019), with higher incidence reported in the Ruzizi plain during the late season of 2019. The high temperatures and semi-arid conditions characteristic of the Ruzizi plain favor rapid development and several generations of FAW within a year (Busato et al., 2005; Westbrook and Sparks, 1986). In contrast, areas with high rainfall, such as Kabare, have lower FAW densities due to increased larval mortality under wetter conditions (Murúa et al., 2006; Early et al., 2018). The results in relation to temperature are consistent with those of Du Plessis et al. (2020), who found that FAW development rates increase with temperatures between 18 and 30°C. Warmer temperatures generally accelerate the rate of development. This leads to faster population growth and higher infestation rates (Barfield et al., 1978; Isenhour et al., 1985). However, constant laboratory temperatures do not reflect actual field conditions, so studying the effects of temperature fluctuations can provide valuable information under real conditions (Early et al., 2018).

The two climatic parameters mentioned above are strongly influenced by climate change phenomena. An increase in temperature is predicted for the coming years (Arnell et al., 2019), which is likely to affect the distribution of FAW in its native range as well as in invaded areas. FAW may expand its range and increase its generational turnover, which may exacerbate infestation rates (Zacarias, 2020; Ramirez-Cabral et al., 2017; Timilsena et al., 2022; Adan et al., 2024). Warmer temperatures favor a greater number of generations per year, as seen in tropical areas where there can be up to eight generations per year (Busato et al., 2005). Rainfall patterns are predicted to change in the future, with large amounts of rain occurring in short periods and irregularly (Dai et al., 2018; Dai et al., 2020). Adjustments to the agricultural calendar should be advocated, and farmers should be informed of the ideal planting time in each season. Unfortunately, this is not the case in South Kivu and in the DRC in general, as there are several planting dates for smallholder agriculture in South Kivu. Agricultural production systems are closely linked to the local climate, and adaptation to climate change involves adjusting planting dates (Minoli et al., 2022). Although the climatic data used to model the distribution of FAW in South Kivu are outdated (50 years old), this still gives a real trend in the results by looking at the number of generations obtained, the bioclimatic zones and the predicted potential corridors for the presence of FAW. Two generations of FAW are actually observed (Section 3 Chapter 2), the first starting at four-five leaves completely unfolded stages (V4-V5) and the second at green mealie stage (R1) as shown in Figure 32. Studies have shown that FAW infestations are low in the early vegetative growth stages (V4-V6) (McGrath et al., 2018) and that plants are more tolerant to FAW attacks and can compensate for damage when soil and climatic conditions are optimal (Baudron et al., 2019; Hruska, 2019). Optimal soil and climate conditions mean that maize is grown in fertile soil with high organic matter content and adequate rainfall. The second generation is usually observed at green mealie stage and a FAW larva is found in the ear after harvest.

Given the impact of climate change on FAW, there is a risk of overlapping generations as reported by Niassy et al. (2021), which could also affect the dynamics and abundance of their natural enemies (Thomson et al., 2010; Durocher-Granger et al., 2024). Accurate modelling of FAW distribution at regional scales and assessment of seasonal infestation rates requires real-time local bioclimatic data (Abdel-Rahman et al., 2023). Such data are often scarce due to the limited number or absence of weather stations in South Kivu. The use of such data can reduce the errors that may be associated with imported bioclimatic data in predicting species distributions (Soria-Auza et al., 2010). An invasive species monitoring Centre equipped with meteorological stations is becoming a necessity in South Kivu. Considering the seasonal aspects, FAW is a migratory species when conditions are no longer favorable (Westbrook et al., 2019). Given the existence of two cropping seasons in South Kivu, it is hypothesized that several generations could be observed each year. With a short three-month dry season in the agricultural calendar (Figure 32), it is imperative to inquire whether FAW occurs during this period if its preferred crop is not grown at that time (Wightman, 2018). In sub-Saharan African farming systems, smallholder farmers try to maximize production by diversifying crops and making the best use of land (Jayne et al., 2010; Makate et al., 2016). To this end, farmers in South Kivu grow maize in the marshlands. This results in FAW populations being harbored during the dry season. In addition, FAW have been observed to attack onions in the maize growing season (Cokola et al., 2021b), cabbage and, more recently, bananas in the dry season (personal observations). The latter two are permanent crops in the agricultural system of the region.



Agricultural calendar					
Early season	S	O	N	D	J
Late season	F	M	A	M	J
Dry season	J	Jl	A	Months	

Figure 32. Understanding the fall armyworm dynamics in maize agricultural system of South Kivu. The figure was created by the author using BioRender.com.

2. Challenges and opportunities of using biological control agents against FAW in South Kivu

FAW is not a new pest in African agriculture, as its presence was reported by farmers even before it was officially declared on the continent in 2016, according to the findings presented in Chapter 3. However, farmers still resort to the use of pesticides in the face of alarming damage to their maize plantations and when they have no other choice in terms of curative control methods against FAW (Hruska, 2019). To do this, farmers in Africa use dangerous products that are no longer allowed on the pesticide market (Kansiime et al., 2019; Kumela et al., 2019). Pesticides are effective in managing pest populations (Nauen and Denholm, 2005), but their effects on non-target organisms such as beneficial insects, birds and even humans in case of exposure have been reported (Gill and Garg, 2014; Pisa et al., 2015). Pesticides can disrupt the ecological balance by harming natural enemies and other pests, which can lead to the resurgence of secondary pests (Gill and Garg, 2014). Relying solely on pesticides for FAW control is unsustainable in the long term due to resistance issues (Bateman et al., 2018), which would make control efforts less effective on farmer households in eastern DRC in the future. This occurs because susceptible larvae are killed, leaving behind those with genetic mutations that confer resistance (Yu, 1992). FAW populations naturally have genetic diversity, and some individuals may have genes that make them less susceptible to certain insecticides (Samanta et al., 2023). When exposed to insecticides, these individuals survive and pass on their resistance genes to the next generation (Gui et al., 2022). In some cases, resistance to one type of insecticide can confer resistance to other insecticides in the same chemical class or with similar modes of action (Nauen and Denholm, 2005; Van den Berg and du Plessis, 2022). In addition, the mechanism of FAW resistance to insecticides has been attributed to an increase in detoxification enzymes that break down insecticides more rapidly, thereby reducing their toxic effects (Gichuhi et al., 2020; Gomes et al., 2020).

The use of insecticides to control FAW in Africa involves several economic considerations that impact on farmers' economies. While insecticides can provide short-term relief from FAW infestations and protect crop yields, their economic viability and sustainability depend on careful consideration of cost, efficacy, environmental impact, health risks and the availability of alternative control methods (McGrath et al., 2021). Insecticides represent a direct cost to farmers. Expenditure includes the purchase of the chemicals themselves, as well as associated costs such as equipment, labor for application and transport (Bourguet and Guillemaud, 2016). For smallholder farmers in Africa, these costs can be significant, adding to already tight budgets. The effectiveness of insecticides in controlling FAW varies depending on factors such as timing of application, dosage and pest resistance (McGrath et al., 2021). Ineffective use of insecticides can result in poor control of FAW, leading to crop losses and wasted investment (Obour et al., 2022). In addition, the economic viability of insecticide use must be weighed against the potential losses due to FAW damage. Growers must assess whether the expected yield increase from insecticide use justifies the costs and risks involved, considering fluctuations in crop prices and market demand (Sexton et al., 2007). In contrast to invaded countries, FAW management in countries of origin is based on the use of Bt resistant varieties (Hruska, 2019; Van den Berg et al., 2021), given all the problems associated with insecticide management of FAW. Field trials and studies have shown that Bt varieties are effective in reducing the damage caused by FAW in crops such as maize and cotton (Siebert et al., 2008; Hardke et al., 2011b). These varieties have significantly reduced larval survival rates and crop losses due to FAW damage. By reducing FAW damage to crops and the need for chemical insecticides, Bt varieties have led to increased yields and profitability for farmers (Buntin, 2010; Gassmann and Reisig, 2023). Despite their effectiveness, there are issues such as the development of resistance and regulatory concerns (Huang et al, 2014; Gassmann and Reisig, 2023). Van den Berg et al. (2021) recommend alternating Bt with other control methods. The efficacy of Bt can be affected by environmental factors such as UV radiation, rainfall and temperature, which can degrade Bt toxins (Zhu et al., 2022). In addition, Bt is most effective when applied to early larval stages, as older larvae are more tolerant to the toxin, as with insecticides (Huang, 2021).

With all these concerns in mind, in Chapter 4 we present alternative methods, including macro- and micro-organism natural enemies that attack FAW in eastern DRC. In Section 1 of Chapter 4, we identified ten parasitoid species, two of which attack eggs, one of which attacks both eggs and larvae, and seven of which attack larvae. The diversity of predatory insects was much greater, with 31 species in 6 groups. The abundance of predatory insects varied according to the phenology of maize and the density of FAW larvae. Three groups of predators - ants, earwigs and ladybirds - were consistently abundant in maize fields in both agro-ecological zones. The results highlight the potential for conservation biological control on small farms in the DRC. Reducing the use of chemical pesticides and promoting crop diversity can create a favorable environment for these natural enemies of FAW (Harrison et al., 2019; Clarkson et al., 2022). Classical biological control is recommended to control FAW populations in newly invaded areas (Kenis, 2023). Although this method can be effective and environmentally friendly, it is associated with several challenges. Biocontrol agents (BCAs) may have difficulty establishing in a new environment due to climatic conditions, prey availability or other ecological factors (Howarth, 1991). Sometimes introduced biocontrol agents become invasive species themselves, causing additional ecological and economic problems (Simberloff and Stiling, 1996). Changes in climatic conditions can alter the effectiveness of BCAs by affecting their survival, reproduction and interactions with pests and other species (Thomson et al., 2010). Predation or parasitism on non-target species can lead to reductions in biodiversity (Simberloff and Stiling, 1996).

Prospectively, detailed morphological and molecular studies are needed to confirm the taxonomy of newly discovered parasitoid species such as *Diadegma sp.*, *Drino sp.* or *Brachymeria sp.* and many other predatory species. Understanding their genetic diversity and evolutionary relationships may provide a better understanding of their adaptation mechanisms and biocontrol potential. Studying the influence of landscape composition and habitat diversity on natural enemy abundance and effectiveness will help to design agricultural landscapes that promote biological control (Harrison et al., 2019). Studies should focus on comparing monoculture systems with more diverse agroecosystems. Analysis of multi-trophic interactions involving EPFs, FAW, maize plants and beneficial natural enemies will shed light on the complex ecological networks that regulate pest populations (Goettel et al., 1990; Shikano et al., 2017). Experimental field trials should be conducted to understand how these interactions can be exploited to improve the efficacy of biocontrol. Understanding the behavioral ecology of key natural enemies, such as foraging patterns, host selection and interspecific interactions, will provide valuable information to optimize their use in biocontrol programs. Studies on the synergistic effects of multiple natural enemies on FAW populations are particularly needed. Research into the effects of conventional pesticides on the abundance and effectiveness of natural enemies is essential. Understanding the non-target effects of pesticides will enable the development of IPM strategies that minimize damage to beneficial insects. Studying the effects of climate change on the dynamics of FAW and their natural enemies will be important for predicting future pest invasions and developing resilient biocontrol strategies. Climate models should be integrated with ecological data to predict changes in pest and natural enemy populations.

Microbial control, particularly the use of EPFs such as *Beauveria bassiana*, has shown promise as an alternative to chemical pesticides (Mascarin and Jaronski, 2016; Guo et al., 2020) In Section 2 of Chapter 4, we report the presence of *B. bassiana* infecting insects in DR Congo and highlight the potential of local fungal isolates KA14 and PL6 for the development of environmentally friendly integrated pest management (IPM) strategies against FAW. The identification and use of indigenous EPFs can improve the sustainability and effectiveness of IPM programs in South Kivu and potentially other regions facing FAW infestations. *B. bassiana* is not the only EPFs that naturally infects FAW. *Metarhizium rileyi* is a promising EPF for FAW management (Wyckhuys et al., 2024a). However, this EPF is highly sensitive to nutrient and environmental conditions, making it difficult to cultivate and produce as a stable biopesticide (Grijalba et al., 2018). This represents a real challenge for the development of targeted biopesticides against FAW and suggests the immediate cultivation and implementation of small-scale production units of this fungus in the environment where it has been observed. There are constraints to the production of EPFs, including production costs, which include substrates, culture media, labor and maintenance of aseptic conditions (Mascarin and Jaronski, 2016;

Jaronski, 2023). Ensuring a long shelf life without loss of viability is essential for the commercial success of EPFs (Feng et al., 1994). This requires optimization of storage conditions and formulations, which may be a technological challenge in the eastern DRC. Advances in bioprocess engineering, such as improved bioreactors and automation, can improve production efficiency and consistency (Jaronski, 2023), even in less industrialized countries (Grzywacz et al., 2023). In Chapter 3, the concept of biological control is unfamiliar to many farmers, who may be reluctant to adopt the use of EPFs because of their familiarity with chemical pesticides and uncertainty about the efficacy and reliability of biological control products. The virulence, viability and mechanisms of action of different FAW isolates need to be studied in detail in the laboratory and in the field. This will include investigation of the enzymatic activities involved in host infection, particularly for the fungus *M. rileyi*, and assessment of the potential for combining FAW with other BCAs for integrated pest management (IPM).

3. IPM fall armyworm-based ecology and biological control considerations

Integrated pest management (IPM) provides a sustainable approach to controlling FAW populations (Tepa-Yotto et al., 2022b), focusing on both ecological and biological control methods to minimize reliance on chemical pesticides and reduce environmental impacts (Kogan, 1998). By reducing reliance on chemical pesticides and promoting natural pest control mechanisms, IPM not only protects crops but also preserves environmental health and biodiversity (Barzman et al., 2015). Effective management of an invasive pest such as FAW is the result of two variables: control methods/technologies and human actions (Kansiime et al., 2019). While control methods/technologies continue to be systematically refined through scientific research (Bateman et al., 2018; Harrison et al., 2019; Guo et al., 2020; Van den Berg et al., 2021; Niassy et al., 2024), research efforts on the human factor in FAW invasion management are limited. Farmer education and community action are essential components of a sustainable FAW control strategy (Human, 2018). Training farmers in natural enemy identification, pest knowledge and the effective use of biological control agents is key to the successful implementation of an integrated approach to FAW in the DRC. This issue has already been highlighted in Chapter 3 of this thesis, which shows that farmers' knowledge of pests and sustainable pest management practices is inadequate in many African countries, despite development programs and projects. Knowledge of the pest includes its life cycle and the timing of its appearance in maize crops, which is influenced by environmental conditions. Most farmers wait until the more advanced stages of the pest before spraying with insecticides, which are sometimes ineffective due to resistance problems (Yu, 1992) and the choice of product, which sometimes does not match the target pest (Kumela et al., 2019).

As mentioned in Section 2 of Chapter 2 and Section 1 of Chapter 4, if maize is sown at the ideal time, two generations of FAW are likely to be observed. However, the existence of several planting dates complicates the management of FAW in South Kivu. It is essential to make farmers aware of the influence of environmental conditions, and particularly the ideal planting time, to predict pest dynamics and implement timely control measures (Niassy et al., 2021). There is an urgent need to revise the agricultural calendar in South Kivu. The use of forecasting models in sub-Saharan Africa is a successful example of combining environmental and biological factors to predict FAW (Adan et al., 2024). As mentioned above, the establishment of a meteorological Centre to alert farmers to the ideal planting time, or the revision of the agricultural calendar based on data from this Centre in the context of climate change, is becoming a matter of urgency. By integrating climatic data with observations of pest populations, researchers have developed statistical and computational models to analyze the relationship between environmental factors, the activity of biological control agents and FAW population dynamics (Niassy et al., 2021; Guimapi et al., 2022; Adan et al., 2024). These models have allowed the anticipation of interventions to reduce crop losses by producing risk maps showing the areas likely to be infested by FAW, depending on the specific environmental conditions in each zone. These maps can be used to target surveillance and control efforts. To date, the economic threshold of damage that would justify chemical intervention is unknown in South Kivu and is proposed as a prospect in the context of this thesis.

All these actions are only possible with political support. Government policies should support IPM by funding research, providing extension services and promoting environmentally friendly pest management practices. In most FAW-affected countries, governments have provided pesticides to farmers in response to FAW damage, which some consider a calamity (Rwomushana et al., 2018; Wightman, 2018). In addition, science-based development agencies and international development research consortia have expressed contrary opinions and suggested integrated pest management measures against FAW for sustainability reasons (Tepa-Yotto et al., 2022b). The planting season warning system also includes monitoring of FAW populations. This concerns both the seasonal abundance of moths and the presence of egg masses and small larvae in the fields.

The first strategy is possible using pheromone traps (Tepa-Yotto et al., 2022a; Sisay et al., 2024), which are not yet available to smallholders and require companies that produce pheromones, which are rare in most African countries. These systems can be used to establish economic thresholds to predict when chemical intervention is necessary, depending on the presence of different larval stages and levels of infestation (Lowry et al., 2022). In addition to avoiding unnecessary use of pesticides, this will encourage the use of control measures that are specific to the context of farmers in South Kivu.

Agricultural practices, including variety selection, cropping systems and intercropping, have a significant impact on FAW populations. Monoculture maize systems are more susceptible to severe FAW infestations than diversified cropping systems (Mutyambai et al., 2022). In this thesis (Chapter 2 Section 3), it has been shown that intercropping maize with legumes such as soybean or groundnut limits FAW larval densities and enhances natural pest control mechanisms (Harrison et al., 2019; Midega et al., 2018). This practice not only disrupts the pest's life cycle by limiting larval movement, but also attracts FAW natural enemies, reducing their populations (Smith and McSorley, 2000; Khan et al., 2010). In regions such as South Kivu, intercropping maize and legumes can be a sustainable approach to FAW management, particularly as it is an approach commonly used by smallholder farmers. The push-pull system, which involves the use of repellent and attractive crops, has also proven effective in reducing FAW infestation by using semiochemicals that repel pests and attract their natural enemies (Midega et al., 2018; Sobhy et al., 2022). Among the agroecological approaches to sustainable FAW management, maintaining habitats for natural enemies can help control pest populations. This includes planting hedgerows and cover crops that provide shelter and other food sources for beneficial organisms (Harrison et al., 2019; Clarkson et al., 2022; Jordon et al., 2022). In terms of variety choice, farmers use local varieties with low production potential and are sensitive to the adoption of new varieties (Mugumaarhahama et al., 2021). To date, there are no maize varieties tolerant to FAW infestation in South Kivu (personal observations), although breeding efforts are expanding rapidly on the African continent (Kasoma et al., 2022; Prasanna et al., 2022). The use of Bt varieties on farmers' farms has been proposed in Africa (Van den Berg et al., 2021), but their adoption is restricted by governments in several African countries.

Physical control of FAW relies on biological processes and ecological relationships to control pest populations (Wightman, 2018). Examples include the use of natural substances such as plant extracts of neem, garlic, etc. The use of soil, ash and detergents to repel or kill FAW has been documented in Africa (Hruska, 2019; Maphumulo et al., 2023). Physical control methods such as hand weeding are used to manage FAW on farms in Africa (Tambo et al., 2020a). All these methods should be explored for the benefit of farmers in South Kivu.

Biological control is an essential component of integrated pest management against FAW in South Kivu, with the discovery of potentially indigenous parasitoids and predators. In this thesis, two approaches to biological control are proposed: augmentative biological control, i.e. increasing the population of natural enemies such as *Te. remus*, *C. luteum*, *Ch. bifoveolatus* and *Ch. diversipes* through mass production and periodic releases; and conservation biological control, which aims to protect and enhance the populations of already existing natural enemies such as parasitoids, ladybirds, earwigs and wasps' predators of FAW. This may include providing habitat and alternative prey for these natural enemies. The use of biopesticides based on entomopathogenic fungi, such as *B. bassiana* and *M. rileyi*, and bacteria, such as *B. thuringiensis* (Bt) (Guo et al., 2020), is a promising approach to FAW management in South Kivu, with the discovery of new isolates of *B. bassiana* and the exploration of other entomopathogenic microorganisms in the future. The diagram representing the IPM strategy in South Kivu in the context of this thesis is shown in Figure 33.

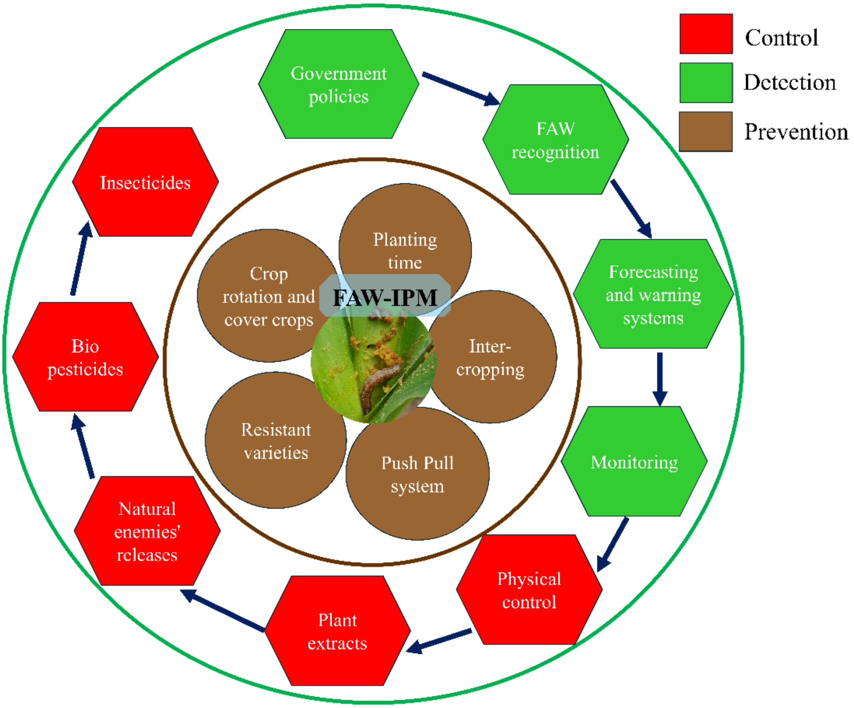


Figure 33. Proposed diagram of integrated management of fall armyworm in South Kivu.

4. Conclusions

Combining environmental factors and biological control methods offers a powerful approach to forecasting fall armyworm outbreaks. By leveraging data on weather conditions and natural enemy activity, it is possible to develop predictive models that enable proactive pest management. This integrated strategy not only enhances the effectiveness of control measures but also promotes sustainable agricultural practices, minimizing reliance on chemical pesticides and preserving ecological balance. The spread and impact of FAW in eastern DRC are intricately linked to various environmental, seasonal, and agricultural factors. Understanding these dynamics is essential for developing effective management strategies to mitigate the pest's impact on maize and other crops. Accurate modeling of FAW distribution, considering local bioclimatic data, and adopting sustainable agricultural practices, such as intercropping and optimized planting dates, can significantly reduce the pest's damage. Continued research and collaboration among stakeholders are vital for enhancing the resilience of agricultural systems against FAW infestations in South Kivu.

Chapter 6

Scientific communication

Photo by Marcellin C. Cokola

Chapter 6. Scientific communication

1. Scientific publications related to the thesis topic

Published articles

Wyckhuys, K.A.G., Akutse, K.S., Amalin, D.M., Araj, S.-E., Barrera, G., Beltran, M.J.B., Ben Fekih, I., Calatayud, P.-A., Cicero, L., **Cokola, M.C.**, Colmenarez, Y.C., Dessauvages, K., Dubois, T., Durocher-Granger, L., Espinel, C., Fallet, P., Fernández-Triana, J.L., Francis, F., Gómez, J., Haddi, K., Harrison, R.D., Haseeb, M., Iwanicki, N.S.A., Jaber, L.R., Khamis, F.M., Legaspi, J.C., Lomeli-Flores, R.J., Lopes, R.B., Lyu, B., Montoya-Lerma, J., Montecalvo, M.P., Polaszek, A., Nguyen, T.D., Nurkomar, I., O'Hara, J.E., Perier, J.D., Ramírez-Romero, R., Sánchez-García, F.J., Robinson-Baker, A.M., Silveira, L.C., Simeon, L., Solter, L.F., Santos-Amaya, O.F., Talamas, E.J., De Souza Tavares, W., Trabanino, R., Turlings, T.C.J., Valicente, F.H., Vásquez, C., Wang, Z., Wengrat, A.P.G.S., Zang, L.-S., Zhang, W., Zimba, K.J., Wu, K., Elkahky, M., Hadi, B.A.R., 2024. Global scientific progress and shortfalls in biological control of the fall armyworm *Spodoptera frugiperda*. Biological Control 191, 105460. https://doi.org/10.1016/j.biocontrol.2024.105460.

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Cokola, M.C., Noël, G., Mugumaarhahama, Y., Caparros Megido, R., Bisimwa, E.B., Francis, F., 2024. Planting date in South Kivu, Eastern DR Congo: a real challenge in the sustainable management of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) by smallholder farmers. Journal: PLoS ONE.

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3. Scientific congresses, workshop and symposiums

Francis, F., **Cokola Cuma, M.**, Dessauvages, K., Kouanda, N., Glacet, L., Badolo, A., & Ben Fekih, I. (05 August 2024). *Fungal Entomopathogens for pest biocontrol in multitrophic approaches* [Paper presentation]. International Congress on Invertebrate Pathology and Microbial Control and 56th Annual Meeting of the Society for Invertebrate Pathology, Vienna, Austria. https://hdl.handle.net/2268/321060.

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Workshop: Arthropod-Fungal Associations: from parasites to pathogens. 13 to 15

May 2024. Meise Botanic Garden and Ghent University.

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Appendixes

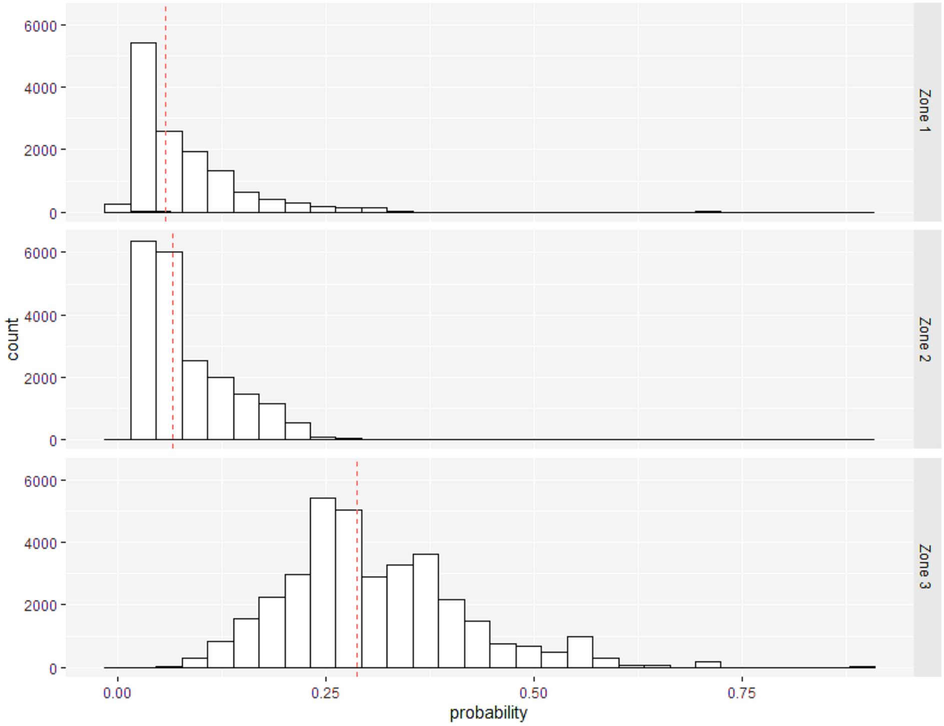

Figure 1. Distribution of probabilities of occurrence of fall armyworm in the bioclimatic zones of South Kivu. The red dashed line on each histogram represents median of occurrence probability in the corresponding bioclimatic zone.

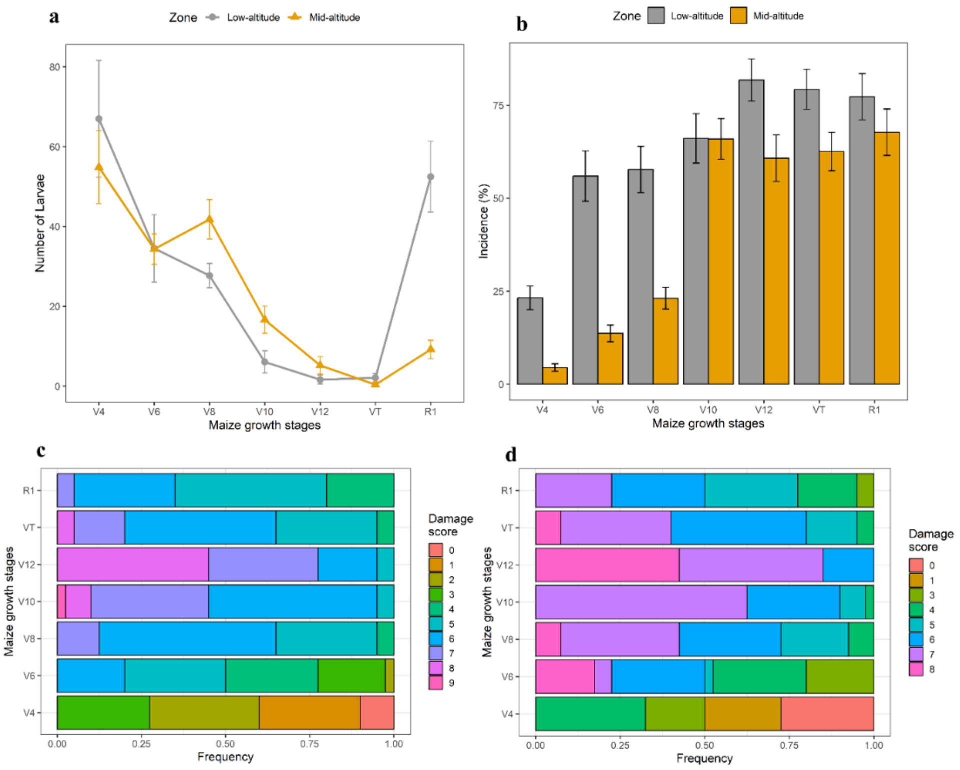

Figure 2. Fall armyworm infestation in relation with maize growth stage and agroecological zone. **a:** variation in fall armyworm larval density; **b:** Incidence of the fall armyworm represented as the number of infested plant and the total number of plants in each quadrat; **c:** severity estimated as damage score in low altitude; **d:** severity estimated as damage score in mid-altitude.

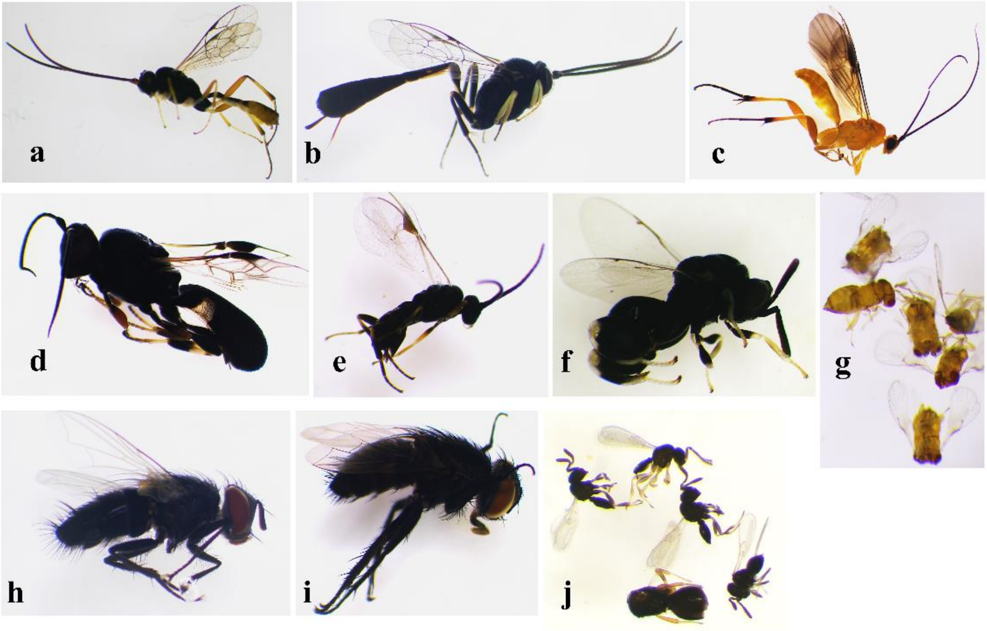

Figure 3. Fall armyworm parasitoids species collected from eastern DRC. **a:** *Diadegma sp.*; **b:** *Charops diversipes*; **c:** *Coccygidium luteum*; **d:** *Chelonus bifoveolatus*; **e:** *Parapanteles sp.*; **f:** *Brachymeria sp.*; **g:** *Trichogramma chilonis*; **h:** *Drino sp.*; **i:** *Drino quadrizonula*; **j:** *Telenomus remus.*

Figure 4. Some FAW predator groups.

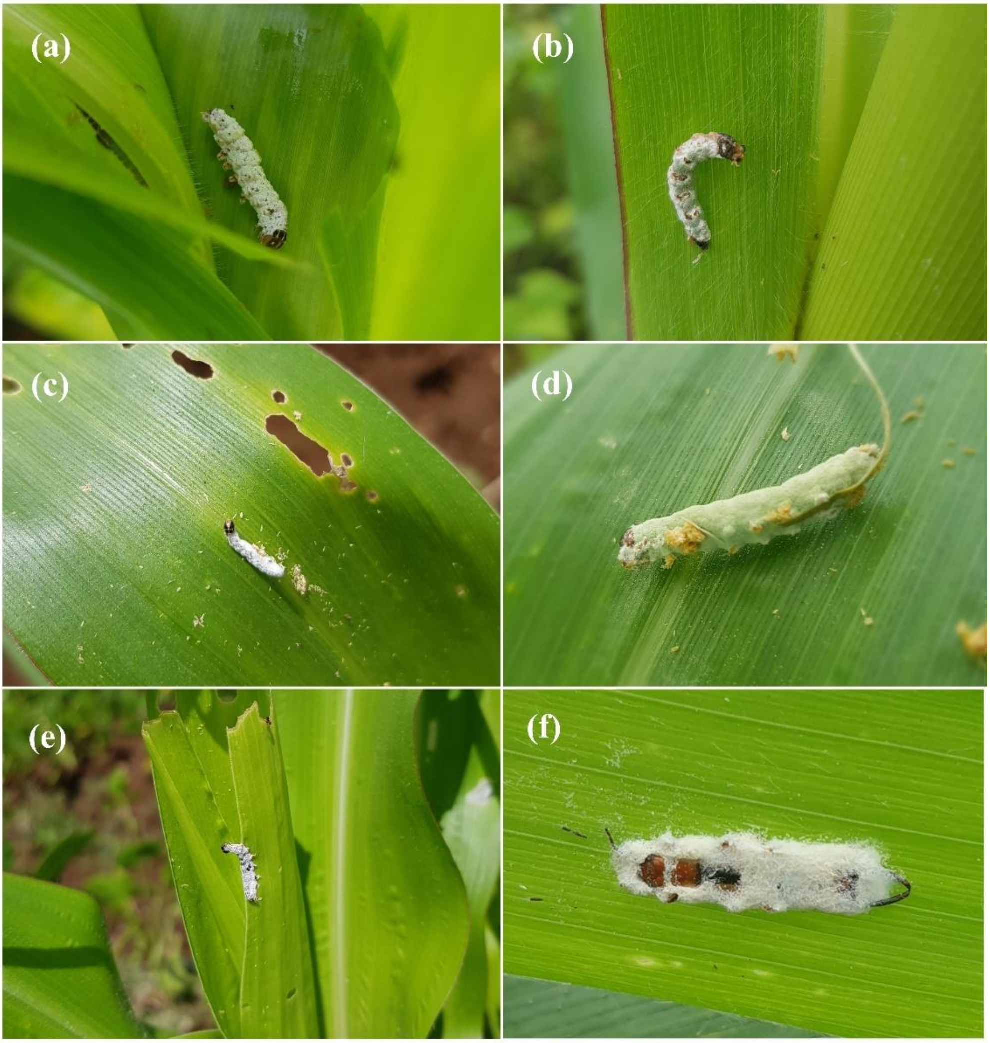

Figure 5. Insect mycosed cadevers collected for entomopathogenic fungi studies. **a-e:** cadavers of fall armyworm; **f:** cadaver of earwig.

Figure 6. Setting up yellow pantraps, collecting FAW larvae and fields monitoring.

Table 1. Characteristics of the fall armyworm larval stages.

Larval stages	Head capsule widths (mm) [a]	Lenghts (mm) [a]	Duration (days) at 25° C [b]
L1	0.35	1.7	3.3
L2	0.45	3.5	1.7
L3	0.75	6.4	1.5
L4	1.3	10.0	1.5
L5	2.0	17.2	2.0
L6	2.6	34.2	3.7

[a] Capinerra (2000); [b] Pitre and Hogg (1983).

Table 2. Indicators for assessing the severity of *Spodoptera frugiperda* attacks on maize crops according to Davis

Explaining/defining damage	**Evaluation**
No visible damage to leaves	0
Pinhole damage only	1
Damage to leaves in the form of pinholes and small circular holes	2
Pinholes, small circular lesions and a few small, elongated lesions (rectangular in shape) up to 1.3 cm long are present on upright and rolled leaves.	3
Several small to medium-sized elongated lesions measuring 1.3 to 2.5 cm are present on a few upright and rolled leaves.	4
Several large, elongated lesions over 2.5 cm long are present on a few upright and rolled leaves and/or a few small to medium-sized, uniformly to irregularly shaped holes (basal membrane consumed) that are eaten from upright and/or rolled leaves.	5
Several large, elongated lesions present on several whorled and rolled leaves and/or several large, uniform, irregularly shaped holes eaten from whorled and rolled leaves.	6
Numerous elongated lesions of all sizes are present on several whorled and rolled leaves, as well as several large holes of identical or irregular shape that are eaten from the whorled and rolled leaves.	7
Numerous elongated lesions of all sizes are present on most of the whorled and rolled leaves, as well as numerous medium to large holes of identical or irregular shape, eaten into the whorled and rolled leaves.	8
The whorled and rolled leaves are almost completely destroyed.	9

Table 3. Pearson Rank correlation between environmental variables.

	bio1	bio2	bio3	bio4	bio5	bio6	bio7	bio10	bio11	bio12	bio13	bio14	bio15	bio16	bio17	dem	llds	mi	miaq	mimq
bio2	**0.757**																			
bio3	0.224	0.381																		
bio4	-0.256	-0.433	**-0.824**																	
bio5	**0.995**	**0.787**	0.167	-0.222																
bio6	**0.991**	0.737	0.331	-0.341	**0.976**															
bio7	0.504	0.575	-0.535	0.340	0.582	0.392														
bio10	**0.999**	**0.752**	0.196	-0.232	**0.996**	**0.987**	0.525													
bio11	**0.999**	**0.764**	0.244	-0.280	**0.994**	**0.993**	0.493	**0.998**												
bio12	-0.260	-0.233	0.619	-0.424	-0.325	-0.163	**-0.772**	-0.285	-0.249											
bio13	-0.372	-0.470	0.257	-0.074	-0.428	-0.307	-0.667	-0.388	-0.371	**0.878**										
bio14	0.443	0.417	**0.879**	-0.653	0.383	0.537	-0.392	0.418	0.455	0.646	0.345									
bio15	-0.609	-0.737	-0.444	0.422	-0.618	-0.620	-0.296	-0.605	-0.616	0.373	0.700	-0.395								
bio16	-0.237	-0.310	0.447	-0.275	-0.300	-0.156	-0.691	-0.258	-0.231	**0.957**	**0.960**	0.525	0.556							
bio17	0.328	0.393	**0.940**	-0.714	0.269	0.429	-0.469	0.301	0.342	0.670	0.325	**0.980**	-0.423	0.511						
dem	**-0.981**	**-0.764**	**-0.343**	0.313	**-0.966**	**-0.984**	-0.406	**-0.976**	**-0.981**	0.154	0.303	-0.563	0.642	0.156	-0.457					
llds	-0.064	-0.127	**-0.827**	0.541	-0.001	-0.163	0.609	-0.039	-0.074	-0.716	-0.439	**-0.855**	0.240	-0.565	**-0.889**	0.199				
mi	**-0.761**	-0.674	0.232	-0.091	**-0.806**	-0.689	**-0.835**	**-0.776**	**-0.755**	**0.801**	**0.827**	0.126	0.661	**0.787**	0.200	0.691	-0.389			
miaq	0.115	0.215	**0.945**	-0.701	0.052	0.227	-0.635	0.088	0.131	0.738	0.395	**0.920**	-0.334	0.560	**0.971**	-0.252	**-0.920**	0.376		
mimq	**-0.765**	-0.744	0.033	0.070	**-0.802**	-0.714	**-0.723**	**-0.775**	**-0.763**	0.712	**0.857**	-0.037	**0.820**	**0.772**	0.007	0.724	-0.206	**0.965**	0.168	
pet	**0.979**	**0.866**	0.308	-0.343	**0.983**	**0.971**	0.528	**0.977**	**0.982**	-0.240	-0.403	0.481	-0.678	-0.248	0.388	**-0.972**	-0.106	**-0.758**	0.176	**-0.786**

Table 4. Principal component analysis of fall armyworm infestation: number of infested plants (NIP); total number of plants (TNP); number of infested leaves per plant (NIL); number of larvae per plant (NLP); number of lesions per leaf (NLL); number of larvae per defined area (NLDA).

	Configuration	Dim.1	Dim.2	Dim.3	Dim.4
Eigen value		2.8495	1.3440	1.0748	1.0120
Percentage of variance		35.6187	16.8000	13.4348	12.6497
Cumulative percentage of variance		35.6187	52.4188	65.8536	78.5033
NIP	Active variable	**0.4586** (7.3812)	**0.3297** (8.0870)	**0.7498** (52.3029)	0.0484 (0.2319)
TNP	Active variable	-0.0443 (0.0688)	**-0.6481** (31.2526)	**0.3865** (13.8967)	**0.5177** (26.4793)
NIL	Active variable	0.0527 (0.0976)	**0.8131** (49.1864)	-0.0445 (0.1841)	**0.3478** (11.9499)
NLP	Active variable	**0.5434** (10.3618)	-0.0150 (0.0166)	**-0.5913** (32.5277)	**0.4236** (17.7288)
NLL	Active variable	**0.3246** (3.6971)	0.1117 (0.9280)	0.0762 (0.5399)	**0.5503** (29.9241)
NLDA	Active variable	**0.8989** (28.3541)	-0.1184 (1.0430)	-0.0529 (0.2606)	-0.0533 (0.2804)
SEVERITY	Active variable	**0.8512** (25.4278)	**-0.3219** (7.7075)	-0.0255 (0.0604)	-0.0944 (0.8813)
INCIDENCE	Active variable	**0.8374** (24.6115)	**0.1546** (1.7789)	0.0495 (0.2276)	**-0.3560** (12.5243)
A2018	Supplementary category	**-0.5628**	**-0.6568**	0.0429	**0.2126**
B2019	Supplementary category	**0.5510**	**0.6432**	-0.0420	**-0.2082**
Kabare	Supplementary category	**-0.7012**	0.0131	**-0.2227**	**-0.2128**
Ruzizi plain	Supplementary category	**0.6865**	-0.0129	**0.2180**	**0.2084**
BIO1	Supplementary variable	**0.4204**	-0.0261	**0.2207**	**0.2051**
BIO2	Supplementary variable	**0.4115**	-0.0053	**0.2219**	**0.1990**
BIO3	Supplementary variable	**-0.4114**	0.0149	**-0.2394**	**-0.1705**
BIO4	Supplementary variable	**0.3178**	0.0223	**0.1539**	0.0439
BIO5	Supplementary variable	**0.4215**	-0.0225	**0.2269**	**0.2056**

BIO6	Supplementary variable	**0.4087**	-0.0347	**0.2150**	**0.2081**
BIO7	Supplementary variable	**0.4181**	-0.0060	**0.2287**	**0.1926**
BIO10	Supplementary variable	**0.4191**	-0.0242	**0.2243**	**0.2055**
BIO11	Supplementary variable	**0.4154**	-0.0278	**0.2221**	**0.2081**
BIO12	Supplementary variable	**-0.4140**	0.0210	**-0.2225**	**-0.2147**
BIO13	Supplementary variable	**-0.4052**	0.0262	**-0.2191**	**-0.2189**
BIO14	Supplementary variable	**-0.4091**	0.0247	**-0.2198**	**-0.2130**
BIO15	Supplementary variable	**-0.3769**	0.0157	**-0.2138**	**-0.2192**
BIO16	Supplementary variable	**-0.4079**	0.0207	**-0.2223**	**-0.2189**
BIO17	Supplementary variable	**-0.4151**	0.0208	**-0.2151**	**-0.2132**
DEM	Supplementary variable	**-0.4177**	0.0163	**-0.2209**	**-0.2014**
LLDS	Supplementary variable	**0.3965**	-0.0200	**0.1912**	**0.1985**
MI	Supplementary variable	**-0.4156**	0.0206	**-0.2251**	**-0.2126**
MIAQ	Supplementary variable	**-0.4126**	0.0224	**-0.2223**	**-0.2116**
MIMQ	Supplementary variable	**-0.4116**	0.0216	**-0.2276**	**-0.2128**
PET	Supplementary variable	**0.4221**	-0.0171	**0.2257**	**0.2030**

Values in bold are significantly different from 0 at $\alpha = 0.05$ (*p-value* < *0.05*)

Table 5. Allocation of the number of monitored fields according to sowing dates, seasons and study sites.

			Early Season 2020		
Planting date	**Timing**	**Miti-Murhesa**	**Katana**	**Mudaka**	**Total**
01 September 2020	Early	4	3	2	9
15 September 2020	Early	5	2	2	9
01 October 2020	Early	3	3	3	9
15 October 2020	Late	4	3	2	9
30 October 2020	Late	3	3	3	9
Total		**19**	**14**	**12**	**45**
			Late Season 2021		
01 February 2021	Early	3	3	3	9
15 February 2021	Early	4	2	3	9
01 March 2021	Early	4	3	2	9
15 March 2021	Late	3	4	2	9
30 March 2021	Late	3	3	3	9
Total		**17**	**15**	**13**	**45**

Table 6. Summary of the results of the Generalized linear mixed models (GLMMs) selection for explaining the variability of the larval density with variables in early season 2020.

Fixed effects	Model 1									
	Estimate	Std. Error	Z value	P value	AICc	AIC	BIC	logLik	Deviance	Df.resid
Intercept	-1.414	1.048	-1.349	0.177	302.32	285.8	312.9	-127.9	255.8	30
Type of field (Exploitation)	0.547	0.344	1.588	0.112						
Type of field (Farmer)	0.446	0.399	1.117	0.263						
Surface (m^2)	-0.048	0.043	-1.127	0.259						
Planting time (Late)	-0.045	0.162	-0.28	0.779						
Variety (M'Roma)	0.089	0.117	0.762	0.446						
Variety (SAM4 Vita)	0.278	0.188	1.477	0.139						
Variety (Z-M)	0.132	0.080	1.639	0.101						
Fertilizers (Manure)	-0.766	0.364	-2.104	**0.035**						
Fertilizers (None)	-0.557	0.239	-2.331	**0.019**						
Fertilizers (NPK)	-0.450	0.232	-1.941	0.052						
Fertilizers (Urea)	-0.747	0.392	-1.905	0.056						
Fertilizers (Urea+Manure)	-0.215	0.289	-0.744	0.456						
Julian calendar	0.016	0.003	4.144	**< 0.001**						
	Model 2									
Intercept	-1.174	0.529	-2.219	**0.026**	297.86	283.9	309.2	-127.9	255.9	31
Type of field (Exploitation)	0.569	0.335	1.7	0.089						
Type of field (Farmer)	0.471	0.389	1.211	0.226						
Surface (m^2)	-0.050	0.042	-1.179	0.238						
Variety (M'Roma)	0.090	0.117	0.773	0.439						
Variety (SAM4 Vita)	0.282	0.188	1.5	0.133						
Variety (Z-M)	0.138	0.077	1.791	0.073						
Fertilizers (Manure)	-0.786	0.357	-2.199	**0.027**						

Fertilizers (None)	-0.584	0.220	-2.647	**< 0.01**						
Fertilizers (NPK)	-0.478	0.211	-2.265	**0.023**						
Fertilizers (Urea)	-0.782	0.370	-2.108	**0.035**						
Fertilizers (Urea+Manure)	-0.233	0.284	-0.82	0.411						
Julian calendar	0.015	0.001	8.962	**< 0.001**						
					Model 3					
Intercept	-0.940	0.469	-2.004	**0.045**	288.37	283.2	299.5	-132.6	265.2	36
Surface (m^2)	-0.011	0.034	-0.338	0.735						
Fertilizers (Manure)	-0.741	0.318	-2.331	**0.019**						
Fertilizers (None)	-0.426	0.144	-2.952	**< 0.01**						
Fertilizers (NPK)	-0.325	0.177	-1.832	0.066						
Fertilizers (Urea)	-0.346	0.300	-1.152	0.249						
Fertilizers (Urea+Manure)	-0.353	0.238	-1.483	0.138						
Julian calendar	0.016	0.001	9.432	**< 0.001**						
					Model 4					
Intercept	-0.913	0.461	-1.979	**0.047**	285.34	281.3	295.8	-132.7	265.3	37
Fertilizers (Manure)	-0.738	0.317	-2.323	**0.020**						
Fertilizers (None)	-0.413	0.138	-2.975	**< 0.01**						
Fertilizers (NPK)	-0.333	0.176	-1.888	0.059						
Fertilizers (Urea)	-0.345	0.300	-1.15	0.250						
Fertilizers (Urea+Manure)	-0.333	0.230	-1.445	0.148						
Julian calendar	0.015	0.001	9.664	**< 0.001**						
					Model 5					
Intercept	-1.214	0.438	-2.769	**< 0.01**	282.00	281.4	286.8	-137.7	275.4	42
Julian calendar	0.015	0.001	10.048	**< 0.001**						

Table 7. Summary of the results of the Generalized linear mixed models (GLMMs) selection for explaining the variability of the larval density with variables in late season 2021.

Fixed effects	Model 1									
	Estimate	**Std. Error**	**Z value**	**P value**	**AICc**	**AIC**	**BIC**	**logLik**	**Deviance**	**Df.resid**
Intercept	3.382	0.468	7.222	**< 0.001**	335.50	321.5	346.8	-146.7	293.5	31
Type of field (Exploitation)	-0.273	0.336	-0.812	0.416						
Type of field (Farmer)	-0.541	0.334	-1.62	0.105						
Surface (m^2)	-0.042	0.062	-0.688	0.491						
Planting time (Late)	0.563	0.149	3.76	**< 0.001**						
Variety (M'Roma)	0.004	0.126	0.035	0.971						
Variety (SAM4 Vita)	0.135	0.194	0.699	0.484						
Variety (Z-M)	-0.016	0.088	-0.182	0.855						
Fertilizers (None)	-0.065	0.162	-0.404	0.686						
Fertilizers (NPK)	-0.278	0.160	-1.735	0.082						
Fertilizers (NPK+Manure)	-0.403	0.236	-1.705	0.088						
Fertilizers (Urea+Manure)	-0.327	0.418	-0.781	0.434						
Julian calendar	0.000	0.004	0.182	0.855						
					Model 2					
Intercept	2.728	0.430	6.336	**< 0.001**	345.71	334.0	357.5	-154.0	308.0	32
Type of field (Exploitation)	-0.105	0.332	-0.318	0.750						
Type of field (Farmer)	-0.563	0.334	-1.687	0.091						
Surface (m^2)	-0.133	0.057	-2.327	**0.02**						
Variety (M'Roma)	-0.147	0.120	-1.219	0.222						
Variety (SAM4 Vita)	0.127	0.193	0.658	0.510						
Variety (Z-M)	-0.108	0.086	-1.258	0.208						

Fertilizers (None)	0.022	0.158	0.141	0.887						
Fertilizers (NPK)	-0.320	0.159	-2.005	**0.044**						
Fertilizers (NPK+Manure)	-0.421	0.235	-1.786	0.074						
Fertilizers (Urea+Manure)	-0.322	0.418	-0.771	0.440						
Julian calendar	0.014	0.001	7.559	**< 0.001**						
Model 3										
Intercept	2.722	0.141	19.19	**< 0.001**	343.50	339.5	354.0	-161.8	323.5	37
Surface (m^2)	0.030	0.031	0.955	0.339						
Fertilizers (None)	-0.259	0.111	-2.337	**0.019**						
Fertilizers (NPK)	-0.343	0.159	-2.155	**0.031**						
Fertilizers (NPK+Manure)	-0.298	0.176	-1.694	0.090						
Fertilizers (Urea+Manure)	-0.009	0.200	-0.05	0.960						
Julian calendar	0.011	0.001	7.468	**< 0.001**						
Model 4										
Intercept	2.724	0.142	19.159	**< 0.001**	341.43	338.4	351.1	-162.2	324.4	38
Fertilizers (None)	-0.276	0.109	-2.522	**0.011**						
Fertilizers (NPK)	-0.336	0.159	-2.115	**0.034**						
Fertilizers (NPK+Manure)	-0.314	0.175	-1.793	0.073						
Fertilizers (Urea+Manure)	-0.063	0.192	-0.333	0.739						
Julian calendar	0.011	0.001	7.684	**< 0.001**						
Model 5										
Intercept	2.451	0.101	24.079	**< 0.001**	338.93	338.3	343.8	-166.2	332.3	42
Julian calendar	0.011	0.001	8.074	**< 0.001**						