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RESEARCH

Crop Mixtures Influence Fall Armyworm Infestation and Natural Enemy Abundance in Maize-based Intercropping Systems

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Abstract

The fall armyworm (FAW), *Spodoptera frugiperda* (J. E. Smith), causes significant damage to maize, threatening the food security and livelihood of millions of smallholder farmers in sub-Saharan Africa (SSA). Crop diversification has been recommended as an ecologically sustainable FAW control option. However, limited information is available on the impacts of companion plants and their control mechanisms against FAW in SSA, being a relatively new pest to the region. Building upon our earlier laboratory study, which elucidated how edible companion intercrops effectively reduce FAW infestation, we conducted field experiments in Kenya to assess the effectiveness of intercropping maize with beans, groundnut, cassava and sweet potato under realistic field conditions. Growing maize with these intercrops consistently resulted in fewer FAW eggs, larvae and lower plant infestation compared to maize monoculture except with cassava. Additionally, maize under these intercrops experienced low FAW damage and higher crop yield compared to maize monoculture. Maize growth stages significantly influenced the population of FAW eggs and larvae, with a peak observed between vegetative stages V4 and V10. Furthermore, intercropped maize plots exhibited a higher presence of FAW predators, such as lady beetles and earwigs. Correlation analysis revealed a significant correlation between temperature, relative humidity, and the population of FAW life stages and natural enemies at the experimental sites. Therefore, intercropping maize with beans, sweet potato, and groundnuts can be incorporated into an integrated FAW management strategy to sustainably control the pest in real farming conditions. These findings are particularly relevant for small-scale farmers in Africa and beyond, who cannot afford expensive FAW control using insecticides.

Keywords *Spodoptera frugiperda* · Intercropping · Natural enemies · Maize · Agroecology · Integrated pest management

Key Message

- We investigated the impacts of functional diversity in maize based edible companion intercrops in reducing an invasive fall armyworm pest in its new habitat.
- Intercropping maize with edible companion plants (beans, sweet potato, and groundnut) reduced FAW infestation, and damage on maize and led to higher crop yield.
- Intercropped maize plots exhibited a higher presence of FAW predators, such as lady beetles and earwigs.
- Maize phenology and weather factors influenced the FAW population dynamics and the severity of crop damage by the pest.
- Crop diversification has a great potential for integration as an ecologically sustainable FAW management strategy.

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Introduction

Maize (*Zea mays*), also known as corn, ranks as the world's third most important cereal crop, following rice and wheat (Khatri et al. 2020). Maize is a valuable source of nutrition containing high levels of carbohydrates (about 70% starch), along with essential vitamins A, C, E, proteins and vital minerals (Sheng et al. 2018). Moreover, it plays a significant role as a primary source of income for resource-limited farmers in many developing nations. In sub-Saharan Africa (SSA), where maize cultivation spans over 36 million hectares each year, a substantial portion of the local population relies on this crop for their food security and livelihood (Tefera et al. 2019).

Despite the wide range of benefits offered by this crop, its production and productivity in SSA faces numerous challenges, with significant hindrances arising from both biotic and abiotic factors (Assefa and Ayalew 2019; Mohamed et al. 2021). A prominent problem among them is the infestation by insect pests (Alam et al. 2014; Bakry and Abdel-Baky 2024). Recently, the situation has been exacerbated due to the invasion by the fall armyworm (FAW), *Spodoptera frugiperda* (J.E. Smith) to the region, adding a layer of complexity to the problem. This insect pest, a nocturnal moth native to the Americas, was first documented in Africa around January 2016 (Goergen et al. 2016) and has been reported to inflict heavy economic losses on maize since then (De Groote et al. 2020). Around the world where the pest has invaded, considerable damage has been reported on maize crop due to FAW feeding on leaf whorls, ears and tassel leading to complete failure of the crop in extreme cases (Khatri et al. 2020; Udayakumar et al. 2021). While FAW causes significant harm to maize, it has also been reported to damage other grass species such as sorghum, sugarcane, millets, rice, oat, Bermuda grass, crabgrass, bluegrass and Johnson grass (Babendreier et al. 2022; Nandhini et al. 2023).

The losses inflicted by FAW may vary depending on the location and severity of infestations (Kamweru et al. 2023). For instance, in Honduras Wyckhuys and O'Neil (2006) reported a 40% reduction, while in Argentina, Murúa et al. (2006) observed losses ranging from 17 to 72%. In 12 African countries, Day et al. (2017) and Overton et al. (2021) documented crop losses ranging between 21 and 53%. The ongoing spread of FAW across continents, including Africa, Asia and Australia has contributed to the global grain crisis (Kamweru et al. 2023). As a result, FAW has been listed as an A1 pest by the European and Mediterranean Plant Protection Organization (EPPO) to prevent its further spread and invasion to Europe, the Middle East and other regions (Mohamed et al. 2021).

As an emergency response to combat the devastation caused by FAW in SSA, there has been a widespread reliance on use of chemical insecticides against the pest (Otim et al. 2021; Van Den Berg et al. 2021; Tepa-Yotto et al. 2022). While the judicious use of chemical insecticides for short-term FAW management can be effective (Kamweru et al. 2023), the excessive and indiscriminate usage poses a serious hazard to human health and the environment (Otim et al. 2021). Moreover, the inaccessibility, high costs and development of insecticide resistance linked to the repeated use of chemical insecticides make this approach unsustainable for majority smallholder farmers (Mutyambai et al. 2022), prompting the need to explore alternative sustainable options.

Agroecological control strategies could be a practical alternatives to mitigate the drawbacks associated with chemical insecticides (Kirui et al. 2023). For example, agroecological control measures, such as intercropping, trap cropping and push-pull companion cropping, have proven to be effective in reducing FAW damage on crops (Smith and McSorley 2000; Hailu et al. 2018; Midega et al. 2018; He et al. 2021; Udayakumar et al. 2021; Jalloh et al. 2023). Farmers, especially in Africa and South America, traditionally grow diverse crops with maize, primarily legumes such as beans or peas, but also other crops including cassava and yam (Babendreier et al. 2022). Such crop diversification has been shown to increase activity and population of natural enemy to enhance pest control (Harrison et al. 2019). Studies have documented that intercrops can decrease FAW oviposition through the emission of repellent volatile organic compounds (VOCs) and olfactory camouflage (Harrison et al. 2019; Sobhy et al. 2022; Kenis et al. 2022). A notable example is the reduction of FAW damage in climate-adapted push-pull systems (Midega et al. 2018), where *Desmodium* spp releases repellent volatiles (Sobhy et al. 2022). However, the effectiveness of these measures may vary across intercrops and situations. For instance, Baudron et al. (2019), observed an association between pumpkin intercropping and increased FAW damage in a study conducted in farmer fields in Zimbabwe. Hence, gaining more insight into the mechanisms that lead to decreased FAW infestation through the utilization of companion crops in a maize-based intercropping system is vital to effectively implement intercropping as a pest management strategy.

Our recent laboratory and screen house studies have shown that incorporating edible companion intercrops holds the potential to reduce FAW infestation (egg-laying) (Peter et al. 2023). This reduction is attributed to the emission of FAW repellent VOCs while simultaneously enhancing the attraction of its natural enemies (parasitoids) (Peter et al. 2023). VOCs are known to play a significant role in mediating interactions between plants and insects (Clavijo Mccormick et al. 2014; Aartsma et al. 2017; Bouwmeester et al. 2019). Specifically, the behaviours of herbivorous in-

Fig. 1 Map of Kenya showing the study sites in two locations (counties)

sect pests are affected by VOCs emitted by host and non-host plant species (Cai et al. 2018). Moreover, the composition and concentrations of VOCs emission may vary across plant species and is often affected by both biotic and abiotic environmental factors (Clavijo McCormick 2016; Effah et al. 2021). The VOCs emitted by plants serve as crucial indicators of their physiological reactions to environmental conditions and temperature has been identified as a key factor influencing both volatile emissions and the ecology of plants (Effah et al. 2021).

In Kenya and other parts of SSA, maize cultivation occurs across diverse agroecological zones, encompassing wet areas to hot semi-arid lands with differing climatic conditions. Moreover, most smallholder farmers in the region grow maize with other intercrops, especially legumes. To maximize the effectiveness of intercropping systems against FAW, it is important to study and test the impacts of different companion plants and their control potential in the new environments and landscapes of Africa. Building upon our earlier laboratory study (Peter et al. 2023), we evaluated the effectiveness of different edible crop combinations in influencing FAW infestation and the abundance of its natural enemies under field conditions in two different locations in Kenya with distinct climatic conditions (Fig. 1). Since weather factors such as temperature and relative humidity (RH) are known to influence FAW population dynamics, they can indirectly affect the severity of crop damage in various maize-growing agroecology (Yan et al. 2022; Tanaka and Matsukura 2023). Thus, we also examined how weather variables impact the population of FAW and its natural enemies.

Materials and Methods

Study Sites

Field trials were carried out in two maize-growing regions of Kenya (Fig. 1) from April to December 2022, during the maize cropping season. In selecting study sites for the trials, we considered elevation to be a crucial factor in influencing climatic variations across locations. Site 1: Kabuku in Limuru, Kiambu County, situated at an elevation of 2120 m above sea level (masl) (coordinates: S 01° 09′ 38.5″ E 036° 40′ 35.2″), and Site 2: Kibembe in Mwea, Kirinyaga County, with an elevation of 1174 masl (coordinates: S 00° 39′ 03.7″ E 037° 22′ 48.1″).

Treatments, Experimental Design and Layout

Five treatments (i.e. maize intercropping systems) namely: (i) maize + beans (*Phaseolus vulgaris* L.), (ii) maize + groundnut (*Arachis hypogaea* L.), (iii) maize + cassava (*Manihot esculenta* Crantz), (iv) maize + sweet potato (*Ipomoea batatas* L.) and (v) maize monocrop (control) were laid out in a Randomized Complete Block Design (RCBD) and replicated five (5) times in each location. The treatments were laid out in a 6 m × 6 m plot size with 2 m spacing between blocks (replicates) and plots respectively

(Figure S1). Maize plants were planted at a 75 cm × 25 cm (inter and intra-row) spacing respectively. The companion intercrops were planted between the rows of maize. Each plot (both maize monocrop and intercropped combination) had 8 rows of maize per plot with 24 maize stands per row and a population of 192 maize stands per plot. In each site, two rows of maize (guard crop) were planted around the borders 2 m away from the experimental plots. In both locations, the experimental plots were laid out in a farm area of 42 m × 42 m (1764 m^2) and the trials were conducted under rainfed conditions and supplemented with irrigation but without any chemical pesticides (insecticides and herbicides) application.

Data Collection

Data on FAW live stages (eggs and larvae) abundance, infestation, damage levels, population of FAW natural enemy on maize plants and yield of all treatment plots including weather and soil data (Table S1) were collected from the two experimental sites. We began sampling and inspecting for live stages of FAW, infestation levels, and the abundance of natural enemies two weeks after maize planting. This process was repeated every two weeks for a total of 8 samplings, i.e. sixteen weeks (four months) from the planting date. We used weeks after planting (WAP) to collect, standardize and compare data across the two sites, while also noting the corresponding maize growth stages [vegetative (V) and reproductive (R)] throughout the sampling periods to ensure an accurate representation of plant development stages across the different locations (Alam et al. 2021).

Fall Armyworm Abundance and Infestation

Fifty (50) maize plants from all the treatment plots were assessed using the 'W' pattern approach (Niassy et al. 2021) where 10 maize plants were randomly selected across 5 points per plot to examine FAW live stage abundance and infestation, excluding the outer two guard rows of maize. A total of 250 maize plants were sampled for each of the 5 treatments, resulting in 1250 plants sampled per location. Maize leaves, whorls, ears and stems were thoroughly checked for the presence of FAW eggs, larvae and damage. The number of eggs (both egg batches and total eggs laid), larvae and maize plants with the active presence of FAW live stages (eggs and larvae) and FAW feeding symptoms were counted and recorded per plot at each location. The number of plants and ears (at harvest) with FAW damage in each plot was converted to proportions and expressed as percentages.

Level of Plant Damage

The level of FAW damage on the randomly selected maize plants per plot (50) was assessed and rated using the 1–9 whole plant leaf damage scale for FAW (Soujanya et al. 2022). The average damage score of the sampled maize plants per plot was determined by calculating the mean score across all sampled plants (both infested and non-infested) (Mutyambai et al. 2022). The rating scores were classified as 1–4 indicating minimal visible leaf damage (Low), 5–7 marginal leaf damage (medium) and 8–9 extensive leaf damage (high).

Natural Enemy Abundance

Fifty (50) maize plants from each plot were randomly selected using a similar approach as mentioned above to assess the population of natural enemies on maize plants in each treatment. The number of predators (lady beetles and earwigs) were collected, counted, and recorded in each treatment plot. Moreover, FAW parasitoid cocoons were collected from maize leaves where we observed parasitised FAW larvae cadavers and then brought them to the laboratory to monitor adult emergence. Adults emerging from unidentified cocoons were subsequently used in parasitism assays to assess their ability to parasitize different FAW larval stages and compare their identities with previous reports (Agboyi et al. 2020; Mohamed et al. 2021; Otim et al. 2021).

Yield

Harvested maize cobs in each treatment plot were weighed using a Berger ACS-300 digital scale (Ningbo Berger, China), the shelling percentage was calculated as described by (Lauer 2002) and the moisture content was determined using Grain Moisture Tester PM-450 (Kett, USA). The yield data (kg/plot) was generated using the formula described by Tandzi and Mutengwa (2020).

$$\text{Yield (kg/plot)} = \frac{\text{Ear weight} \times (100 - \text{MC}) \times \text{shelling percentage}}{(100 - \text{Adjusted moisture content}) \times \text{Plot Area}}$$

Where MC = Moisture content determined at harvest:

$$\text{Shelling percentage} = \frac{\text{Grain weight (shelled)}}{\text{Ear weight}} \times 100$$

Weather Data

Weather variables such as temperature, relative humidity and precipitation of the two experimental sites were ob-

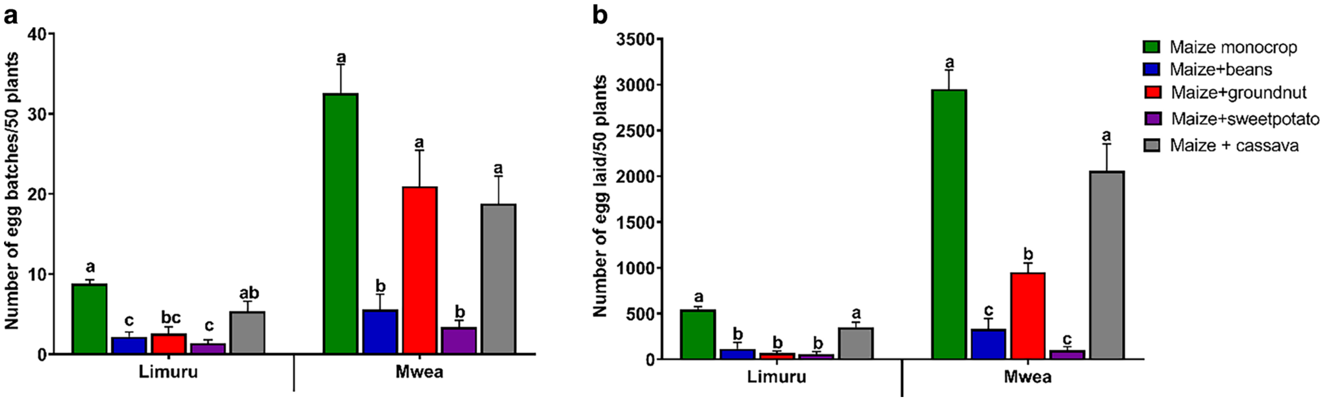

Fig. 2 Egg deposition by *Spodoptera frugiperda* across treatments at two experimental sites, Limuru and Mwea ($n = 5$). Mean (± SE) number of (**a**) egg batches (**b**) total eggs laid on maize plants. Treatments with similar letters above the bars in each location are not significantly different based on Tukey post-hoc test ($P < 0.05$)

tained from NASA Power Project Metrological database (https://power.larc.nasa.gov/data-access-viewer/) and Google Earth Engine Data Catalog (https://developers.google.com/earth-engine/datasets/catalog/UCSB-CHG_CHIRPS_DAILY) using the GPS coordinates of each farm site.

Statistical Analyses

All data generated were tested for normality using the Shapiro-Wilk test. We analyzed the quantities of egg batches, total eggs laid, larvae, and FAW parasitoids (cocoons) and predators in each treatment using a generalized linear model with quasipoisson distribution to address overdispersion in the datasets. The differentiation of significant means was carried out through the Tukey post-hoc test. We used a linear mixed effect model using the' lmer' function from the 'lme4' package to determine the effect of maize phenology (growth stages) on the abundance of FAW live stages (eggs and larvae) as well as its natural enemies. The number of eggs, larvae, and natural enemies were the response variables, treatments and sampling duration (weeks) fixed effects, while replication was kept as a random effect. We further used beta regression with the betareg package (Cribari-Neto and Zeileis 2010) with a Tukey post hoc test to analyze proportion data (FAW damaged maize plants and ears). We used one-way ANOVA to analyze the damage score and yield data for each treatment. The differentiation of significant means was performed through the Newman-Keuls post hoc test ($P < 0.05$). Additionally, we conducted a correlation analysis to investigate the relationship between the population of FAW, natural enemy live stages and weather variables at the experimental sites. All data analyses were carried out using R statistical software (R Core Team 2021).

Results

Fall Armyworm Eggs

The number of FAW eggs (egg batches and total egg count) deposited on maize plants was influenced by the different crop mixtures (treatments) used in the maize intercropping trials at both locations (Fig. 2). Female FAW deposited significantly more egg batches in plots with maize plants alone (monocrop) compared to maize plots intercropped with beans, groundnuts and sweet potatoes in Limuru ($\chi^2 = 54.26$, df = 4, $P < 0.001$, Fig. 2a). Similarly, significantly lower number of egg batches were recorded in maize plots intercropped with beans and sweet potatoes in Mwea ($\chi^2 = 69.23$, df = 4, $P < 0.001$, Fig. 2a). More so, the total number of FAW eggs laid was significantly higher in maize monocrop and maize + cassava plots compared to maize plots intercropped with beans, groundnut and sweet potato in both locations (Limuru: $\chi^2 = 54.71$, df = 4, $P < 0.001$, Mwea: $\chi^2 = 210.81$, df = 4, $P < 0.001$, Fig. 2b).

Equally, we observed that maize growth stages had effects on the number of eggs deposited by female FAW across treatments in both locations (Fig. 3). In Mwea, a significantly higher number of FAW egg batches were recorded at four WAP, corresponding to the four-leaf stage (V4) in maize monocrop ($\chi^2 = 197.12$, df = 28, $P < 0.001$, Fig. 3b). In Limuru, we recorded a significantly higher number of egg batches at six WAP, corresponding to the V6 maize growth stage ($\chi^2 = 50.32$, df = 7, $P < 0.001$, Fig. 3a), but there was no significant interaction between maize growth stages and treatments ($\chi^2 = 31.21$, df = 28, $P = 0.30$). In terms of the total number of eggs laid, a significant interaction effect was observed between growth stages and treatments in both locations (Mwea: $\chi^2 = 630.79$, df = 28, $P < 0.001$, Fig. 3d, Limuru: $\chi^2 = 44.27$, df = 28, $P = 0.02$, Fig. 3c). More eggs

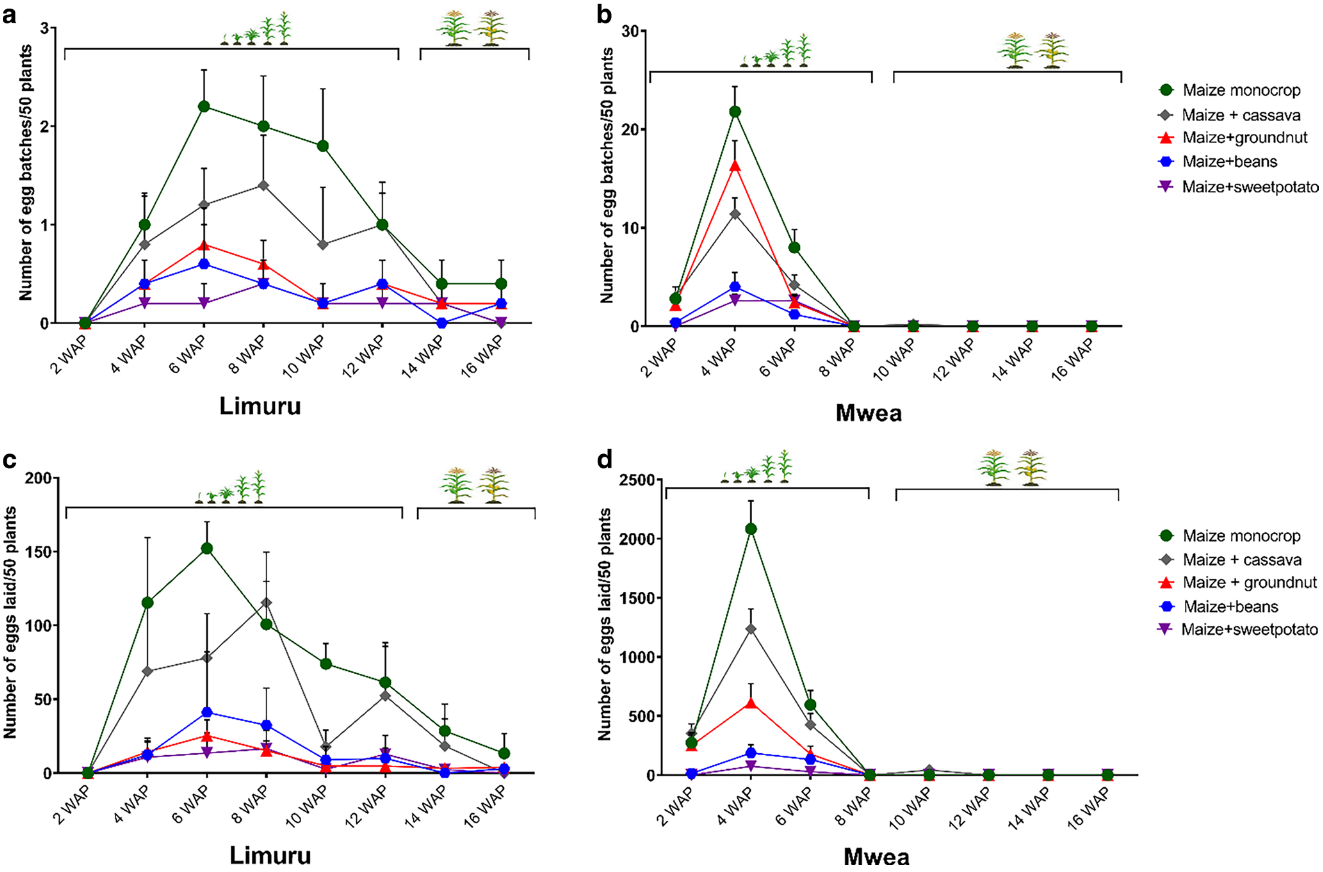

Fig. 3 Egg deposition by *Spodoptera frugiperda* on maize crop at different maize growth stages at two study sites. Weeks after planting (WAP) correlation with maize growth stages was done according to Alam et al. (2021). Limuru: mean (± SE) number of *S. frugiperda* egg batches (**a**) eggs (**c**) deposited. Mwea: mean (± SE) number of egg batches (**b**) eggs (**d**) laid on maize plants across sampling weeks. The scales on the Y-axes differed between the response variables across experimental sites to accommodate the range of observed values

were laid in maize monocrop at V4 and V6 stages in Mwea and Limuru, respectively.

Fall Armyworm Larvae

Overall, higher number of FAW larvae were recorded in Mwea than Limuru (Fig. 4). However, the number of live FAW larvae was greater in maize monocrop than maize plots intercropped with beans, groundnuts and sweet potatoes except for cassava in both locations (Limuru: $\chi^2 = 28.84$, df = 4, $P < 0.001$, Mwea: $\chi^2 = 119.06$, df = 4, $P < 0.001$, Fig. 4). Furthermore, a significant interaction effect was observed between maize growth stages and treatments in both locations (Limuru: $\chi^2 = 46.30$, df = 28, $P = 0.01$, Fig. 5a, Mwea: $\chi^2 = 201.66$, df = 28, $P < 0.001$, Fig. 5b). The highest number of live FAW larvae were recorded at 8 WAP, corresponding to the V10 maize growth stage, in maize monocrop at both experimental sites (Fig. 5a and b).

Fall Armyworm Infestation

Infestation of maize plants with FAW eggs and larvae was markedly greater in maize monocrop than maize plots intercropped with beans, groundnuts and sweet potatoes at both experimental sites (Limuru: $\chi^2 = 24.82$, df = 4, $P < 0.001$, Mwea: $\chi^2 = 0.06$, df = 4, $P < 0.001$, Fig. 6a). Notably, we observed, at both experimental plots, there was a significant difference between the treatments in the percentage of maize plants with visible foliar damage symptoms (Limuru: $\chi^2 = 23.38$, df = 4, $P < 0.001$, Mwea: $\chi^2 = 31.88$, df = 4, $P < 0.001$, Fig. 6b), FAW damaged maize ear (Limuru: $\chi^2 = 106.85$, df = 4, $P < 0.001$, Mwea: $\chi^2 = 122.24$, df = 4, $P < 0.001$, Fig. 6d) and the level of plant damage (Limuru: $F_{(4, 20)} = 18.16$, $P < 0.001$, Mwea: $F_{(4, 20)} = 66.54$, $P < 0.001$, Fig. 6c).

Fall Armyworm Natural Enemies

The parasitoids reared from the field collected cocoons comprised *Cotesia icipe, Campoletis pedunculata* and *Charops ater* while the main FAW predators were lady

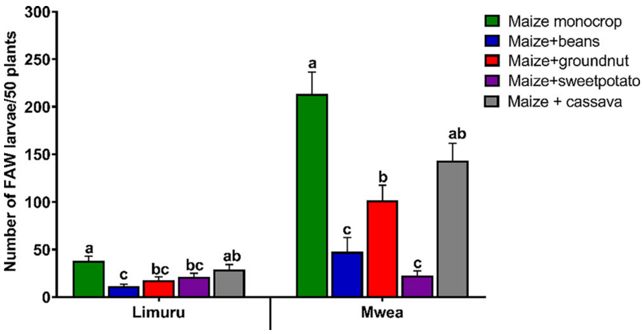

Fig. 4 Abundance (mean ± SE) of *Spodoptera frugiperda* larvae on maize plants across treatments in two experimental sites ($n = 5$). Treatments with similar letters above the bars in each location are not significantly different based on Tukey post-hoc test ($P < 0.05$)

beetles and earwigs. The number of FAW predators (lady beetles and earwigs) collected were significantly greater in maize plots intercropped with beans, sweet potatoes and groundnuts compared to plots with maize alone and maize + cassava in Limuru ($\chi^2 = 17.73$, df = 4, $P = 0.001$, Fig. 7). In Mwea, a higher number of FAW predators were recorded in maize plots intercropped with beans, followed by maize + groundnut and maize + sweet potato plots compared to the other treatments ($\chi^2 = 31.19$, df = 4, $P < 0.001$, Fig. 7). Furthermore, the population of FAW predators in Limuru were significantly higher at 14 WAP, corresponding to the milking stage (reproductive phase) of maize ($\chi^2 = 48.69$, df = 7, $P < 0.001$, Fig. 8a), but there was no significant interaction between treatments and maize growth stages ($\chi^2 = 17.65$, df = 4, $P = 0.93$). Whereas, a significant interaction effect was observed in Mwea, where the highest number of FAW predators were recorded at 8 WAP (V10) in maize plots intercropped with beans ($\chi^2 = 60.16$, df = 28, $P < 0.001$, Fig. 8b).

Correlation Analysis

We conducted a correlation analysis to examine the impact of weather parameters, such as temperature, relative humidity, and precipitation, on the abundance of live FAW stages and its natural enemy population at both locations. This analysis was aimed at understanding the relationship between the number of FAW and natural enemy live stages collected and the prevailing weather conditions across the experimental sites. We observed a significant positive correlation between temperature and the number of FAW egg batches ($r_s = 0.69$, $P < 0.01$), larvae ($r_s = 0.82$, $P < 0.001$) and predators ($r_s = 0.83$, $P < 0.001$) in Mwea (Table 1). Also, at the same location, there was a significant negative correlation between relative humidity (RH) and the numbers of FAW egg batches ($r_s = -0.95$, $P < 0.001$), larvae ($r_s = -0.98$, $P < 0.001$), and predators ($r_s = -0.58$, $P = 0.02$) (Table 1). Similarly, significant negative correlation was observed in Limuru between RH and the number of FAW larvae ($r_s = -0.92$, $P < 0.01$) and predators ($r_s = -0.90$, $P = 0.014$) (Table 1). However, precipitation had no significant correlation ($P > 0.05$) with the population of FAW and its natural enemy abundance at both locations (Table 1).

Yield

We observed a distinct difference in maize yield among the treatments at both locations (Fig. 9). In Limuru, maize plots intercropped with beans and sweet potatoes resulted in a significantly higher yield compared to plots with maize + cassava and maize alone, which had the lowest yield ($F_{(4, 20)} = 7.16$, $P < 0.001$, Fig. 9). A comparable pattern was noticed in Mwea, where the lowest yield was recorded in plots with sole maize, and this difference was statistically significant when compared to the other treatments,

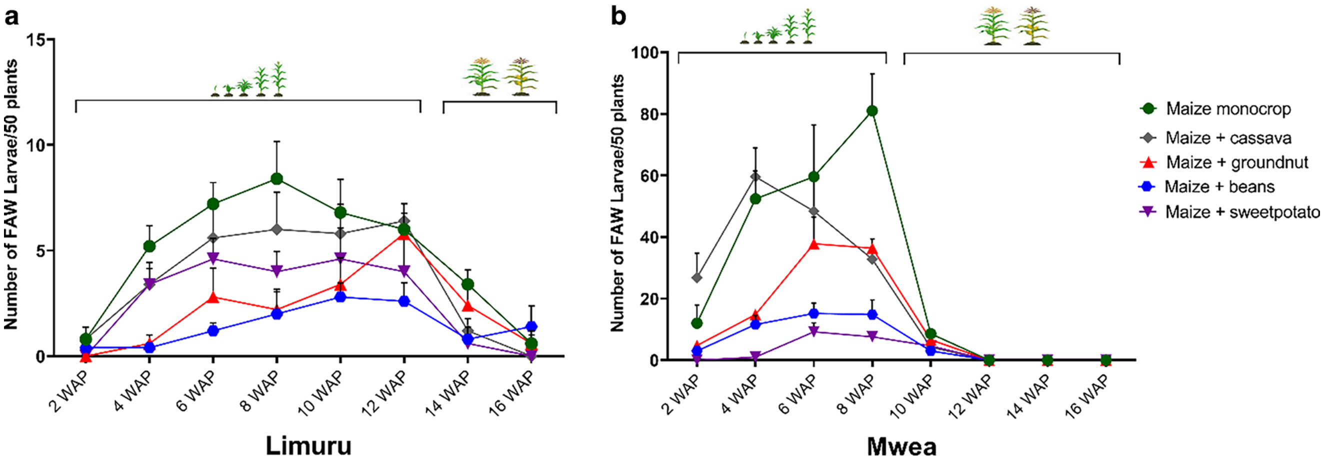

Fig. 5 The number (Mean ± SE) of *Spodoptera frugiperda* larvae collected in (**a**) Limuru and (**b**) Mwea at different maize growth stages. Weeks after planting (WAP) correlation with maize growth stages was done according to Alam et al. (2021). The scales on the Y-axes differ between the response variables across experimental sites to accommodate the actual observed values

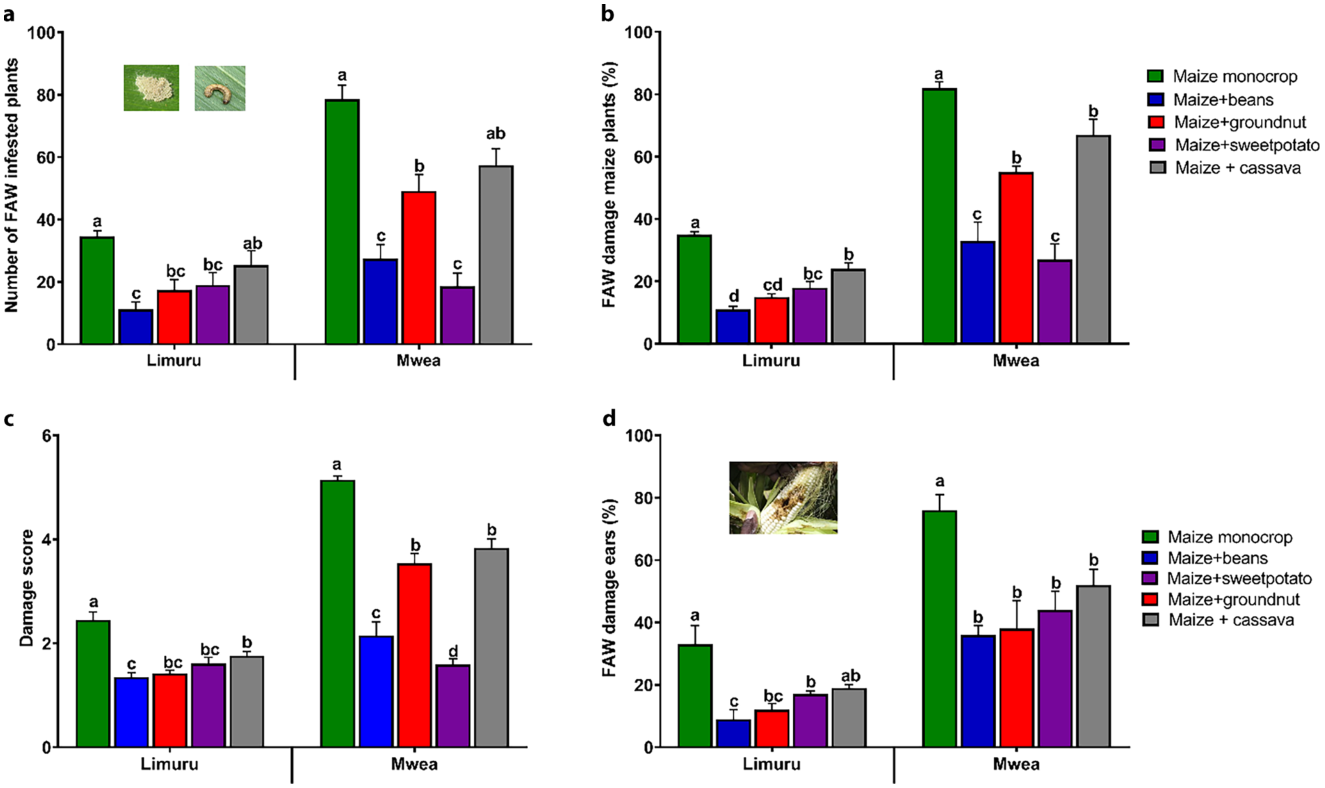

Fig. 6 Infestation by *Spodoptera frugiperda* on maize plants across treatments at two experimental sites ($n = 5$). Mean (± SE) number of FAW (**a**) infested plants (**b**) damage plants (**c**) level of plant damage and (**d**) damage ears (cobs). Treatments with similar letters above the bars in each location are not significantly different (Tukey post-hoc test, $P < 0.05$)

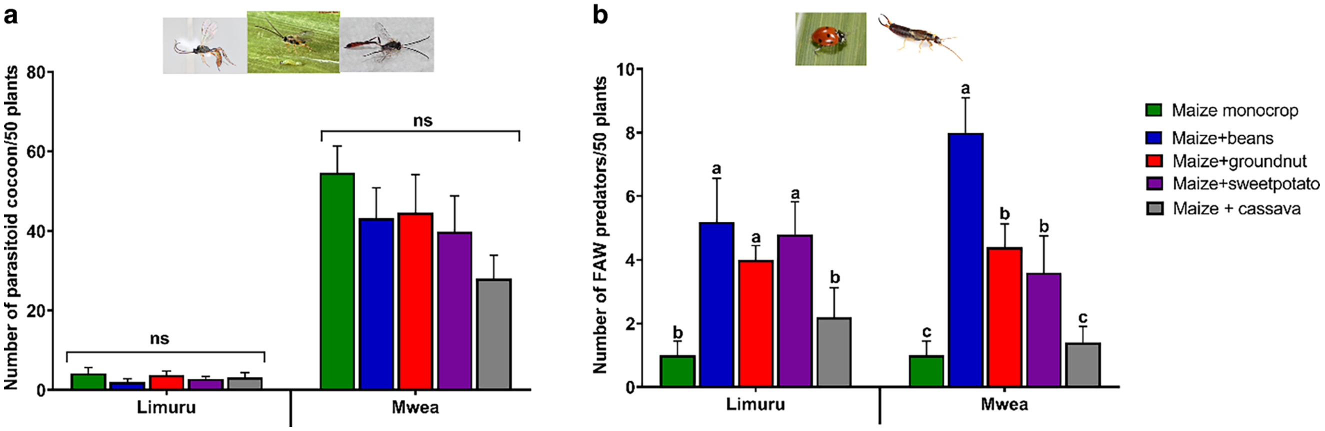

Fig. 7 Abundance of *Spodoptera frugiperda* natural enemies on maize plants across treatments at two experimental sites ($n = 5$). Mean (± SE) number of FAW (**a**) parasitoid (*Cotesia icipe*, *Campoletis pedunculata* and *Charops ater*) cocoons (**b**) predators (lady beetles and earwigs). Treatments with similar letters above the bars in each location are not significantly different (Tukey post-hoc test, $P < 0.05$)

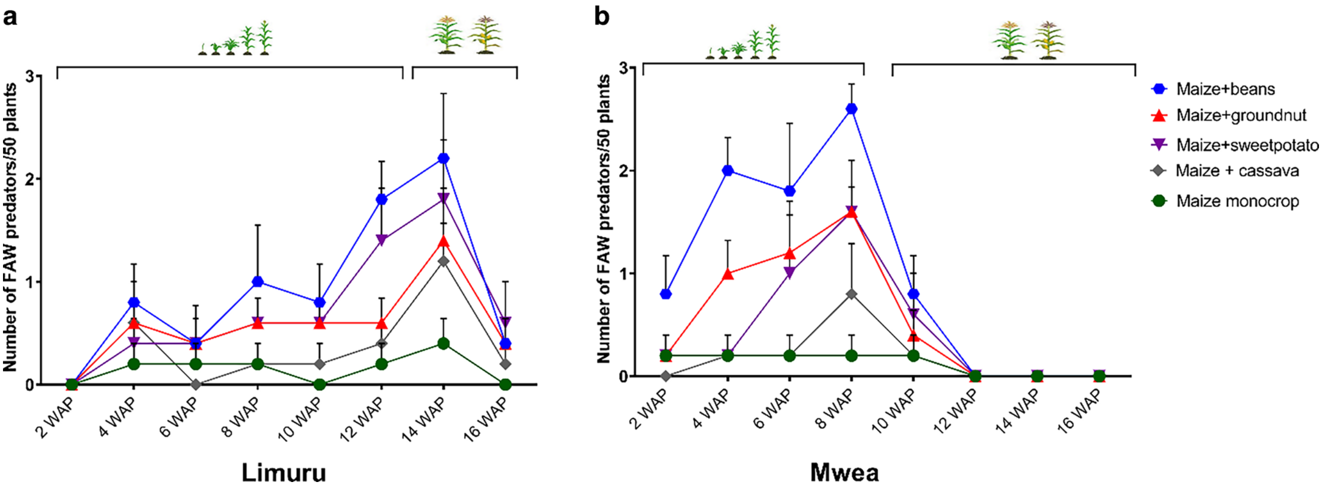

Fig. 8 Number (Mean ± SE) of *Spodoptera frugiperda* predators collected from maize plants at different growth stages in (**a**) Limuru and (**b**) Mwea. Weeks after planting (WAP) correlation with maize growth stages was done according to Alam et al. (2021)

Table 1 Spearman's correlation analysis between the population of fall armyworm life stages, its natural enemies, and weather variables at the study locations

	LIMURU			MWEA		
	Egg batches	Larvae	Predators	Egg batches	Larvae	Predators
Weather Variables	R_s	R_s	R_s	R_s	R_s	R_s
Temperature	0.55	0.58	0.55	0.69**	0.82***	0.83***
Relative Humidity	–0.28	–0.92**	–0.90*	–0.95***	–0.98***	–0.58*
Precipitation	–0.19	0.52	0.30	–0.42	–0.51	–0.51

r_s Spearman's correlation coefficient for respective parameters compared

Statistically significant correlations are given in asterisks *** for $p < 0.001$, ** for $p < 0.01$, * for $p < 0.05$

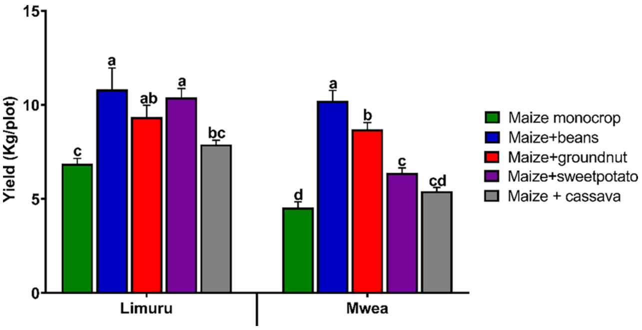

Fig. 9 Yield (mean ± SE) of maize (kg/plot) across treatments at two experimental sites ($n = 5$). Treatments with similar letters above the bars at each location are not significantly different. (Tukey post-hoc test, $P < 0.05$)

except for plots with maize + cassava intercrop ($F_{(4, 20)} = 44.43$, $P < 0.001$, Fig. 9). Remarkably, we observed a decrease in maize yield within the maize + sweet potato plots in Mwea as opposed to the yield obtained in Limuru.

Discussion

One way to manage insect pests in an agricultural cropping system is by incorporating companion plants, a control strategy known as crop diversification. Previous studies have shown that crop diversification promote pest management directly through bottom-up effects of reducing pest population, and/or indirectly through top-down effects of enhancing natural enemies controlling the pest populations (Jaworski et al. 2023). In this process, volatile organic compounds (VOCs) released by these companion plants play a crucial role in mediating the interactions between plants and insects (Bouwmeester et al. 2019). Despite the known benefits of crop diversification in pest management, most studies considered the effects of non-crop habitat management such as flowering plants and banker plant systems (Arnò et al. 2018; Chen et al. 2022). Hence, there is an increasing need to determine crop functional diversity which provides effective pest management benefit while intensifying the existing production land. In this study, we investigated the impacts of functional diversity in maize based intercropping system comprising different edible companion crops in reducing the invasive fall armyworm pest in its new habitat as well as its influence on the pest's natural enemy abundance.

Our results, from field studies at two maize growing agroecologies in Kenya with distinct climatic conditions, demonstrated that intercropping companion plants could provide protection to maize plants from FAW damage by reducing infestation by the pest, further validating our previous laboratory findings (Peter et al. 2023). At both study sites, Limuru and Mwea, we recorded a significantly lower number of FAW eggs on maize plants intercropped with beans, sweet potato and groundnut as opposed to maize monoculture and maize plots with cassava intercrop. These results indicate that intercropping appropriate companion plants together with maize can reduce FAW oviposition and subsequent damage by the emerging larvae. Our findings corroborate with previous studies which highlighted the potential of companion crops in reducing FAW oviposition in mixed cropping systems (Hailu et al. 2018; Midega et al. 2018; Kenis et al. 2022). Yet, this generalization may not always hold true for every combination of crops in all circumstances as observed in maize plots intercropped with cassava where similar effects were not observed. Previous studies by Baudron et al. (2019) and Nwanze et al. (2021), have reported an association of FAW with intercrops (pumpkin and cassava) planted with maize leading to higher FAW infestation (oviposition) in the field.

Similarly, at both study locations, intercropping maize with beans, sweet potato and groundnut significantly reduced the number of live FAW larvae compared to maize monocrop. This is in line with previous findings which reported a reduction in population of FAW larvae in maize intercrops compared to sole maize plots (Hailu et al. 2018; Tanyi et al. 2020; Khatri et al. 2020; Udayakumar et al. 2021). Beside altering the detection cues of the main host crop (maize) and the repellent effects of companion plant volatiles to FAW moths (Sobhy et al. 2022), having intercrops in a maize field creates a distinct ecological space for FAW larvae, preventing the pest's dispersal, especially through ballooning, within the crop field (Tanyi et al. 2020; Scheidegger et al. 2021). Moreover, the intercrops could also mechanically trap and decimate dispersing larvae (Kaur and Kariyat 2020). Our findings further demonstrated that maize monoculture had significantly higher FAW egg and larval infestations compared to plots intercropped with beans, sweet potato, and groundnut, except cassava. Intercropped systems also had lower rates of FAW feeding symptoms, damaged cobs, and overall plant damage. Similar results have been documented by Mutyambai et al. (2022) in related study conducted in various maize-growing agroecologies of Kenya. They observed that plots with maize alone exhibited higher FAW infestation and damage compared to maize grown under mixed cropping systems at various agroecological zones. Additionally, their study indicated increased FAW infestation in maize plots intercropped with cassava, particularly in the midland zones, aligning with our current findings. In Uganda, Hailu et al. (2018) found that intercropping maize with beans, soybeans, or groundnuts had a beneficial effect in reducing *S. frugiperda* incidence and damage to maize plants. An earlier study by Altieri et al. (1978) have reported a 23% reduction in FAW incidence (whorl feeding) when maize was intercropped with beans in Columbia. In the present study, the average leaf damage score of maize monoculture was 2.45 (low) in Limuru and medium 5.15 in Mwea experimental sites. These figures fall within the range reported in earlier studies that documented the level of FAW damage on unprotected maize plants in Africa and Asia (Patidar et al. 2022; Chisonga et al. 2023).

In both locations, we observed that maize growth stages had a significant effect on the population of *S. frugiperda* live stages. Fall armyworm eggs and larvae were most abundant between V4 and V10 maize growth stages, which suggests the critical period for FAW incidence. Previous research has consistently shown that the presence and distribution of FAW life stages (eggs and larvae) depend on the plant's age and growth (Caniço et al. 2020; Omoregie et al. 2023; Bakry and Abdel-Baky 2024). Our current study supports this observation, noting a higher abundance of FAW eggs and larvae during the early vegetative stage. Conversely, their numbers decrease as the maize enters its full reproductive phase, marked by tasseling and silking. This finding aligns with and substantiates results obtained in earlier studies (Jaramillo-Barrios et al. 2019; Adjimoti et al. 2023; Bakry and Abdel-Baky 2024; Durocher-Granger et al. 2024). Hence, safeguarding maize plants from FAW infestation during the critical stages of vegetative growth is crucial to achieve the maximum yield (Van Den Berg et al. 2021; Sisay et al. 2024).

Farming methods that consider ecological principles, like intercropping, play a crucial role in integrated pest management (IPM) strategies (Barzman et al. 2015). These methods impact pests either directly by repelling phytophagous insects or by boosting the numbers and effectiveness of their natural enemies (Khan et al. 1997; Khatri et al. 2020; Shanmugam et al. 2021). Various native parasitoids and predators target FAW both in its native and newly invaded habitats (Agboyi et al. 2020; Kenis et al. 2022). In our study, we recorded FAW parasitoid (*C. icipe, C. pedunculata* and *C. ater*) and predator natural enemies such as lady beetles (Coccinellidae) and earwigs (*Doru* sp.). A greater number of FAW predators such as lady beetles (Coccinellidae) and earwigs (*Doru* sp.) were observed in maize plots intercropped with beans, sweet potatoes and groundnuts compared to maize monocrop at both locations. Intercropping has been shown to enhance the on-field diversity of natural enemies of FAW (Girma et al. 2000; Udayakumar et al. 2021; Kenis et al. 2022).

In this study, we have only examined field collected parasitoid cocoons from FAW larval cadavers as FAW predator natural enemies were the main focus of the current study. Rearing field collected FAW immature stages (eggs, larvae, pupae) and monitoring adult parasitoid emergence could provide a more objective comparison of parasitoid abundance between treatments. Among the parasitoids that emerged from field collected cocoons in the present study, *C. icipe* and *C. ater* have been reported to attack the FAW in SSA (Agboyi et al. 2020; Mohamed et al. 2021; Otim et al. 2021). Parasitoids from the genus *Campoletis*, such as *Campoletis sonorensis, C. flavicincta* and *C. grioti* have been extensively used to suppress the field population of *S. frugiperda* in the Americas (Jourdie et al. 2010; Abbas et al. 2022). However, in Africa, little or no report of these parasitoids from the genus *Campoletis*, attacking *S. frugiperda* has been documented. Interestingly, in this study, *C. pedunculata* was identified as one of the parasitoids parasitizing FAW larvae from the cocoons collected in Limuru. Our parasitism assays confirmed that *C. pedunculata* females successfully parasitized 1st, 2nd, and 3rd instar FAW larvae (Unpublished data, 2023). These experiments also revealed the parasitoid's preference and effectiveness across different FAW larval stages, offering valuable insights into its potential as a biological control agent. Research has shown that volatiles produced by the main crop in response to herbivory typically indicate the presence of potential insect pests (host) (War et al. 2012; Turlings and Degen 2022); while, similar sets of volatiles have also been reported to be produced by some intact intercrop plants (Khan et al. 1997; Sobhy et al. 2022). Parasitoid wasps exploit cues produced either after herbivory or constitutively by some plants to locate their hosts (Khan et al. 1997; Åhman et al. 2010; Tamiru et al. 2011, 2015). Numerous investigations have shown that introducing diversity at the farm level leads to a higher presence of natural enemies and enhances their ability to effectively control FAW (Altieri 1980; Harrison et al. 2019; Shanmugam et al. 2021; Udayakumar et al. 2021). Overall, higher FAW infestation and natural enemy abundance were recorded in the experimental field located at Mwea (midland agroecology) compared to Limuru (highland agroecology). These differences may be linked to the differences in altitude and associated climate variations between the two locations. Previous studies indicated that variations in altitude and weather can impact the population and infestation of FAW, as well as the abundance of its natural enemies (Mengesha et al. 2021; Yan et al. 2022; Tanaka and Matsukura 2023; Singh et al. 2023; Omoregie et al. 2023). Studies by Mutyambai et al. (2022) and Singh et al. (2023) have reported that low and mid-land altitudes provide more favourable conditions for FAW survival, leading to corresponding significant infestation and damage to maize compared to higher altitudes. Additionally, study by De Groote et al. (2020) found that FAW infestation and damage were more than doubled in low and mid-land regions of Kenya as compared to the highlands since the initial reports of FAW invasion in the country.

Furthermore, in this study, our correlation analysis revealed a significant relationship between temperature, relative humidity (RH) and the FAW population life stages and natural enemies. In Mwea, temperature showed a significant positive correlation with the numbers of FAW egg batches, larvae and predators. This suggests that higher temperatures may promote increased FAW activity and reproduction, as well as enhance the development and activity of natural enemies. Warmer conditions could accelerate the lifecycles of both FAW and its natural enemies leading to higher observed numbers. In contrast, a significant negative correlation was observed between RH and the number of FAW larvae and predators both in Mwea and Limuru. Higher RH levels may create less favourable conditions for FAW development and survival, possibly due to increased moisture affecting larval growth. Additionally, higher RH could influence the activity and effectiveness of natural enemies, potentially reducing their impacts on FAW populations which corroborates with previous findings (Yan et al. 2022; Tanaka and Matsukura 2023; Singh et al. 2023; Omoregie et al. 2023). Temperature and RH have been recognized as the primary abiotic factors impacting herbivorous insects (Tamiru et al. 2012). It has been opined that higher temperatures accelerate the developmental rate, shorten generation time and increase the infestation of crops by the FAW (Tamiru et al. 2012; Yan et al. 2022). These play a significant role in the geographic distribution, phenology of FAW and abundance of its natural enemies (Singh et al. 2023; Omoregie et al. 2023). Consequently, this may have implications for crop damage across locations.

Various studies have assessed the influence of FAW damage on maize yield (Abrahams et al. 2017; Mengesha et al. 2021; Bakry and Abdel-Baky 2024), and documented that a decrease in yield can become more evident as the severity of FAW infestation and damage on maize plants increases. According to Trenbath (1993), in certain situations, intercropping can be advantageous in controlling pest populations and minimizing crop yield losses. In our current study, we observed maize intercropped with beans, sweet potato and groundnut had greater yield compared to maize monocrop in both locations which confirmed previous reports (Trenbath 1993; Hailu et al. 2018; Jalloh et al. 2023). However, we noticed a decrease in maize yield in maize plots intercropped with sweet potato in Mwea, as opposed to the same treatment in Limuru. This decline in yield could be attributed to the intense competition between plants resulting in the suppression of maize growth in the plots where maize was intercropped with sweet potato (Arubalueze et al. 2017). Crop yields in intercropping systems have been noted to vary based on the populations of the component crops (Asiimwe et al. 2016). The potential advantages of intercropping systems appear to be significantly dependent on the specific conditions of a given locality and agronomic management. As such, the productivity and profitability of intercropping systems are enhanced when the selection of crops, their spatial arrangement, and the population density of component crops are carefully chosen and well-managed (Islam et al. 2015).

Conclusion

The findings from this study offer tangible evidence from realistic field conditions that crop diversification serves as a practical and effective strategy for combating the FAW. This study specifically showcased that intercropping maize with beans, sweet potato, and groundnut has the potential to prevent crop yield losses due to the pest by shielding maize crops from fall armyworm infestation and indirectly enhance the recruitment of its natural enemies such as ladybeetles and earwigs. Ensuring crop yield advantages in intercropping systems may require careful selection and proper management of the companion intercrops. This agroecological approach (intercropping /crop mixture) is cost-effective and ecologically sustainable way of FAW management as it does not require using toxic chemical pesticides, which are often expensive in the context of smallholder farming. Hence, it presents a viable intervention that can be readily adopted by small-scale farmers in Africa and beyond, and seamlessly incorporated into Integrated FAW Management programs.

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Author Contribution A. Tamiru, E. Peter, S. Subramanian, and B. Torto conceived and designed research. E. Peter conducted experiments and analyzed data. E. Peter and A. Tamiru wrote the manuscript. All authors read, revised critically and approved the manuscript.

Data Availability The data sets generated during the current study are available from the corresponding author upon reasonable request.

Conflict of interest The authors have no competing interests to declare that are relevant to the content of this article.

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