

# Effects of distance from semi-natural habitat on fall armyworm (*Spodoptera frugiperda*, J. E. Smith) and its potential natural enemies in Ghana

## Research Paper

**Cite this article:** Jordon MW, Hackett TD, Aboagye-Antwi F, Eziah VY, Lewis OT (2022). Effects of distance from semi-natural habitat on fall armyworm (*Spodoptera frugiperda*, J. E. Smith) and its potential natural enemies in Ghana. *Bulletin of Entomological Research* **112**, 343–353. <https://doi.org/10.1017/S0007485321000894>

Received: 11 November 2020

Revised: 5 August 2021

Accepted: 28 August 2021

First published online: 7 October 2021


### Keywords:

Biocontrol; biological pest control; maize; parasitism; predation; sub-Saharan Africa

### Author for correspondence:

Matthew W. Jordon,

Email: [matthew.jordon@zoo.ox.ac.uk](mailto:matthew.jordon@zoo.ox.ac.uk)

Matthew W. Jordon<sup>1</sup> , Talya D. Hackett<sup>1</sup>, Fred Aboagye-Antwi<sup>2</sup>, Vincent Y. Eziah<sup>3</sup> and Owen T. Lewis<sup>1</sup>

<sup>1</sup>Department of Zoology, University of Oxford, Mansfield Road, Oxford, OX1 3SZ, United Kingdom; <sup>2</sup>Department of Animal Biology and Conservation Science, University of Ghana, P.O. Box LG 67, Accra, Ghana and <sup>3</sup>Department of Crop Science, University of Ghana, Accra, Ghana

### Abstract

Insect crop pests are a major threat to food security in sub-Saharan Africa. Configuration of semi-natural habitat within agricultural landscapes has the potential to enhance biological pest control, helping to maintain yields whilst minimising the negative effects of pesticide use. Fall armyworm (*Spodoptera frugiperda*, J. E. Smith) is an increasingly important pest of maize in sub-Saharan Africa, with reports of yield loss between 12 and 45%. We investigated the patterns of fall armyworm leaf damage in maize crops in Ghana, and used pitfall traps and dummy caterpillars to assess the spatial distribution of potential fall armyworm predators. Crop damage from fall armyworm at our study sites increased significantly with distance from the field edge, by up to 4% per m. We found evidence that Araneae activity, richness and diversity correspondingly decreased with distance from semi-natural habitat, although Hymenoptera richness and diversity increased. Our preliminary findings suggest that modifying field configuration to increase the proximity of maize to semi-natural habitat may reduce fall armyworm damage and increase natural enemy activity within crops. Further research is required to determine the level of fall armyworm suppression achievable through natural enemies, and how effectively this could safeguard yields.

### Introduction

The human population of sub-Saharan Africa is expected to at least double by 2050, necessitating a corresponding increase in food availability (Ittersum *et al.*, 2016; Cleland and Machiyama, 2017). Yields per hectare have, however, remained largely static in recent decades, and many African countries are net importers of food (Cleland and Machiyama, 2017). Sustainable intensification to close the yield gap between current and maximum possible production could help improve food security in this region (Godfray *et al.*, 2010; Godfray and Garnett, 2014).

One barrier to improving food security is yield loss from invertebrate pest damage. Sustainable intensification includes an increased reliance on biological pest control (Garibaldi *et al.*, 2017). As part of integrated pest management, this could increase yields while minimising the negative impacts of pesticide application such as environmental pollution and compromised human health (Bianchi *et al.*, 2006; Kansime *et al.*, 2019; Tambo *et al.*, 2020; Haggblade *et al.*, 2021). The configuration of landscape natural capital stocks (e.g. semi-natural habitat surrounding cropland) can potentially be managed to increase the flow of biological pest control services, particularly on smallholder farms (Steward *et al.*, 2014).

One such biological pest control service could come from habitat spillover effects, where populations of invertebrates from surrounding semi-natural habitat move into crop areas to consume or parasitize pests (Tscharntke *et al.*, 2005). Here, we refer to these predators and parasitoids as ‘natural enemies’. Complex landscapes consistently contain higher natural enemy populations than simple landscapes (Bianchi *et al.*, 2006). Furthermore, richness and diversity of natural enemy communities is important in delivering effective biological pest control (Wilby and Thomas, 2002; Cardinale *et al.*, 2003; Crowder *et al.*, 2010). However, measures to diversify crop landscapes are not guaranteed to enhance natural enemies, decrease pests, or increase yields (Bianchi *et al.*, 2006; Poveda *et al.*, 2008). Semi-natural habitat can act as reservoirs for crop pests, increasing their abundance and corresponding crop damage (Tscharntke *et al.*, 2005). The inconsistent impact of semi-natural habitat limits the ability to make general recommendations for landscape management. Therefore, localized case-specific studies are required to inform management recommendations.

© The Author(s), 2021. Published by Cambridge University Press. This is an Open Access article, distributed under the terms of the Creative Commons Attribution licence (<http://creativecommons.org/licenses/by/4.0/>), which permits unrestricted re-use, distribution and reproduction, provided the original article is properly cited.

Fall armyworm (FAW, *Spodoptera frugiperda* J. E. Smith, Lepidoptera: Noctuidae), native to the Americas, has been invasive in West Africa since 2016 and attacks several economically important crops such as maize, millet, sorghum, rice, wheat, and sugar cane (Goergen *et al.*, 2016). FAW is a particular problem on maize (*Zea mays*) (Day *et al.*, 2017; Early *et al.*, 2018); estimates of yield loss in sub-Saharan Africa range between 12 and 45%, with 26% losses reported by Ghanaian farmers in 2018 (Njuguna *et al.*, 2021). Although a variety of natural enemies of FAW have been identified in Ghana (Agboyi *et al.*, 2020; Koffi *et al.*, 2020) and studies on landscape management for its control are emerging from sub-Saharan Africa (e.g. Midega *et al.*, 2017), studies investigating how abundance of FAW or its natural enemies changes with distance from field edges are lacking (Harrison *et al.*, 2019). This is fundamental to understanding the potential for semi-natural habitat to enhance biological control of this economically important pest, which in turn is required to inform management recommendations for landscape configuration to minimise pest abundance and maximise crop yield.

Using a combination of empirical observation and experimental dummy caterpillars in Ghanaian maize fields we examine the relationship between distance from semi-natural habitat and FAW-mediated crop damage, and the abundance, richness and diversity of its potential natural enemies. We hypothesise that natural enemies colonise maize from semi-natural habitat, and therefore predict that FAW crop damage will be lower, and the activity of natural enemies higher, closer to field edges. Conversely, if semi-natural habitat acts as a reservoir for FAW from which it colonises crops, this may be a more important determinant of FAW abundance, and FAW damage could therefore be higher closer to field edges.

## Methods

### *FAW damage in relation to distance from field edge*

To assess how herbivory from FAW varied with distance from field margins in a rural smallholder agricultural setting, on 5 February 2019 we surveyed two fields of unharvested maize bordered by semi-natural habitat (grass, shrubs, and small trees) in Abutia Amegame (Volta Region of Ghana; 6.46°N, 0.32°E), referred to throughout as village maize (VM). We sampled along a 7 m transect running from the mid-point of a field edge into the centre of the maize crop (fig. 1a). Maize plants within a 2-m wide zone along this transect were surveyed for the total number of leaves per plant and number of leaves showing herbivory. The proportion of leaves with herbivore damage correlates with FAW abundance (Hruska and Gould, 1997; Midega *et al.*, 2017). FAW infestation had occurred earlier in the growing season, so no FAW were present in the fields when surveyed, but the damage recorded was characteristic of FAW damage; i.e. windowed whorls with larval frass and skeletonised leaves (Goergen *et al.*, 2016). We were unable to sample additional fields as intended due to the majority of maize fields having already been harvested.

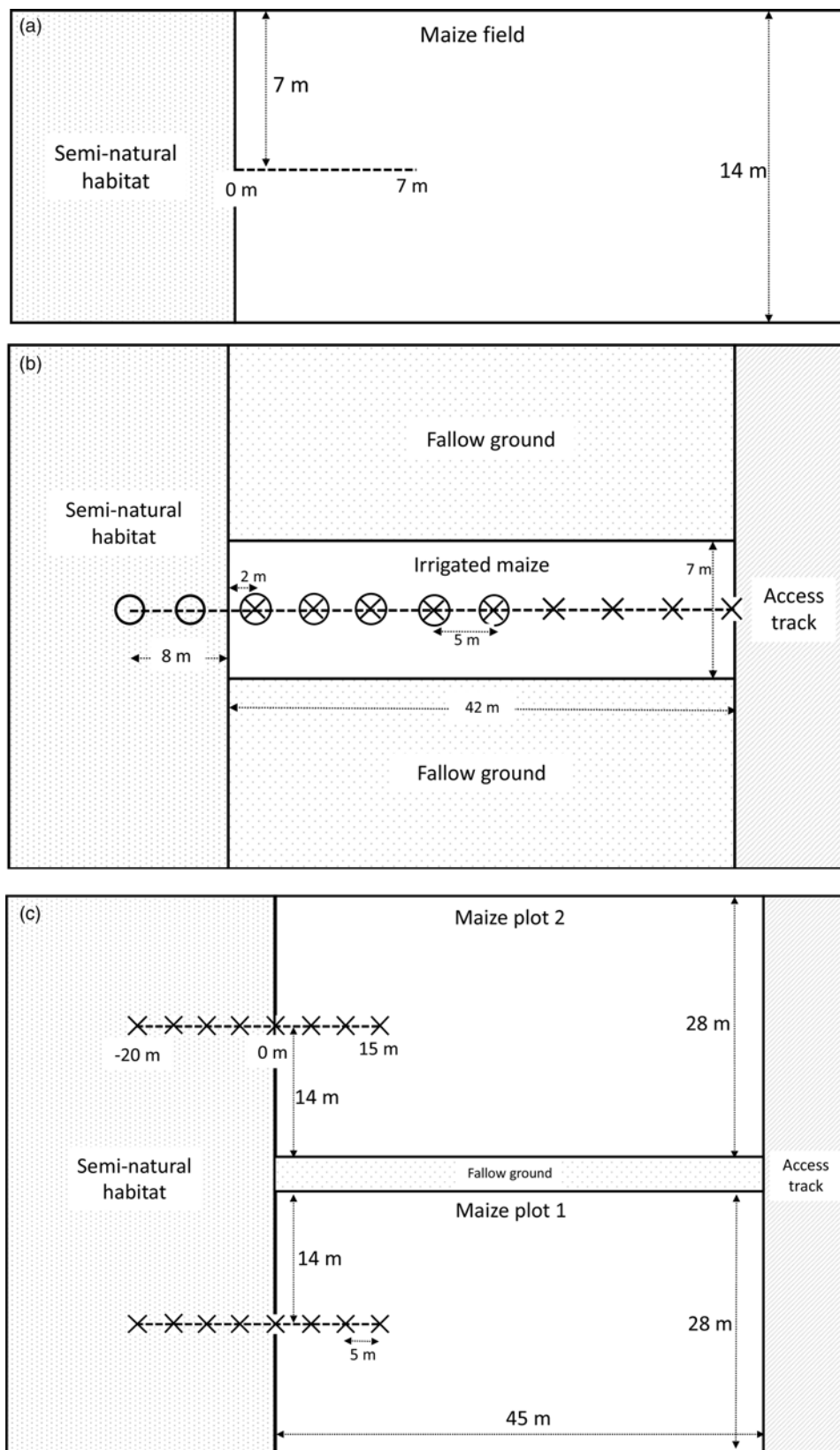
To observe the infestation process of FAW on young maize plants in a more controlled experimental setting, on 5 February 2019 we established a 42 m × 7 m irrigated maize plot at the University of Ghana experimental farm (5.66°N, 0.19°W), referred to here as University maize 1 (UM1). The plot was bordered by bare cultivated earth on the long edges and semi-natural vegetation (predominantly grass) or a dirt access track on the short

edges (fig. 1b). We ran a 50 m transect starting 8 m into semi-natural vegetation at one margin of the crop, through the whole experimental crop plot, and ending at the opposite margin bordering an access track. During 12–22 February 2019, we daily monitored 6–8 maize plants every 5 m along the transect in the two planting rows on either side of the transect. We recorded the total number of leaves and the number of leaves showing herbivore damage for the same plants each day. The number of FAW larvae per plant was not observed directly; this would have required destructive sampling, since FAW larvae typically retreat into leaf whorls (Day *et al.*, 2017; Early *et al.*, 2018).

### *Natural enemy activity in relation to distance from field edge*

To link the development of FAW-mediated crop damage in young maize to natural enemy activity, richness and diversity, between 12 and 22 February 2019 we placed pitfall traps every 5 m along the 50 m transect in the University maize plot described above (UM1, fig. 1b). Traps were emptied every 24 h and invertebrate morphospecies abundances recorded. The four pitfall traps closest to the access track were excluded from analysis, due to inability to determine whether invertebrates in these samples had entered the crop from the edge of interest (bordering semi-natural habitat) or had crossed the access track to reach the maize. We also assessed parasitism rates of FAW larvae from a three plant by three plant quadrat (totalling nine plants) every 5 m along the transect within the crop. Seventeen days after planting the maize, each plant was searched systematically for FAW larvae, and all larvae were collected (up to a maximum of 20 larvae per quadrat). Each larva was reared individually on maize leaves in transparent plastic cups covered with nylon mesh in the Department of Crop Sciences, University of Ghana, until either an adult moth or a parasitoid emerged, or the larva or pupa died; monitoring for parasitoid emergence continued for 1 week after death. Further collection of larvae took place at 14-day intervals, on 8 and 22 March 2019 (Supplementary Table 4).

We complemented our study of natural enemy activity in the young maize crop by surveying previously established maize at the tasselling stage on the experimental farm (University maize 2, UM2). Two un-irrigated maize plots 28 m × 45 m had been planted on 9 November 2018. One of the 28 m margins of both plots was bordered by uncultivated land, predominantly exposed ground with patchy shrubs and grass clumps. One plot had previously been treated with a pesticide targeting FAW, but as pesticide treatment was not ongoing and is not of interest in our study, we sampled both plots to increase replication and included plot ID as a fixed effect in data analysis. We set a 35 m transect perpendicular to the edge bordering uncultivated habitat in both plots, starting 20 m into the semi-natural vegetation and continuing 15 m into the maize plot (fig. 1c). On 11 February 2019, we placed pitfall traps (6 cm in diameter) partially filled with water and detergent, every 5 m along this transect. We emptied traps after 24 h and recorded invertebrate morphospecies. As a further indicator of natural enemy activity, ten plasticine caterpillars were placed every 5 m on the transect on 12 February 2019. Model caterpillars made from modelling clay or plasticine are widely used to assess potential predation pressure on invertebrate herbivores from arthropods, birds and mammals (Howe *et al.*, 2009; Low *et al.*, 2014). Dummy caterpillars (30 mm × 3 mm) were made from brown Newplast (Newclay Products Ltd), to mimic later instars of FAW (EPPO, 2015; Jeger



**Fig. 1.** Layout of maize plots sampled. (a) VM. Two fields in Abutia Amegame were surveyed for FAW herbivory, both 14 m wide. Leaf damage was assessed on maize plants within a 2 m zone along the transect (dashed line) and plant distant point recorded to the nearest 0.5 m. (b) UM1. February-planted irrigated maize plot on the University of Ghana experimental farm. 50 m transect (dashed line) ran through 42 m of crop and 8 m of semi-natural habitat. Sampling took place at 5 m intervals; crosses indicate where maize leaf herbivory damage was assayed and FAW larvae were collected, and circles indicate where pitfall traps were set. (c) UM2. November-planted tasselling-stage maize plots, University farm. 35 m transects (dashed lines) ran through each plot and adjacent semi-natural habitat. Crosses indicate where pitfall traps and dummy caterpillars were set. The plots were separated by fallow ground.

*et al.*, 2017). Caterpillars were attached to maize/semi-natural vegetation using UHU super glue. After 48 h, we used a hand lens to score the presence or absence of attack and the identity

of the potential predator (categorised as arthropod, mammal, or bird) (Low *et al.*, 2014). Mammal and bird attacks were rare (two and one caterpillars, respectively), so analyses were restricted

**Table 1.** Change in proportion of leaf damage with distance into maize field from semi-natural habitat, for VM and UM1

Dataset	<i>n</i>	Difference in proportion of maize leaves damaged		Significance of variable on proportion of leaves damaged		
		Field 1	Field 2	Distance	Field ID	
VM	36	Distance (3–4 m)		*	–	
		Field 1	Field 2			
		0.0418	0.0387			
UM1	671	Distance (17–22 m)		***	*	***
		Day 7	Day 17			
		0.000776	–0.00591			
		Day (at 22 m)				
		Day 7	Day 17			
		0.120	0.896			

VM model back-transformed values are between 3 and 4 m on transect. UM1 models are back-transformed between 17 and 22 m to evaluate change in proportion with distance on the first and last day of surveying (7 and 17 days after planting), and also evaluated at 22 m to indicate the effect of time since planting alone. Statistical significance of variables is indicated (– not significant, \*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$ ). For the full summary of model estimates, standard errors and  $R^2$  values, see Supplementary Table 2.

to overall attack rates. Missing caterpillars were excluded from the analysis (as in Sam *et al.*, 2015; Mansion-Vaquie *et al.*, 2017).

### Statistical analysis

R version 3.5.2 was used for statistical analysis and to plot graphs. Details of the variables and response distribution included in the generalised linear models (GLM, fitted using the *glm* function), along with details of dispersion tests and adjusted  $R^2$  used to assess model fit are given in Supplementary Table 1 and Supplementary Text 1.

Araneae (spider) and Hymenoptera (mostly Formicidae, i.e. ant) data from pitfall traps were analysed as likely natural enemies of FAW. Three metrics were used to summarise Araneae and Hymenoptera activity and diversity: abundance (total number of individuals), species richness (number of species), and inverse Simpson's diversity index.

## Results

### FAW crop damage

The proportion of leaves showing herbivore damage in the VM fields increased significantly with distance from semi-natural habitat by 4.2 and 3.9% per metre in the two fields ( $P < 0.05$ , Table 1, fig. 2a). However, relatively little of the variation in herbivory was explained by distance ( $R^2_{D, D\gamma} = 0.0761$ , Supplementary Table 2).

In the UM1 plot, the relationship between level of herbivory and distance from semi-natural habitat changed with time since planting (i.e. a significant time  $\times$  distance interaction;  $P < 0.001$ , Supplementary Table 2). Our hypothesis was primarily concerned with the effect of distance on herbivory, but since leaf damage accumulates as FAW infestation progresses, we included time as a fixed effect to account for this and to determine any interaction effect with distance. On the first day of sampling (7 days after planting), the proportion of leaves showing herbivore damage increased 0.078% over 10 m (15–25 m) from the semi-natural habitat, whereas 17 days after planting the proportion of leaves damaged decreased 0.59% over this same distance (Table 1, fig. 2b). The proportion of leaves with herbivory increased with time since planting from 12.0% 7 days after planting to 89.6%

on day 17 (Table 1), but the increase in damage was less pronounced further from the field margin bordering semi-natural habitat (fig. 2b). The binomial GLM had a very good fit to the data ( $R^2_{D, \gamma} = 0.476$ , Supplementary Table 2), equivalent to a conventional  $R^2$  value of over 0.9 (Louviere *et al.*, 2000).

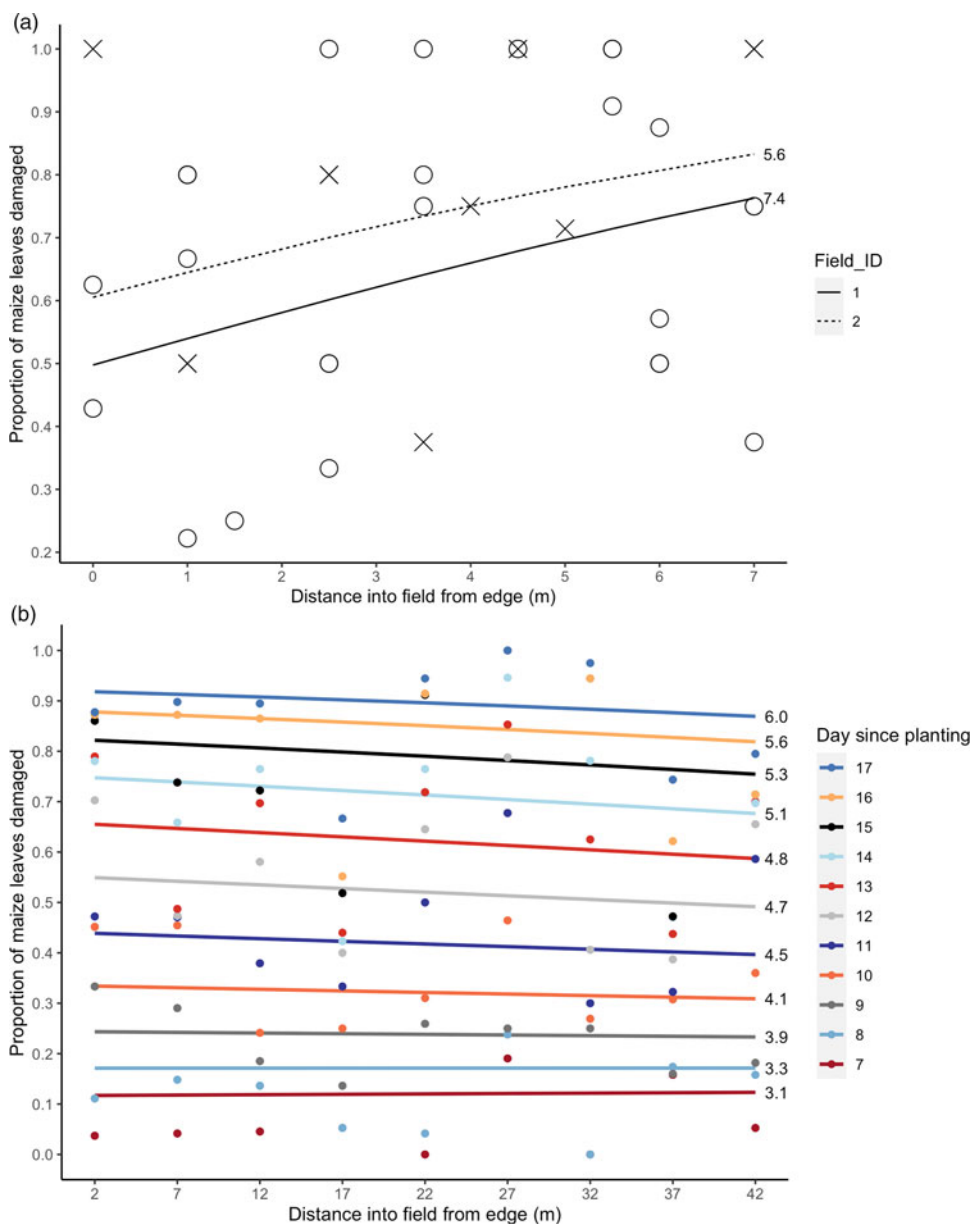
### Natural enemy activity – abundance, richness, and diversity

In UM1, a total of 2138 invertebrates were collected in pitfall traps over 11 days of sampling. Araneae accounted for 169 individuals assigned to 33 morphospecies, while a further 1670 were Hymenoptera, predominantly Formicidae (ants) and attributed to 64 morphospecies. The samples were dominated by three Araneae morphospecies (each with over 20 specimens across all days of sampling) and seven Hymenoptera morphospecies (combined abundance greater than 100).

Araneae activity was affected by an interaction between distance from semi-natural habitat and time since planting ( $P < 0.05$  for total abundance,  $P < 0.1$  for richness and diversity, Table 2). As the maize grew, Araneae activity changed from moderately increasing with distance from semi-natural habitat to decreasing with distance (fig. 3a–c). The total abundance data contained an outlier at 20 m on day 7 (abundance of 18) and re-analysis without this data point removed the statistical significance of this result, but not the direction of the effect (Supplementary Table 3). Araneae diversity was also significantly higher in semi-natural habitat than in the crop ( $P < 0.05$ , Table 2).

Hymenoptera diversity was affected by an interaction between distance and time since planting ( $P < 0.05$ , Table 2), declining with increasing distance from semi-natural habitat into crop initially but, over time, changing to an increase with distance from crop edge (fig. 3f). All GLMs used to analyse the Araneae and Hymenoptera metrics from the UM1 pitfall trap data explained little variation in the data, indicated by low  $R^2$  values (Supplementary Table 3).

From the 260 FAW larvae collected at three 14-day intervals from UM1, 53 emerged as moths and eight as parasitoids, giving an average parasitism rate of 13.1% (Table 3) which is typical of parasitism of FAW in Ghana (Agboyi *et al.*, 2020; Koffi *et al.*, 2020) and East Africa (Sisay *et al.*, 2018, 2019). Most other larvae died as larvae or pupae (Supplementary Table 5). Future work



**Fig. 2.** Proportion of maize leaves showing herbivory damage with distance from semi-natural habitat in (a) VM and (b) UM1 (cumulative total damage over successive days). Lines display model-fitted values and points show the raw data. The mean number of leaves per field (VM) or per day (UM1) are shown next to the respective lines, to indicate maize development stage during sampling. Colour of lines and points in (b) indicate day since maize was planted, with 11 days surveyed in total.

would benefit from also considering egg parasitism, given candidates have already been identified in West Africa (Kenis *et al.*, 2019).

Of the 449 invertebrates collected using pitfall traps in UM2, 22 Araneae and 385 Hymenoptera were identified (11 and 22 morphospecies, respectively).

Hymenoptera species richness and diversity significantly increased with distance along the transect ( $P < 0.05$ , Table 4, fig. 4e, f), but did not differ significantly between habitat types. Statistical models used for analysis of Hymenoptera metrics fitted the data well, indicated by high  $R^2$  values (Supplementary Table 3); total abundance and species richness models have adjusted pseudo- $R^2$  values in the range 0.2–0.4, equivalent to conventional  $R^2$  values of 0.7–0.9 or above (Louviere *et al.*, 2000). In contrast, the models used to analyse Araneae metrics explained little variation in the data (Supplementary Table 3).

Attack rate of dummy caterpillars placed in UM2 increased significantly with distance from crop edge in both the crop and

semi-natural habitat ( $P < 0.05$ , Table 4, fig. 4g). Attack rate was significantly different between plots ( $P < 0.01$ ). The model fitted very well, explaining a substantial amount of the variation in the data ( $R^2_{D, D\gamma}$  of 0.446, Supplementary Table 3).

### Discussion

We found that apparent FAW herbivory on maize (mature at the point of observation) increased with distance from semi-natural habitat in the realistic conditions of smallholder fields (VM). Our daily monitoring of herbivory on young maize plants at the University of Ghana research farm (UM1) indicated that FAW damage changed from increasing to decreasing with distance from semi-natural habitat as the maize grew. Araneae activity, richness and diversity decreased with distance from semi-natural habitat over time in this crop, whilst Hymenoptera diversity increased. Further data from mature maize plots at the research farm (UM2) also found increased Hymenoptera richness

**Table 2.** Values of natural enemy metrics from UM1 pitfall trap data, evaluated as the difference between the 7 and 12 m sampling points from the crop edge for the first and last day of sampling (7 and 17 days after maize planting)

Natural enemy metric		<i>n</i> <sup>a</sup>	Difference in natural enemy metric between 7—and 12 m from crop edge		Significance of variable on natural enemy metric			
			First sample (7 days after planting)	Last sample (17 days after planting)	Distance × Day since planting	Distance	Day since planting	Habitat type
Araneae	Total abundance	76	0.0214	−0.462	−	−	−	−
	Species richness	77	0.0828	−0.360	.	−	*	−
	Diversity (inverse Simpsons)	58	0.0828	−0.217	.	−	.	*
Hymenoptera	Total abundance	77	−0.169	2.82	−	−	−	−
	Species richness	77	−0.388	0.999	−	−	−	−
	Diversity (inverse Simpsons)	76	−0.466	0.0700	*	*	**	−

Values given are back-transformed from models fitted. Statistical significance of variables is indicated (− not significant, .  $P < 0.1$ , \*  $P < 0.05$ , \*\*  $P < 0.01$ ). For the full summary of model estimates, standard errors and  $R^2$  values, see Supplementary Table 3.

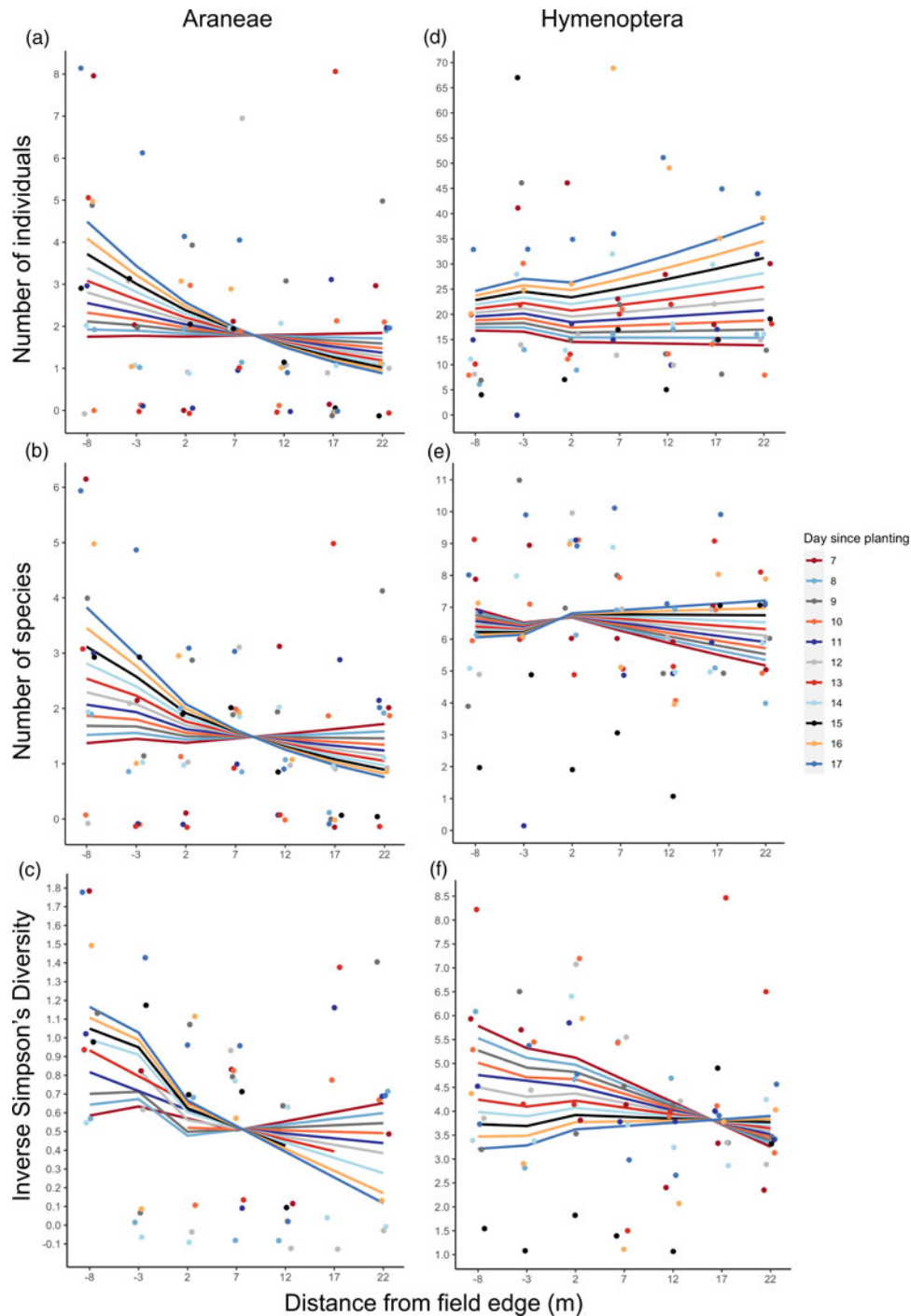
<sup>a</sup>Seven intervals on the transect were sampled over 11 days, resulting in  $n = 77$ . However, an outlier was removed for Araneae total abundance. Samples with zero individuals were removed from analyses of inverse Simpsons index.

and diversity, and dummy caterpillar attack rate, with distance from uncultivated ground at the crop edge.

The maize plots on the university farm were relatively small and the semi-natural habitat bordering these plots is not consistently representative of semi-natural habitat surrounding fields in rural villages, which can include complex matrices of grass, shrubs and small trees. We did not record the maize varieties grown or plant species composition of the semi-natural habitat bordering the plots in this study, which would have allowed us to further qualify our findings and evaluate the prevalence of alternate hosts for FAW surrounding crop fields. Our study suffers from low replication, the magnitude of the effects we identified was very small and the differences between the VM and UM sites make comparison of results difficult. However, our results are useful as preliminary indicators of trends in a data-poor region. There are few published studies from West Africa that consider the relationship between semi-natural habitat and natural enemy activity. A limited number of studies from the Americas consider the influence of extra-field characteristics (Wyckhuys and O'Neil, 2007), weeds within crops (Altieri and Whitcomb, 1980), and distance from semi-natural habitat (forest) (Sousa *et al.*, 2011) on natural enemy and FAW abundance. Successful biological control of crop pests can be highly context-specific (Tscharntke *et al.*, 2005; Bianchi *et al.*, 2006), so regional studies of FAW in sub-Saharan Africa are necessary to fill this important knowledge gap. Future research would benefit from ongoing sampling of a greater number of fields throughout the maize growing season, with some measure of surrounding habitat and landscape complexity included in analyses, as this has been shown to be significant for other crop pests in sub-Saharan Africa (Kebede *et al.*, 2018a, 2018b).

While there are no published data from Africa, FAW abundance has been found to increase with distance from semi-natural habitat in the Americas (Sousa *et al.*, 2011), consistent with our VM results. This trend could be due to edge effects resulting in

decreasing FAW abundance closer to a non-preferred habitat (Ries *et al.*, 2004) or natural enemy pressure being greater near the field edge due to spillover of enemies from adjacent non-crop habitat (Bianchi *et al.*, 2006). In contrast, the pattern of herbivore damage in UM1 is consistent with crop pests infesting the field from the edge, re-colonising following post-harvest clearance (Tscharntke *et al.*, 2005). The distance-dependent difference in herbivory emerged from around day 10 (fig. 2b), corresponding to when FAW infestation is likely to have commenced; FAW frass – a characteristic sign of FAW infestation (Hruska and Gould, 1997; Goergen *et al.*, 2016; Jeger *et al.*, 2017) – first appeared on leaves 11 days after planting. However, it is unlikely that the trend in herbivory we observed is due to a gradient in FAW infestation from the crop edge. Although some pest species may benefit from specific components of semi-natural vegetation (e.g. Baggen *et al.*, 1998), the primary source of most pest species are crop fields (Bianchi *et al.*, 2006) and FAW adult females disperse long distances and oviposit directly onto maize throughout the field (Goergen *et al.*, 2016). Crop yield measurements would provide a more robust and economically relevant measure of the impact of FAW. The yield loss from leaf damage depends on the maize growth stage; early infestation causes the largest yield losses, but yield loss plateaus with increasing pest pressure in later growth stages (Evans and Stansly, 1990; Overton *et al.*, 2021). Other limitations of using leaf damage as a proxy for FAW abundance, particularly in the mature maize of the VM fields, include (i) inability to determine the maize growth stage when FAW attack occurred, (ii) difficulty distinguishing FAW leaf damage from other Lepidopteran crop pests, and (iii) leaf damage remaining in instances where FAW are removed by natural enemies. Despite its weaknesses, we feel leaf damage provided an adequate proxy to initially test our hypotheses and would seek to measure crop yields in future work.



**Fig. 3.** Natural enemy activity (abundance, richness and diversity) data from pitfall traps in UM1; 8 m into semi-natural habitat (from crop edge) to 22 m into irrigated maize plot. Lines display model-fitted values, points show the raw data, and colours indicate day since maize was planted (11 days surveyed in total). (a) Araneae abundance (total number of individuals), (b) Araneae species richness (number of species), (c) Araneae diversity (inverse Simpsons Diversity Index, log scale), (d) Hymenoptera abundance (total number of individuals), (e) Hymenoptera species richness (number of species), (f) Hymenoptera diversity (inverse Simpsons Diversity Index). As the maize grew, Araneae activity tended to decrease with distance into the maize plot, whereas Hymenoptera activity increased.

The decrease in Araneae abundance with increased distance from edge in UM1, and similar findings in early samples of Hymenoptera, are consistent with theoretical and empirical evidence that natural enemies colonise crops from surrounding semi-natural habitat in fragmented landscapes (Kruess and Tschardtke, 2000; Tschardtke *et al.*, 2005; Bianchi *et al.*, 2006; Sousa *et al.*, 2011). Semi-natural habitats can enable the

persistence of natural enemies during inter-crop periods when pests are not present by providing: (i) a source of alternative plant hosts and prey and nectar sources (important for parasitoids), (ii) a favourable microclimate, (iii) refuge, and (iv) sites for hibernation (Tschardtke *et al.*, 2005; Bianchi *et al.*, 2006; Harrison *et al.*, 2019). The subsequent reversal in trend for Hymenoptera in UM1 – consistent with the trends in

**Table 3.** Parasitism rate for FAW larvae collected from UM1 at 17, 31 and 45 days after planting

Collection date	Number of FAW reared			Proportion parasitised
	Total collected	Emerged as FAW moth	Emerged as parasitoid	
22 Feb 2019	83	4	3	0.429
8 Mar 2019	63	21	3	0.125
22 Mar 2019	114	28	2	0.0667
Total	260	53	8	0.131

For numbers of larvae collected at each distance, and the outcomes of all larvae collected, see Supplementary Tables 4 and 5, respectively.

**Table 4.** Values of natural enemy metrics from UM2 pitfall trap and dummy caterpillar data, evaluated as the difference between –10 m and –15 m for semi-natural habitat samples, and between 5 m and 10 m for crop samples, for both plots

Natural enemy metric	<i>n</i> <sup>a</sup>	Difference in natural enemy metric (plot 1, plot 2)		Significance of variable on natural enemy metric				
		Semi-natural (–10 to –15 m)	Crop (5–10 m)	Distance × Habitat type	Distance	Habitat type	Plot	
Proportion of dummy caterpillars attacked		0.168, 0.0414	0.0745, 0.129	*	*	–	**	
Araneae	Total abundance	16	0, 0	0.145, 0.254	–	–	–	–
	Species richness	16	$5.00 \times 10^{-12}$ , $1.00 \times 10^{-11}$	$6.54 \times 10^{-10}$ , $1.31 \times 10^{-9}$	–	–	–	–
	Diversity (inverse Simpsons)	12	$2.22 \times 10^{-16}$ , $2.22 \times 10^{-16}$	0.472, 0.408	–	–	–	–
Hymenoptera	Total abundance	16	5.01, 1.55	9.50, 2.93	–	–	–	*
	Species richness	16	–0.0635, –0.0365	1.93, 1.11	–	*	–	*
	Diversity (inverse Simpsons)	15	–0.220, –0.220	0.784, 0.784	–	*	–	–

Values given are back-transformed from models fitted. Significance of variables on natural enemy metric are also given (– not significant, ·  $P < 0.1$ , \*  $P < 0.05$ , \*\*  $P < 0.01$ ). For the full summary of model estimates, standard errors and  $R^2$  values, see Supplementary Table 3.

<sup>a</sup>Eight intervals on the transect were sampled over across two plots, resulting in  $n = 16$ . Samples with zero individuals were removed from analyses of inverse Simpsons index.

Hymenoptera and dummy caterpillar attack rate in UM2 – is expected if natural enemies have moved from the semi-natural habitat and stayed in the crop as the maize grew, perhaps facilitated by the increased suitability of the crop as habitat and/or availability of crop pests as food sources. If this is the case, it is possible that Araneae are slower to move into the crop following the arrival of crop pests, or require a more developed crop to provide a suitable matrix, potentially explaining why we detected this trend reversal for Hymenoptera but not Araneae in UM1. Our results therefore highlight the influence of time since planting on the distribution of potential natural enemies with distance from semi-natural habitat. Early FAW infestation of maize results in the largest yield losses (Evans and Stansly, 1990), and our study found evidence of FAW infestation 11 days after planting. As such, natural enemies from semi-natural habitat surrounding crops may not effectively minimise yield loss if they do not disperse into the crop rapidly enough.

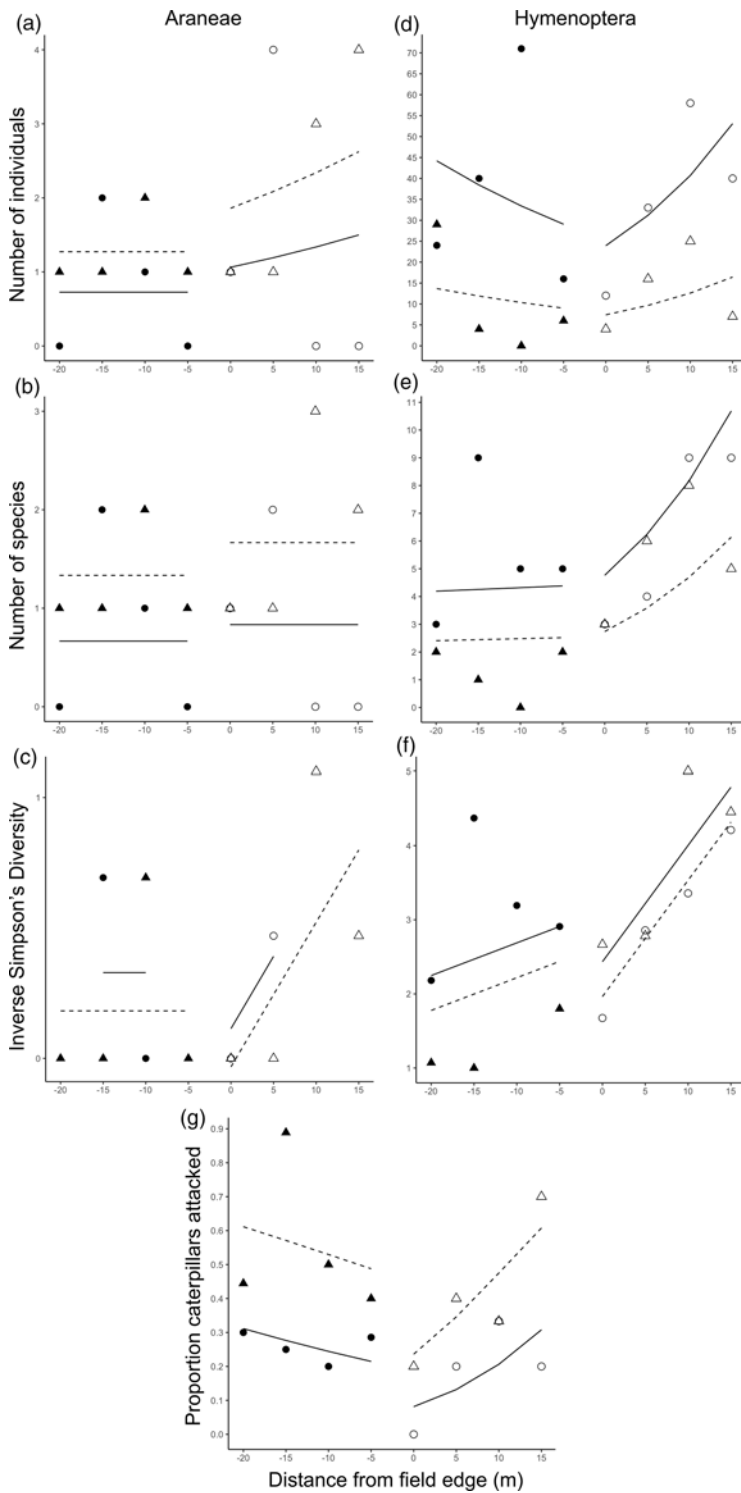
FAW infestations in sub-Saharan Africa are causing substantial damage to maize crops (Sisay *et al.*, 2019) with severe yield consequences (Njuguna *et al.*, 2021) in a context where food security is already of concern (FAO *et al.*, 2019). Control of FAW to date is focusing almost exclusively on the use of synthetic insecticides (Harrison *et al.*, 2019; Agboyi *et al.*, 2020; Tambo *et al.*, 2020) despite recognition of the negative impacts of pesticide application on

human health and the environment (Kansiime *et al.*, 2019; Tambo *et al.*, 2020; Haggblade *et al.*, 2021). Enhancing landscape complexity by increasing the proximity of crops to semi-natural habitat has been suggested as a means to increase natural enemy predation of crop pests, both generally (Bianchi *et al.*, 2006) and specifically for FAW (Harrison *et al.*, 2019), thus reducing the need for synthetic insecticides as part of an integrated pest management approach. Our results support further investigation of changing maize field configuration to increase proximity of crops to semi-natural habitat (e.g. through dividing larger fields with semi-natural vegetation strips), to reduce FAW damage and increase natural enemy abundance and diversity within crops. Future work should assess the impact of such a strategy on maize yield, to ensure reductions in FAW damage translate into improved or safeguarded yields that more than compensate for potential loss of cropping area from habitat enhancement.

## Conclusion

This study provides the first quantification of changes in FAW crop damage and activity of its potential natural enemies with distance from semi-natural habitat bordering maize crops in West Africa. We observed increased herbivore damage with distance from semi-natural habitat in a small sample of





**Fig. 4.** Natural enemy activity in UM2; abundance, richness and diversity data from pitfall traps plus dummy caterpillar attack rate. Transect run from 20 m into semi-natural habitat (negative distance increments) to 15 m into crop (positive distance increments), with the 0 m point representing the crop edge. Lines display model-fitted values and points show the raw data; circle points and solid lines represent plot 1, and triangle points and dashed lines represent plot 2 (see [fig. 1c](#)). (a) Araneae abundance (total number of individuals), (b) Araneae species richness (number of species), (c) Araneae diversity (inverse Simpsons Diversity Index, log scale), (d) Hymenoptera abundance (total number of individuals), (e) Hymenoptera species richness (number of species), (f) Hymenoptera diversity (inverse Simpsons Diversity Index), (g) proportion of dummy caterpillars attacked. Missing data points in (c) (circles at -20 and -5 m) and (f) (triangle at -10 m) are due to these traps having a Simpsons Diversity Index of 0 so these points were removed from the analysis.

smallholder maize fields and provide initial evidence that abundance of some natural enemies declines with distance from semi-natural habitat in young maize around the time of FAW infestation – a particularly critical stage for reducing pest-mediated yield loss. Further work is required to quantify the extent to which natural enemy pressure reduces FAW abundance, and whether this occurs rapidly enough to prevent significant yield loss due to herbivore damage, before the effectiveness of such management practices as a means of improving food security can be assessed.

**Supplementary material.** The supplementary material for this article can be found at <https://doi.org/10.1017/S0007485321000894>

**Acknowledgements.** We would like to thank Miriam Mantey and Kurt Matey for assisting with fall armyworm larvae collection and rearing, and Dr Chris Terry for advice on statistical analysis. We would also like to thank the anonymous reviewers whose comments greatly improved the paper. This work was supported by funding from the Biotechnology and Biological Sciences Research Council (BBSRC) (grant number BB/M011224/1).

**Conflict of interest.** The authors declare none.

## References

- Agboyi LK, Goergen G, Beseh P, Mensah SA, Clotney VA, Glikpo R, Buddie A, Cafà G, Offord L, Day R, Rwomushana I and Kenis M (2020) Parasitoid complex of fall armyworm, *Spodoptera frugiperda*, in Ghana and Benin. *Insects* **11**, 1–15.
- Altieri MA and Whitcomb WH (1980) Weed manipulation for insect pest management in corn. *Environmental Management* **4**, 483–489.
- Baggen LR, Gurr GM and Meats A (1998) Flowers in tri-trophic systems: mechanisms allowing selective exploitation by insect natural enemies for conservation biological control. *Entomologia Experimentalis et Applicata* **91**, 155–161.
- Bianchi FJJA, Booij CJH and Tscharrntke T (2006) Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. *Proceedings of the Royal Society B: Biological Sciences* **273**, 1715–1727.
- Cardinale BJ, Harvey CT, Gross K and Ives AR (2003) Biodiversity and bio-control: emergent impacts of a multi-enemy assemblage on pest suppression and crop yield in an agroecosystem. *Ecology Letters* **6**, 857–865.
- Cleland J and Machiyama K (2017) The challenges posed by demographic change in sub-Saharan Africa: a concise overview. *Population and Development Review* **43**, 264–286.
- Crowder DW, Northfield TD, Strand MR and Snyder WE (2010) Organic agriculture promotes evenness and natural pest control. *Nature. Nature Publishing Group* **466**, 109–112.
- Day R, Abrahams P, Bateman M, Beale T, Clotney V, Cock M, Colmenarez Y, Corniani N, Early R, Godwin J, Gomez J, Moreno PG, Murphy ST, Oppong-Mensah B, Phiri N, Pratt C, Silvestri S and Witt A (2017) Fall armyworm: impacts and implications for Africa. *Outlooks on Pest Management* **28**, 196–201.
- Early R, González-Moreno P, Murphy ST and Day R (2018) Forecasting the global extent of invasion of the cereal pest *Spodoptera frugiperda*, the fall armyworm. *Neobiota* **40**, 25–50.
- EPPO (European and Mediterranean Plant Protection Organisation) (2015) PM 7/124 (1) *Spodoptera littoralis*, *Spodoptera litura*, *Spodoptera frugiperda*, *Spodoptera eridania*. *EPPO Bulletin* **45**, 410–444.
- Evans DC and Stansly PA (1990) Weekly economic injury levels for fall armyworm (Lepidoptera : Noctuidae) infestation of corn in lowland Ecuador. *Journal of Economic Entomology* **83**, 2452–2454.
- FAO, IFAD, UNICEF, WFP and WHO (2019) The State of Food Security and Nutrition in the World 2019. Safeguarding against economic slowdowns and downturns. Rome.
- Garibaldi LA, Gemmill-Herren B, D'Annolfo R, Graeb BE, Cunningham SA and Breeze TD (2017) Farming approaches for greater biodiversity, livelihoods, and food security. *Trends in Ecology and Evolution* **32**, 68–80.
- Godfray HCJ and Garnett T (2014) Food security and sustainable intensification. *Philosophical Transactions of the Royal Society B* **369**, 20120273.
- Godfray HCJ, Beddington JR, Crute IR, Haddad L, Lawrence D, Muir JE, Pretty J, Robinson S, Thomas SM and Toulmin C (2010) Food security: the challenge of feeding 9 billion people. *Science* **327**, 812–819.
- Goergen G, Kumar PL, Sankung SB, Togola A and Tamò M (2016) First report of outbreaks of the fall armyworm *Spodoptera frugiperda* (J E Smith) (Lepidoptera, Noctuidae), a new alien invasive pest in west and Central Africa. *PLoS ONE* **11**(10), e0165632.
- Haggblade S, Diarra A and Traoré A (2021) Regulating agricultural intensification: lessons from West Africa's rapidly growing pesticide markets. *Development Policy Review* **00**, 1–24.
- Harrison RD, Thierfelder C, Baudron F, Chinwada P, Midega C, Schaffner U and Berg JVD (2019) Agro-ecological options for fall armyworm (*Spodoptera frugiperda* J.E. Smith) management: providing low-cost, small-holder friendly solutions to an invasive pest. *Journal of Environmental Management* **243**, 318–330.
- Howe A, Lövei GL and Nachman G (2009) Dummy caterpillars as a simple method to assess predation rates on invertebrates in a tropical agroecosystem. *Entomologia Experimentalis et Applicata* **131**, 325–329.
- Hruska AJ and Gould F (1997) Fall Armyworm (Lepidoptera : Noctuidae) and *Diatraea lineolata* (Lepidoptera : Pyralidae): impact of larval population level and temporal occurrence on maize yield in Nicaragua. *Journal of Economic Entomology* **90**, 611–622.
- Ittersum MKV, Bussel LGJV, Wolf J, Grassini P, Wart JV, Guilpart N, Claessens L, Groot HD, Wiebe K, Mason-D'Croz D, Yang H, Boogaard H, Oort PAJV, Loon MPV, Saito K, Adimo O, Adjei-Nsiah S, Agali A, Bala A, Chikowo R, Kaizzi K, Kouressy M, Makoi JHJR, Ouattara K, Tesfaye K and Cassman KG (2016) Can sub-Saharan Africa feed itself? *Proceedings of the National Academy of Sciences* **113**, 14964–14969.
- Jeger M, Bragard C, Caffier D, Candresse T, Chatzivassiliou E, Dehnen-Schmutz K, Gilioli G, Gregoire JC, Miret JAJ, Navarro MN, Niere B, Parnell S, Potting R, Rafoss T, Rossi V, Urek G, Bruggen AV, Werf WVD, West J, Winter S, Gardi C, Aukhjee M and MacLeod A (2017) Pest categorisation of *Spodoptera frugiperda*. *European Food Standard Safety Authority Journal* **15**, 4927.
- Kansiime MK, Mugambi I, Rwomushana I, Nunda W, Lamontagne-Godwin J, Rware H, Phiri NA, Chipabika G, Ndlovud M and Day RK (2019) Farmer perception of fall armyworm (*Spodoptera frugiperda* J.E. Smith) and farm-level management practices in Zambia. *Pest Management Science* **75**, 2840–2850.
- Kebede Y, Bianchi F, Baudron F, Abraham K and de Valença TP (2018a) Implications of changes in land cover and landscape structure for the bio-control potential of stemborers in Ethiopia. *Biological Control* **122**, 1–10.
- Kebede Y, Baudron F, Bianchi F and Tittone P (2018b) Unpacking the push-pull system: assessing the contribution of companion crops along a gradient of landscape complexity. *Agriculture, Ecosystems and Environment* **268**, 115–123.
- Kenis M, du Plessis H, Van den Berg J, Ba MN, Goergen G, Kwadjo KE, Baoua I, Tefera T, Buddie A, Cafà G, Offord L, Rwomushana I and Polaszek A (2019) *Telenomus remus*, a candidate parasitoid for the biological control of *Spodoptera frugiperda* in Africa, is already present on the continent. *Insects* **10**, 92.
- Koffi D, Kyerematen R, Eziah VY, Agboka K, Adom M, Goergen G and Meagher RL (2020) Natural enemies of the fall armyworm, *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae) in Ghana. *Florida Entomologist* **103**, 85.
- Kruess A and Tscharrntke T (2000) Species richness and parasitism in a fragmented landscape: experiments and field studies with insects on *Vicia sepium*. *Oecologia* **122**, 129–137.
- Louviere JJ, Hensher DA and Swait JD (2000) *Stated Choice Methods: Analysis and Applications*. Cambridge, United Kingdom: Cambridge University Press.
- Low PA, Sam K, McArthur C, Posa MRC and Hochuli DF (2014) Determining predator identity from attack marks left in model caterpillars: guidelines for best practice. *Entomologia Experimentalis et Applicata* **152**, 120–126.
- Mansion-Vaquie A, Ferrante M, Cook SM, Pell JK and Lövei GL (2017) Manipulating field margins to increase predation intensity in fields of winter wheat (*Triticum aestivum*). *Journal of Applied Entomology* **141**, 600–611.
- Midega CAO, Pittchar JO, Pickett JA, Hailu GW and Khan ZR (2017) A climate-adapted push-pull system effectively controls fall armyworm, *Spodoptera frugiperda* (J E Smith), in maize in East Africa. *Crop Protection* **105**, 10–15.
- Njuguna E, Nethononda P, Maredia K, Mbabazi R, Kachapulula P, Rowe A and Ndolo D (2021) Experiences and perspectives on *Spodoptera frugiperda* (Lepidoptera: Noctuidae) management in Sub-Saharan Africa. *Journal of Integrated Pest Management* **12**, 1–9.
- Overton K, Maino JL, Day RK, Umina PA, Bett B, Carnovale D, Ekesi S, Meagher R and Reynolds OL (2021) Global crop impacts, yield losses and action thresholds for fall armyworm (*Spodoptera frugiperda*): a review. *Crop Protection* **145**, 105641.
- Poveda K, Gomez M and Martinez E (2008) Diversification practices: their effect on pest regulation and production. *Revista Colombiana de Entomologia* **34**, 131–144.
- Ries L, Fletcher RJ, Battin J and Sisk TD (2004) Ecological responses to habitat edges: mechanisms, models and variability explained. *Annual Review of Ecology, Evolution, and Systematics* **35**, 491–522.

- Sam K, Rimmel T and Molleman F** (2015) Material affects attack rates on dummy caterpillars in tropical forest where arthropod predators dominate: an experiment using clay and dough dummies with green colourants on various plant species. *Entomologia Experimentalis et Applicata* **157**, 317–324.
- Sisay B, Simiyu J, Malusi P, Likhayo P, Mendesil E, Elibariki N, Wakgari M, Ayalew G and Tefera T** (2018) First report of the fall armyworm, *Spodoptera frugiperda* (Lepidoptera: Noctuidae), natural enemies from Africa. *Journal of Applied Entomology* **142**, 800–804.
- Sisay B, Simiyu J, Mendesil E, Likhayo P, Ayalew G, Mohamed S, Subramanian S and Tefera T** (2019) Fall armyworm, *Spodoptera frugiperda* infestations in east Africa: assessment of damage and parasitism. *Insects* **10**, 1–10.
- Sousa EHS, Matos MCB, Almeida RS and Teodoro AV** (2011) Forest fragments' contribution to the natural biological control of *Spodoptera frugiperda* Smith (Lepidoptera: Noctuidae) in maize. *Brazilian Archives of Biology and Technology* **54**, 755–760.
- Steward PR, Shackelford G, Carvalheiro LG, Benton TG, Garibaldi LA and Sait SM** (2014) Pollination and biological control research: are we neglecting two billion smallholders. *Agriculture and Food Security* **3**, 1–13.
- Tambo JA, Kansiime MK, Mugambi I, Rwomushana I, Kenis M, Day RK and Lamontagne-Godwin J** (2020) Understanding smallholders' responses to fall armyworm (*Spodoptera frugiperda*) invasion: Evidence from five African countries. *Science of the Total Environment* **740**, 140015.
- Tscharntke T, Rand TA and Bianchi FJ** (2005) The landscape context of trophic interactions: insect spillover across the crop-noncrop interface. *Annales Zoologici Fennici* **42**, 421–432.
- Wilby A and Thomas MB** (2002) Natural enemy diversity and pest control: patterns of pest emergence with agricultural intensification. *Ecology Letters* **5**, 353–360.
- Wyckhuys KAG and O'Neil RJ** (2007) Influence of extra-field characteristics to abundance of key natural enemies of *Spodoptera frugiperda* Smith (Lepidoptera : Noctuidae) in subsistence maize production. *International Journal of Pest Management* **53**, 89–99.