

The biocontrol agents of fall armyworm, *Spodoptera frugiperda* in Togo: moderating insecticide applications for natural control of the pest?

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Abstract

Although there has been intensive use of insecticides for fall armyworm, *Spodoptera frugiperda* (Lepidoptera: Noctuidae) management, their effects on population reduction and performance of natural enemies have not been adequately investigated. Therefore, this study assessed the diversity and performance of natural biocontrol agents under insecticide and insecticide-free applications. Bio-agents were annually collected from 2016 to 2022 in 348 maize farms throughout the West African nation of Togo. The collections included the entomopathogenic nematode *Ovomermis sinensis* (Nematoda: Mermithidae), unidentified bacteria from Enterobacteriaceae and Enterococcus, unidentified viruses from Ascoviruses and Baculoviruses, and fungi *Isaria* spp. (Hypocreales: Clavicipitaceae) and *Metarhizium rileyi* (Hypocreales: Cordycipitaceae). Eggs were parasitized by *Telenomus remus* (Hymenoptera: Platygasteridae), and the egg-larval parasitoid *Chelonus bifoveolatus* (Hymenoptera: Braconidae). Larval parasitoids included *Anatrichus erinaceus* (Diptera: Chloropidae), *Archytas* spp. and *Lespesias* spp. (Diptera: Tachinidae), *Bracon* sp., *Coccygidium luteum*, *Cotesia icipe* and *Meteoridea testacea* (Hymenoptera: Braconidae), and *Campoletis grioti* and *Ophion* spp. (Hymenoptera: Ichneumonidae). The collected predators included *Orius insidiosus* (Heteroptera: Anthracoridae), *Haematochara obscuripennis*, *Peprius nodulipes*, *Rhynocoris* sp. and *Zelus renardii* (Heteroptera: Reduviidae), *Calleida* sp. (Coleoptera: Carabidae), *Cheilomenes sulphurea*, *Coccinella septempunctata* and *Cycloneda sanguinea* (Coleoptera: Coccinellidae), *Euborellia annulipes*, *Forficula auricularia* and *F. senegalensis* (Dermaptera: Forficulidae), *Pheidole megacephala* and *Polyrhachis lamellidens* (Hymenoptera: Formicidae), *Chrysoperla carnea* (Neuroptera: Chrysopidae), and *Mantis religiosa* (Mantodea: Mantidae). The parasitism rates were from 14.72% in 2018 to 45.38% in 2022 for egg masses, and from 1.32% in 2016 to 41.85% in 2021 for larvae. The parasitism rates were three to four times higher in unsprayed farms than sprayed farms.

Key Message

Even though there have been high applications of insecticides against fall armyworm in West Africa, natural control agents continue to develop and help to reduce damaging populations. However, insecticide use, especially in the early years of the fall armyworm invasion, affected the population densities of these agents. Therefore, this study draws attention to moderate use of insecticides to increase natural control of this pest.

Introduction

The equilibrium among living organism populations is due to the interdependency relationships among plants, herbivores, carnivores, parasites, and pathogenic agents that regulate and balance the bio-ecosystem (Szwabiński et al. 2010). Unfortunately, this equilibrium is constantly challenged by human activities that cause routine interruptions (Ruppert et al. 2018). Agricultural production is one of the human activities that throw off the biodiversity balance, and increased agricultural pest populations can lead to food and economic losses (Zamagni et al. 2012; Sala et al. 2013). To avoid these losses, different crop protection methods have been developed against phytopathogens and crop pests from mammals, birds, reptiles and arthropods (Bery et al. 2010; Roger et al. 2014). Pesticide uses has been the most applied method to control pests. Unfortunately, some pest species have developed different resistance mechanisms to various pesticide families (Anderson et al. 2018; Tay and Gordon 2019), while other species escape and migrate to new regions. In the absence of consistence control measures or indigenous natural enemies, successful pest invasions are usually followed by rapid population increase and movement, resulting in severe plant injury to crops and potentially serious yield and economic losses (De Barro et al. 2011; Haile et al. 2021).

One currently known invasive pest is the fall armyworm (FAW), *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae), an insect that has moved from its native occurrence in the Neotropical Americas to many parts of the Eastern Hemisphere. This polyphagous insect has already been reported on over 350 host plants including many crops of economic importance (Montezano et al. 2018). Unfortunately, since 2016, it has invaded sub-Saharan Africa (Goergen et al. 2016; Nagoshi et al. 2017, 2018, 2022; Koffi et al. 2020a, b) to Asia (Nagoshi et al. 2020; Kim et al. 2021), and now has reached Oceania (Bourke and Sar 2020). Spread of this pest has caused severe economic damage to cereal production (mostly maize) and has disrupted global agricultural systems and food security (Koffi et al 2020a, b, 2022). To reduce food and economic losses, insecticides are mainly used by millions of farmers with the support of several governments (Koffi et al. 2020b, 2021). However, the indiscriminate uses

of insecticides are not only threatening the human health and environmental protection (O'Dowd et al. 2003), but also disrupting the natural interdependencies of biodiversity species by killing non-target organisms that include natural enemies of pests.

Over hundred species of natural biocontrol agents of FAW have already been reported worldwide (Molina-Ochoa et al. 2003a; Murúa et al. 2009; Meagher et al. 2016). In Africa, many indigenous entomopathogens, parasitoids, and predators have been reported from FAW (Sisay et al. 2018; Agboyi et al. 2020; Koffi et al. 2020c). But due to the indiscriminate application of insecticides in the invaded areas, the population evolutions and potentiality of natural control of the indigenous agents are poorly known. However, in Togo, infestation of FAW was three times lower from 2018 to 2020 compared to the previous two years following the invasion (Koffi et al. 2020a, 2022). Thus, the aim of this study was to identify, evaluate the geospatial distributions, and the impacts of insecticides applications on indigenous entomopathogenic virus, bacteria, fungi and nematodes, parasitoids, and predators established with FAW populations during the seven years following the invasion of the pest in Togo.

Materials And Methods

Sites of collections and sampling

Fall armyworm egg masses and larvae were collected during the cropping seasons from April to November of seven consecutive years (2016 to 2022). The collections of specimens were initiated at the on-set of the FAW invasion in Togo. In 2016, selected collection sites covered the geo-latitude from Lomé (6.176 N) to Kara (9.377 N). In the following years, collections covered the entire country from Lomé to Dapaong (10.474 N). The collection sites were randomly selected (Fig. 1) during the survey trips for inspections of maize farms by the Entomological Research team from the Ecole Supérieure d'Agronomie, Université de Lomé. Specimen collections were separated into two periods, 1) intensive insecticide applications (2016 and 2018), and 2) occasional insecticide applications (2018 to 2022). During the inspections, insecticide application information was documented from the farmers to determine the percent of farms with insecticide applications per year (sprayed farms). However, calculations did not consider farms where the owner was not present. Within the selected farms, quadrants were designed at the four angles and middle of each farm. Egg masses and larvae were collected from plants within the quadrants as well the living organisms that were preying on egg masses or larvae. The collected egg masses and larvae were individually placed in rearing boxes as described by Koffi et al. (2020c) and carried in coolers to the Université de Lomé laboratory to continue rearing at $25 \pm 5^\circ \text{C}$, $78 \pm 15\%$ relative humidity, and 12:12 photoperiod.

Isolation of biocontrol agents

From the field collection sites, predators were immediately preserved in crystal vials containing 70% ethanol (Koffi et al. 2020c). During inspections, egg masses and larvae were collected to complete their life cycle with laboratory individual rearing. The non-infected specimens were reared to adulthood, while the infected or parasitized specimens were reared until the dead of individuals with symptoms of entomopathogens or emergence of parasitoids. Natural biological control agents were classified into entomopathogenic nematodes, virus, bacteria and fungi, parasitoids, and predators. The emerged parasitoids and nematodes were preserved into crystal vials containing 70% ethanol. Dead larvae with evidence of viral or bacterial symptoms were isolated and preserved in the freezer at 4°C . Symptoms of infections from entomopathogenic fungi were germination of hyphae from dead larvae. The infected samples were removed from their rearing boxes and individually conserved in an empty petri dish under the same laboratory rearing conditions. They were later individually transmitted into a petri dish containing Potato Dextrose Agar (PDA) previously prepared for fungi germinations and isolations. The preparations were incubated at laboratory rearing conditions for 10–21 days for identification.

Identifications Of Biocontrol Agents

Description keys were used to identify the entomopathogenic nematodes (Crosskey 1968; Baker and Capinera 1997; Firake and Behere 2020) and bacteria (Eilenberg et al. 2015). Two categories of virus were identified using morphology of the dead larvae.

Stunted larvae with production of virus-filled vesicles and milky-white discoloration were classified as Ascoviruses (Federici et al. 2008). Larvae with whitish-grey discoloration and a swollen body with a ruptured integument leading to liquefaction, were assigned to the Baculoviruses (Haase et al. 2015; Valicente 2019). Entomopathogenic fungi were determined by hyphal germination from the larvae, and a few samples were morphologically identified by the USDA-ARS in Ithaca, NY, USA. Dead larvae presenting green-like microflora germinations were assigned to undetermined entomopathogenic bacteria. Identification keys were used to identify emerged parasitoids (van Achterberg 1990; Braet et al. 2012; O'Hara and Cerretti 2016), and collected predators (Brindle 1967; Waller et al. 1999; Kwadjo et al. 2012; Nicolas et al. 2015; Gerod and Lassalle 2017).

Data curations and analysis

After identification of specimens, several variables were calculated. Infection rates (number of larvae infected by a given entomopathogen species over total number of collected larvae), parasitism rates (number of egg masses or larvae parasitized by a given parasitoid species over the total number of egg masses or larvae collected), population density (number of a given species over the total number of sampled plants), and relative abundances (number of egg masses or larvae infected or parasitized by a given biocontrol agent over the total egg masses or larvae infected or parasitized) were calculated at the farm level. The index of dispersion (ratio of the number of farms hosting a given nematode, bacterium, virus, fungus, parasitoid or predator species over the total number of farms inspected for each year) and percent of sprayed farms (number of sprayed farms over total inspected farms per year) were calculated on a national level (Koffi et al. 2020c).

These data were arranged per location and grouped per year. The percentage data were arcsine square root transformed prior to statistical analysis. All the calculations, arrangements, and transformations were carried out using Excel before being submitted to a Shapiro test for normality (GenStat Twelfth Edition GenStat Procedure Library Release PL20.1). Normal data were submitted to one-way analysis of variance at 95% confident interval, and the non-normal data to a non-parametric test (Kruskal-Wallis) at 5% significance level. Multiple means obtained from ANOVA were subjected to a Tukey test for separation, while means comparing the parasitism rates between the sprayed and unsprayed farms were subjected to a *t*-test. The assessment of correlation between the numbers of collected egg masses and larvae were also calculated using GenStat.

Results

Impact of insecticides on the performance natural biocontrol

The two years following the invasion of FAW in Togo showed higher numbers of egg masses collected per farm than the next several years. Although there were high numbers of egg masses those first two years, none were found to be parasitized. However, the low numbers of egg masses collected since 2018 showed parasitism rates increasing from 14.72% in 2018 to 45.38% in 2022 (Table 1). The same trend was shown with larvae as higher numbers were collected per farm in 2016 and 2017 than the following years. Correlation analysis between collected egg masses and larvae showed no relationship ($r= 0.0002$, $P= 0.869$). Larval parasitism rates were very low in 2016 (1.32%) and 2017 (2.53%), but increased to 15.96% in 2018 and 42.23% in 2022 (Table 1).

Table 1
Numbers and parasitism rates of egg masses and larvae across years of collections

Year	Farm	Egg mass				Larvae			
		n	P	Per farm	Pr (%)	n	P	Per farm	Pr (%)
2016	61	103	0	1.67 ± 0.23b	0a	1025	15	17.02 ± 1.36b	1.32 ± 0.36a
2017	37	42	0	1.14 ± 0.41b	0a	692	17	18.53 ± 3.05b	2.53 ± 0.34a
2018	27	13	2	0.46 ± 0.32a	14.72 ± 2.03b	139	23	4.82 ± 1.23a	15.96 ± 1.35b
2019	79	35	9	0.44 ± 0.11a	23.63 ± 1.35b	425	123	5.07 ± 0.31a	28.72 ± 1.82bc
2020	71	29	11	0.42 ± 0.21a	36.28 ± 2.41bc	296	93	4.11 ± 1.51a	31.37 ± 2.35bc
2021	28	9	4	0.31 ± 0.18a	42.76 ± 3.85c	108	46	3.76 ± 1.65a	41.85 ± 3.61c
2022	45	11	5	0.22 ± 0.14a	45.38 ± 1.69c	153	65	3.36 ± 0.86a	42.23 ± 2.54c
df				6, 347	6, 91			6, 347	6, 269
F				4.65	12.26			8.69	6.82
P				0.032	< 0.001			0.009	0.018
<i>n</i> = total number, <i>P</i> = number of parasitized individuals, <i>Pr</i> = parasitism rate.									
Means (± SE) followed by the same letter in the column are not statistically different									

During the survey, farmers were interviewed regarding the insecticide applications and depending on the year, between 52.1–74.1% responded. The percentage of sprayed farms were very high in 2017 (91.38% of farms inspected) and 2016 (73.25%), compared with the range of 23.52–11.08% obtained between 2018 and 2022. Higher egg and larval parasitism rates were recorded in unsprayed farms than sprayed farms every year of the seven-year study (Fig. 2).

Entomopathogenic organisms associated with FAW

Entomopathogenic agents associated with FAW larvae included a nematode, *Ovomermis sinensis* (Nematoda: Mermithidae), unidentified species in the bacteria family of Enterobacteriaceae and *Enterococcus* species, unidentified viruses belonging to Ascoviruses and Baculoviruses, and fungal species *Isaria* spp. (Hypocreales: Clavicipitaceae) and *Metarhizium rileyi* (Hypocreales: Cordycipitaceae). The nematode, *O. sinensis* had low infection rates, relative abundance and indice of dispersion until 2018, compared to the following years (Table 2). The infection rate of bacteria species belonging to Enterobacteriaceae were not constant during the period of collections, but its relative abundances were high in 2016 and 2017. The indexes of dispersion were constant over the study period. Infection rates of *Enterococcus* species increased from 2018 onward, while its relative abundance decreased, and its indexes of dispersion remained constant along the study (Table 2). Larvae infected by Ascovirus were collected from 2018 and Baculovirus was collected in 2017. However, the two virus and fungal groups had constant infection rates, relative abundance, and indice of dispersion throughout the study (Table 2).. Although the spatial distribution of entomopathogens yearly increased (Fig. 3), the population densities of each species are similar.

Table 2
Entomopathogenic associated with FAW from 2016 to 2022 in Togo and their infection rates, relative abundances, and index of dispersions

Species		2016	2017	2018	2019	2020	2021	2022	df	F	P
Entomopathogenic nematode											
<i>O. sinensis</i>	Ir (%)	0.29 ± 1.02a	0.29 ± 1.01a	2.16 ± 1.05a	12.94 ± 2.31b	16.55 ± 2.51b	17.59 ± 2.63bc	20.92 ± 1.03c	6, 347	7.32	0.011
	pd	0.03 ± 0.01a	0.01 ± 0.05a	0.02 ± 0.03a	0.02 ± 0.01a	0.01 ± 0.06a	0.01 ± 0.03a	0.01 ± 0.4a	6, 347	0.23	0.362
	RA (%)	20 ± 3.56b	11.76 ± 2.23a	13.04 ± 2.32a	44.72 ± 3.05c	52.69 ± 2.12d	41.30 ± 3.03c	49.23 ± 2.02d	6, 347	11.82	< 0.001
	iD	0.02 ± 0.02a	0.06 ± 0.03a	0.07 ± 0.03a	0.39 ± 0.02b	0.51 ± 0.06c	0.54 ± 0.04c	0.56 ± 0.05c	6, 347	13.59	< 0.001
Entomopathogenic bacteria											
Enterobacteriaceae	Ir (%)	0.20 ± 0.12a	0.29 ± 0.14a	0.72 ± 0.23b	0.71 ± 0.22b	0.34 ± 0.15a	0.93 ± 0.2bc	0.65 ± 0.2b	6, 347	6.23	0.014
	pd	0.02 ± 0.03a	0.02 ± 0.03a	0.01 ± 0.02a	0.02 ± 0.04a	0.01 ± 0.02a	0.01 ± 0.03a	0.01 ± 0.3a	6, 347	0.15	0.315
	RA (%)	13.33 ± 0.65b	11.76 ± 0.32b	4.3s5 ± 0.18a	2.44 ± 0.09a	1.08 ± 0.33a	2.17 ± 0.11a	1.54 ± 0.06a	6, 347	4.23	0.024
	iD	0.02 ± 0.1a	0.03 ± 0.06a	0.04 ± 0.02a	0.03 ± 0.05a	0.01 ± 0.03a	0.04 ± 0.04a	0.02 ± 0.03a	6, 347	1.23	0.117
Enterococcus	Ir (%)	0.29 ± 0.23a	0.29 ± 0.05a	0.72 ± 0.04b	0.94 ± 0.35bc	1.01 ± 0.51c	0.93 ± 0.12bc	1.31 ± 0.34c	6, 347	12.03	< 0.001
	pd	0.02 ± 0.02a	0.02 ± 0.03a	0.01 ± 0.04a	0.02 ± 0.02a	0.03 ± 0.02a	0.01 ± 0.02a	0.02 ± 0.03	6, 347	0.423	0.412
	RA (%)	20 ± 3.21bc	11.76 ± 1.23b	4.35 ± 0.57a	3.23 ± 0.33a	3.23 ± 0.13a	2.17 ± 0.31a	3.08 ± 0.21a	6, 347	5.58	0.035
	iD	0.03 ± 0.2a	0.03 ± 0.12a	0.04 ± 0.13a	0.03 ± 0.02a	0.01 ± 0.01a	0.04 ± 0.12a	0.02 ± 0.10	6, 347	0.98	0.095
Entomopathogenic virus											
Ascoviruses	Ir (%)	*	*	0.72 ± 0.021a	2.35 ± 0.71a	2.03 ± 0.58a	1.85 ± 0.085a	1.96 ± 0.75a	4, 249	1.63	0.069
	pd	*	*	0.01 ± 0.02a	0.03 ± 0.04a	0.05 ± 0.02a	0.03 ± 0.2a	0.3 ± 0.03a	4, 249	0.37	0.428

*no collection, iD-index of dispersion, Ir-infection rate, pd-population density, RA-relative abundance; means (± SE) in the same row with same letter are not statistically different

Species		2016	2017	2018	2019	2020	2021	2022	df	F	P
	RA (%)	*	*	4.35 ± 1.02a	8.13 ± 1.15a	6.45 ± 1.19a	4.35 ± 1.35a	4.62 ± 0.86a	4, 249	0.85	0.112
	iD	*	*	0.04 ± 0.1a	0.04 ± 0.09a	0.04 ± 0.12a	0.04 ± 0.11a	0.02 ± 0.05a	4, 249	0.68	0.231
Baculoviruses	Ir (%)	*	0.14 ± 0.23a	0.72 ± 0.12a	3.06 ± 0.56a	3.04 ± 0.81a	2.78 ± 0.69a	3.27 ± 1.05a	5, 286	1.09	0.183
	pd	*	0.01 ± 0.02a	0.01 ± 0.02a	0.03 ± 0.05a	0.02 ± 0.01a	0.02 ± 0.02a	0.03 ± 0.01a	5, 286	1.07	0.065
	RA (%)	*	5.88 ± 1.02a	4.35 ± 1.15a	10.57 ± 2.03a	9.68 ± 1.85a	6.52 ± 1.35a	7.69 ± 2.31a	5, 286	0.85	0.076
	iD	*	0.03 ± 0.02a	0.04 ± 0.10a	0.05 ± 0.12a	0.03 ± 0.21a	0.04 ± 0.12a	0.04 ± 0.09a	5, 286	1.21	0.097
Entomopathogenic fungi											
<i>Isaria</i> spp.	Ir (%)	*	*	0.72 ± 0.25a	0.47 ± 0.12a	0.34 ± 0.32a	0.93 ± 0.25a	0.65 ± 0.16a	4, 249	1.02	0.135
	pd	*	*	0.01 ± 0.03a	0.02 ± 0.01a	0.01 ± 0.03a	0.01 ± 0.02a	0.01 ± 0.05a	4, 249	0.36	0.512
	RA (%)	*	*	4.35 ± 0.38a	1.63 ± 0.25a	1.08 ± 0.68a	2.17 ± 0.62a	1.54 ± 0.23a	4, 249	1.36	0.125
	iD	*	*	0.04 ± 0.11a	0.01 ± 0.09a	0.01 ± 0.02a	0.04 ± 0.05a	0.02 ± 0.06a	4, 249	0.96	0.139
<i>M. rileyi</i>	Ir (%)	*	0.14 ± 0.05a	0.72 ± 0.08a	*	0.68 ± 0.12a	0.93 ± 0.31a	0.65 ± 0.08a	4, 207	1.32	0.067
	pd	*	0.01 ± 0.02a	0.01 ± 0.01a	*	0.02 ± 0.03a	0.01 ± 0.02a	0.01 ± 0.02a	4, 207	0.34	0.623
	RA (%)	*	5.88 ± 1.02a	4.35 ± 1.06a	*	2.15 ± 0.81a	2.17 ± 0.09a	1.54 ± 0.12a	4, 207	1.23	0.098
	iD	*	0.03 ± 0.21a	0.04 ± 0.05a	*	0.01 ± 0.06a	0.04 ± 0.05a	0.02 ± 0.05a	4, 207	0.52	0.238
*no collection, iD-index of dispersion, Ir-infection rate, pd-population density, RA-relative abundance; means (± SE) in the same row with same letter are not statistically different											

Complex Of Parasitoids

During this study, 11 species of parasitoids were collected and identified. The egg parasitoid *Telenomus remus* (Hymenoptera: Platygasteridae) was consistently collected from 2018 with increasing parasitism rates from 15.38–45.44% in 2022 and equally dispersed during the collection period (Table 3). One species of egg-larva parasitoid, *Chelonus bifoveolatus* (Hymenoptera:

Braconidae), was also collected with low parasitism rates that increased from 0.39% in 2016 to 3.70% in 2021. This species had an increasing index of dispersion and decreasing relative abundance during the study (Table 3). The larval parasitoids included three dipteran species, *Anatrichus erinaceus* (Chloropidae), *Archytas* spp. and *Lespesia* spp. (Tachinidae), six hymenopteran species including *Bracon* sp., *Coccygidium luteum*, *Cotesia icipe* and *Meteoridea testacea* (Braconidae), and *Campoletis grioti* and *Ophion* spp. (Ichneumonidae). The parasitism rate of *A. erinaceus* was low but increased slightly in 2020; the index of dispersion was consistent throughout the study and the relative abundance increased in 2016 and 2017. The indexes of dispersion of *Archytas* spp. and *Lespesia* spp. were the same across all years of collection, with small variations found among the parasitism rates and relative abundances (Table 3). Parasitism rates of all the other larval parasitoids increased moderately from 2018 onward, with low variation in relative abundance and index of dispersion (Table 3). Although the spatial distribution of parasitoids yearly increased (Fig. 4), the population densities of each species are similar.

Table 3

Egg, egg-larval and larval parasitoids with annually parasitism rates, population densities, relative abundance and index of dispersion

Species		2016	2017	2018	2019	2020	2021	2022	df	F	P
Egg Parasitoid											
<i>T. remus</i>	Pr (%)	*	*	15.38 ± 2.31a	25.71 ± 3.25b	37.93 ± 3.65bc	44.44 ± 4.23c	45.46 ± 3.95c	4, 249	6.85	0.025
	pd	*	*	0.01 ± 0.02a	0.02 ± 0.01a	0.02 ± 0.03a	0.01 ± 0.03a	0.01 ± 0.02a	4, 249	0.35	0.324
	RA (%)	*	*	100	100	100	100	100	4, 249	*	*
	iD	*	*	0.07 ± 0.12ab	0.05 ± 0.08a	0.07 ± 0.10ab	0.11 ± 0.14b	0.09 ± 0.11b	4, 249	4.38	0.046
Egg-larval Parasitoids											
<i>C. bifoveolatus</i>	Pr (%)	0.39 ± 0.06a	0.29 ± 0.12a	2.16 ± 0.21b	2.12 ± 0.18b	2.03 ± 0.18b	3.70 ± 0.28b	2.61 ± 0.22b	6, 347	6.31	0.033
	pd	0.01 ± 0.03a	0.02 ± 0.04a	0.02 ± 0.02a	0.02 ± 0.03a	0.01 ± 0.01a	0.01 ± 0.03a	0.01 ± 0.02a	6, 347	0.32	0.624
	RA (%)	26.67 ± 1.35b	11.76 ± 1.12ab	13.04 ± 1.23ab	7.32 ± 1.06a	6.45 ± 0.95a	8.70 ± 1.25a	6.15 ± 0.79a	6, 347	4.35	0.042
	iD	0.05 ± 0.02a	0.03 ± 0.11a	0.07 ± 0.12ab	0.08 ± 0.06ab	0.07 ± 0.06ab	0.11 ± 0.21b	0.09 ± 0.18b	6, 347	3.58	0.048
Larval Parasitoids											
<i>A. erinaceus</i>	Pr (%)	*	0.14 ± 0.17a	0.72 ± 0.35ab	0.71 ± 0.23ab	0.34 ± 0.12a	0.93 ± 0.21bc	1.31 ± 0.58c	5, 286	5.64	0.017
	pd	*	0.01 ± 0.01a	0.01 ± 0.03a	0.02 ± 0.02a	0.01 ± 0.01a	0.02 ± 0.01a	0.02 ± 0.03a	5, 286	0.09	0.853
	RA (%)	*	5.88 ± 1.33b	4.35 ± 1.35b	2.44 ± 0.58a	1.08 ± 0.35a	2.17 ± 0.48a	3.08 ± 0.25ab	5, 286	6.25	0.036
	iD	*	0.03 ± 0.08a	0.04 ± 0.05a	0.03 ± 0.12a	0.01 ± 0.08a	0.04 ± 0.05a	0.02 ± 0.03a	5, 286	1.58	0.359
<i>Archytas</i> spp.	Pr (%)	*	0.14 ± 0.06a	0.72 ± 0.12ab	0.47 ± 0.35a	0.34 ± 0.18a	0.93 ± 0.32ab	1.31 ± 0.68b	5, 286	3.85	0.043
	pd	*	0.01 ± 0.03a	0.01 ± 0.03a	0.02 ± 0.02a	0.01 ± 0.02a	0.01 ± 0.02a	0.02 ± 0.01a	5, 286	0.36	0.647
	RA (%)	*	5.88 ± 1.68b	4.35 ± 1.23ab	1.63 ± 0.58a	1.08 ± 0.65a	2.17 ± 0.66a	3.08 ± 1.02a	5, 286	4.05	0.048
	iD	*	0.03 ± 0.08a	0.04 ± 0.02a	0.01 ± 0.01a	0.01 ± 0.03a	0.04 ± 0.05a	0.04 ± 0.03a	5, 286	1.58	0.235
<i>Bracon</i> sp.	Pr (%)	0.20 ± 0.2a	0.14 ± 0.32a	1.44 ± 0.57bc	0.47 ± 0.35ab	1.01 ± 0.28b	1.85 ± 0.25c	1.96 ± 0.38c	6, 347	8.32	0.023
	pd	0.01 ± 0.03a	0.01 ± 0.01a	0.02 ± 0.03a	0.01 ± 0.02a	0.01 ± 0.01a	0.01 ± 0.03a	0.01 ± 0.02a	6, 347	0.52	0.634
	RA (%)	13.33 ± 2.35b	5.88 ± 1.38a	8.70 ± 2.03ab	1.63 ± 0.85a	3.23 ± 0.38a	4.35 ± 1.08a	4.62 ± 1.12a	6, 347	5.02	0.031

*no collection, iD-index of distribution, pd-population density, Pr-parasitism rate, RA-relative abundance; means in the same row with the same letter are not statistically different

Species		2016	2017	2018	2019	2020	2021	2022	df	F	P
	iD	0.03 ± 0.12a	0.03 ± 0.15a	0.03 ± 0.18a	0.01 ± 0.06a	0.04 ± 0.08a	0.07 ± 0.12b	0.07 ± 0.18b	6, 347	4.68	0.028
<i>C. grioti</i>	Pr (%)	*	0.14 ± 0.35a	0.72 ± 0.03a	0.71 ± 0.09a	1.01 ± 0.12b	1.85 ± 0.65bc	2.61 ± 0.35c	5, 286	7.23	0.019
	pd	*	0.01 ± 0.02a	0.01 ± 0.02a	0.02 ± 0.01a	0.01 ± 0.02a	0.02 ± 0.02a	0.01 ± 0.03a	5, 286	0.95	0.324
	RA (%)	*	5.88 ± 0.123a	4.35 ± 1.09a	2.44 ± 0.68a	3.23 ± 1.05a	4.35 ± 1.09a	6.15 ± 1.52a	5, 286	1.23	0.135
	iD	*	0.03 ± 0.13a	0.04 ± 0.11a	0.03 ± 0.09a	0.04 ± 0.14a	0.04 ± 0.08a	0.07 ± 0.08b	5, 286	3.68	0.041
<i>C. luteum</i>	Pr (%)	*	0.14 ± 0.15a	0.72 ± 0.24bc	0.47 ± 0.15b	0.68 ± 0.19bc	0.93 ± 0.26c	*	4, 241	7.38	0.023
	pd	*	0.01 ± 0.02a	0.01 ± 0.02a	0.02 ± 0.02a	0.01 ± 0.01a	0.01 ± 0.02a	*	4, 241	0.035	0.852
	RA (%)	*	5.88 ± 1.37a	4.35 ± 1.29a	1.63 ± 0.65a	2.15 ± 0.54a	2.17 ± 0.51a	*	4, 241	2.08	0.118
	iD	*	0.03 ± 0.12a	0.04 ± 0.28a	0.01 ± 0.19a	0.03 ± 0.26a	0.04 ± 0.32a	*	4, 241	1.95	0.109
<i>C. icipe</i>	Pr (%)	*	0.14 ± 0.23a	0.72 ± 0.35b	0.71 ± 0.28b	0.68 ± 0.25b	1.85 ± 0.05c	0.65 ± 0.14b	5, 286	8.35	0.011
	pd	*	0.01 ± 0.01a	0.01 ± 0.02a	0.02 ± 0.02a	0.02 ± 0.01a	0.02 ± 0.01a	0.01 ± 0.02a	5, 286	0.032	0.625
	RA (%)	*	5.88 ± 1.09a	4.35 ± 0.96a	2.44 ± 0.51a	2.15 ± 0.23a	4.35 ± 0.32a	1.54 ± 0.22a	5, 286	2.09	0.075
	iD	*	0.03 ± 0.01a	0.04 ± 0.05a	0.04 ± 0.03a	0.01 ± 0.12a	0.04 ± 0.10a	0.02 ± 0.09a	5, 286	1.95	0.102
<i>Lespesia</i> spp.	Pr (%)	0.10	0.14 ± 0.08a	0.72 ± 0.07ab	0.24 ± 0.07a	0.34 ± 0.05a	1.85 ± 0.59bc	1.31 ± 0.18b	6, 347	4.82	0.038
	pd	0.01 ± 0.01a	0.01 ± 0.01a	0.01 ± 0.02a	0.01 ± 0.01a	0.01 ± 0.03a	0.02 ± 0.01a	0.01 ± 0.03a	6, 347	0.86	0.215
	RA (%)	6.67	5.88 ± 1.32b	4.35 ± 0.28ab	0.81 ± 0.05a	1.08 ± 0.15a	4.35 ± 0.51ab	3.08 ± 0.28ab	6, 347	4.36	0.041
	iD	0.02	0.03 ± 0.01a	0.04 ± 0.01a	0.01 ± 0.12a	0.01 ± 0.05a	0.04 ± 0.023a	0.04 ± 0.04	6, 347	1.03	0.247
<i>M. testacea</i>	Pr (%)	*	*	1.44 ± 0.21a	0.47 ± 0.21a	0.34 ± 0.12a	0.93 ± 0.31a	0.65 ± 0.22a	4, 249	0.68	0.234
	pd	*	*	0.01 ± 0.02a	0.02 ± 0.02a	0.1 ± 0.01a	0.01 ± 0.01a	0.01 ± 0.02a	4, 249	0.026	0.567
	RA (%)	*	*	8.70 ± 1.69b	1.63 ± 0.35a	1.08 ± 0.41a	2.17 ± 0.68a	1.54 ± 0.65a	4, 249	4.95	0.035
	iD	*	*	0.07 ± 0.23b	0.01 ± 0.25a	0.01 ± 0.31a	0.04 ± 0.036a	0.02 ± 0.23a	4, 249	4.65	0.037
<i>Ophion</i> spp.	Pr (%)	*	*	0.72 ± 0.35a	0.47 ± 0.29a	0.34 ± 0.09a	0.93 ± 0.34a	0.65 ± 0.19a	4, 249	0.63	0.238

*no collection, iD-index of distribution, pd-population density, Pr-parasitism rate, RA-relative abundance; means in the same row with the same letter are not statistically different

Species		2016	2017	2018	2019	2020	2021	2022	df	F	P
	pd	*	*	0.01 ± 0.02a	0.02 ± 0.01a	0.01 ± 0.02a	0.01 ± 0.03a	0.01 ± 0.02a	4, 249	0.56	0.538
	RA (%)	*	*	4.35 ± 1.08a	1.63 ± 0.85a	1.08 ± 0.65a	2.17 ± 0.57a	1.54 ± 0.87a	4, 249	0.68	0.215
	iD	*	*	0.04 ± 0.08a	0.01 ± 0.06a	0.01 ± 0.03a	0.04 ± 0.02a	0.02 ± 0.02a	4, 249	0.95	0.312

*no collection, iD-index of distribution, pd-population density, Pr-parasitism rate, RA-relative abundance; means in the same row with the same letter are not statistically different

Species Diversity Of Faw Predator

A total of 16 species of FAW arthropod predators were collected during this study. These were five heteropterans, *Orius insidiosus* (Anthocoridae), and *Haematochara obscuripennis*, *Peprius nodulipes*, *Rhynocoris* sp. and *Zelus renardii* (Reduviidae); four beetles, *Calleida* sp. (Carabidae), *Cheilomenes sulphurea*, *Coccinella septempunctata* and *Cycloneda sanguinea* (Coccinellidae); three earwigs, *Euborellia annulipes*, *Forficula auricularia* and *Forficula senegalensis* (Forficulidae); two ants, *Pheidole megacephala* and *Polyrhachis lamellidens* (Formicidae); one lacewing, *Chrysoperla carnea* (Chrysopidae); and one mantid, *Mantis religiosa* (Mantidae).

Except for *O. insidiosus* and *Z. renardii*, all the heteropteran species were collected from 2018 and had similar relative abundances and indices of dispersion during the collection years (Table 4). The beetle species were collected from 2017 and had similar relative abundance across the years of collection with slight increasing index of dispersion (Table 4). Except for *E. annulipes*, the earwig species were collected from the on-set of the FAW invasion with a slight increase of relative abundances and dispersion in the following years (Table 4). Ants collected were social Formicidae that increased in their locations found during the study. The lacewing *C. carnea* and mantid *M. religiosa* were collected in higher numbers during the first years of the FAW invasion in Togo, and their dispersion increased during the study (Table 4). Although the spatial distribution of predators annually increased (Fig. 5), the population densities of each species are similar.

Table 4

The predator species collected from 2016 to 2022 in Togo with their relative abundances and index of dispersions

Species		2016	2017	2018	2019	2020	2021	2022	df	F	P
<i>H. obscuripennis</i>	RA (%)	*	*	3.80 ± 1.02a	5.86 ± 1.25a	3.96 ± 0.89a	7.41 ± 1.58a	5.29 ± 1.24a	4, 249	0.85	0.253
	pd	*	*	0.02 ± 0.03a	0.02 ± 0.01a	0.01 ± 0.03a	0.01 ± 0.02a	0.01 ± 0.02a	4, 249	0.68	0.694
	iD	*	*	0.07 ± 0.08a	0.10 ± 0.02a	0.11 ± 0.07a	0.25 ± 0.06a	0.2 ± 0.15a	4, 249	0.67	0.152
<i>P. nodulipes</i>	RA (%)	*	*	3.80 ± 1.05a	4.39 ± 1.09a	4.85 ± 1.09a	5.93 ± 1.15a	4.71 ± 1.22a	4, 249	1.38	0.358
	pd	*	*	0.02 ± 0.02a	0.01 ± 0.02a	0.02 ± 0.02a	0.02 ± 0.03a	0.01 ± 0.02a	4, 249	0.68	0.523
	iD	*	*	0.07 ± 0.08a	0.10 ± 0.05a	0.08 ± 0.15a	0.18 ± 0.11a	0.16 ± 0.08a	4, 249	0.94	0.125
<i>Rhynocoris</i> sp	RA (%)	*	*	5.06 ± 0.11a	5.37 ± 0.08a	3.96 ± 0.12a	4.44 ± 0.09a	4.71 ± 0.08a	4, 249	0.28	0.358
	pd	*	*	0.01 ± 0.03a	0.02 ± 0.02a	0.02 ± 0.03a	0.02 ± 0.01a	0.01 ± 0.02a	4, 249	0.32	0.428
	iD	*	*	0.11 ± 0.02a	0.08 ± 0.08a	0.07 ± 0.12a	0.14 ± 0.07a	0.13 ± 0.06a	4, 249	1.08	0.240
<i>Orius insidiosus</i>	RA (%)	*	5.88 ± 2.08b	2.53 ± 1.08a	2.44 ± 1.03a	*	2.22 ± 1.03a	2.94 ± 0.09a	4, 215	3.95	0.045
	pd	*	0.02 ± 0.01a	0.01 ± 0.03a	0.02 ± 0.01a	*	0.01 ± 0.02a	0.01 ± 0.01a	4, 215	0.32	0.726
	iD	*	0.03 ± 0.02a	0.07 ± 0.08a	0.04 ± 0.02a	*	0.11 ± 0.12b	0.09 ± 0.08ab	4, 215	3.56	0.048
<i>Z. renardii</i>	RA (%)	*	5.88 ± 2.04b	*	1.46 ± 0.85a	2.64 ± 0.65a	2.22 ± 0.56a	2.94 ± 0.68a	4, 259	3.89	0.042
	pd	*	0.01 ± 0.02a	*	0.02 ± 0.02a	0.02 ± 0.01a	0.01 ± 0.03a	0.01 ± 0.02a	4, 259	0.35	0.591
	iD	*	0.05 ± 0.05a	*	0.03 ± 0.01a	0.06 ± 0.08a	0.11 ± 0.06a	0.09 ± 0.09a	4, 259	1.35	0.158
<i>Calleida</i> sp	RA (%)	*	*	*	2.44 ± 1.34a	3.52 ± 1.05a	4.44 ± 1.63a	4.71 ± 1.38a	3, 222	1.86	0.354
	pd	*	*	*	0.01 ± 0.01a	0.02 ± 0.02a	0.02 ± 0.01a	0.02 ± 0.02a	3, 222	0.29	0.635
	iD	*	*	*	0.06 ± 0.08a	0.06 ± 0.17a	0.10 ± 0.09a	0.11 ± 0.03a	3, 222	0.96	0.358
<i>C. sulphurea</i>	RA (%)	*	8.82 ± 2.38a	8.86 ± 2.98a	*	4.85 ± 1.54a	9.63 ± 2.86a	7.65 ± 2.34a	4, 207	1.13	0.125
	pd	*	0.02 ± 0.03a	0.02 ± 0.01a	*	0.01 ± 0.04a	0.02 ± 0.01a	0.01 ± 0.03a	4, 207	0.35	0.436
	iD	*	0.05 ± 0.21a	0.15 ± 0.15ab	*	0.11 ± 0.08ab	0.25 ± 0.19b	0.24 ± 0.13b	4, 207	4.65	0.032

*no collection, iD-index of distribution, pd-population density, RA-relative abundance; means in the same row with same letter are not statistically different

Species		2016	2017	2018	2019	2020	2021	2022	df	F	P
<i>C. septempunctata</i>	RA (%)	*	*	15.19 ± 3.28a	12.68 ± 3.02a	15.86 ± 3.15a	21.48 ± 3.58a	18.24 ± 2.95a	4, 249	1.61	0.325
	pd	*	*	0.02 ± 0.2a	0.02 ± 0.01a	0.02 ± 0.01a	0.02 ± 0.02a	0.02 ± 0.03a	4, 249	0.09	0.832
	iD	*	*	0.19 ± 0.12a	0.20 ± 0.08a	0.24 ± 0.24a	0.46 ± 0.15b	0.36 ± 0.13b	4, 249	5.14	0.036
<i>C. sanguinea</i>	RA (%)	*	8.82 ± 2.05a	10.13 ± 2.31a	11.71 ± 2.57a	10.13 ± 2.85a	16.30 ± 3.21a	15.29 ± 3.52a	5, 286	1.59	0.085
	pd	*	0.02 ± 0.1a	0.03 ± 0.03a	0.02 ± 0.01a	0.02 ± 0.03a	0.02 ± 0.01a	0.01 ± 0.03a	5, 286	0.87	0.791
	iD	*	0.05 ± 0.05a	0.11 ± 0.08a	0.16 ± 0.15a	0.20 ± 0.34ab	0.40 ± 0.04b	0.42 ± 0.09b	5, 286	5.34	0.041
<i>E. annulipes</i>	RA (%)	*	*	3.80 ± 1.02a	6.34 ± 2.21a	4.85 ± 1.05a	6.67 ± 1.91a	9.41 ± 0.34a	4, 249	1.58	0.086
	pd	*	*	0.03 ± 0.02a	0.02 ± 0.02a	0.02 ± 0.01a	0.03 ± 0.04a	0.02 ± 0.01a	4, 249	1.12	0.062
	iD	*	*	0.04 ± 0.02a	0.10 ± 0.07a	0.10 ± 0.02a	0.11 ± 0.12a	0.2 ± 0.05a	4, 249	0.58	0.124
<i>F. auricularia</i>	RA (%)	15 ± 3.28b	5.88 ± 0.23a	7.59 ± 0.15a	10.24 ± 2.04ab	11.45 ± 1.58ab	9.63 ± 2.58ab	11.18 ± 2.65ab	6, 347	4.31	0.042
	pd	0.02 ± 0.03a	0.02 ± 0.02a	0.02 ± 0.01a	0.03 ± 0.02a	0.02 ± 0.01a	0.02 ± 0.04a	0.01 ± 0.01a	6, 347	0.89	0.085
	iD	0.03 ± 0.08a	0.03 ± 0.017a	0.15 ± 0.06ab	0.10 ± 0.22ab	0.15 ± 0.21ab	0.29 ± 0.05b	0.29 ± 0.09b	6, 347	5.35	0.035
<i>F. senegalensis</i>	RA (%)	25 ± 3.25b	8.82 ± 2.13a	16.46 ± 2.18ab	15.12 ± 3.28ab	18.50 ± 2.96ab	17.04 ± 3.08ab	18.24 ± 3.85ab	6, 347	4.35	0.047
	pd	0.02 ± 0.01a	0.02 ± 0.03a	0.02 ± 0.02a	0.03 ± 0.02a	0.02 ± 0.01a	0.02 ± 0.03a	0.01 ± 0.01a	6, 347	0.93	0.075
	iD	0.05 ± 0.12a	0.05 ± 0.17	0.15 ± 0.21ab	0.19 ± 0.24ab	0.25 ± 0.19b	0.36 ± 0.09b	0.29 ± 0.31b	6, 347	4.85	0.039
<i>P. megacephala</i>	RA (%)	*	Social	Social	Social	Social	Social	Social	*	*	*
	pd	*	Social	Social	Social	Social	Social	Social	*	*	*
	iD	*	0.08 ± 0.07a	0.22 ± 0.14ab	0.20 ± 0.12ab	0.18 ± 0.08ab	0.40 ± 0.15c	0.31 ± 0.07b	5, 286	7.25	0.015
<i>Ps lamellidens</i>	RA (%)	Social	Social	Social	Social	Social	Social	Social	*	*	*
	pd	Social	Social	Social	Social	Social	Social	Social	*	*	*
	iD	0.08 ± 0.04a	0.22 ± 0.16b	0.15 ± 0.08ab	0.30 ± 0.05bc	0.30 ± 0.16bc	0.43 ± 0.31c	0.42 ± 0.24c	6, 347	6.28	0.028

*no collection, iD-index of distribution, pd-population density, RA-relative abundance; means in the same row with same letter are not statistically different

Species		2016	2017	2018	2019	2020	2021	2022	df	F	P
<i>C. carnea</i>	RA (%)								6, 347	12.42	< 0.001
		60 ± 8.35c	47.06 ± 5.22b	22.79 ± 4.32a	21.95 ± 4.62a	15.42 ± 3.75a	18.52 ± 4.35a	18.82 ± 3.29a			
	pd	0.01 ± 0.02a	0.02 ± 0.01a	0.03 ± 0.01a	0.02 ± 0.03a	0.02 ± 0.03a	0.03 ± 0.4a	0.02 ± 0.01a	6, 347	1.02	0.071
	iD	0.15 ± 0.24a	0.22 ± 0.32a	0.15 ± 0.28a	0.32 ± 0.15b	0.32 ± 0.19b	0.36 ± 0.28b	0.38 ± 0.024b	6, 347	6.35	0.031
<i>M. religiosa</i>	RA (%)	30 ± 3.65b	26.47 ±	15.19 ± 2.38ab	13.17 ± 2.85ab	10.13 ± 3.52a	9.63 ± 2.69a	11.18 ± 3.50a	6, 347	5.36	0.044
	pd	0.02 ± 0.02a	0.01 ± 0.02a	0.02 ± 0.01a	0.01 ± 0.03a	0.01 ± 0.02a	0.01 ± 0.02a	0.02 ± 0.01a	6, 347	0.42	0.534
	iD	0.05 ± 0.08a	0.22 ± 0.08b	0.44 ± 0.12c	0.29 ± 0.24b	0.30 ± 0.06b	0.36 ± 0.16bc	0.29 ± 0.17b	6, 347	8.12	0.026
*no collection, iD-index of distribution, pd-population density, RA-relative abundance; means in the same row with same letter are not statistically different											

Discussion

Many of these natural enemy species have been documented before in several areas of the world, especially the parasitoids and predators (Sisay et al. 2018; Koffi et al. 2020c; Abang et al. 2021; Dassou et al. 2021; Otim et al. 2021). The nematode species, *O. sinensis*, has been described attacking several noctuid species (Li et al. 2003), including *S. frugiperda* (Sun et al. 2020). The bacteria found, *Enterococcus* sp., is a common gut bacteria found in many Lepidoptera species and is most likely not pathogenic (Voirol et al. 2018; Kenis et al. 2022). Viruses have been studied for many years to be used as microbial insecticides against FAW (Molina-Ochoa et al. 2003b; Guo et al. 2020; Hussain et al. 2021). Fungi, including *Isaria* spp. and *M. rileyi*, have also been studied for many years as biopesticides against noctuid larvae (Guo et al. 2020).

The invasion of FAW in Africa was successful as increased population growth and rapid spread was followed by the severe damage on maize farms and important yield and economic losses (Koffi 2020a, b, 2022). The response of maize producers and governments to this threatened food security phenomenon was the application of insecticides (Koffi et al. 2021). In Togo, up to 73.25% of maize farms were sprayed with insecticides to reduce the severe infestation of FAW. This increased up to 91.38% in 2017 and was expected to stabilize or to increase in 2018 (Ramírez-Cabral et al 2020). Surprisingly, insecticide applications decreased to 23.52% in 2018 and reached 11.08% in 2022. Lowering of insecticide applications coincided with the increasing numbers and performance of the natural biocontrol agents which were already collected during maize production in 2016 and 2017. Fortunately, the infestations of FAW between 2018 and 2020 were three times lower than the previous two years (Koffi et al. 2020a, 2022), which may explain growers reducing their sprays. This unexpected phenomenon calls into question the efficiency of many insecticides applied against the FAW in Togo. The performance of natural biocontrol may be underestimated or other natural factors (i.e., rainfall) may be involved into the FAW infestation reduction.

Even if low number and efficiency of natural biocontrol were expected during the two years following the invasion of the new pest, the three to four times higher parasitism rates of egg masses and larvae in the unsprayed than sprayed farms demonstrated the negative effects of insecticides on biocontrol agents. Therefore, the moderation observed on applications of insecticides from 2018 may contribute to high emergence of biocontrol agents and improve their performance.

Declarations

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Figures

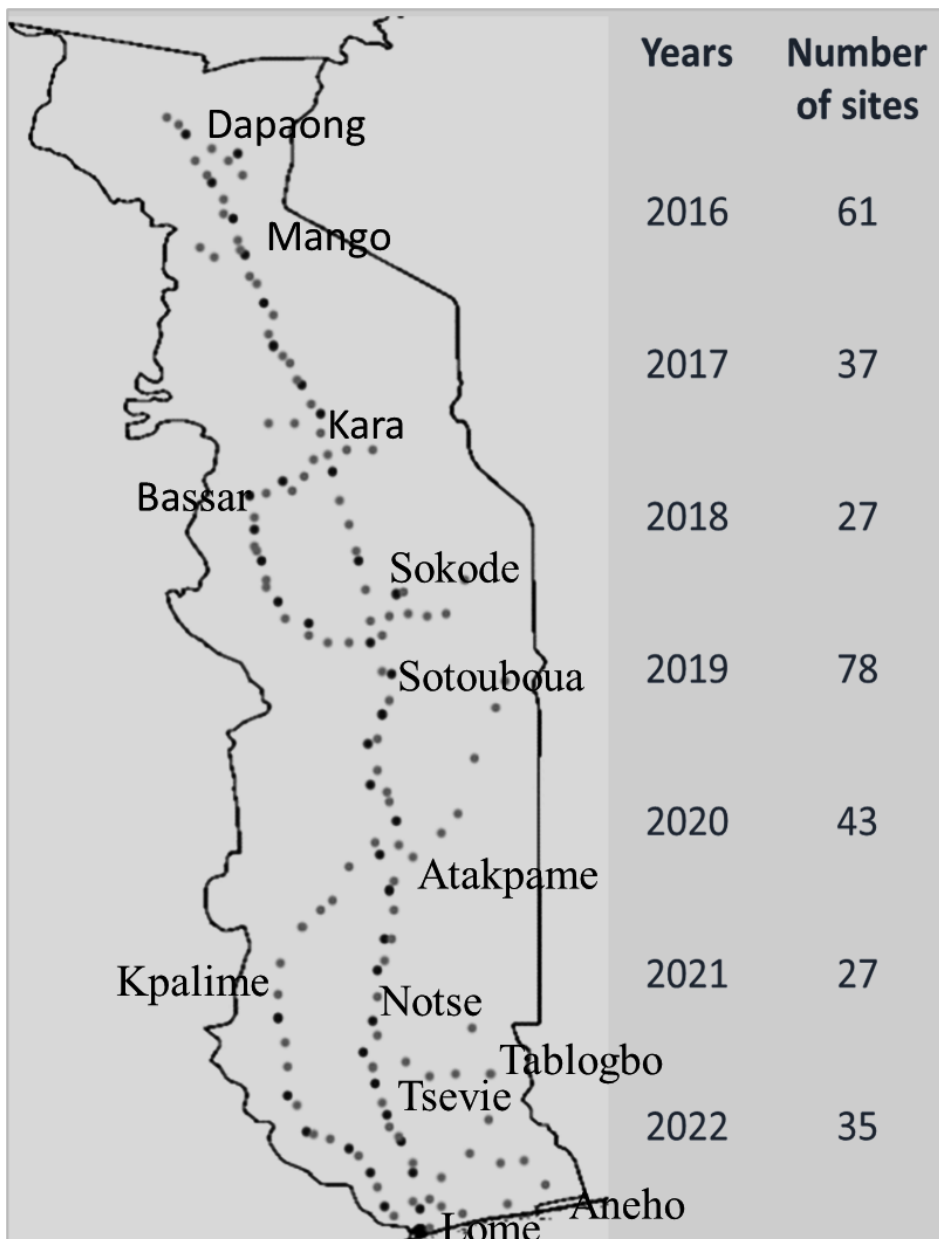


Figure 1

Collection locations with some reference cities, the years of collections and numbers of maize farms inspected from 2016 to 2022

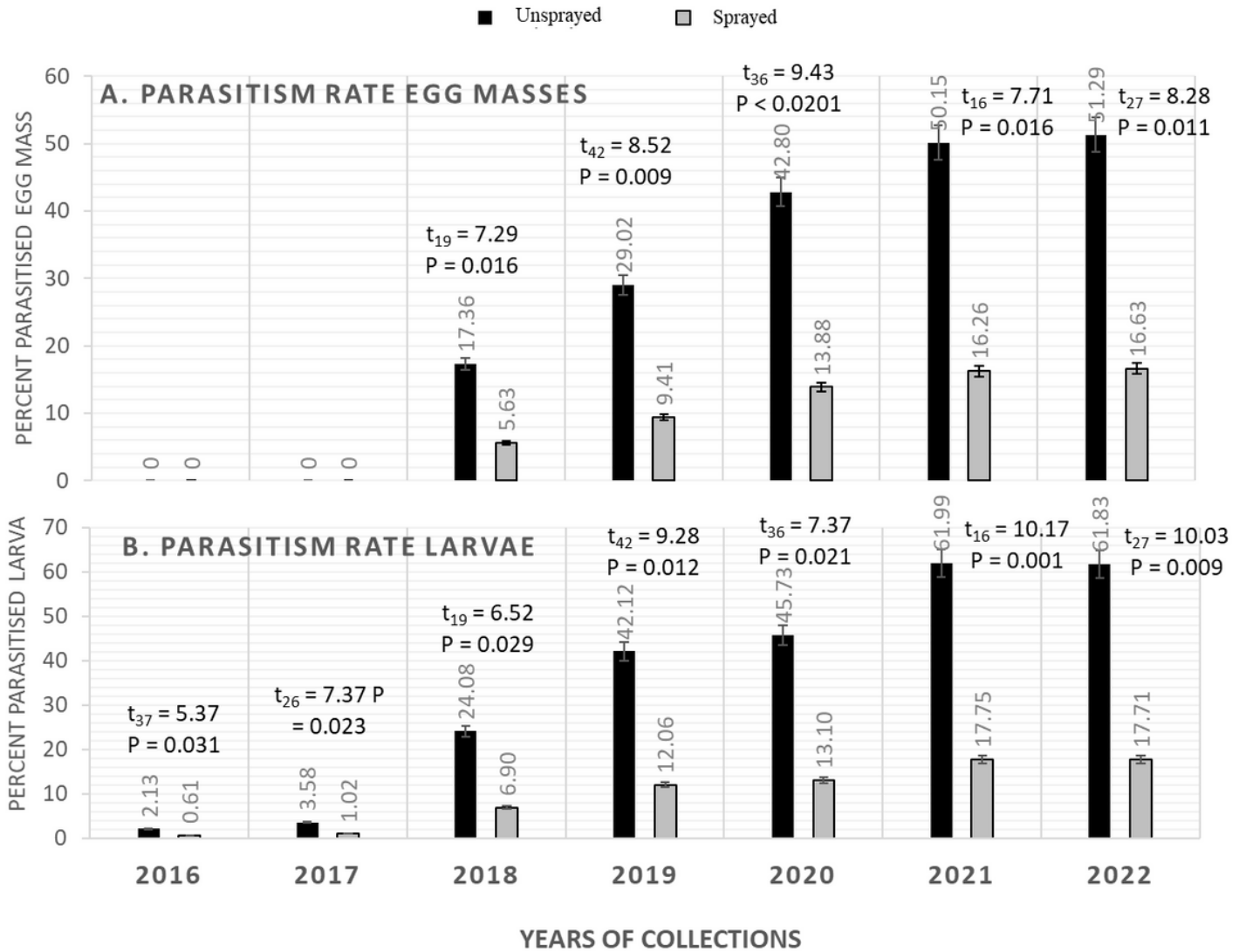


Figure 2

Percent of egg masses and larvae parasitized or infected from 2016 to 2022 in Togo

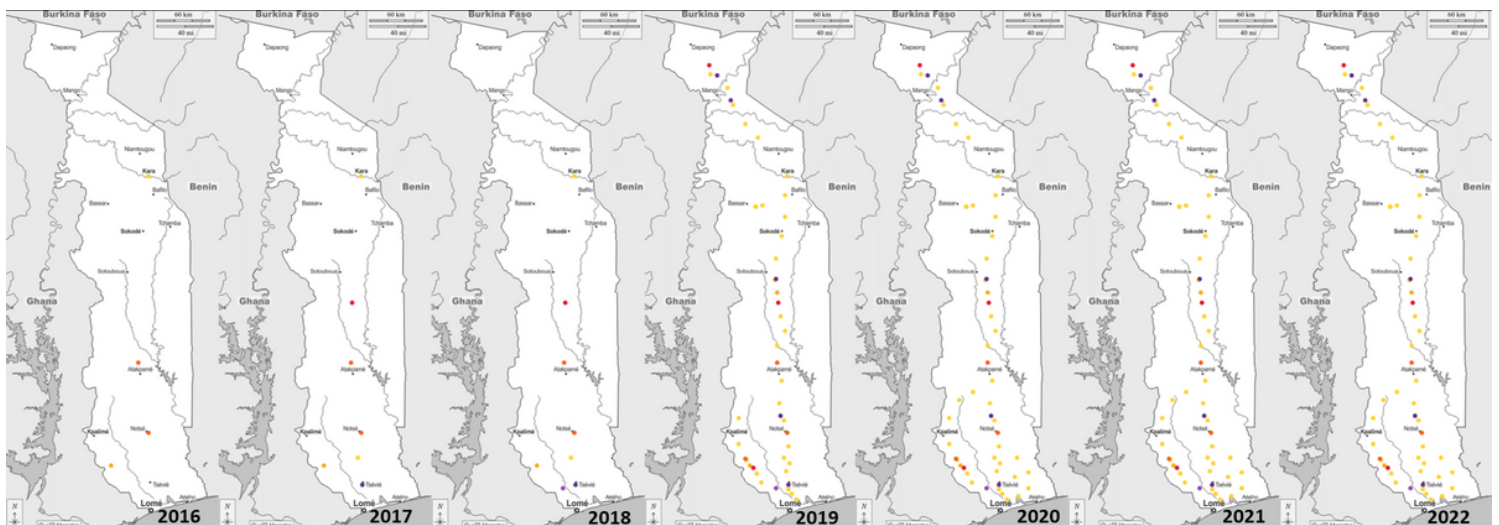


Figure 3

Sites of collections of entomopathogenic agents - *O. sinensis* (yellow), Enterobacteriaceae (dark yellow), *Enterococcus*(orange), Ascoviruses (red), Baculoviruses (purple), *Isariasp.* (violet), and *M. rileyi* (pink) associated to FAW larvae from 2016 to 2022 in Togo

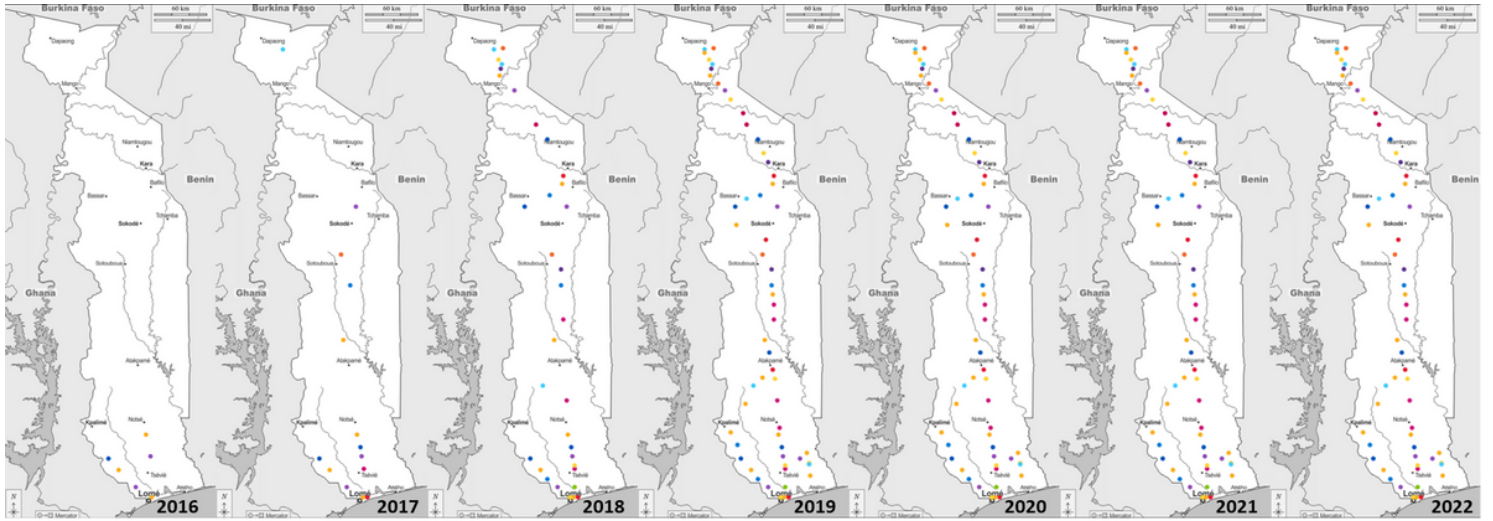


Figure 4

Sites of collections of parasitoids – *T. remus* (yellow), *C. bifoveolatus*, (dark yellow), *C. luteum* (orange), *C. icipe* (red), *M. Testacea*, (purple), *Bracon* sp. (violet), *C. grioti* (pink) *Ophion* spp. (light pink), *A. erinaceus* (light green), *Archytas* spp. (blue), and *Lespesia* spp (dark blue) associated to FAW egg masses and larvae from 2016 to 2022 in Togo

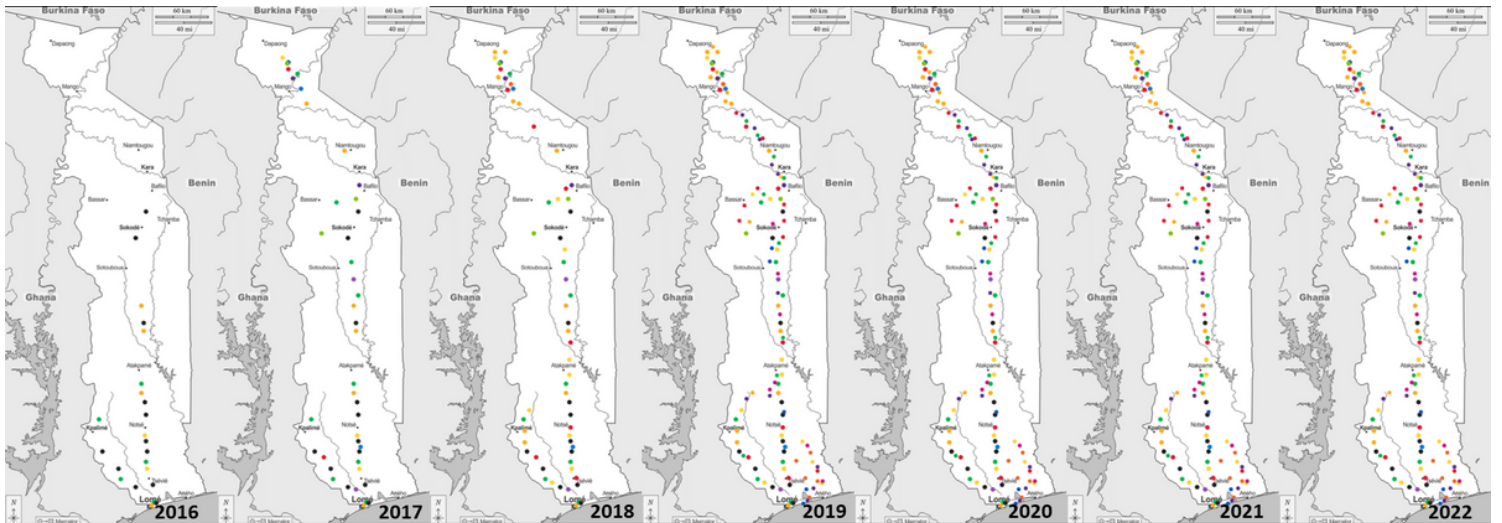


Figure 5

Sites of collections of predators – *F. Auricularia* (yellow), *F. senegalensis* (dark yellow), *E. annulipes* (orange), *C. septempunctata* (red), *C. sanguinea* (purple), *C. sulphurea* (violet), *Calleida* sp. (pink), *P. nodulipes* (light-pink), *Rhynocorissp.* (light-green), *Z. renardii* (blue), *O. insidiosus* (dark blue), *P. megacephala* (green) *P. lamellidens* (dark-green) *H. obscuripennis* (hash), *C. carnea*(dark-hash), *M. religiosa* (dark) associated to FAW larvae from 2016 to 2022 in Togo