Journal of Pest Science (2023) 96:1405–1416
https://doi.org/10.1007/s10340-023-01662-0

ORIGINAL PAPER

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

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Received: 24 February 2023 / Revised: 7 June 2023 / Accepted: 24 June 2023 / Published online: 6 July 2023

Abstract

Although there has been intensive use of insecticides for the fall armyworm, *Spodoptera frugiperda* (Lepidoptera: Noctuidae) management, their effects on population reduction and natural enemies' performance have not been adequately studied. Therefore, this study investigated the diversity and activity of natural enemies under insecticide and insecticide-free applications. Natural enemies were collected annually from 2016 to 2022 from 348 maize farms throughout the West African nation of Togo. The collections included an entomopathogenic nematode, unidentified bacteria from Enterobacteriaceae and *Enterococcus*, unidentified viruses from Ascoviruses and Baculoviruses, and several fungal species. Parasitoids collected included hymenopteran and dipteran species that attacked eggs and larvae. The collected predators included species in the following families: Anthocoridae, Carabidae, Chrysopidae, Coccinellidae, Forficulidae, Formicidae, Mantidae, and Reduviidae. 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.

Keywords Microbial natural enemies · *Ovomermis sinensis* · *Telenomus remus* · Coccinellidae · Formicidae

Key message

- High use of insecticides against fall armyworm in West Africa, and performance of natural enemies.
- The use of insecticides has affected population densities and performances of these species.
- This study draws attention to moderate use of insecticides to improve natural control of this pest.

Communicated by Hannalene Du Plessis.

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Introduction

The equilibrium among populations of living organisms is due to the interdependent relationships among plants, herbivores, carnivores, parasites, and pathogens that regulate and balance the bio-ecosystem (Szwabiński et al. 2010). Unfortunately, this balance is constantly challenged by human activities that cause routine disruptions (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 2012; Sala et al. 2013). To avoid these losses, various crop protection methods have been developed against phytopathogens and crop pests from mammals, birds, reptiles, and arthropods (Berny et al. 2010; Roger et al. 2014). The use of pesticides has been the most common method of pest control. 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 consistent control measures or indigenous natural enemies, a successful pest invasion is usually followed by rapid population increase and movement, resulting in severe crop damage and potentially serious yield and economic losses (De Barro et al. 2015; Haile et al. 2021).

A currently known invasive pest is the fall armyworm (FAW), *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae), an insect that has spread from its native occurrence in the neotropical Americas to many parts of the Eastern Hemisphere. This polyphagous insect has been reported on over 350 host plants, including many crops of economic importance (Montezano et al. 2018). Unfortunately, since 2016, it has been detected in sub-Saharan Africa (Goergen et al. 2016; Nagoshi et al. 2017, 2018, 2022; Koffi et al. 2020a, b), south and east Asia (Nagoshi et al. 2020; Kim et al. 2021), and Oceania and Australia (Bourke and Sar 2020). The 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, indiscriminate use of insecticides not only threatens the human health and environmental protection (O'Dowd et al. 2003) but also disrupts natural biodiversity interdependencies by killing non-target organisms, that includes natural enemies.

Over one hundred species of natural enemies of FAW have been reported worldwide (Molina-Ochoa et al. 2003a; Murúa et al. 2009; Meagher et al. 2016). In Africa, many indigenous entomopathogens, parasitoids, and predators of FAW have been reported (Sisay et al. 2018; Agboyi et al. 2020; Koffi et al. 2020c). However, due to the indiscriminate application of insecticides in the invaded areas, population trends and the potential of natural control from indigenous agents are poorly known. In the west African nation of 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 and evaluate the spatial distribution and impact of insecticide applications on indigenous entomopathogenic viruses, 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

Fall armyworm egg masses and larvae were collected during the cropping seasons from April to November of seven consecutive years (2016–2022). The collections of specimens were initiated at the onset of the FAW invasion in Togo. In 2016, selected collection sites covered the area from Lomé (6.176 N) to Kara (9.377 N). From 2017 to 2022, collections covered the entire country from Lomé to Dapaong (10.474 N). The collection sites were randomly selected during survey trips for maize farm inspections by the Entomological Research team from the Ecole Superieure d'Agronomie, Université de Lomé (Fig. 1).

Collection and preservation of specimens

Within the selected farms, quadrants were designated at the four cardinal points and middle of each farm. Egg masses and larvae were collected from 100 plants within the quadrants as well the living organisms that were preying on egg masses or larvae. The collected egg masses and larvae were placed individually in rearing boxes as described by Koffi et al. (2020c) and transferred in coolers (Mobicool ME24, 23 L, 12 V, Hannover, Germany) to the Université de Lomé laboratory. Predators were immediately preserved in crystal vials containing 70% ethanol (Koffi et al. 2020c). The egg masses and larvae completed their life cycle during laboratory rearing (25 ± 5 ℃, 78 ± 15% relative humidity, and 12:12 photoperiod) to adulthood of non-infected specimens

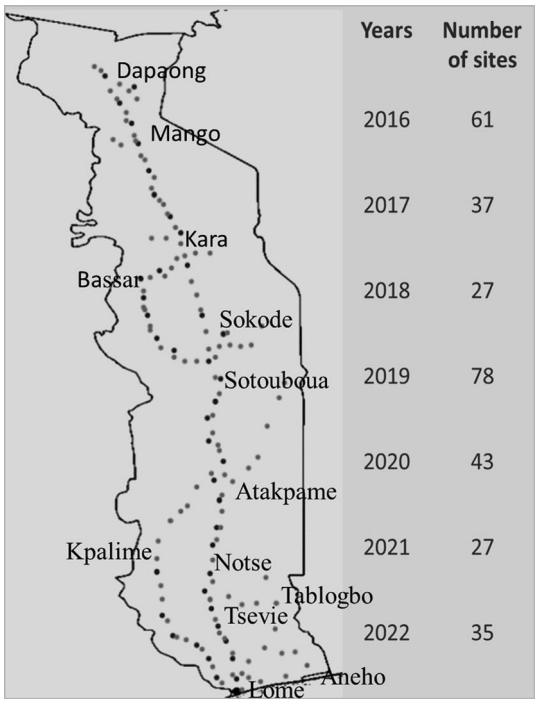

Fig. 1 Collection locations with some reference cities, the years of collections and numbers of maize farms inspected from 2016 to 2022

or to the death of individuals with symptoms of entomopathogens or emergence of parasitoids.

Microbial natural enemies

Dead larvae with evidence of bacterial or viral symptoms were isolated and preserved in the freezer at 4 ℃. Description keys were used to identify bacteria (Eilenberg et al. 2015). Dead larvae presenting green-colored microflora germinations were assigned to undetermined entomopathogenic bacteria. Two categories of viruses were identified using morphology of 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-gray discoloration and a swollen body with a ruptured integument leading to liquefaction, were assigned to the Baculoviruses (Haase et al. 2015; Valicente 2019).

Symptoms of infections from entomopathogenic fungi were germination of hyphae from dead larvae, although a few samples were morphologically identified by scientists at the USDA-ARS in Ithaca, NY, USA. The infected samples were removed from their rearing boxes and individually placed in an empty Petri dish under the same laboratory rearing conditions. They were then individually transferred to 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.

Nematodes, parasitoids, and predators

Nematodes and parasitoids that emerged from FAW eggs, and larvae were preserved in 70% ethanol in crystal vials. Description keys were used to identify the entomopathogenic nematodes (Crosskey 1968; Baker and Capinera 1997; Firake and Behere 2020).

Identification keys (Braet et al. 2012; Koffi et al. 2020c) and characteristics of insects already identified using molecular barcodes from Africa (Agboyi et al. 2020; Durocher-Granger et al. 2021; Otim et al. 2021) were used to identify emerged parasitoids and collected predators (Brindle 1967; Waller et al. 1999; Kwadjo et al. 2012; Nicolas et al. 2015; Girod and Lassalle 2017).

Calculations and statistical analysis

During the inspections, insecticide application information was documented from the farmers to determine the percentage of farms with insecticide applications per year (sprayed farms). However, calculations did not consider farms where the owner was not present to provide information. Specimen collections were separated into two periods, (1) intensive insecticide applications, where more than 75% of the farms made insecticide applications for FAW management (2016 and 2018) and (2) occasional insecticide applications, where less than 25% of the farms made insecticide applications (2018–2022).

After specimen identifications, several variables were calculated according to the following equations (Koffi et al. 2020c):

$$y = \frac{n}{N} * 100 \quad (1)$$

or

$$i = \frac{t}{T} \quad (2)$$

where infection rates (Ir) (y), n = number of larvae infected by a given entomopathogen species and N = total number of collected larvae. For parasitism rates (Pr) (y), n = number of egg masses or larvae parasitized by a given parasitoid species and N = total number of egg masses or larvae collected. For relative abundances (RA) (y), n = number of a given species and N = total number of collected species. For percent of sprayed farms (y), n = number of sprayed farms and N = total inspected farms per year. For index of dispersion (iD) (i), t = ratio of the number of farms hosting a given nematode, bacterium, virus, fungus, parasitoid or predator species, and T = total number of farms inspected for each year

Data were arranged per location and grouped per year. The percentage data were arcsine square root transformed prior to statistical analysis. All calculations 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 the 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 was also calculated using GenStat.

Results

Impact of insecticides on the performance of natural control

The two years following the invasion of FAW in Togo showed higher numbers of egg masses collected per farm

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

		Egg mass				Larvae			
Year	Farm	*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

Means (± SE) within the same column followed by the same letter are not statistically different

n total number, *P* number of parasitized individuals, *Pr* parasitism rate

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).

During the survey, farmers were interviewed regarding insecticide applications and depending on the year, between 52.1 and 74.1% responded. The percentage of sprayed farms was 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, respectively. Higher egg and larval parasitism rates were recorded in unsprayed

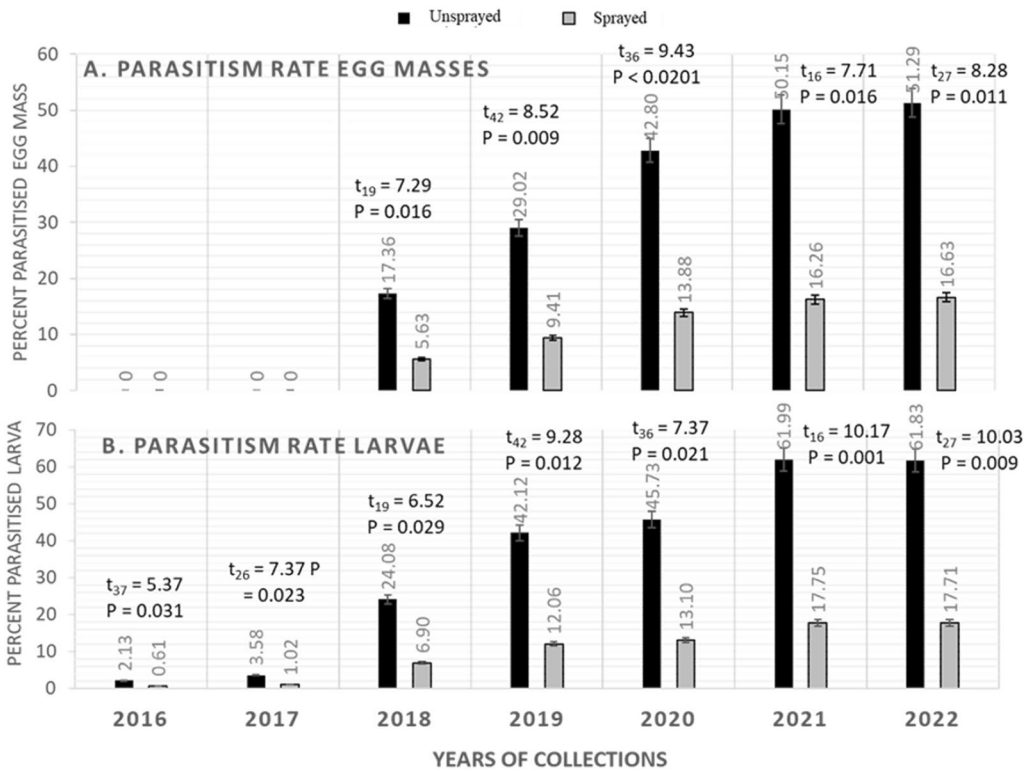

Fig. 2 Percent of egg masses and larvae parasitized or infected from 2016 to 2022 in Togo

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											
Ovomermis sinensis	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
	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
	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 sp.	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
	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
	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
	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											
Isaria sp.	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
	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
Metarhizium rileyi	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
	RA (%)	*	5.88 ± 1.02a	4.35 ± 1.06a	*	2.15 ± 0.81a	2.17 ± 0.09a	1.540.12a	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, *RA* relative abundance; means (± SE) in the same row with same letter are not statistically different

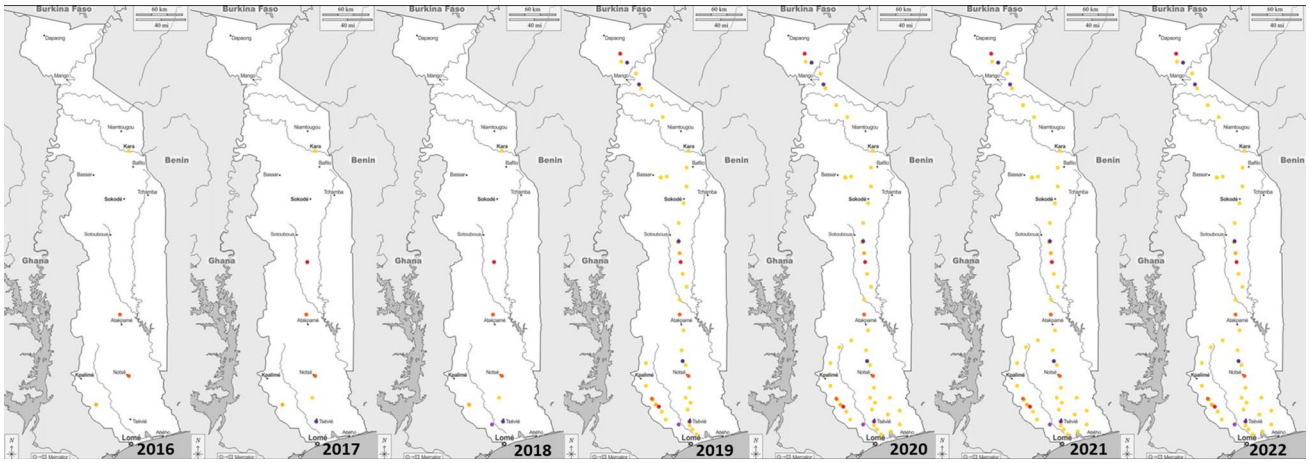

Fig. 3 Sites of collections of entomopathogenic agents—*O. sinensis* (yellow), Enterobacteriaceae (dark yellow), *Enterococcus* spp. (orange), Ascoviruses (red), Baculoviruses (purple), *Isaria* spp. (violet), and *M. rileyi* (pink) associated to FAW larvae from 2016 to 2022 in Togo

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* Chen, Jian, & Ren (Nematoda: Mermithidae), unidentified species in the bacteria family of Enterobacteriaceae and *Enterococcus* sp., unidentified viruses belonging to Ascoviruses and Baculoviruses, and fungal species *Isaria* sp. (Hypocreales: Clavicipitaceae) and *Metarhizium rileyi* (Farl.) Kepler, Rehner, & Humber (Hypocreales: Cordycipitaceae). The nematode, *O. sinensis* had low infection rates, relative abundance and index of dispersion until 2018, compared to the following years (Table 2). The infection rate of bacteria species belonging to Enterobacteriaceae was 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* sp. increased from 2018 onward, while its relative abundance decreased, and its indexes of dispersion remained constant during the study (Table 2). Larvae infected by Ascovirus were collected from 2018 to 2022, and Baculovirus was collected from 2017 to 2022. However, the two viruses and fungal groups had constant infection rates, relative abundance, and indexes of dispersion throughout the study (Table 2). Although the spatial distribution of entomopathogens increased during the study (Fig. 3), the population densities of each species were similar.

Parasitoids

During this study, 10 species of parasitoids were collected and identified. The egg parasitoid *Telenomus remus* Nixon (Hymenoptera: Platygastridae) was consistently collected from 2018, with increasing parasitism rates from 15.38 to 45.44% in 2022. This species index of dispersion was higher during the last two years of the collection period (Table 3). One species of egg-larval parasitoid, *Chelonus bifoveolatus* (Szépligeti) (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 two unidentified species of Tachinidae, five hymenopteran species including *Coccygidium luteum* (Brullé), *Cotesia icipe* (Fernandez-Triana and Fiaboe), an unidentified Braconidae, and two unidentified Ichneumonidae, and the larval-pupal parasitoid species *Meteoridea testacea* (Granger) (Braconidae). The indexes of dispersion of the tachinid species 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 increased every year (Fig. 4), the population densities of each species were similar.

Predators

A total of 16 species of arthropod predators were collected attacking FAW during this study. These were five heteropterans, *Orius* sp. (Anthocoridae), *Haematochares*

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											
Telenomus remus	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
	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											
Chelonus bifoveolatus	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
	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											
Unidentified Tachnidae	Pr (%)	0.10 ± 0.02a	0.27 ± 0.04a	1.41 ± 0.27ab	0.71 ± 0.02a	0.69 ± 0.15a	4.09 ± 0.79bc	4.39 ± 0.08b	6, 347	5.09	0.032
	RA (%)	6.67 ± 1.06b	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 ± 0.02a	0.05 ± 0.02a	0.04 ± 0.01a	0.01 ± 0.12a	0.02 ± 0.05a	0.05 ± 0.02a	0.04 ± 0.02	6, 347	1.21	0.247
Unidentified Braconidae	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
	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
	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
Unidentified Ichneumonidae	Pr (%)	*	0.14 ± 0.35a	1.43 ± 0.23b	1.19 ± 0.17b	1.35 ± 0.21b	2.78 ± 0.33b	3.25 ± 0.49b	5, 286	6.24	0.021
	RA (%)	*	11.66 ± 0.13a	8.715 ± 1.32a	4.06 ± 0.92a	4.31 ± 0.47a	6.52 ± 0.38a	7.69 ± 0.95a	5, 286	1.28	0.091
	iD	*	0.03 ± 0.13a	0.04 ± 0.08a	0.03 ± 0.09a	0.04 ± 0.14a	0.04 ± 0.08a	0.07 ± 0.08b	5, 286	3.25	0.036
Coccygidium luteum	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
	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
Cotesia icipe	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
	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
Meteoridea testacea	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
	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

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

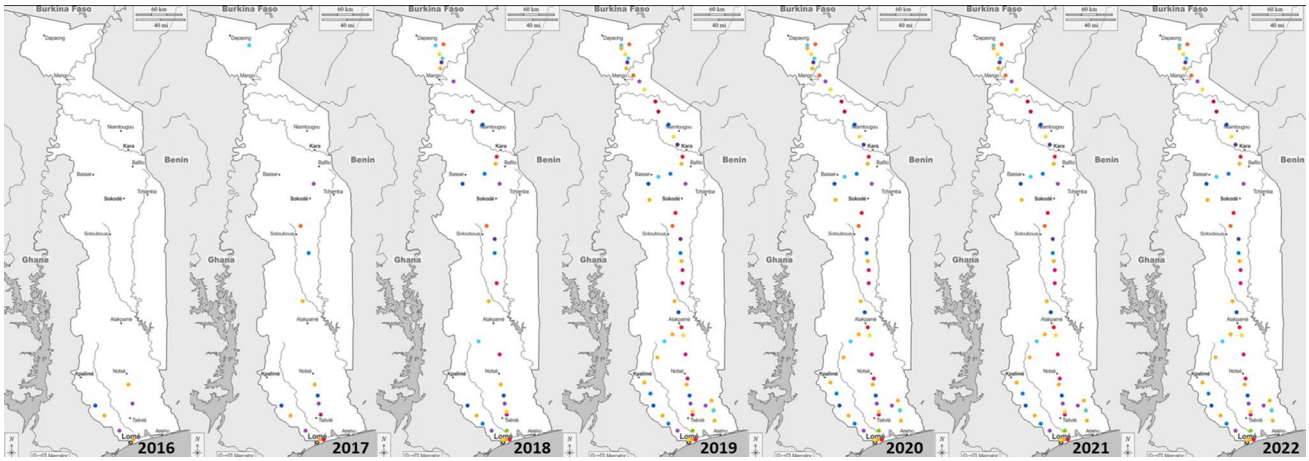

Fig. 4 Sites of collections of parasitoids—*T. remus* (yellow), *C. bifoveolatus,* (dark yellow), *C. luteum* (orange), *C. icipe* (red), *M. testacea,* (purple), braconid (violet), ichneumonid (pink), and tachinids (blue) associated to FAW egg masses and larvae from 2016 to 2022 in Togo

obscuripennis Stål, *Peprius nodulipes* (Signoret), *Rhynocoris* sp., and *Zelus* sp. (Reduviidae); four beetles, *Calleida* sp. (Carabidae), *Cheilomenes sulphurea* (Olivier), *Coccinella* sp. and an unidentified coccinellid (Coccinellidae); three earwigs, *Euborellia* sp., *Forficula senegalensis* Audinet-Serville, and *Forficula* sp. (Forficulidae); two ants, *Pheidole megacephala* F. and *Polyrhachis* sp. (Formicidae); one lacewing, *Chrysoperla* sp. (Chrysopidae); and one mantid, *Sphodomantis viridis* Forsskal (Mantidae).

Except for *Orius* sp. and *Zelus* sp., 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 slightly increasing indices of dispersion (Table 4). Except for *Euborellia* sp., the earwig species were collected from the onset of the FAW invasion with a slight increase in relative abundances and dispersion in the following years (Table 4). Ants collected were social Formicidae that increased in their locations found during the study. *Chrysoperla* sp. and *Mantis* sp. 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 the predators expanded during the study (Fig. 5), the population densities of each species were similar.

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 to infest several noctuid species (Li et al. 2003), including *S. frugiperda* (Sun et al. 2020). The bacterium found, *Enterococcus* sp., is a common gut bacterium found in many Lepidoptera species and is most likely non-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 as biopesticides against noctuid larvae for many years (Guo et al. 2020).

The invasion of FAW in Africa was successful as increased population growth and rapid spread were followed by severe damage to maize plants and important yield and economic losses (Koffi 2020a, b, 2022). The response of maize producers and governments to threatened food security was the application of insecticides (Koffi et al. 2021). In Togo, up to 73.25% of maize farms were sprayed with insecticides to reduce heavy infestations 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. The decrease in insecticide applications coincided with the increasing numbers and activity of natural control agents which were already being 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 why growers reduced their sprays. This unexpected phenomenon calls into question the efficiency of many insecticides applied against the FAW in Togo. The activity of natural control may be underestimated or other abiotic factors (i.e., rainfall) may be involved in reducing FAW infestation.

Even if natural enemy populations were expected to be low and inefficient during the two years following the

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*
Haematochares obscuripennis	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
	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
Peprius nodulipes	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
	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
Rhynocoris 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
	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
Orius sp.	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
	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
Zelus sp.	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
	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
Calleida sp.	RA (%)	*	*	*	2.44 ± 1.34a	3.52 ± 1.05a	4.44 ± 1.63a	4.71 ± 1.38a	3, 222	1.86	0.354
	iD	*	*	*	0.06 ± 0.08a	0.06 ± 0.17a	0.10 ± 0.09a	0.11 ± 0.03a	3, 222	0.96	0.358
Cheilomenes sulphurea	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
	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
Coccinella sp.	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
	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
Unidentified Coccinellidae	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
	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
Euborellia sp.	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
	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
Forficula sp.	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
	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
Forficula senegalensis	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
	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
Pheidole megacephala	RA (%)	*	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
Polyrhachis sp.	RA (%)	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
Chrysoperla sp.	RA (%)	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	6, 347	12.42	< 0.001
	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
Sphodomantis viridis	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
	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 dispersion, *RA* relative abundance; means in the same row with same letter are not statistically different

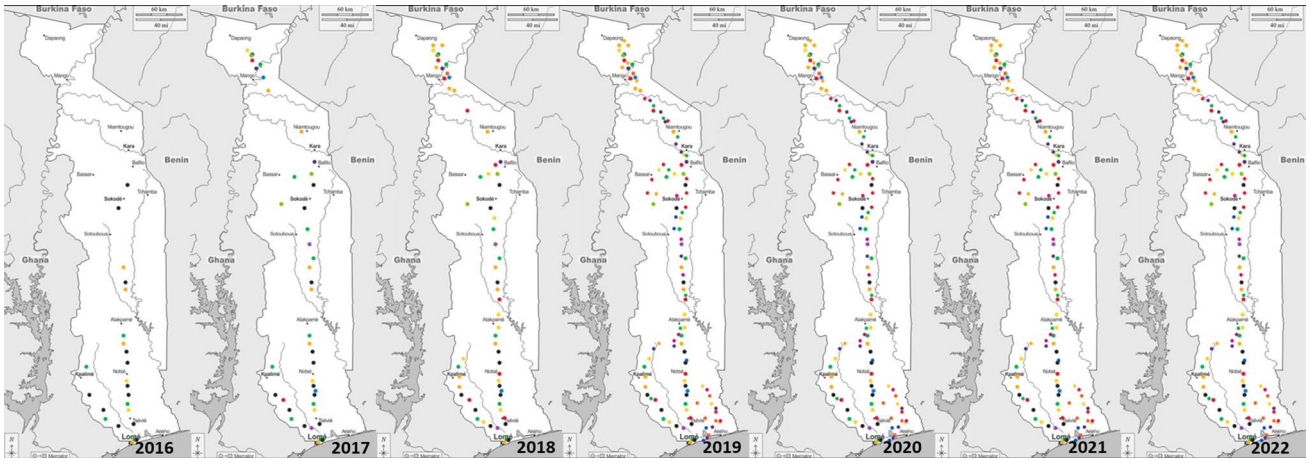

Fig. 5 Sites of collections of predators—*Forficula* sp. (yellow), *F. senegalensis* (dark yellow), *Euborellia* sp. (orange), *Coccinella* sp. (red), coccinellid (purple), *C. sulphurea* (violet), *Calleida* sp. (pink), *P. nodulipes* (light-pink), *Rhynocoris* sp. (light-green), *Zelus* sp. (blue), *Orius* sp. (dark blue), *P. megacephala* (green) *P. lamellidens* (dark-green) *H. obscuripennis* (hash), *Chrysoperla* sp. (dark-hash), *Mantis* sp. (dark) associated to FAW larvae from 2016 to 2022 in Togo

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 these natural enemy populations. Therefore in Togo, the reduction in the number of insecticide applications since 2018 most likely contributes to the emergence of higher populations of pathogens, parasitoids, and predators and improvement in their performance.

Author contributions

All authors designed the research methods.DK, KA, MKAA, MA, and KT collected the data.DK, KA, and RLM wrote the manuscript.All authors reviewed the manuscript.

Acknowledgements The data collection and laboratory works were sponsored by the International Foundation of Sciences (IFS/C/6255-1). We thank Dr. Louela Castrillo, Acting Curator; USDA-ARS Collection of Entomopathogenic Fungal Cultures at the Robert W. Holley Center for Agriculture & Health, Ithaca, NY, USA for identification of fungal samples.

Funding The authors have not disclosed any funding.

Declarations

Conflict of interest The authors have not disclosed any competing interests.

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