


Associated cultivated plants in tomato cropping systems structure arthropod communities and increase the *Helicoverpa armigera* regulation

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Abstract

Cultivating plant mixtures is expected to provide a higher productivity and a better control of pests and diseases. The structure of the arthropod community is a major driver of the magnitude of natural pest regulations.

With the aim of optimizing pest management, a study was carried out to determine the effect of the cropping system type (tomato mono-cropping vs. mixed-cropping) on the diversity and abundance of arthropods from three trophic groups (herbivores, omnivores, predators) and the abundance of *Helicoverpa armigera*. Therefore, the diversity of cultivated plants and arthropod communities was assessed within tomato fields from 30 farmer's fields randomly selected in South of Benin. Results showed that the arthropod abundance was significantly higher in mixed-cropping systems compared with mono-cropping systems, although the crop type did not alter significantly the arthropod diversity, evenness, and richness. At the level of taxa, the abundances of generalist predators including ants (*Pheidole* spp., and *Paltothyreus tarsatus*) and spiders (*Araneus* spp. and *Erigone* sp.) were significantly higher in mixed fields than in mono-crop fields. Then, the abundances of omnivore-predator trophic groups have a negative significant effect on the *H. armigera* abundance. This study allowed better understanding of how plant diversity associated to tomato fields structures arthropod's food webs to finally enhance the ecological management of *H. armigera*.

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Introduction

Cultivating plant mixtures is expected to generally provide a higher overall productivity (Hooper *et al.*, 2005), a better control of pests and diseases (Ratnadass *et al.*, 2012), and enhanced ecological services (Vandermeer, 1989; Gurr *et al.*, 2003; Malézieux *et al.*, 2009). Mixed-cropping systems are often seen as a strategy to reduce the risk of pest incidence through barrier, dilution, and trophic effects (Ratnadass *et al.*, 2012). Increasing natural regulation constitutes an important component of more sustainable cropping systems. The management of animal and plant communities in agroecosystems represents one of most important levers to improve these regulations (Macfadyen *et al.*, 2015). Understanding trophic and non-trophic interactions between different species in agroecosystems is essential to develop more efficient pest control strategies based on natural regulation processes.

Crop diversification at different scales, from field scales to diversified landscape scales, is often presented as a means to alter pest regulation processes by increasing the incidence of natural enemies, reducing pest pressure and enhancing crop production (Andow, 1991; Poveda *et al.*, 2008). However, the effect of plant diversity is not always positive for the control of pests. For instance, increasing plant diversity may support alternative prey that diverts generalist predators from the pest. Furthermore, systems more rich in plants may support a richer community of predators in which intraguild predation may dampen the potential of pest control. Therefore, understanding what type of cropping system is more suitable to reduce pest damage is of major importance to ultimately improve agricultural productivity and avoid pesticides applications. The type of plants embedded in agroecosystems strongly influences habitats for arthropods altering the refuges or shelters available for generalist predators (Bianchi *et al.*, 2006; Dassou *et al.*, 2017). These mixed-cropping systems may also shelter alternate hosts and prey for parasitoids and predators (Bianchi *et al.*, 2006). The development of alternative prey may increase the abundance of generalist predators and improve pest regulation (Landis *et al.*, 2000; Chailleux *et al.*, 2014). In addition, according to the resource concentration hypothesis (Root, 1973), mixed-cropping systems may benefit from resource dilution of a particular pest.

In Benin, tomatoes are grown in cropping systems ranging from monoculture to intercropping with diverse food crops including maize, roots, tubers, and vegetables. These unmechanized cropping systems rely on family labor and receive very little chemical inputs. The local cultivation of tomato contributes to the nutrition security of populations through diet quality (Simeni *et al.*, 2009). Indeed, the tomato fruit is involved in several daily dishes and is a source of minerals and vitamins that can help reduce micronutrient and vitamin deficiencies (Beecher, 1998).

Pests and diseases greatly reduce the yield and the market value of the tomato fruits. In Benin, the main tomato insect pest is *Helicoverpa armigera* (Hübner) (Elégbédé *et al.*, 2014) which feeds on tomato fruits. This polyphagous pest (Cunningham *et al.*, 1999) causes massive damage to the

tomato fruit, thus greatly reducing tomato yield. A broad range of families of predators have been listed as potential predators for the *Helicoverpa* spp., especially in cotton plots (Mensah *et al.*, 1995). Predatory beetles, bugs, lacewings, and spiders are mentioned as predators of *H. armigera* (Mensah *et al.*, 1995; Cherry *et al.*, 2003). Anthocorids and ants of the genera *Pheidole* and *Myrmicaria* have been identified as potential generalist predators of *H. armigera* in smallholders' fields in Kenya (Van Den Berg & Cock, 1995).

We hypothesize that the cultivated plants associated with tomatoes are expected to change the structure of arthropod trophic groups in tomato-based agroecosystems and *in fine* may modify the control of *H. armigera* by generalist predators. Here, we assessed the effect of the cropping system type (tomato mono-cropping vs. mixed-cropping) on (i) the diversity and abundance of arthropods from three trophic groups (herbivores, omnivores, predators) and (ii) the abundance of *H. armigera*. We also investigated whether the abundance of *H. armigera* was correlated to the abundance of higher trophic groups (omnivore and predators).

Materials and methods

Study sites

The study was carried out at the southern part of Benin in the departments of Atlantic, Mono and Couffo. The tomato fields were located in the small villages of Southern Benin in areas where tomato is the major production. These villages are in the districts of Abomey-Calavi: Latitude 6°26'54O Longitude 2°21'20N; Ouidah: Latitude 6°21'47O Longitude 2°5'6N; Comè: Latitude 6°24'27O Longitude 1°52'55N; Dogbo: Latitude 6°49'0O Longitude 1°46'59N; Lokossa: Latitude 6°38'19O Longitude 1°43'0N; Allada: Latitude 6°39'55N Longitude 2°9'4O. The climate is humid tropical with an average temperature of 28 °C and rainfall up to 1400 mm per year. The soil is sandy clay. Four fields were monocultures of tomato and 26 fields were tomato crops associated to a diverse array of other annual (e.g. maize, groundnut, and vegetable crops) and perennial crops (e.g. palms and pineapples), covering a gradient of situations ranging from one to ten associated crops. We studied farmer's fields that were set up since decades. Farmers make a mix of all crops in the fields without a particular spatial organization. No chemical fertilizers or insecticides were used for the field management. Soil fertilization was made with composts, and biopesticides based on neem seeds were used for pest control.

Measurements of plant diversity and arthropod communities in tomato cropping systems

The effect of the diversity of cultivated plants in tomato fields on the food web structure of arthropods was measured in the 30 fields. We characterized the cultivated species composition at the field scale. In the center of each tomato field, an experimental plot (20 × 20 m) was delimited. Each experimental plot was subdivided into 25 (4 m by 4 m) quadrats in which

Table 1. Abundance and occurrence of the arthropod species (with occurrence >10), on the whole experiment and for the two studied seasons.

| Species | Abundance | Occurrence | Abundance SRS | Occurrence SRS | Abundance LRS | Occurrence LRS | Trophic groups |
|---------------------------------|-----------|------------|---------------|----------------|---------------|----------------|----------------|
| <i>Paltothyreus tarsatus</i> | 916 | 356 | 602 | 248 | 314 | 108 | Predator |
| <i>Pheidole</i> sp2 | 285 | 25 | 92 | 22 | 193 | 3 | Omnivore |
| <i>Pheidole</i> sp1 | 278 | 41 | 202 | 28 | 76 | 13 | Omnivore |
| <i>Gonocephalum simplex</i> | 268 | 149 | 248 | 137 | 20 | 12 | Herbivore |
| <i>Araneus</i> sp1 | 228 | 152 | 109 | 77 | 119 | 75 | Predator |
| <i>Aiolopus simulatrix</i> | 222 | 146 | 105 | 65 | 117 | 81 | Herbivore |
| <i>Erigone</i> sp1 | 110 | 84 | 89 | 65 | 21 | 19 | Predator |
| <i>Zonocerus variegatus</i> | 67 | 49 | 57 | 39 | 10 | 10 | Herbivore |
| <i>Helicoverpa armigera</i> | 62 | 38 | 41 | 26 | 21 | 12 | Herbivore |
| <i>Camponotus</i> sp1 | 58 | 23 | 55 | 21 | 3 | 2 | Omnivore |
| <i>Hycleus</i> sp1 | 34 | 22 | 21 | 15 | 13 | 7 | Herbivore |
| <i>Gastrimargus africanus</i> | 31 | 29 | 27 | 25 | 4 | 4 | Herbivore |
| <i>Araneus</i> sp2 | 28 | 19 | 24 | 16 | 4 | 3 | Predator |
| <i>Altise</i> sp1 | 23 | 19 | 19 | 16 | 4 | 3 | Herbivore |
| <i>Modicogryllus</i> sp1 | 22 | 19 | 15 | 12 | 7 | 7 | Omnivore |
| <i>Camponotus brutus</i> | 18 | 14 | 10 | 8 | 8 | 6 | Omnivore |
| Porcellionidae | 18 | 14 | 11 | 9 | 7 | 5 | Detritivore |
| <i>Catopsilla florella</i> | 17 | 15 | 8 | 7 | 9 | 8 | Herbivore |
| <i>Parapoderus</i> sp1 | 16 | 13 | 15 | 12 | 1 | 1 | Herbivore |
| <i>Anepictata</i> sp1 | 13 | 11 | 7 | 6 | 6 | 5 | Herbivore |
| Lyniphiidae | 13 | 13 | 13 | 13 | 0 | 0 | Predator |
| <i>Acanthaspis vidua</i> | 12 | 11 | 9 | 8 | 3 | 3 | Predator |
| <i>Homeogryllus reticulatus</i> | 12 | 12 | 8 | 8 | 4 | 4 | Omnivore |

SRS, short rainy season; LRS, long rainy season.

all cropped plants were identified and counted. In the center of each quadrat, one pitfall trap (12 cm of diameter, half-filled with soapy water) was placed and removed after 72 h to capture the soil and litter arthropods. In total, 25 pitfall traps were used per field in order to maximize the trapping. Additionally, in each experimental plot, flying insects were (i) captured with an entomological net during 5 min and (ii) collected directly on ten entire tomato plants using a mouth aspirator. On each of the ten tomato plants, all the damaged tomato fruits were cut in order to collect the larvae of *H. armigera*. We also visually inspected all tomato plants in each experimental plot to search for the different stages of development of *H. armigera*. The 30 studied fields covered evenly a broad gradient of plant diversity (Table S1). The same measurements were achieved between 8 and 12 am in two periods: 3 months in the long rainy season (May, June, and July) and 3 months in the short rainy season (August, September, and October). The identification of arthropod taxa collected in the fields was completed at Entomological Museum of IITA – Benin. All arthropod individuals collected with the traps, nets, and aspirator were identified up to the genus or to the species and counted. When an individual was not identified at the species level, a morphospecies was attributed to each individual based on morphological specificities, allowing further calculation of richness (Barratt *et al.*, 2003). Finally, each taxon was associated to a trophic group (herbivore, omnivore, and predator) according to the literature (Table S2).

Data analysis

The abundance of both taxa and trophic groups was calculated by summing abundance of individuals of the same

species or trophic group. Poisson Generalized Linear Models (GLMs) were used to analyze the effect of the type of system (tomato mono-cropping vs. mixed-cropping) on the abundance of arthropod taxa or trophic groups. The effect of the crop type on the overall diversity, richness, and evenness was tested with a linear model. In the case of the herbivore trophic group and of *H. armigera*, we also tested the effect of the combined abundance of omnivore and predator trophic group (log and log quadratic values) as predictors of their abundance. The maximum likelihood of parameters of GLMs was approximated by the Laplace method (Bolker *et al.*, 2009). Statistical analyses were performed with R 3.4.2 (R Development Core Team, 2018) at a significant level of 1%.

Results

Abundance of the arthropod species in tomato agroecosystems

As a whole, 3351 individual arthropods from 12 orders were collected in the overall tomatoes fields. The most abundant orders were Hymenoptera with 1937 individuals followed by Orthoptera with 391 individuals, Araneae with 384 individuals, Coleoptera with 353 individuals. Based on the literature, five arthropod trophic groups were constituted as follows: omnivores (1905 individuals), herbivores (940 individuals), generalist predators (467 individuals), detritivores (30 individuals), and parasitoids (seven individuals). We retained for further analyses the arthropods for which the trophic group abundances were >400 individuals. The arthropod species or genus that are the most abundant and for which the occurrence was >50 in tomato agroecosystems were from omnivore-predator trophic group including the ants taxa (*Pheidole* spp. and *Camponotus* sp.), spiders

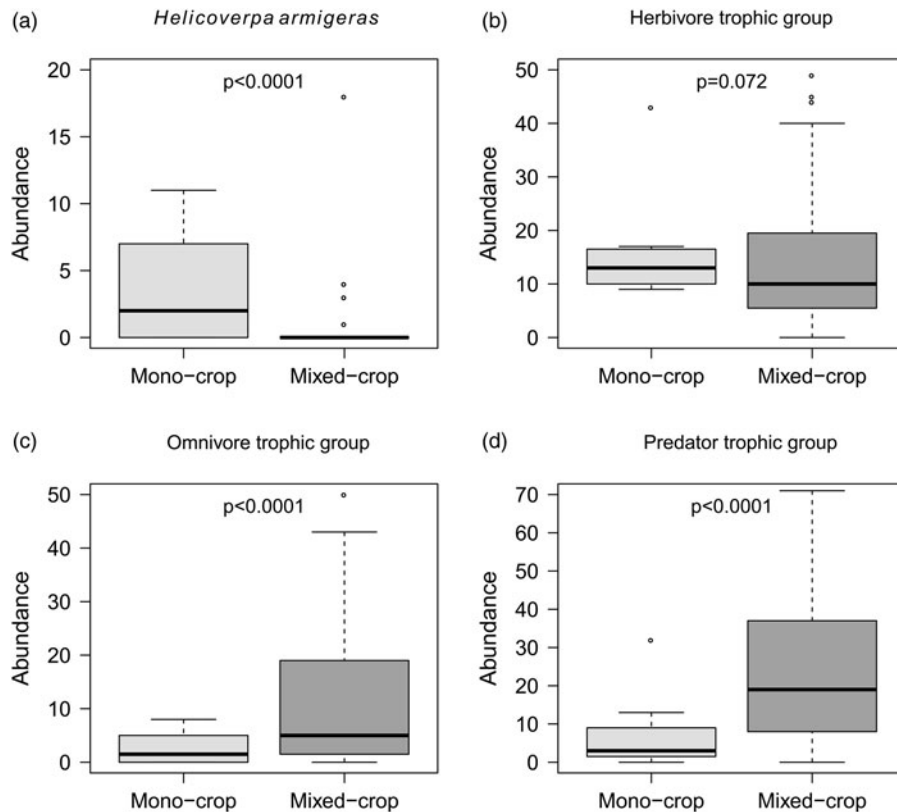


Fig. 1. Distributions of the field-scale abundance of *Helicoverpa armigera* and of the three trophic groups according to the type of cropping system. The *P* values are corresponding to the test of the effect of the crop type on the abundance, tested in a Poisson GLM.

(*Araneus* sp. and *Erigone* sp.), and from herbivores trophic group including the false wireworm (*Gonocephalus simplex* (F.) (Coleoptera: Tenebrionidae)), two grasshoppers (*Aiolopus simulatrix* (Walker) (Orthoptera: Acrididae) and *Zonocerus variegatus* (Orthoptera: Pyrgomorphidae)), and *H. armigera* (table 1).

Difference of abundance and diversity of arthropod trophic groups between mono-crops and mixed-crops in tomato agro-ecosystems

The abundance of *H. armigera* was significantly lower in the mixed-crop fields than in mono-crop. Inversely, the abundance of herbivores was not correlated with the crop type but there was a trend for more abundant herbivores in mono-crop fields. The abundance of the predators and omnivores was significantly higher in the mixed-crop fields than in mono-crop fields (fig. 1).

The abundance of all arthropods was significantly higher in mixed-cropping systems compared with mono-cropping systems (fig. 2a). The crop type did not alter significantly the arthropod diversity, evenness, and richness (fig. 2b–d). At the level of taxa, the abundances of *Pheidole* spp., *Paltothyreus tarsatus*, and spiders (including *Araneus* spp. and *Erigone* sp.) were significantly higher in mixed fields than in mono-crop fields (fig. 3). In total, the abundance of 14 out of 63 taxa was significantly affected by the crop type (Table S3). Among these taxa that significantly responded to crop type,

there were the five taxa of ants *P. tarsatus*, *Monomorium bicolor*, *Monomorium* sp., *Crematogaster* sp., *Pheidole* spp.

Relationship between the abundance of herbivores and *H. armigera* with the abundance of the omnivore-predator trophic group

The abundance of the omnivore-predator trophic groups had a positive (but plateauing) significant effect on the herbivores abundance (fig. 4a, table 2). Inversely, this omnivore-predator abundance had a negative significant effect on the *H. armigera* abundance (fig. 4b, table 2).

Discussion

Difference of abundance and diversity of the three arthropod trophic groups between mono-crop and mixed-crops systems

In this study, the abundances of the predators were significantly higher in the mixed-crop fields than in mono-crop fields. This result corroborates previous studies from biodiversity experiment or meta-analyses (Letourneau *et al.*, 2011). This could be explained by an increase in predator abundance due to the diversification of the plant resources as suggested by other studies (Mollot *et al.*, 2012; Dassou *et al.*, 2015). Plant diversity often modifies the structure of arthropod communities, increases the abundance of generalist predators (Song *et al.*, 2010), and reduces the abundance of pests (Baliddawa, 1985). This case, found also in this study, could also be

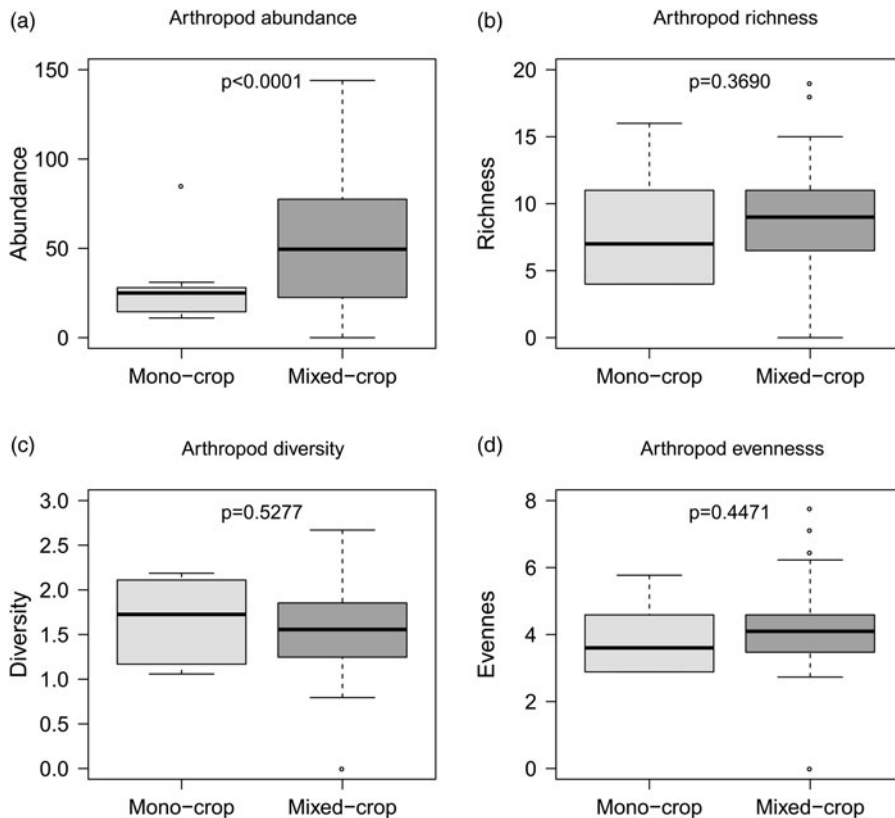


Fig. 2. Distributions of the field-scale arthropod community metrics according to the type of cropping system. The P values are corresponding to the test of the effect of the crop type on the metrics, tested in a Poisson GLM for the total arthropod abundance and in a LM for other metrics.

explained by the fact that tomato is a seasonal crop in which the intercropped plants provide a favorable habitats and plant resources to the predators.

This finding could be the result of two complementary processes in diversified cropping systems: (i) more provision of favorable habitats for predators and (ii) increased availability of alternative resources for predators (Vasconcelos *et al.*, 2008; Dassou & Tixier, 2016). Interestingly, in our experiment, the crop type affected the omnivore and the predator trophic groups but not the herbivore trophic group (fig. 1). The positive effects of mixing plants on the abundance of the omnivore and of the predator trophic groups, but not of the herbivore group, suggest that the abundance of higher trophic groups was driven by habitat diversification rather than by an increase of their resources (herbivores). The positive and plateauing trend between herbivore and omnivore-predator trophic groups (fig. 4a) suggests (i) that at low abundances of both trophic groups, habitat effect is positive for both, and (ii) that at higher abundances of the omnivore-predator trophic group, the predation of herbivores progressively increases with their abundance. The absence of effect of associated cultivated plants on the abundance of the herbivore trophic group may be the result of the resource concentration effect (Root, 1973). Indeed, the herbivore trophic group was dominated by specialist species (*Tetranychus* sp., *Altise* sp., *Dacus ciliatus*, and *Lyriomyza sativae*) that are likely to respond to a dilution of their resources. *Tetranychus* sp. is a mite reported on tomato and can be responsible for important damages

with leaves chlorotic spots on and under the limb of the tomato leaves thus reducing the photosynthesis of the tomato. Adults of the fruit fly *D. ciliatus* bite early to deposit their eggs. After hatching, their larvae sink into the healthy pulp to feed. The leafminer *Liriomyza sativae* such as *Tetranychus* sp. attacks the leaves and is responsible for the sinuous galleries on the leaves reducing photosynthesis. The association of other crop inside tomato fields had probably reduced the ability of herbivores to locate their host plants. Furthermore, non-host plants could obstruct the movement of the insect pest within the fields (Poveda *et al.*, 2008) as described by the barrier crop hypothesis.

In our study, the effect of the crop type was positively significant on both omnivore and predator abundances and not significant on herbivores abundances. This finding shows how mixed-crop systems favor omnivore and predator communities that consume majority herbivores. Surprisingly, mixed systems increased overall arthropod abundance but not diversity (fig. 2) as predicted by the resource concentration hypothesis and mentioned by Ebeling *et al.* (2018), the diversity of communities is not always positively correlated to plant diversity. We can hypothesize that in our case, higher abundance in more diversified systems led to more connection between species, which is a key factor associated with community stability (Hooper *et al.*, 2005) and also probably to pest control. This absence of effect on arthropod diversity could also be attributed to the fact that even in mixed systems the habitat remains a highly perturbed cultivated area; it is

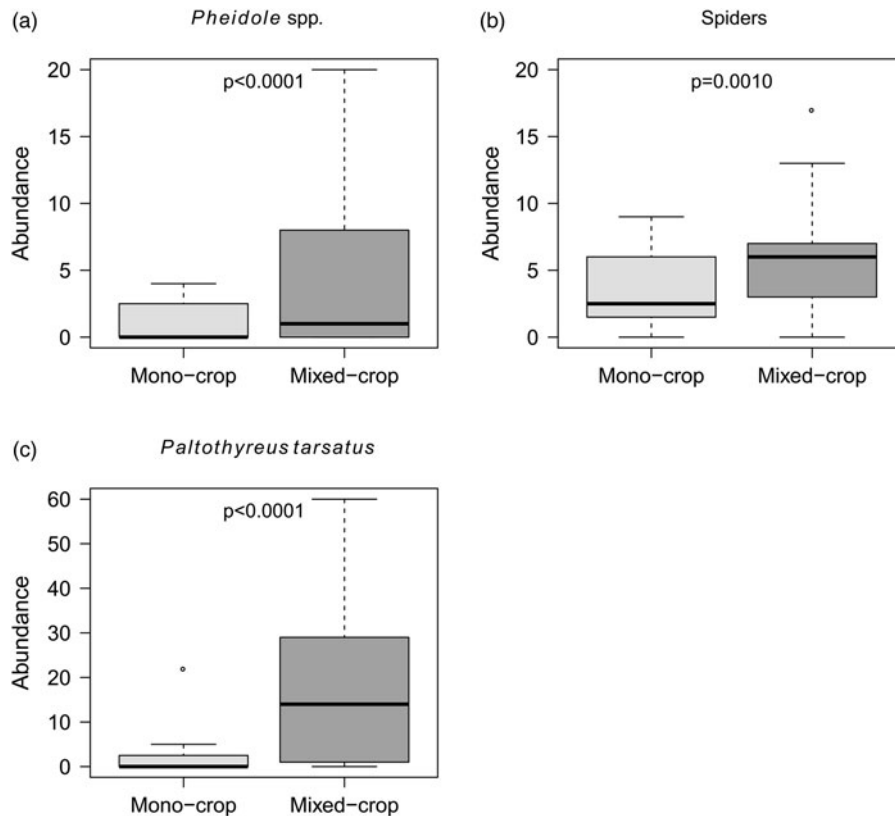


Fig. 3. Distributions at the field-scale of the abundances of *Pheidole* spp., spiders and *Paltothyreus tarsatus* according to the type of cropping system. The *P* values are corresponding to the test of the effect of the crop type on the abundance, tested in a Poisson GLM.

perhaps even more perturbed in mixed-crops since there were more diverse cultural practices applied to each crop of the field.

Difference of *H. armigera* abundance between mono-crops and mixed-crops in tomato agro-ecosystems

Our results show that *H. armigera* abundance was greater in mono-cropping than in mixed-cropping systems. The cultivated plant diversity increased the predator abundance and in-turn probably increased the control of lower trophic levels including *H. armigera*, through predator-mediated interactions (Chailleux *et al.*, 2014). This agrees with the findings of Dassou *et al.* (2016) and Haddad *et al.* (2009) who reported that plant diversity increases the abundance of arthropods at higher trophic levels and reduces the abundance of lower trophic levels. Ants are potential predators of *H. armigera* as showed by Mansfield *et al.* (2003) on *H. armigera* eggs. In our study, ants such as *Pheidole* spp. and *P. tarsatus* and other arthropods such as beetles *Gonocephalum simplex* and spiders *Araneus* sp. and *Erigone* sp. were more abundant in tomato mixed-cropping systems than in tomato mono-cropping systems. These arthropods are generalist predators of many pests. Liu *et al.* (2000) have enumerated many of these predators including ants and spiders as potential predators of *H. armigera*. Other studies have shown the suppression of *H. armigera* by a large complex of predators including *Pheidole* spp. and *Camponotus* spp. (Van Den Berg & Cock, 1995). In addition to ants, spiders were among the most

abundant predators recorded in our tomato cropping systems. Some families including Lycosidae, Clubionidae, Oxyopidae, Salticidae, and Thomsidae could be integrated in biological control programs since they were shown to consume 2.5–5 *Helicoverpa* spp. eggs per day and per spider (Pfannenstiel, 2008). The generalist predator *G. simplex* is abundant in these systems and feeds on several species of plants. The dilution of resources is favorable to their proliferation.

Our study gives element to increase the ecological regulation of *H. armigera* in tomato cropping systems. First we showed that mixed-cropping systems create suitable ecological structures for omnivores and predators that in-turn are likely to control *H. armigera*. Interestingly higher abundance of omnivores and predators did not dampen the abundance of other herbivore (except *H. armigera*). The habitat effect is probably the main effect that explains higher abundance of the omnivores and predators, e.g. by providing shelter from adverse conditions (Landis *et al.*, 2000). Our results suggest that a good way to improve this control would be to go further in the magnitude of the field plant diversity. For instance, we could recommend to farmers to not only increase the richness of plants inside tomato fields, but also to maximize the type of plants that create more diverse habitats for the omnivore-predator trophic group. Including more perennial plants would also be an interesting mean to structure the community of natural enemies especially ants (Dassou *et al.*, 2017).

Ants occurred frequently at relatively high abundance and we suggest that future research should focus on ant species,

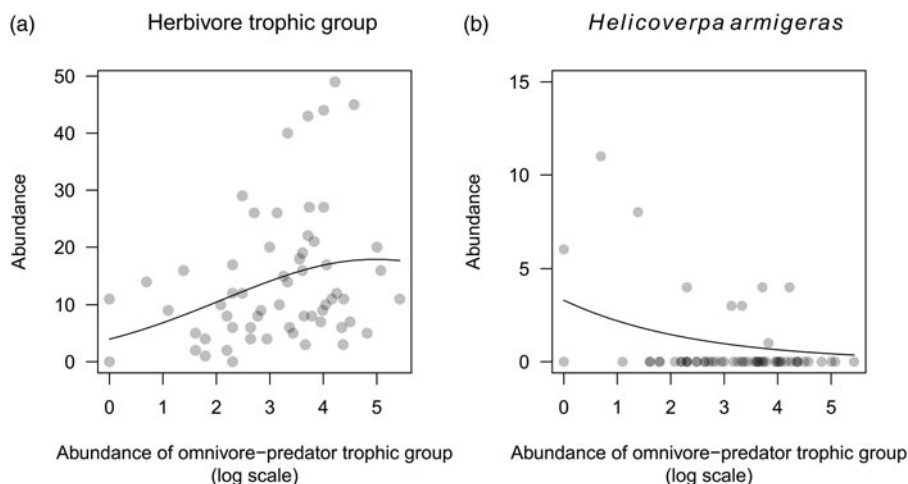


Fig. 4. Relationship between the field-scale (one point per season) abundance of the herbivore trophic group (A) and *Helicoverpa armigera* (B) with the abundance of the omnivore-predator trophic group. The curves show the prediction of the GLM (Poisson distribution) when significant (see table 2 for the description of the models).

Table 2. Effect of the abundance of the omnivore-predator trophic groups on the abundance of the herbivore trophic group and of the *Helicoverpa armigera* abundance.

| Response variable/predictors | DF | Deviance | AIC | deltaAIC | LRT | P |
|--|----|----------|--------|----------|-------|---------|
| Abundance of herbivore trophic group | | | | | | |
| Null model | 59 | 453.31 | 705.04 | | | |
| log(Omnivores + Predators) | 1 | 472.89 | 722.61 | 20.26 | 19.58 | <0.0001 |
| log(Omnivores + Predators) ² | 1 | 460.83 | 710.55 | 8.20 | 7.52 | 0.0061 |
| Abundance of <i>Helicoverpa armigera</i> | | | | | | |
| Null model | 59 | 231.88 | 272.24 | | | |
| log(Omnivores + Predators) | 1 | 243.60 | 281.96 | 7.75 | 11.72 | 0.0006 |
| log(Omnivores + Predators) ² | 1 | 236.73 | 275.09 | 0.88 | 4.85 | 0.0276 |

such as the predaceous ant *P. tarsatus*, and investigate its potential role in biological control of *H. armigera*. In future experiments, it will be valuable to go deeper in the assessment of the process of control, for example, in carrying out experiments with the exclusion of predators.

This study is representative of traditional African agricultural systems that are less chemically intensive than most tomato cropping systems across the world, and also cover a broad range in crops mixing. This makes it a particularly rich case to better understand how favorable habitats and refuges may be managed to enhance pest control.

Supplementary material

The supplementary material for this article can be found at <https://doi.org/10.1017/S0007485319000117>

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