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To cite this version:

Camille Imbert, Julien Papaix, Léa Husson, François Warlop, Claire Lavigne. Pests, but not predators, increase in mixed fruit tree–vegetable plots compared to control vegetable plots in a Mediterranean climate. Agroforestry Systems, 2020, 94, pp.627-638. 10.1007/s10457-019-00430-3 . hal-02622820

HAL Id: hal-02622820
https://hal.inrae.fr/hal-02622820v1

Submitted on 1 Sep 2023

Pests, but not predators, increase in mixed fruit tree-vegetable plots compared to control vegetable plots in a Mediterranean climate.

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Running head: Pests and predators in fruit tree-vegetable plots

Word count: 5981

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Abstract

Mixed fruit tree-vegetable systems simultaneously combine the production of vegetables at the ground level with that of fruits in tree canopies. We tested whether such crop diversification may reduce herbivores on the vegetable crop in the case of an apple fruit-cabbage association. For this purpose, we monitored arthropod pests and natural enemies during six sampling sessions over one growing season with direct observations and pitfall traps. Unexpectedly, we found that four out of seven pest stages (the aphid *Myzus persicae* Sulzer (Aphididae), lepidoptera eggs and caterpillars, and pupae of whiteflies) were more abundant or more frequent in the mixed fruit tree-vegetable plots than in control plots. In contrast, we observed more of three out of the six main predator taxa (chilopods, earwigs and ants) in the control plots. The mechanisms possibly explaining our results include better microclimatic conditions, the dilution of predators and increased bird abundance in the agroforestry plots as well as the longer generation time of predators versus pests.

Keywords: Alley cropping; *Brassica*; Conservation biological control; *Malus*; Mixed fruit-vegetable; Temperate agroforestry.

Introduction

Mixed fruit tree-vegetable systems, also known as fruit alley cropping, simultaneously combine the production of vegetables at the ground level and that of fruits in tree canopies. Such diversified systems are expected to be ecologically efficient by making the best use of the available 3D space in fields (Wolz and DeLucia, 2018). Furthermore, being diversified systems, they are expected to have low pest abundance (Letourneau et al., 2011). Direct impacts of diversification on the pest population may result from a resource dilution that decreases the pest colonisation rate and population growth ("resource concentration hypothesis") (Ratnadass et al., 2012; Root, 1973). Most effects, however, are expected from changes in the natural enemy communities. A main expectation concerns the enhancement of natural enemy abundance and diversity that would increase the predation pressure, the probability of the presence of key voracious predator species and the functional complementarity of species ("enemies hypothesis"), (Loreau, 2001; Root, 1973; Russell, 1989). Such expected changes in the composition of the natural enemy community are mediated by the heterogeneity of crop composition and structure, which provide natural enemies with a diversity of habitats and resources (Langellotto and Denno, 2004; Sunderland and Samu, 2000). These effects may be exacerbated by the presence of trees because they assure long-term refuges and their vegetation structure is a source of new habitats both in the canopy and in the understorey vegetation (Landis et al., 2000).

The presence of trees within plots, however, leads to equivocal effects on the control of annual crop pests (Pumariño et al., 2015; Smits et al., 2012). There are a number of possible explanations linked to pest dynamics or their interactions with their natural enemies. Lower temperatures, higher humidity, and reduced light and wind speed under the trees may create favourable conditions for pest and disease development, particularly in hot conditions (e.g. slugs in Griffiths et al., 1998). Microclimatic conditions may directly affect the pests or may be mediated by lower crop defences in milder environments (Coley et al., 1985). Predators may also be favoured by a milder microclimate, but they may consume fewer of the annual crop pests because they are diverted away from them by alternative prey (i.e., the dilution effect, Koss and Snyder, 2005), experience increased intraguild predation, or both (Halaj and Wise, 2002). Consequently, pest control efficiency in diversified systems results from the balance of the effects of diversification on pest and predator abundances and on the rate of pest consumption by each individual predator.

Other factors explaining the variability in results are pest ecological preferences, habitat complexity, the surrounding landscape and agricultural techniques (Brezzi et al., 2017; Jonsson et al., 2015; Pumariño et al., 2015; Schroth et al., 2000; Smits et al., 2012).

In the present study, we investigated whether growing vegetables between orchard tree rows affects the abundance of vegetable pests and predators using an experimental case study based on apple trees and cabbages. We chose such a simple alley cropping system to limit the number of factors possibly affecting pest control. We monitored the main cabbage pests and focused on generalist predator groups known to attack cabbage pests or similar species. These included spiders, which are predators of both caterpillars and aphids, including cabbage pests (e.g., Furlong et al., 2014); earwigs, which are predators of aphids (e.g., Dib et al., 2010); harvestmen, that prey on pest caterpillars on cabbage (e.g., Schmaedick and Shelton, 2000), predatory chilopods, and Coleoptera families known to include predatory species. Our hypotheses were that, overall, vegetables in mixed fruit tree-vegetable plots would host fewer pests than those in control plots and that they would host a higher abundance of predators. Furthermore, given the diversity of results from the literature, we also investigated whether the response to plot type differed among pest species.

Materials and methods

Experimental design

Study area and experimental plots

The study was carried out at Avignon, south-east France (43°54’55”N 4°52’49”E), from March to June 2016. The climate is Mediterranean with an average (± sd) monthly precipitation of 33.6 ± 19.00 mm, an average monthly temperature of 17.56 ± 6.12°C and an average monthly wind speed of 2.46 ±

0.23 m.s^{-1} during the study period (source: INRA CLIMATIK platform, weather station located less than 500 m from the study site).

Two pairs of experimental plots (hereafter named blocks, Supporting Information, Fig. S1) were established at the local French National Agricultural Research Institute (INRA) experimental site. Each block was composed of one “mixed fruit tree-vegetables” (FV) plot and one “vegetables only” (control) plot. The distance between blocks was approximately 250 m. Within a block, the FV and control plots were at distances of approximately 13 m for block 1 and 35 m for block 2. These distances were meant to ensure that the landscape was similar around the two plots within one block. Cabbage was chosen as the vegetable because it hosts a large variety of pests. Two cultivars, broccoli (*Brassica oleracea* L. var *Belstar*) and the pointed cabbage (*Brassica oleracea* L. var *Poët*), were used in the experiment (both cutivars are thereafter called “cabbage”).

The FV plots were established in experimental apple orchards. The orchard in block 1 was planted in 2004 with 6 rows of 48 apple trees (*Malus domestica* Borkh.) of the cultivar ‘Ariane’. The distance between rows was 4 m. The FV plot was established in one central alley of the orchard by planting two parallel lines of cabbages 80 cm apart when the plants were approximately 10 cm high. The line closest to the trees was located 50 cm from the tree trunks, while the other line was near the centre of the alley. Cabbages were spaced 70 cm apart on the line, alternating one pointed cabbage and one broccoli cabbage, resulting in a total of 238 cabbages. The orchard in block 2 was planted in 1996 with 10 rows of 24 apple trees of the cultivars ‘Granny’ and ‘Gala’ (5 rows each). The distance between rows was also 4 m. The FV plot was established on the same date and followed the same pattern as for block 1 except that cabbage lines were planted along two central orchard alleys. In total, the FV plot in the second orchard contained 216 cabbages.

Control plots contained two lines of 102 cabbages and 69 cabbages per line for block 1 and 2, respectively. Similar to the FV plots, the distance between lines was 80 cm, and the distance between plants within the line was 70 cm.

All plots were planted on 10th March 2016. Each plant was fertilised at planting with 50 g of organic fertiliser (OVIBIO™, Terres et Traditions, France). The plots were free of pesticides and hand weeded, and the four plots were simultaneously irrigated when necessary with 70 cm-high sprinklers.

Sampling design

The sampling design was based on 48 sampling points per plot, i.e., 192 points, on six sampling occasions that occurred every two weeks from mid-April to the end of June 2016. The sampling points were determined as follows: each plot was first subdivided into six subplots (Supporting Information, Fig. S1), and during each sampling session, we randomly chose 2 pointed cabbages and 2 broccoli cabbages on each of the two lines in each subplot, resulting in 8 points per subplot and 48 points per plot. Such a sampling strategy made it possible to randomly choose cabbages that were evenly distributed in the plot. The resulting distributions of sampling occasions for each sampling point are provided for pests and predators in Supporting Information, Fig. S2 and S3. Most cabbages (76%) were sampled only once or twice.

Pest monitoring

The adults, larvae and eggs of pests were monitored on the 48 cabbages per plot on each sampling occasion, resulting in 1152 observations. Green peach aphids (*Myzus persicae* Sulzer) and Cabbage grey aphids (*Brevicoryne brassicae* L.) were counted individually. The number of Lepidoptera caterpillars and the presence of Lepidoptera eggs were assessed without distinguishing between those of the Large white (*Pieris brassicae* L. Pieridae), the Small white (*P. rapae* L. Pieridae), the Green veined-white (*P. napi* L. Pieridae), the Garden pebble moth (*Evergestis forficalis* L. Crambidae), and the Diamondback moth (*Plutella xylostella* L. Plutellidae). Cocoons of the Diamondback moth were pooled with the caterpillars. The presence of eggs, larvae, pupae and adults of the whitefly (*Aleyrodes proletella* L. Aleyrodidae) was also assessed. Larvae and pupae were pooled.

Natural enemy monitoring

Monitoring was performed on or in the vicinity of 16 cabbages per plot on 6 sampling sessions one week following pest monitoring, resulting in 384 observations. These 16 cabbages were a subset of those monitored for pests and were located in two randomly chosen subplots per plot. Three complementary non-lethal methods were used to assess predator abundance. These methods made it possible to monitor predators with distinct movement abilities with minimal impact on predator abundances or behaviour. Predators were identified at the taxonomic level of order.

Flying predators were counted during 5-min observations within 20 cm around each cabbage. Only flying Coleoptera (mostly Cantharidae) are reported, other taxa (including Syrphidae) being too rare. The activity-density of ground-dwelling predators was assessed using 5.4 cm diameter pitfall traps containing stones and leaves to avoid intraguild predation within the trap. Traps were deployed for 24 hours. The predators were monitored and released at the same location immediately after counting. We classified them as spiders, terrestrial Coleoptera, chilopods and harvestmen. The presence of ants was also recorded. Finally, sedentary predators and predators that stayed on the cabbages, such as larvae of Diptera, Coleoptera and predatory Hemiptera, earwigs (Dermaptera) and Acari, were counted directly on the cabbages.

Data analyses

Variation in pest and predator abundance or occurrence was analysed using autoregressive models to account for possible temporal correlations in population dynamics resulting from the same cabbage being visited during different sessions. To address the fact that all cabbages were not sampled on each date, the autoregressive structure was assumed on the basis of an unobserved latent variable conditioning the observations. This allowed us to predict the full dynamics for each cabbage even if no observation was available for a given session. The model is thus as follows:

$$\begin{cases} \epsilon_{i,t} \sim N(0,\sigma) \\ \log(\lambda_{i,t}) = \alpha^0 + \alpha^1_{b(i)} + \alpha^2_{p(i)} + \alpha^3_{c(i)} + \alpha^4_{b(i)p(i)} + \rho\lambda_{i,t-1} + \epsilon_{i,t}\,, \\ Y_{i,t} \sim \text{Poisson}(\lambda_{i,t}) \end{cases} \qquad \text{(Equation 1)}$$

in the case of count data and

$$\begin{cases} \epsilon_{i,t} \sim N(0,\sigma) \\ \text{logit}(\lambda_{i,t}) = \alpha^0 + \alpha^1_{b(i)} + \alpha^2_{p(i)} + \alpha^3_{c(i)} + \alpha^4_{b(i)p(i)} + \rho\lambda_{i,t-1} + \epsilon_{i,t}\,, \\ Y_{i,t} \sim \text{Bernouilli}(\lambda_{i,t}) \end{cases} \qquad \text{(Equation 2)}$$

in the case of occurrence data. In equations 1 and 2, α^0 is an intercept, α^1, α^2, α^3 and α^4 are, respectively, a block effect (1 or 2), a plot type effect (FV or control), a cabbage cultivar effect (broccoli or pointed), and a block x plot type interaction effect. Parameter ρ accounts for temporal correlations. No a priori information was assumed to be available for the parameters, and non-informative priors were thus used. Parameter estimation was performed in a Bayesian framework (details in supporting information S4).

Comparisons of abundance or probability of occurrence between the control and FV plots were performed by computing the posterior probability that the estimated parameter for the FV plot type was higher than that for control plots. Below, only differences leading to a probability higher than 0.90 or lower than 0.1 are discussed unless otherwise stated.

Results

Pests

Pests on the cabbages were diverse, with an overall average of 3.04±0.05 (mean ± se) different pests per cabbage.

Temporal dynamics

Pests showed specific seasonal dynamics, with abundance or occurrence peaking from the fourth to the sixth sampling session (mid-May to the end of June), except for Lepidoptera eggs and caterpillars, which had more or less steady values during the season (Fig. 1). The overall average caterpillar abundance was 1.3±0.17individuals per cabbage, and the overall Lepidoptera egg frequency was

0.50±0.01. The two aphids showed a typical bell-shaped curve, with maximum values (all plots pooled) of 5.4±1.9 and 16.4±2.8 individuals per cabbage during the 5th session for *M. persicae* and *B. brassicae*, respectively. The adult whitefly frequency increased during the season, reaching a plateau with an average presence of 65.5% over the last three sessions. The frequency of whitefly pupae followed the same pattern, while that of eggs tended to decrease by the end of the season (Fig. 1).

Factors affecting individual pest abundance or occurrence

There was a clear pattern when comparing pest abundance or occurrence in the FV and control plots. Contrary to our expectations, four out of seven pest stages were more abundant or frequent in FV plots; these were *M. persicae*, lepidoptera eggs and caterpillars, and pupae of whiteflies. (Fig. 2). The three other differences between plot types were not significant (Fig. 3). The differences between plot types peaked during the 5th sampling session, i.e., during the population peaks, for *M. persicae* with 23.4 times more individuals per cabbage in the FV than control plots. In contrast, differences were larger at the 3rd sampling session for whitefly pupae, with 1.9 times larger frequencies in the FV than control plots, and no clear temporal pattern was observed for lepidoptera eggs and caterpillars (Fig. 1). As observed from mean values (Fig. 2) and the analyses of block x plot type interactions (Fig. S6), higher abundances in FV plots were mostly due to observations from block 2 for *M. persicae* and from block 1 for lepidoptera eggs.

There were also a few differences between the cultivars: *B. brassicae* aphids were more abundant and whitefly pupae were more frequent on pointed cabbages, while whitefly adults and eggs were more frequent on broccolis (Supporting information, Fig. S7). There was only one difference between blocks, with whitefly pupae being more abundant in block 1 (Supporting information, Fig. S8). Large probabilities associated to block x plot type interactions further indicate that differences between plot types differed between blocks for whitefly eggs and adults, the pest stages being particularly frequent in FV plots in block 2.

Natural enemies

The most common ground-dwelling predators in the pitfall traps were ants, spiders and Coleoptera. The overall average frequency of ants in the traps was 0.55, and we caught a total of 840 spiders and 455 Coleoptera, corresponding to an average of 2.20 ± 0.25 (mean ± se) and 1.19 ± 0.08 individuals per trap, respectively. Harvestmen and chilopods were much less abundant, with overall averages of 0.15 ± 0.03 and 0.12 ± 0.02 individuals per trap, respectively. Spiders were mostly from the families Lycosidae, Gnaphosidae and Linyphiidae. Coleoptera were mostly from the families Carabidae and Staphylinidae, many of which are predatory (Thiele et al., 1977; Warner et al., 2008). Independent sampling further showed that most ants belonged to the species *Lasius grandis* (Formicidae) and *Messor structor* (Formicidae). The most common predators observed directly on cabbages were earwigs of the species *Forficula auricularia* (Forficulidae, Dermaptera), with an overall average of 0.19 ± 0.03 individuals per cabbage (Fig. 4).

Other predator taxa, i.e., Diptera larvae, Hemiptera larvae, Coleoptera larvae, Acari and flying Coleoptera, were rarely observed (fewer than 40 individuals over the duration of the experiment each), and their abundance was not further analysed. These rare taxa were mainly observed during the later sampling sessions (Supporting information, Fig. S9).

Temporal dynamics

Except for Coleoptera and ants, the abundance of predator taxa was low during the first sampling session and increased during the later sampling sessions (Fig. 4). Coleoptera tended to show steady dynamics throughout the season, while ants increased in the FV plots, reaching in the FV plots the highest frequency observed in the control plots (Fig. 4).

Factors affecting individual predator abundance or occurrence

Overall, there was a clear tendency towards differences between plot types. Contrary to our expectations, three predator taxa (chilopods, earwigs and ants) were more abundant or frequent in the control plots (Fig. 3). The same pattern was observed for coleoptera but in block 2 only (Fig. 5 and Fig. S6). The other two predator species showed no differences (Fig. 3). While overall significant, the differences between plot types were particularly marked at the beginning of the season for ants and towards the end of the season for earwigs and chilopods (Fig. 5).

The abundance of predator taxa varied little between blocks and cultivars. Harvestmen were more abundant in block 2 (Supporting information, Fig. S8) and earwigs were more abundant on pointed cabbages than broccolis (Supporting information, Fig. S7).

Discussion

In the present study, contrary to our expectations, we found that four out of the seven tested pest stages were more abundant in FV plots and that predators were generally less abundant in these plots.

Lower pest abundance in more diversified systems is a general expectation (Letourneau et al., 2011), but there are many exceptions to this pattern especially in agroforestry systems (Pumariño et al., 2015). Pest identity has been argued to be one variable explaining the variety in the published results (Jonsson et al., 2015; Pumariño et al., 2015). In the present study, we indeed found different results depending on the pest. The two aphid species, in particular, were not affected similarly; *M. persicae* was more abundant in the FV plots, while *B. brassicae* tended to be more abundant in the control plots (probability: 0.12). Overall, however, there was a clear trend towards a higher abundance of pests in the mixed plots. In contrast, there was a trend for the activity-density or abundance of predators to be higher in control plots. Three out of six taxa differed between plots, and, in contrast to pests, they were more numerous in control plots.

Microclimate, resource dilution and natural enemies have been suggested to explain differences in pest abundance between monocultures and temperate agroforestry plots (Tamps and Linits, 1998). Microclimate is a possible explanation for the higher pest abundance in the present study. This study took place in a Mediterranean region characterised by both strong winds and hot temperatures. During the study period, the maximum daily temperatures reached 33°C in the shade. There were also 12 days with maximum wind speeds above 50 km/h. It is likely that the wind and temperature were lower and more favourable for pest survival and reproduction in the FV plots. The oviposition rates of other whitefly species, for example, have been shown to decrease with increasing temperatures (Alonso et al., 2009; Cui et al., 2008) which may explain why whiteflies had a higher abundance in FV plots. Similarly, feeding and growth of *P. rapae* caterpillars have also been shown to decline at temperatures above 35°C (Kingsolver, 2000). Finally, the higher abundance of *M. persicae* in FV plots is consistent with its lower optimal temperature than *B. brassicae* (35°C for *B. brassicae* and 30°C for *M. persicae* (Satar, 2005; Whalon and Smilowitz, 1979)).

Resource dilution in mixed plots would result in a lower immigration of pests to crops because of the barrier effect of trees and a reduction in crop attractiveness (Ratnadass et al., 2012). Lesser colonisation of aphids on *Brassica* crops grown in mixed stands has been reported (Hooks and Johnson, 2003). There are, however, exceptions. *P. rapae*, for example, has adapted to finding scattered host plants (Root and Kareiva, 1984), and its caterpillars were found to be more abundant on intercropped broccolis (Hooks and Johnson, 2002), a result consistent with its higher observed abundance in mixed plots. In the present study, the temporal dynamics of pest abundance show no indication of earlier colonisation in the control plots for any of the pest species (Figs 1, 4. Thus, it is unlikely that trees limited access to the crop, although the trees were grown and had their leaves during the study period (leaf onset started at the beginning of April).

Finally, it is possible that the higher observed abundance of pests in the FV plots partly resulted from lower predation due to a lower predator abundance. Indeed, predator/prey ratios are common indicators of the intensity of pest control (e.g., Vandervoet et al. 2018). Pest control by generalist predators is most efficient early in the season, when pest abundance is low (Symondson et al., 2002). During this period, among the predators that were more numerous in the control plots, antsshowed marked differences between the control and FV plots. As *M. persicae* and *B. brassicae* are not attended by ants, ants may thus have contributed to the control of most pests. Earwigs, which are known as efficient aphid predators, particularly in orchards (Romeu-Dalmau et al., 2012), were abundant in control plots but only over the last three sampling sessions. At that time, *B. brassicae* colonies had already increased in size in the control plots, so that the higher abundance of earwigs in these plots was likely not sufficient to reduce populations significantly. Chilopods were also mostly abundant at the end of the season, and their abundance was therefore unlikely to explain the pest differences.

The tendency towards the lower predator abundance in FV plots was unexpected (Russel, 1989; Stamps and Linit, 1997; Sunderland and Samu, 2000). Similar to pests, better microclimatic conditions could have benefited predator reproduction and survival. Furthermore, trees increased the plot habitat heterogeneity at the ground level, increasing niche diversity and possibly the colonisation of arthropods, whose habitat preferences take place not only at the plot scale but also at smaller scales (Langellotto and Denno, 2004). Finally, some predators, such as spiders or coccinellids, also use resources from the tree canopy (e.g., Sunderland and Samu, 2000). However, we found no evidence for increased predator populations in the mixed plots.

One explanation may lie in the presence of more insectivorous birds in the mixed plots than pure stands (Torralba et al., 2016) that may have affected pest control by preying on arthropod predators (Martin et al., 2013). Insectivorous birds, however, also feed on pests and the presence of vertebrate predators does not on average increase herbivore abundance (Mooney et al., 2010).

A major difference between the pests and the predators that we monitored is that the predators are more generalist regarding their food sources and less restricted to cabbages. Their abundance on or near cabbages thus resulted not only from their population growth but also from their spatial distribution within the plot. It is possible that predators aggregated on the cabbages in the control plots, as cabbages grew on bare ground and probably hosted most prey in these plots. In contrast, mobile predators such as spiders, harvestmen, Coleoptera, earwigs and ants may have been diverted from the cabbages in the mixed plots, looking for alternative prey in the trees or in the vegetation between trees (Prasad and Snyder, 2006). Aggregation on the cabbage is particularly likely for earwigs that furthermore seek refuge in shelters during the day (Lamb 1976) and were frequently observed in humid spots between the pointed cabbage leaves. This ‘dilution effect’ may have masked a possibly positive effect of trees on the local predator abundance. It may have been particularly large in our experiment because the time needed for predator abundance to respond through reproduction to the increased amount of prey brought by the cabbages exceeds the duration of the experiment. Ground beetles, and earwigs generally have one or two generations per year, and spiders only one (Foelix, 2011; Moerkens et al. 2009; Thiele, 1977). In contrast, aphids perform continuous asexual reproduction, and whiteflies can have up to five generations per year; therefore, better environmental conditions may directly translate to higher population abundances for these pests. The temporal pattern for ants is particularly interesting, suggesting that colonies became established in the FV plots throughout the season.

In the present study, we thus confirmed that the response to FV cropping may differ among pests, and we did not find an overall short-term benefit in terms of pest control for farmers growing cabbages within apple orchards. Results concerning pest abundance in temperate agroforestry systems are few and not consistent (Guenat et al., 2019; Pumariño et al., 2015; Smits et al., 2012) possibly because pest abundance highly depends on complex ecological networks (e.g., Mooney et al. 2010) and on both top-down and bottom-up processes (Guenat et al., 2019). The results observed in the present study may highly depend on the cropping system that we investigated, which was both simple and little managed, and on the Mediterranean climatic conditions. It was, further, a short-term study with only two replicates. A higher diversification level and longer time scales may also have provided different results (Taylor-Lovell et al., 2018). Positive impacts of crop diversification may, in particular, rely on the buffering of between-year variations or pest outbreaks (Altieri et al., 2015), which could not be observed in our experiment. Nevertheless, mixed fruit-vegetable systems have been shown to provide other benefits to farmers (Jose, 2009; Morel, 2016). Improving the plot spatial design to decrease predator dilution (Collard et al., 2018), designing practices that reduce pest densities and longer-term studies are thus next steps to further investigate how to improve pest control in mixed fruit tree-vegetable systems.

Acknowledgements

This work and C.I. PhD were funded by Fondation de France (grant 00056292). The authors thank Jérémy Cortello and Ruoyin Long for helping with the field and lab work.

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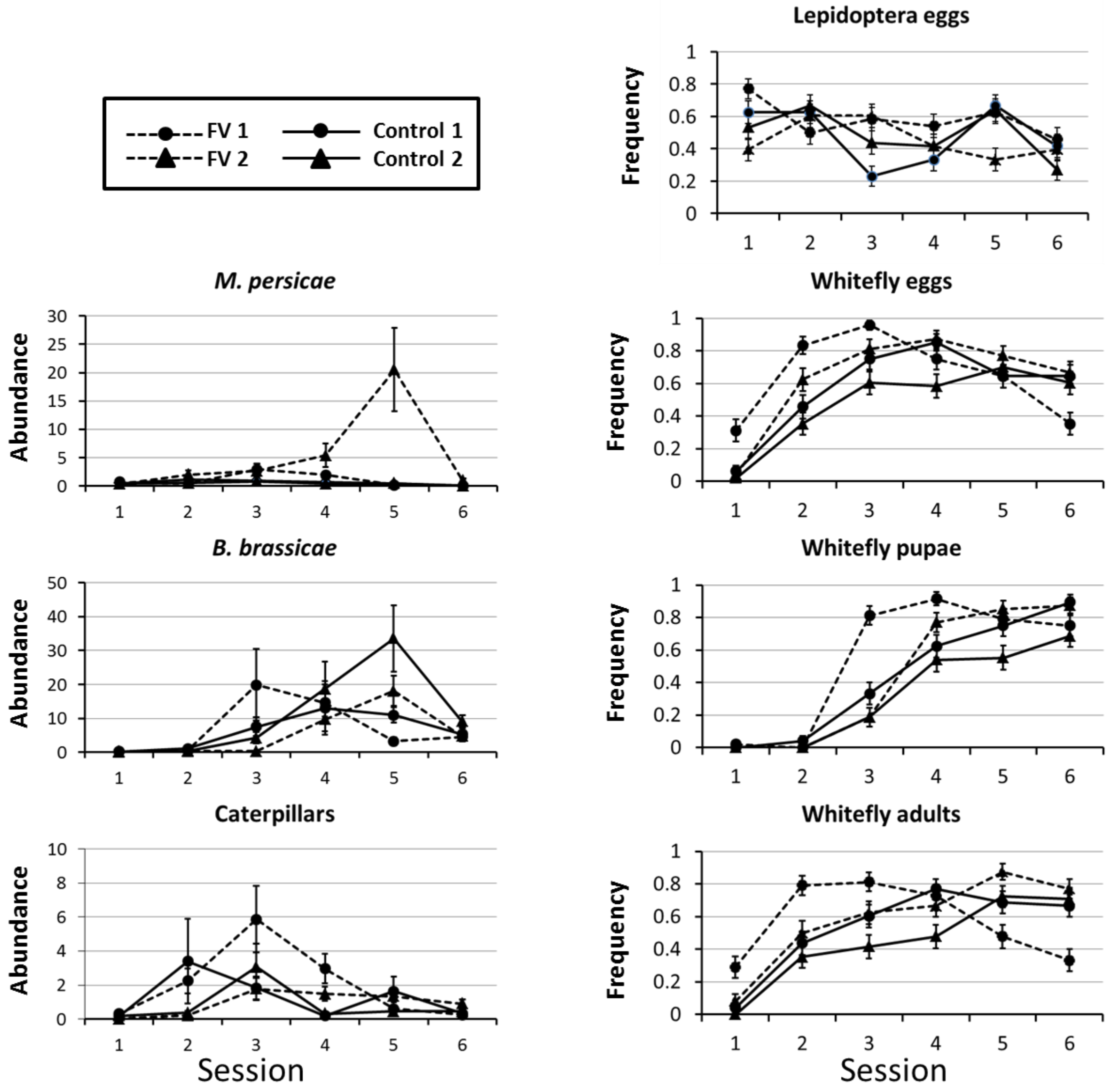

Figure 1. Mean pest abundance (a) and occurrence frequency (b) in control and FV plots as a function of the sampling session. Circles: block 1, triangles: block2. Full line: control plots, hatched line: FV plots. Error bars represent standard errors over cabbages. Note that the y-axes differ.

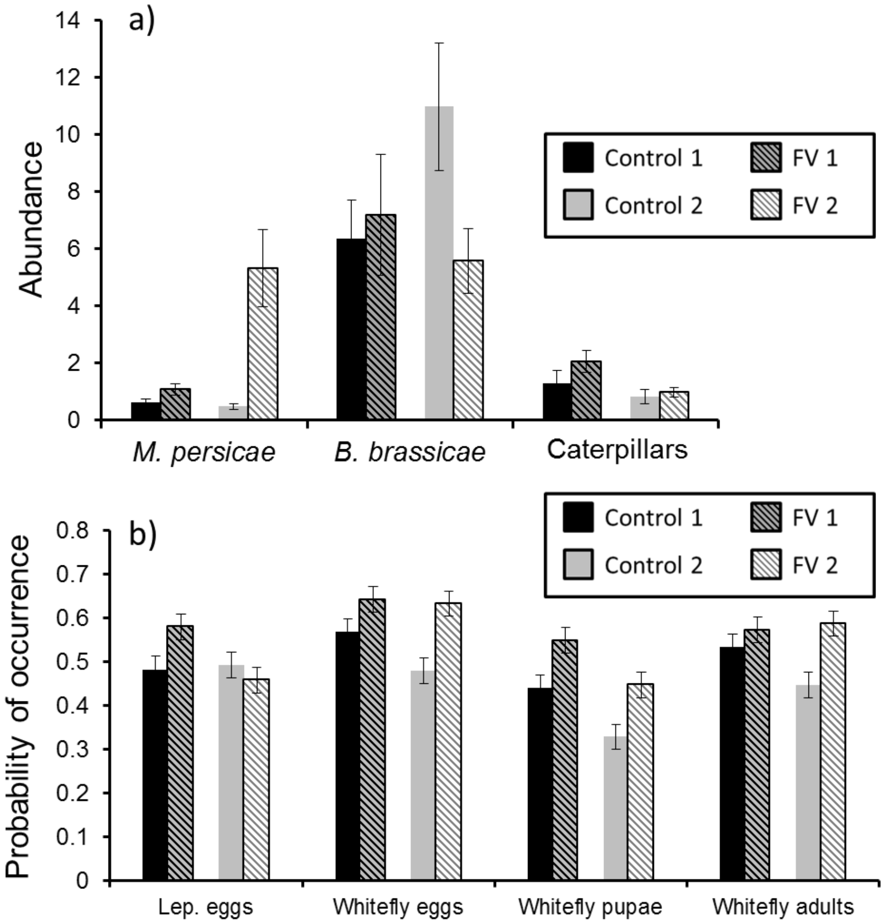

Figure 2 Mean pest abundance (a) and occurrence frequency (b) in control and FV plots. Black: block 1, grey: block2. Filled: control plots, hatched: FV plots. Error bars represent standard errors over cabbages.

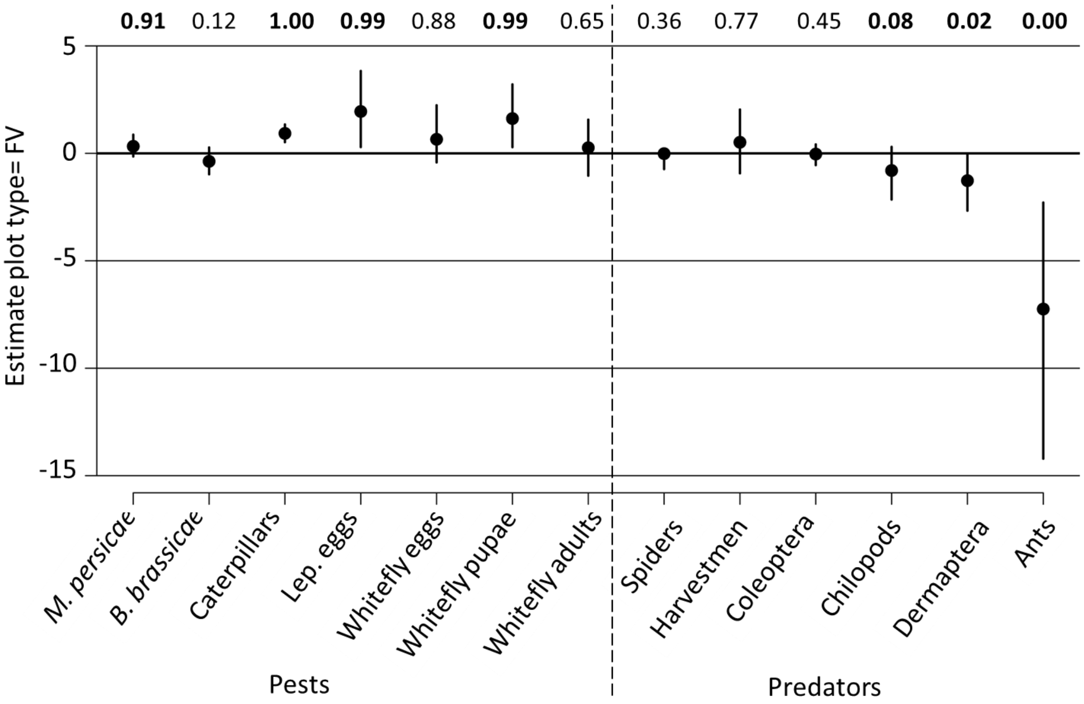

Figure 3. Posterior density of the plot type effect (control =0). Positive values indicate higher abundance or probability of occurrence in FV plots, while negative values indicate higher abundance or probability of occurrence in control plots. Points represent the posterior median, and vertical bars represent the [0.025, 0.975] credibility intervals. The probability that the plot type effect for FV is positive is provided above each individual graph. Values below 0.1 and above 0.9 in bold.

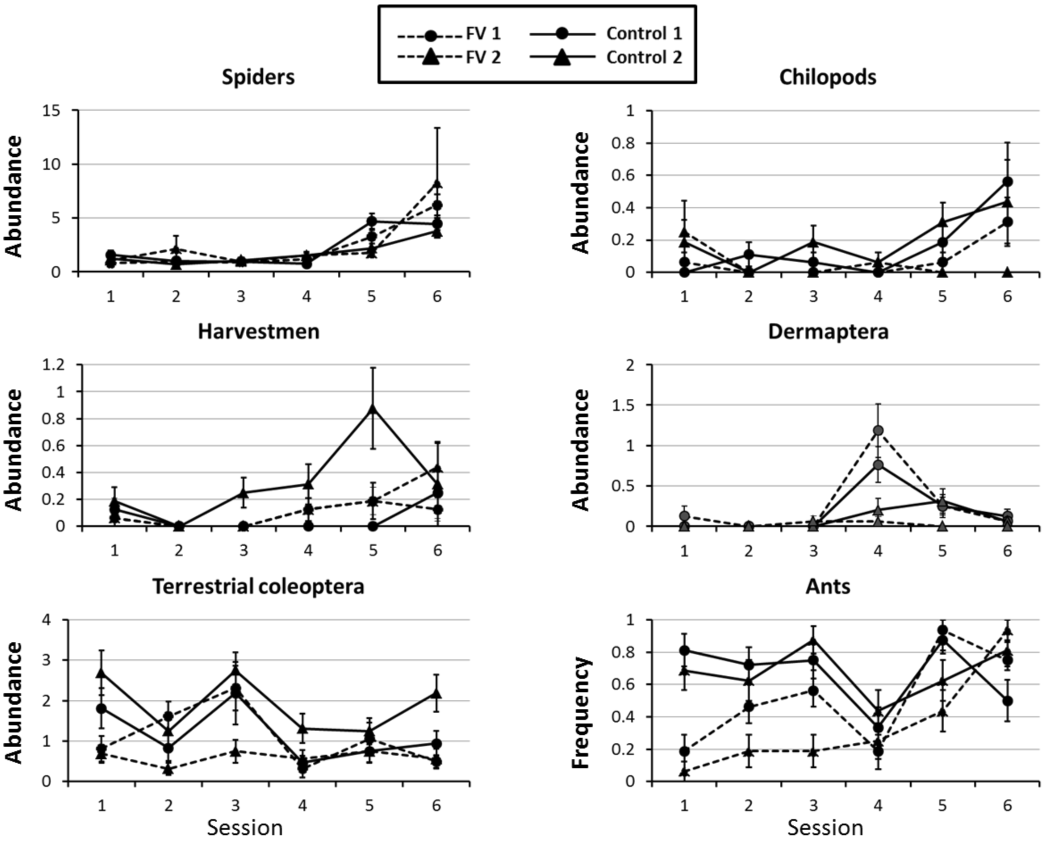

Figure 4. Mean predator abundance or occurrence frequency (ants) in control and FV plots as a function of the sampling session. Circles: block 1, triangles: block2. Full line: control, hatched line: FV plots. Error bars represent standard errors over cabbages. Note that y-axes differ.

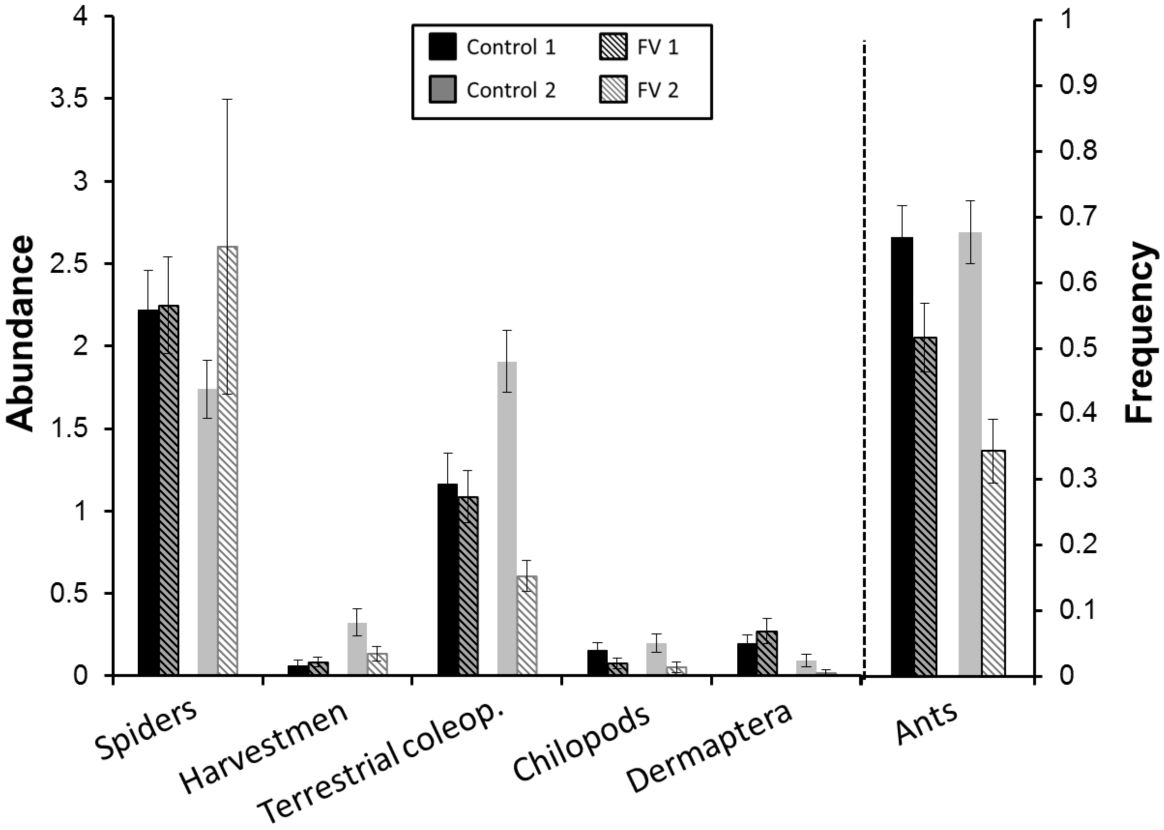

Figure 5. Mean predator abundance or occurrence frequency (ants) in control and FV plots. Error bars represent standard errors over cabbages.