



HAL
open science

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

Camille Imbert, Julien Papaix, Léa Husson, François Warlop, Claire Lavigne

► **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-02622820>

Submitted on 1 Sep 2023

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1 *This version of the article has been accepted for publication, after peer review (when*
2 *applicable) and is subject to Springer Nature's [AM terms of use](#), but is not the Version of*
3 *Record and does not reflect post-acceptance improvements, or any corrections. The Version*
4 *of Record is available online at: <https://doi.org/10.1007/s10457-019-00430-3>.*

5

6

7 **Pests, but not predators, increase in mixed fruit tree-vegetable plots compared to control**

8 **vegetable plots in a Mediterranean climate.**

9

10

11 **Camille Imbert¹, Julien Papaïx², Léa Husson¹, François Warlop³, Claire Lavigne^{1*}**

12

13 ¹INRA, UR 1115 PSH, Plantes et Systèmes de culture Horticoles, F- 84000 Avignon, France

14 ²INRA, UR 546 BioSP, Biostatistique et Processus Spatiaux, F-84000 Avignon, France

15 ³GRAB, Maison de la Bio, 255 Chemin de la Castelette, 84911 Avignon, France

16

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

18

19 **Word count: 5981**

20

21

22 **Correspondence:**

23 Claire Lavigne. INRA PSH, Domaine Saint-Paul, site Agroparc, 228 route de l'aérodrome, 84914 Avignon

24 cedex 9, France. Tel. : +33(0)4 32 72 26 66 ; email : claire.lavigne@inra.fr

25

26

27 **Abstract**

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

39

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

42

43 **Introduction**

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

60 The presence of trees within plots, however, leads to equivocal effects on the control of annual
61 crop pests (Pumariño et al., 2015; Smits et al., 2012). There are a number of possible explanations
62 linked to pest dynamics or their interactions with their natural enemies. Lower temperatures, higher
63 humidity, and reduced light and wind speed under the trees may create favourable conditions for pest
64 and disease development, particularly in hot conditions (e.g. slugs in Griffiths et al., 1998).
65 Microclimatic conditions may directly affect the pests or may be mediated by lower crop defences in
66 milder environments (Coley et al., 1985). Predators may also be favoured by a milder microclimate,
67 but they may consume fewer of the annual crop pests because they are diverted away from them by
68 alternative prey (i.e., the dilution effect, Koss and Snyder, 2005), experience increased intraguild

69 predation, or both (Halaj and Wise, 2002). Consequently, pest control efficiency in diversified systems
70 results from the balance of the effects of diversification on pest and predator abundances and on the
71 rate of pest consumption by each individual predator.

72 Other factors explaining the variability in results are pest ecological preferences, habitat
73 complexity, the surrounding landscape and agricultural techniques (Brezzi et al., 2017; Jonsson et al.,
74 2015; Pumariño et al., 2015; Schroth et al., 2000; Smits et al., 2012).

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

87

88 **Materials and methods**

89 *Experimental design*

90 *Study area and experimental plots*

91 The study was carried out at Avignon, south-east France (43°54'55"N 4°52'49"E), from March to
92 June 2016. The climate is Mediterranean with an average (\pm sd) monthly precipitation of 33.6 ± 19.00
93 mm, an average monthly temperature of $17.56 \pm 6.12^\circ\text{C}$ and an average monthly wind speed of $2.46 \pm$

94 0.23 m.s⁻¹ during the study period (source: INRA CLIMATIK platform, weather station located less than
95 500 m from the study site).

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

105

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

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

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

124

125 *Sampling design*

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

135

136 *Pest monitoring*

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

146

147 *Natural enemy monitoring*

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

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

163

164 *Data analyses*

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

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

172 in the case of count data and

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

174 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,
175 respectively, a block effect (1 or 2), a plot type effect (FV or control), a cabbage cultivar effect (broccoli
176 or pointed), and a block x plot type interaction effect. Parameter ρ accounts for temporal correlations.
177 No a priori information was assumed to be available for the parameters, and non-informative priors
178 were thus used. Parameter estimation was performed in a Bayesian framework (details in supporting
179 information S4).

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

184

185 **Results**

186 *Pests*

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

189 *Temporal dynamics*

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

194 0.50±0.01. The two aphids showed a typical bell-shaped curve, with maximum values (all plots
195 pooled) of 5.4±1.9 and 16.4±2.8 individuals per cabbage during the 5th session for *M. persicae* and *B.*
196 *brassicae*, respectively. The adult whitefly frequency increased during the season, reaching a plateau
197 with an average presence of 65.5% over the last three sessions. The frequency of whitefly pupae
198 followed the same pattern, while that of eggs tended to decrease by the end of the season (Fig. 1).

199

200 *Factors affecting individual pest abundance or occurrence*

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

212

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

220 *Natural enemies*

221 The most common ground-dwelling predators in the pitfall traps were ants, spiders and Coleoptera.
222 The overall average frequency of ants in the traps was 0.55, and we caught a total of 840 spiders and
223 455 Coleoptera, corresponding to an average of 2.20 ± 0.25 (mean \pm se) and 1.19 ± 0.08 individuals per
224 trap, respectively. Harvestmen and chilopods were much less abundant, with overall averages of 0.15
225 ± 0.03 and 0.12 ± 0.02 individuals per trap, respectively. Spiders were mostly from the families
226 Lycosidae, Gnaphosidae and Linyphiidae. Coleoptera were mostly from the families Carabidae and
227 Staphylinidae, many of which are predatory (Thiele et al., 1977; Warner et al., 2008). Independent
228 sampling further showed that most ants belonged to the species *Lasius grandis* (Formicidae) and
229 *Messor structor* (Formicidae). The most common predators observed directly on cabbages were
230 earwigs of the species *Forficula auricularia* (Forficulidae, Dermaptera), with an overall average of 0.19
231 ± 0.03 individuals per cabbage (Fig. 4).

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

236

237 *Temporal dynamics*

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

242

243 *Factors affecting individual predator abundance or occurrence*

244 Overall, there was a clear tendency towards differences between plot types. Contrary to our
245 expectations, three predator taxa (chilopods, earwigs and ants) were more abundant or frequent in

246 the control plots (Fig. 3). The same pattern was observed for coleoptera but in block 2 only (Fig. 5 and
247 Fig. S6). The other two predator species showed no differences (Fig. 3). While overall significant, the
248 differences between plot types were particularly marked at the beginning of the season for ants and
249 towards the end of the season for earwigs and chilopods (Fig. 5).

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

253

254 Discussion

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

257 Lower pest abundance in more diversified systems is a general expectation (Letourneau et al.,
258 2011), but there are many exceptions to this pattern especially in agroforestry systems (Pumariño et
259 al., 2015). Pest identity has been argued to be one variable explaining the variety in the published
260 results (Jonsson et al., 2015; Pumariño et al., 2015). In the present study, we indeed found different
261 results depending on the pest. The two aphid species, in particular, were not affected similarly; *M.*
262 *persicae* was more abundant in the FV plots, while *B. brassicae* tended to be more abundant in the
263 control plots (probability: 0.12). Overall, however, there was a clear trend towards a higher abundance
264 of pests in the mixed plots. In contrast, there was a trend for the activity-density or abundance of
265 predators to be higher in control plots. Three out of six taxa differed between plots, and, in contrast
266 to pests, they were more numerous in control plots.

267 Microclimate, resource dilution and natural enemies have been suggested to explain differences in
268 pest abundance between monocultures and temperate agroforestry plots (Tamps and Linitis, 1998).
269 Microclimate is a possible explanation for the higher pest abundance in the present study. This study
270 took place in a Mediterranean region characterised by both strong winds and hot temperatures. During
271 the study period, the maximum daily temperatures reached 33°C in the shade. There were also 12 days

272 with maximum wind speeds above 50 km/h. It is likely that the wind and temperature were lower and
273 more favourable for pest survival and reproduction in the FV plots. The oviposition rates of other
274 whitefly species, for example, have been shown to decrease with increasing temperatures (Alonso et
275 al., 2009; Cui et al., 2008) which may explain why whiteflies had a higher abundance in FV plots.
276 Similarly, feeding and growth of *P. rapae* caterpillars have also been shown to decline at temperatures
277 above 35°C (Kingsolver, 2000). Finally, the higher abundance of *M. persicae* in FV plots is consistent
278 with its lower optimal temperature than *B. brassicae* (35°C for *B. brassicae* and 30°C for *M. persicae*
279 (Satar, 2005; Whalon and Smilowitz, 1979)).

280 Resource dilution in mixed plots would result in a lower immigration of pests to crops because of
281 the barrier effect of trees and a reduction in crop attractiveness (Ratnadass et al., 2012). Lesser
282 colonisation of aphids on *Brassica* crops grown in mixed stands has been reported (Hooks and Johnson,
283 2003). There are, however, exceptions. *P. rapae*, for example, has adapted to finding scattered host
284 plants (Root and Kareiva, 1984), and its caterpillars were found to be more abundant on intercropped
285 broccolis (Hooks and Johnson, 2002), a result consistent with its higher observed abundance in mixed
286 plots. In the present study, the temporal dynamics of pest abundance show no indication of earlier
287 colonisation in the control plots for any of the pest species (Figs 1, 4. Thus, it is unlikely that trees
288 limited access to the crop, although the trees were grown and had their leaves during the study period
289 (leaf onset started at the beginning of April).

290 Finally, it is possible that the higher observed abundance of pests in the FV plots partly resulted
291 from lower predation due to a lower predator abundance. Indeed, predator/prey ratios are common
292 indicators of the intensity of pest control (e.g., Vandervoet et al. 2018). Pest control by generalist
293 predators is most efficient early in the season, when pest abundance is low (Symondson et al., 2002).
294 During this period, among the predators that were more numerous in the control plots, antsshowed
295 marked differences between the control and FV plots. As *M. persicae* and *B. brassicae* are not attended
296 by ants, ants may thus have contributed to the control of most pests. Earwigs, which are known as
297 efficient aphid predators, particularly in orchards (Romeu-Dalmau et al., 2012), were abundant in

298 control plots but only over the last three sampling sessions. At that time, *B. brassicae* colonies had
299 already increased in size in the control plots, so that the higher abundance of earwigs in these plots
300 was likely not sufficient to reduce populations significantly. Chilopods were also mostly abundant at
301 the end of the season, and their abundance was therefore unlikely to explain the pest differences.

302

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

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

315 A major difference between the pests and the predators that we monitored is that the predators
316 are more generalist regarding their food sources and less restricted to cabbages. Their abundance on
317 or near cabbages thus resulted not only from their population growth but also from their spatial
318 distribution within the plot. It is possible that predators aggregated on the cabbages in the control
319 plots, as cabbages grew on bare ground and probably hosted most prey in these plots. In contrast,
320 mobile predators such as spiders, harvestmen, Coleoptera, earwigs and ants may have been diverted
321 from the cabbages in the mixed plots, looking for alternative prey in the trees or in the vegetation
322 between trees (Prasad and Snyder, 2006). Aggregation on the cabbage is particularly likely for earwigs
323 that furthermore seek refuge in shelters during the day (Lamb 1976) and were frequently observed in

324 humid spots between the pointed cabbage leaves. This ‘dilution effect’ may have masked a possibly
325 positive effect of trees on the local predator abundance. It may have been particularly large in our
326 experiment because the time needed for predator abundance to respond through reproduction to the
327 increased amount of prey brought by the cabbages exceeds the duration of the experiment. Ground
328 beetles, and earwigs generally have one or two generations per year, and spiders only one (Foelix,
329 2011; Moerkens et al. 2009; Thiele, 1977). In contrast, aphids perform continuous asexual
330 reproduction, and whiteflies can have up to five generations per year; therefore, better environmental
331 conditions may directly translate to higher population abundances for these pests. The temporal
332 pattern for ants is particularly interesting, suggesting that colonies became established in the FV plots
333 throughout the season.

334

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

349 studies are thus next steps to further investigate how to improve pest control in mixed fruit tree-
350 vegetable systems.

351

352 **Acknowledgements**

353 This work and C.I. PhD were funded by Fondation de France (grant 00056292). The authors thank

354 Jérémy Cortello and Ruoyin Long for helping with the field and lab work.

355

356

357 **References**

- 358 Alonso, D., Gómez, A.A., Nombela, G. & Muñiz, M. (2009). Temperature-dependent development of
359 *Aleyrodes proletella* (Homoptera: Aleyrodidae) on two cultivars of broccoli under constant
360 temperatures. *Environmental Entomology* 38, 11–17.
- 361 Altieri, M.A., Nicholls, C.I., Henao, A. & Lana, M.A. (2015). Agroecology and the design of climate
362 change-resilient farming systems. *Agronomy for Sustainable Development* 35, 869-890.
- 363 Brezzi, M., Schmid, B., Niklaus, P.A. & Schuldt, A. (2017). Tree diversity increases levels of herbivore
364 damage in a subtropical forest canopy: evidence for dietary mixing by arthropods? *Journal of Plant*
365 *Ecology* 10, 13-27.
- 366 Campos, M., Fernandez, L., Ruano, F., Cotes, B., Cardenas, M. & Castro, J. (2011). Short term response
367 of ants to the removal of ground cover in organic olive orchards. *European Journal of Entomology*
368 108, 417-423.
- 369 Coley, P.D., Bryant, J.P. & Chapin, F.S. (1985). Resource availability and plant antiherbivore defense.
370 *Science* 230, 895–899.
- 371 Collard, B., Tixier, P., Carval, D., Lavigne, C. & Delattre, T. (2018) Spatial organisation of habitats in
372 agricultural plots affects per-capita predator effect on conservation biological control: An individual
373 based modelling study. *Ecological Modelling* 388: 124–135.
- 374 Cui, X., Wan, F., Xie, M. & Liu, T. (2008). Effects of heat shock on survival and reproduction of two
375 whitefly species, *Trialeurodes vaporariorum* and *Bemisia tabaci* Biotype B. *Journal of Insect Science*
376 8, 1–10.
- 377 Dib, H., Simon, S., Sauphanor, B., Capowiez, Y. (2010). The role of natural enemies on the population
378 dynamics of the rosy apple aphid, *Dysaphis plantaginea* Passerini (Hemiptera: Aphididae) in organic
379 apple orchards in south-eastern France. *Biological Control* 55, 97-109.
- 380 Foelix, R.F. (2011). *Biology of spiders*, 3rd ed. ed. Oxford University Press, Oxford ; New York.

381 Furlong, M.J., Rowley, D.L., Murtiningsih, R. & Greenstone, M.H. (2014). Combining ecological methods
382 and molecular gut-content analysis to investigate predation of a lepidopteran pest complex of
383 Brassica crops. *Entomologia Experimentalis Et Applicata* 153, 128-141.

384 Griffiths, J., Phillips, D.S., Compton, S.G., Wright, C. & Incoll, L.D. (1998). Responses of slug numbers
385 and slug damage to crops in a silvoarable agroforestry landscape. *Journal of Applied Ecology* 35, 252-
386 260.

387 Guenat, S., Kaartinen, R., Jonsson, M., (2019). Shade trees decrease pest abundances on brassica crops
388 in Kenya. *Agroforestry Systems* 93, 641-652.

389 Halaj, J. & Wise, D.H. (2002). Impact of a detrital subsidy on trophic cascades in a terrestrial grazing
390 food web. *Ecology* 83, 3141–3151.

391 Hooks, C.R.R. & Johnson, M.W. (2002). Lepidopteran pest populations and crop yields in row
392 intercropped broccoli. *Agricultural and Forest Entomology* 4, 117-125.

393 Hooks, C.R.R. & Johnson, M.W. (2003). Impact of agricultural diversification on the insect community
394 of cruciferous crops. *Crop Prot.* 22, 223-238.

395 Jonsson, M., Raphael, I.A., Ekbohm, B., Kyamanywa, S. & Karungi, J. (2015). Contrasting effects of shade
396 level and altitude on two important coffee pests. *Journal of Pest Science* 88, 281–287.

397 Jose, S. (2009). Agroforestry for ecosystem services and environmental benefits: an overview.
398 *Agroforestry Systems* 76, 1–10.

399 Kingsolver, J.G. (2000). Feeding, growth, and the thermal environment of cabbage white caterpillars,
400 *Pieris rapae* L. *Physiological and Biochemical Zoology* 73, 621–628.

401 Koss, A.M. & Snyder, W.E. (2005). Alternative prey disrupt biocontrol by a guild of generalist predators.
402 *Biological Control* 32, 243–251.

403 Lamb, R.J. (1976). Dispersal by nesting earwigs, *Forficula auricularia* (Dermaptera-Forficulidae).
404 *Canadian Entomologist* 108, 213-216.

405 Landis, D.A., Wratten, S.D. & Gurr, G.M. (2000). Habitat management to conserve natural enemies of
406 arthropod pests in agriculture. *Annual review of entomology* 45, 175-201.

407 Langellotto, G. A., & Denno, R. F. (2004). Responses of invertebrate natural enemies to complex-
408 structured habitats: a meta-analytical synthesis. *Oecologia*, 139(1), 1-10.

409 Letourneau, D.K., Armbrrecht, I., Rivera, B.S., Lerma, J.M., Carmona, E.J., Daza, M.C., Escobar, S.,
410 Galindo, V., Gutiérrez, C., López, S.D., Mejía, J.L., Rangel, A.M.A., Rangel, J.H., Rivera, L., Saavedra,
411 C.A., Torres, A.M. & Trujillo, A.R. (2011). Does plant diversity benefit agroecosystems? A synthetic
412 review. *Ecological Applications* 21, 9–21.

413 Loreau, M. (2001). Biodiversity and Ecosystem Functioning: Current Knowledge and Future Challenges.
414 *Science* 294, 804–808.

415 Martin, E.A., Reineking, B., Seo, B. & Steffan-Dewenter, I. (2013). Natural enemy interactions constrain
416 pest control in complex agricultural landscapes. *Proceedings of the National Academy of Sciences*
417 USA 110:5534–5539.

418 Moerkens, R., Leirs, H., Peusens, G. & Gobin, B. (2009). Are populations of European earwigs, *Forficula*
419 *auricularia*, density dependent? *Entomologica experimentalis et applicata* 130, 198-206.

420 Mooney K.A., Gruner, D.S., Barber, N.A., Van Bael, S.A., Philpott S.M., Greenberg, R. (2010) *Proceedings*
421 *of the National Academy of Sciences USA* 107, 7335-7340.

422 Morel, K. (2016). Viabilité des microfermes maraîchères biologiques. Une étude inductive combinant
423 méthodes qualitatives et modélisation. Phd thesis Université Paris-Saclay.

424 Prasad, R.P., Snyder, W.E., 2006. Polyphagy complicates conservation biological control that targets
425 generalist predators. *Journal of Applied Ecology* 43, 343-352.

426 Pumariño, L., Sileshi, G.W., Gripenberg, S., Kaartinen, R., Barrios, E., Muchane, M.N., Midega, C. &
427 Jonsson, M. (2015). Effects of agroforestry on pest, disease and weed control: A meta-analysis. *Basic*
428 *and Applied Ecology* 16, 573–582.

429 R Core Team (2015). R: A language and environment for statistical computing. R Foundation for
430 Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.

431 Ratnadass, A., Fernandes, P., Avelino, J. & Habib, R. (2012). Plant species diversity for sustainable
432 management of crop pests and diseases in agroecosystems: a review. *Agronomy for Sustainable*
433 *Development* 32, 273–303.

434 Romeu-Dalmau, C., Pinol, J. & Agusti, N. (2012). Detecting aphid predation by earwigs in organic citrus
435 orchards using molecular markers. *Bulletin of Entomological Research* 102, 566-572.

436 Root, R. B. (1973). Organization of a plant-arthropod association in simple and diverse habitats: the
437 fauna of collards. *Ecological Monographs*, 43, 95-124.

438 Root, R.B. & Kareiva, P.M. (1984). The search for resources by cabbage butterflies (*Pieris rapae*) -
439 ecological consequences and adaptive significance of Markovian movements in a patchy
440 environment. *Ecology* 65, 147-165.

441 Russell, E.P. (1989). Enemies hypothesis - a review of the effect of vegetational diversity on predatory
442 insects and parasitoids. *Environmental Entomology* 18, 590-599.

443 Satar, S. (2005). Temperature Dependent Life History Traits of *Brevicoryne brassicae* (L.) (Hom.,
444 Aphididae) on White Cabbage. *Turkish Journal of Agriculture and Forestry* 29:1-6.

445 Schmaedick, M.A. & Shelton, A.M. (2000). Arthropod predators in cabbage (Cruciferae) and their
446 potential as naturally occurring biological control agents for *Pieris rapae* (Lepidoptera : Pieridae).
447 *Canadian Entomologist* 132, 655-675.

448 Schroth, G., Krauss, U., Gasparotto, L., Duarte Aguilar, J.A. & Vohland, K. (2000). Pests and diseases in
449 agroforestry systems of the humid tropics pp 199–241.

450 Smits, N., Dupraz, C. & Dufour, L. (2012). Unexpected lack of influence of tree rows on the dynamics of
451 wheat aphids and their natural enemies in a temperate agroforestry system. *Agroforestry Systems*
452 85, 153–164.

453 Stamps, W. T. & Linit, M. J. (1997). Plant diversity and arthropod communities: implications for
454 temperate agroforestry. *Agroforestry Systems*, 39: 73–89.

455 Sunderland, K. & Samu, F. (2000). Effects of agricultural diversification on the abundance, distribution,
456 and pest control potential of spiders: a review. *Entomologia Experimentalis et Applicata* 95, 1–13.

457 Symondson, W.O.C., Sunderland K.D. & Greenstone, M.H. (2002) Can generalist predators be efficient
458 biocontrol agents? *Annual Review of Entomology* 47, 561-594.

459 Taylor-Lovell, S., Dupraz, C., Gold, M., Shibu Jose, S., Revord, R., Stanek, E. & Wolz, K.J. (2018)
460 Temperate agroforestry research: considering multifunctional woody polycultures and the design of
461 long-term field trials. *Agroforestry Systems* 92, 1397–1415.

462 Thiele, H.-U. (1977). *Carabid beetles in their environments: a study on habitat selection by adaptations*
463 *in physiology and behaviour*. Springer Berlin Heidelberg, Berlin, Heidelberg.

464 Torralba, M., Fagerholm, N., Burgess, P.J., Moreno, G., Plieninger, T. (2016). Do European agroforestry
465 systems enhance biodiversity and ecosystem services? A meta-analysis. *Agriculture, Ecosystems and*
466 *Environment* 230: 150-161.

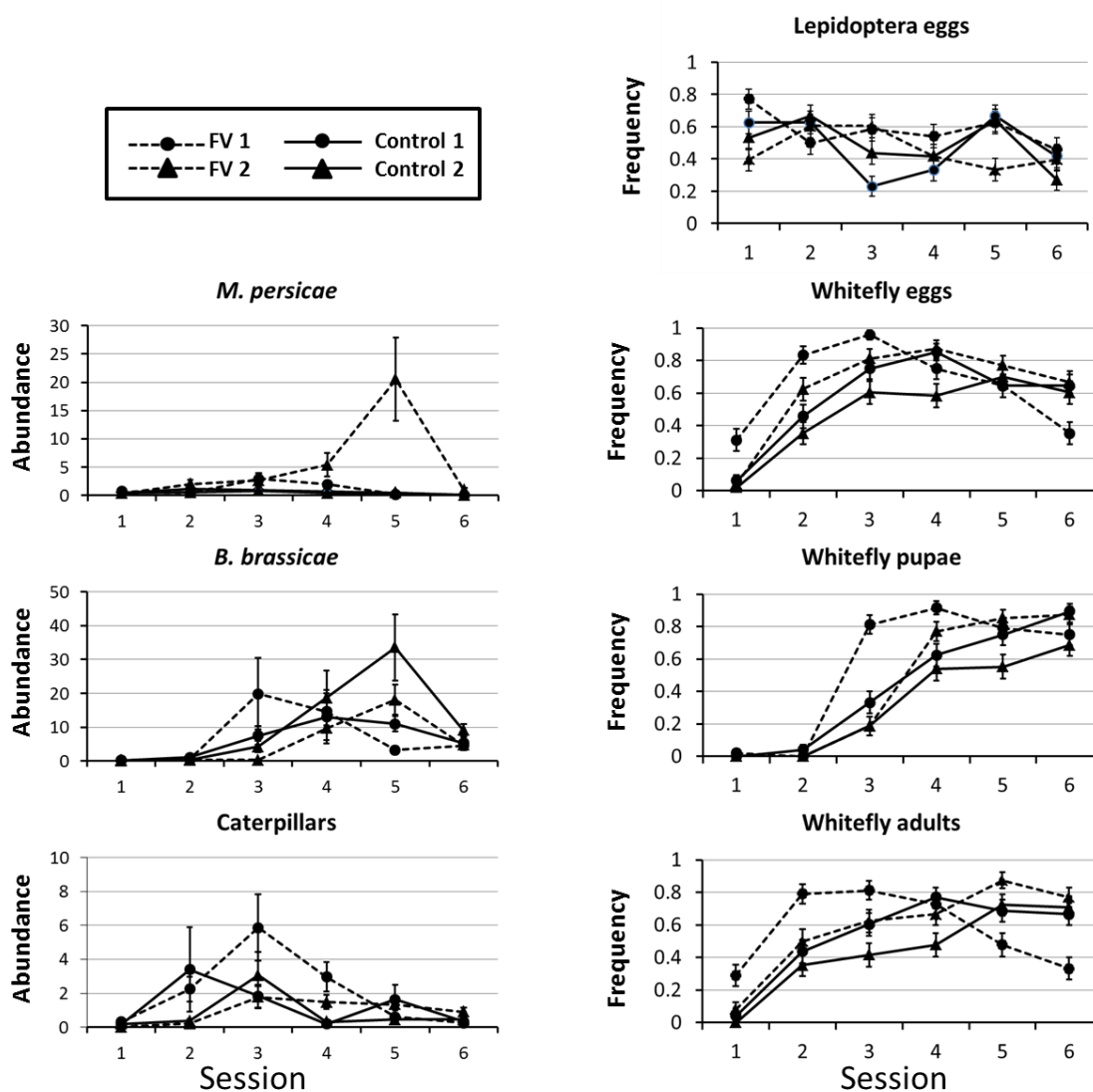
467 Vandervoet, T.F., Ellsworth, P.C., Carriere, Y. & Naranjo, S.E. (2018). Quantifying conservation
468 biological control for management of *Bemisia tabaci* (Hemiptera: Aleyrodidae) in cotton. *Journal of*
469 *Economic Entomology* 111, 1056-1068.

470 Warner, D.J., Allen-Williams, L.J., Warrington, S., Ferguson, A.W. & Williams, I.H. (2008). Implications
471 for conservation biocontrol of spatio-temporal relationships between carabid beetles and
472 coleopterous pests in winter oilseed rape. *Agricultural and Forest Entomology* 10, 375-387

473 Whalon, M.E. & Smilowitz, Z. (1979). Temperature-dependent model for predicting field populations
474 of green aphid, *Myzus persicae* (Homoptera: Aphididae). *The Canadian Entomologist* 111, 1025–
475 1032.

476 Wolz, K.J. & DeLucia, E.H. (2018). Alley cropping: Global patterns of species composition and function.
477 *Agriculture, Ecosystems & Environment* 252, 61–68.

478



480

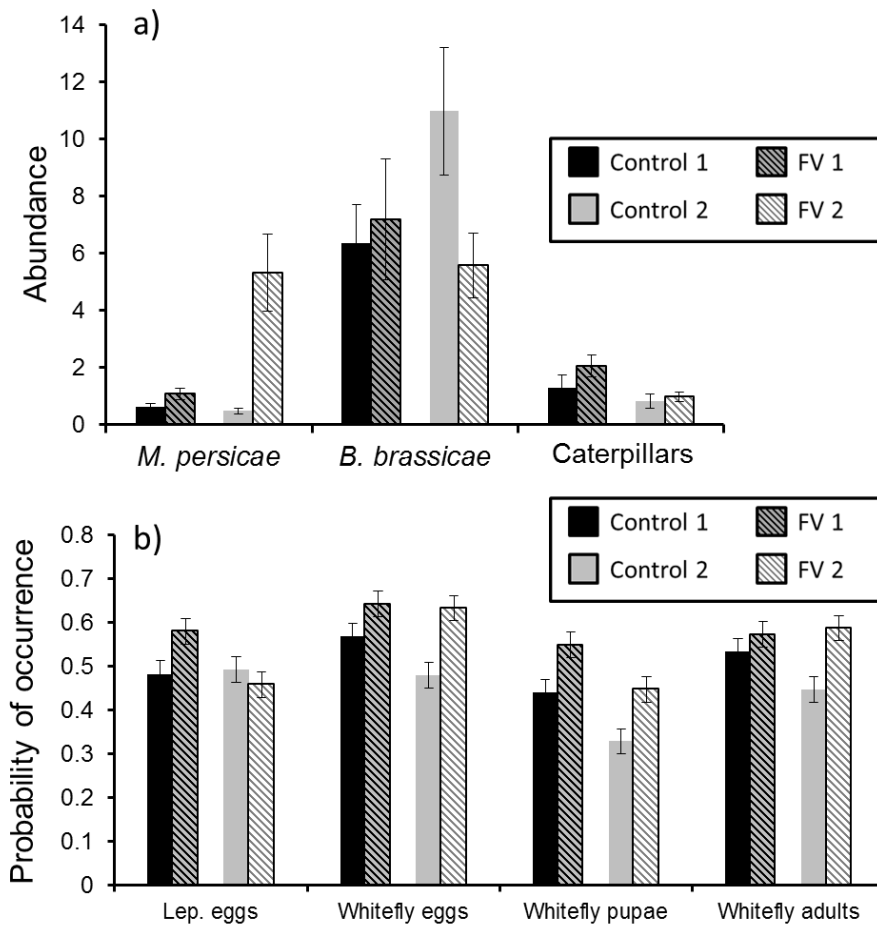
481

482 Figure 1. Mean pest abundance (a) and occurrence frequency (b) in control and FV plots as a function

483 of the sampling session. Circles: block 1, triangles: block2. Full line: control plots, hatched line: FV plots.

484 Error bars represent standard errors over cabbages. Note that the y-axes differ.

485



487

488

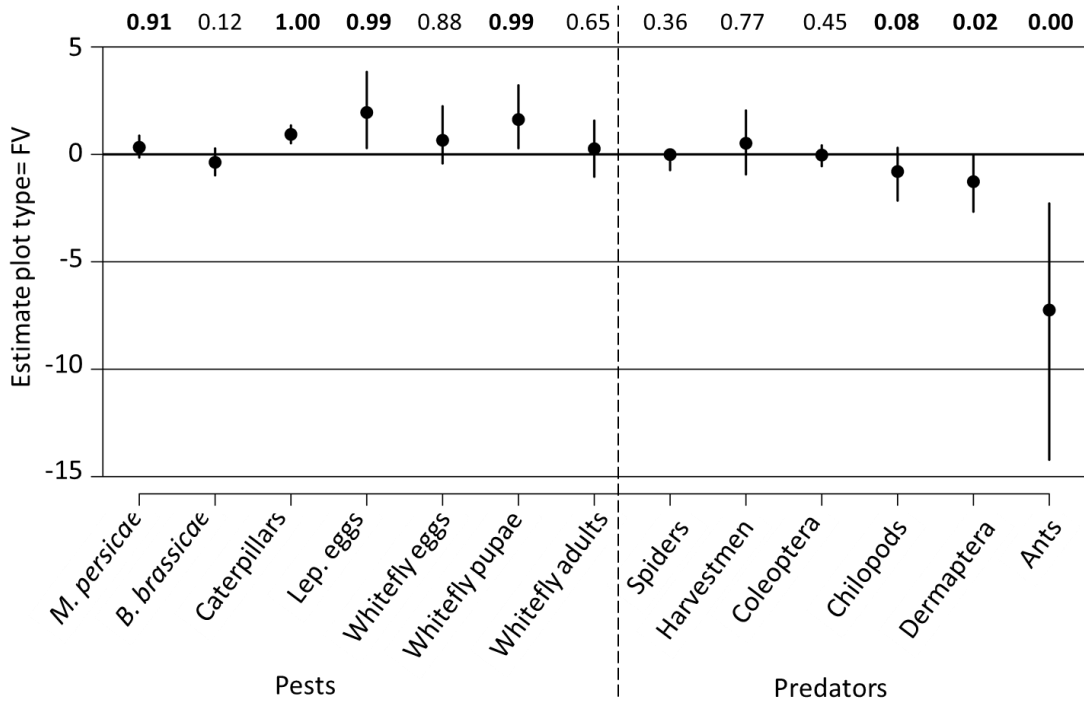
489 Figure 2 Mean pest abundance (a) and occurrence frequency (b) in control and FV plots. Black: block

490 1, grey: block2. Filled: control plots, hatched: FV plots. Error bars represent standard errors over

491 cabbages.

492

493

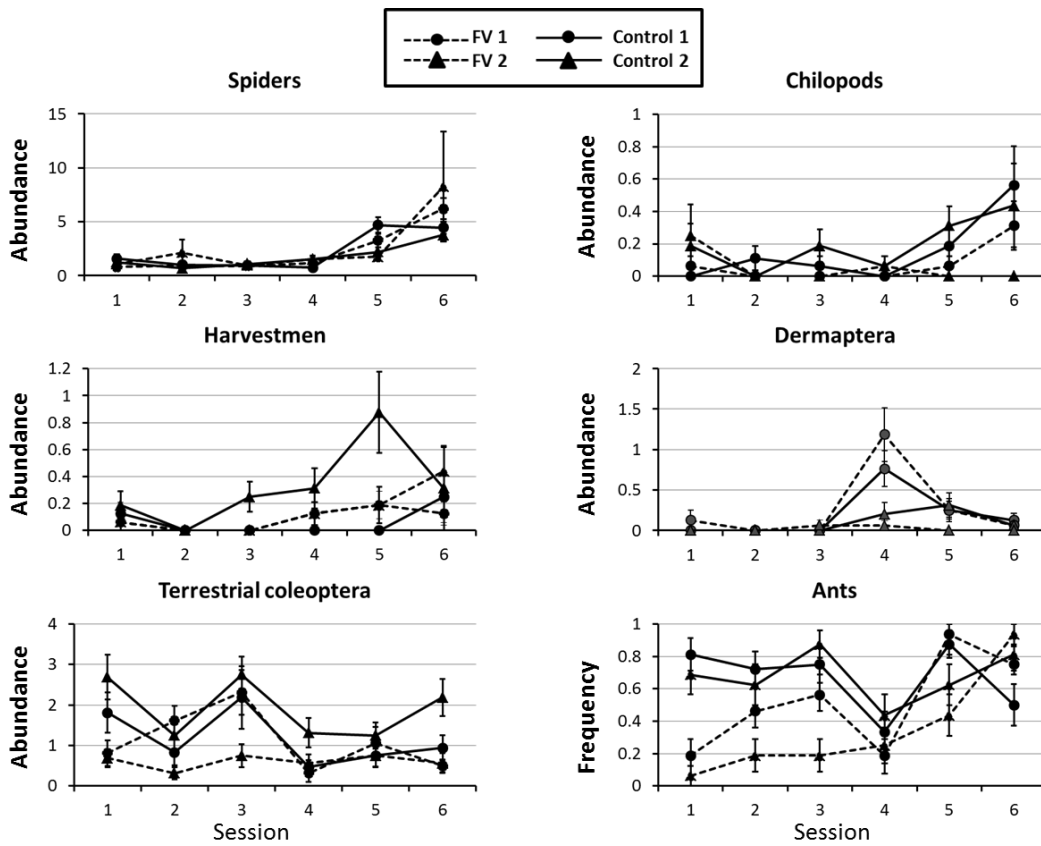


495

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

501

502
503
504

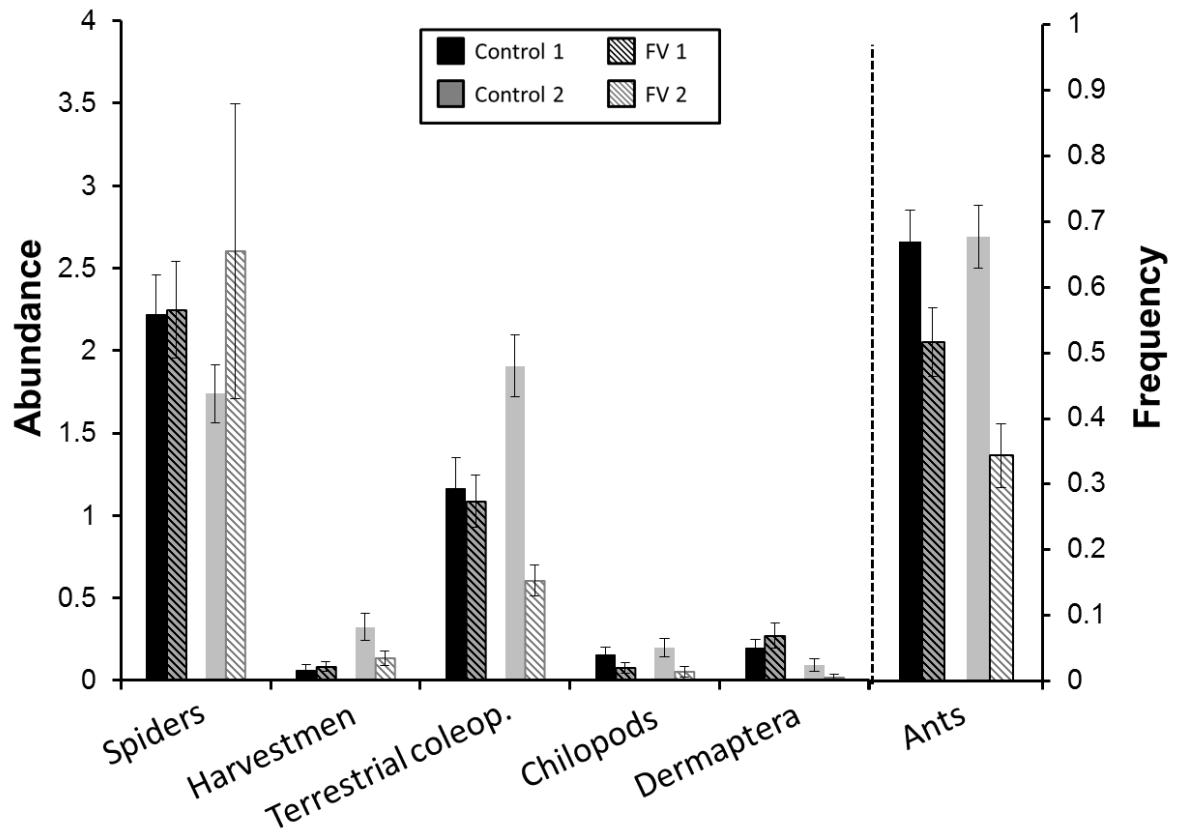


505

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

509

510
511
512



513
514
515
516

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