

1 **The behaviour of hoverfly larvae (Diptera, Syrphidae) lessens the effects of floral**  
2 **subsidy in agricultural landscapes**

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18 Running head: Scale mismatch in conservation biological control

19

20 **Abstract**

21 Modern agricultural landscapes favour crop pests: herbivores benefit from resource  
22 concentration and/or the absence of natural enemies in large areas of intensively farmed fields  
23 interspersed by small fragments of natural or non-crop habitats.

24 Conservation biological control (CBC) aims at increasing the functional diversity of  
25 agricultural landscapes to make them more hospitable to natural enemies, and less to  
26 herbivores. Although natural enemies readily respond to this management, very few studies  
27 assess if they succeed in effectively protecting crops.

28 We set up a field experiment to study if an ecological infrastructure varying in size and  
29 consisting of the provision of floral resources at the centre of lettuce plots would influence the  
30 number of eggs laid by hoverflies, and ultimately the control of lettuce aphids. We found that  
31 the hoverfly females lay more eggs in the plots with the larger flower resource compared to  
32 the control. However, this response had no impact on the abundance of aphids on the lettuces.

33 We designed two laboratory experiments to understand this absence of response. We found  
34 mutual interference between hoverfly larvae, and suggest it may undermine the biological  
35 control of aphids.

36 This mismatch between landscape management and the response of hoverflies indicates CBC  
37 should take into account insect behaviour, particularly their response to conspecific density,  
38 additionally to landscape ecology.

39

40 **Keywords:** conservation biological control, hoverfly, *Episyrphus balteatus*, *Melangyna*  
41 *novaezelandiae*, *Melanostoma fasciatum*, aphids, floral subsidy, mutual interference.

42 **Introduction**

43 Modern agricultural landscapes display large areas of intensively farmed fields interspersed  
44 by small fragments of natural or non-crop habitats (1-3). Crops are susceptible to pest because  
45 arable lands are frequently disturbed by cropping practices that impede the development of  
46 food webs that may deliver pest regulation (4-6). Herbivorous insects can emigrate from  
47 refuges in crop or non-crop habitats and colonize new crops (4, 7), eventually benefiting from  
48 the spatial concentration of their host-plants (8, 9). Natural enemies have lower dispersal and

49 reproductive rates; they are disadvantaged if non-crop refuges are rare or absent, and too far  
50 from the crops (10). Herbivores may therefore experience an enemy free space (11, 12); that  
51 may explain why farmers tend to use more insecticides in simplified landscapes (13, 14) but  
52 see (15).

53 Conservation biological control (CBC) aims at correcting the above mentioned imbalances in  
54 favour of herbivores by managing agricultural landscapes to make them more hospitable to  
55 natural enemies (5, 16-18). Ecological infrastructures are added to agricultural landscapes to  
56 provide natural enemies either with shelters to survive adverse conditions, alternative sources  
57 of prey/hosts or nectar and/or pollen (16, 19). Therefore, a stronger numerical response of  
58 natural enemies to prey, and a better synchrony between the arrival of prey and natural  
59 enemies are anticipated. This should lead to efficient biological control of pests (20).

60 Natural enemies have a strong positive response to management practices that increase  
61 landscape complexity (11, 16, 21). However, very few studies assess if this positive response  
62 translates into crop protection (11, 22-25). The few that went as far as measuring the  
63 relationships between landscape complexity, natural enemies and crop protection produce  
64 contradictory results that are not easily explained (26-28).

65 Four knowledge gaps are frequently invoked for this absence of pattern: the relative  
66 importance of emigration and immigration of natural enemies between crops and non-crop  
67 habitats, the lack of information on the birth and death rate of natural enemies in the various  
68 compartments of the mosaics of habitats, the effect of crop management practices on the  
69 above mentioned processes, and finally the timing, frequency and amplitude of movement  
70 between non-crop and crop habitats (3, 10, 22, 27).

71 To contribute to this debate we firstly set up a field experiment to assess the effects of the  
72 abundance of natural enemies while controlling for the confounding effects of all the  
73 processes related to emigration and immigration between the various compartments of the  
74 agro-landscape. To manipulate the abundance of natural enemies, we provided floral subsidy  
75 to aphidophagous hoverflies (Diptera, Syrphidae) by planting buckwheat (*Fagopyrum*  
76 *esculentum* Moench) at the centre of lettuce plots, and we also varied the area of this subsidy.  
77 In this manner, all the lettuces were equally closed to buckwheat. We expected that larger  
78 subsidy would be positively correlated to the presence of more eggs of hoverflies on the  
79 surrounding lettuces infested with aphids. As a consequence, we were expecting fewer aphids

80 on the lettuces planted around the larger subsidy of buckwheat. Secondly, we assessed in the  
81 laboratory if the larval density affected the behaviour of hoverfly larvae. We anticipated that  
82 the larvae at high density would kill fewer aphids as a result of their interactions with other  
83 larvae. Mutual interference reduces predation efficiency of individual natural enemies and is  
84 one of the major ecological limits to biological control (29). It occurs when the amount of  
85 intraspecific interactions increases with the density of natural enemies up to a point where it  
86 reduces the time available for searching and handling prey, eventually triggering aggressive  
87 behaviour and cannibalism (29, 30).

88 We selected this biological model because aphids are among the major pests for several crops  
89 of economic importance in temperate regions, including lettuces (31). Hoverflies are natural  
90 enemies that have an influence on aphid abundance (32), and they respond to ecological  
91 infrastructures such as floral subsidies (33-36).

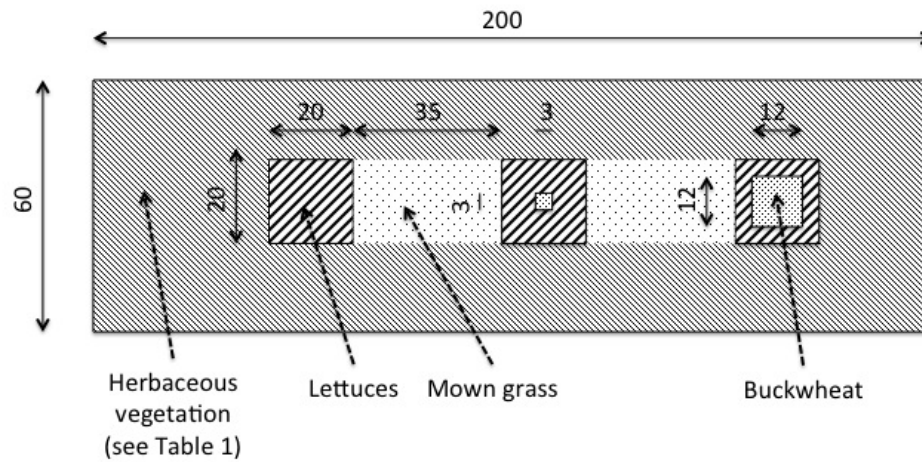
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### 93 **Material and methods**

#### 94 *Incidence of added floral resources on hoverfly and aphid abundance in the field*

95 To assess the influence of supplementary pollen and nectar on the abundance of hoverflies  
96 and aphids, a field experiment was set up at the Horticultural Research Area (HRA) and at  
97 Iverson Field (IF), on the campus of Lincoln University, New Zealand. The HRA comprises  
98 26 ha of land divided into 19 blocks, and IF consists of an area of 13 ha divided into 14  
99 blocks. Five blocks of similar dimensions at the HRA and one at IF were used (Table 1). The  
100 5 blocks at the HRA were located within a circle of 370 m while IF's was 500 m away to the  
101 Southwest. On December 15, 2005, at the centre of each of these six blocks, a 130 x 20 m  
102 strip was prepared for sowing. Then, in each of these strips, three 20 x 20 m plots were  
103 delineated and separated from each other by 35 m (Fig 1). A mixture of grass species was  
104 sown in the areas between the plots. Later, the turf was regularly mown. Those strips were  
105 surrounded by herbaceous vegetation briefly described in Table 1. One of the following  
106 treatments was randomly allocated to each 20 x 20 m plot: 1) a control only consisting of  
107 lettuces (*Lactuca sativa* L. cv. Target) planted at a spacing of 45 cm x 90 cm; 2) lettuces  
108 planted as above but the centre of the plot was occupied by a 3 m x 3 m area of buckwheat  
109 (*Fagopyrum esculentum* Moench cv. Katowase), and 3) lettuces plus a 12 m x 12 m area of

110 buckwheat at the centre of the plot. Buckwheat provides nectar and pollen, which adult  
111 hoverflies readily use (34). It was sown on December 28, 2005 and January 13, 2006; the  
112 lettuces were transplanted on January 19 and 20, 2006. This experimental design allows  
113 testing if CBC is dependent on the abundance of floral resources while controlling for the  
114 confounding issue of natural enemy movement between non-crop and crop habitats.



115 Buckwheat was indeed sown at the centre of the lettuce plots and all the lettuces were equally  
116 distant from the flowers.

117

118 **Fig 1** Plan of one experimental block, showing the dimensions and location of lettuces and  
119 buckwheat plots.

120

121

122 **Table 1** The geographical coordinates, dimensions, type of vegetation around the  
 123 experimental area, and information on the field enclosure of the 6 experimental fields.

Plot name	Geographical coordinates	Dimensions (m)	Vegetation	Field enclosure
<b>Horticultural Research Area</b>				
H2	-43°38'47.87'' 172°27'12.95''	200 x 60	Grasses	Located side by side within a poplar ( <i>Populus nigra Italica</i> ) hedgerow (approximately 20 m height)
H3	-43°38'47.53'' 172°27'15.58''	200 x 60	Tall and dry grasses (about 60 cm height)	
H11	-43°38'53.87'' 172°27'20.12''	200 x 60	Dry grass on the West side ; vine yard on the East side	Surrounded by a 20 m height poplar hedgerow
H13	-43°38'51.30'' 172°27'28.88''	200 x 60	Tall and dry grasses (about 60 cm height)	Located side by side within a poplar hedgerow (approximately 20 m height)
H14	-43°38'54.09'' 172°27'29.59''	200 x 60	Grasses	
<b>Iverson Field</b>				
I13	-43°38'53.56'' 172°27'47.62''	185 x 40	A mixture of grasses and alfalfa	Open field with the exception of a 20 m height poplar hedgerow on the Northern side

124 Plots were kept free of weeds by hoeing and were visited every day to record the presence of  
 125 hoverflies. Adult hoverflies were seen for the first time on February 15, 2006, when  
 126 buckwheat started to flower. Sampling for aphids, hoverfly eggs and larvae started the next  
 127 day. Six lettuces were randomly selected in each plot and their shoot carefully cut at ground  
 128 level on February 16, 2006. They were individually put in large plastic bags and brought back

129 to the laboratory. There, each leaf was carefully cut off, unfolded and inspected. The aphids,  
130 and the hoverfly eggs and larvae were counted. This was repeated on February 27, March 13,  
131 and March 22 when the lettuces reached marketable size.

132 The numbers of aphids, syrphid eggs and larvae were analysed using General Linear Mixed  
133 Models with a Poisson distribution (package lme4 in R 2.11.1). The added floral resource (no  
134 buckwheat, small or large area of buckwheat) was a fixed factor. The weeks and blocks were  
135 random factors. The weeks were pseudoreplications within each treatment nested in the  
136 blocks. *A priori* orthogonal contrasts were implemented to compare the floral subsidies (large  
137 and small) to the control, and then the large subsidy to the small (37).

138 *The behaviour of hoverfly larvae in the laboratory*

139 *Insect choice and culture*

140 The numerical response of hoverfly females to aphids in the presence of floral subsidy is  
141 expected to lead to high density of larvae. Two experiments were set up in the laboratory to  
142 see whether mutual interference would appear in such circumstances.

143 The two dominant species of hoverflies in the experimental fields were *Melangyna*  
144 *novaezelandiae* (Macquart) and *Melanostoma fasciatum* (Macquart). However, we never  
145 succeeded in developing a stable and reliable culture of these species in the laboratory to  
146 support the experiments. Therefore, we decided to work with *Episyrphus balteatus* De Geer.  
147 This choice is firstly justified by the ease of rearing this species, secondly by its phylogenetic  
148 relatedness to the two species observed in the field, suggesting ecological resemblance (38-  
149 40). *M. novaezelandiae*, *M. fasciatum* and *E. balteatus* belong to the subfamily Syrphinae ; *E.*  
150 *balteatus* and *M. novaezelandiae* are the most closely related because they are members of the  
151 tribe Syrphini while *M. fasciatum* belongs to the Bacchini tribe (41). Because phylogenetic  
152 conservatism of interactions occurs in many taxa (42), we believe that knowledge on the  
153 behaviour of *E. balteatus* in the laboratory will prove useful to predict how *M.*  
154 *novaezelandiae* and *M. fasciatum* behave in similar conditions.

155 Adult *E. balteatus* were reared in mesh cages (40 x 75 x 50 cm) in a greenhouse, from April  
156 to September 2006. Hoverflies were offered every other day fresh flowers from the field in  
157 water. Broad bean plants (*Vicia faba* L.) infested with pea aphids (*Acyrtosiphon pisum*  
158 Harris) were periodically introduced into the cages to induce the hoverflies to lay eggs. The

159 beans were checked every other day and the leaves with eggs were removed and kept in the  
160 laboratory at  $21 \pm 1^\circ\text{C}$ , under a photoperiod of LD 16:8 h. Larvae were reared in the same  
161 environmental conditions, in  $175 \text{ cm}^3$  plastic boxes that contained a piece of corrugated filter  
162 paper to reduce the frequency of encounter and therefore the risks of cannibalism. Three times  
163 a week the larvae were fed an excess of mixed instars of *A. pisum*. Two cut stems of broad  
164 bean were added to each box to improve the survival of the aphids. As hoverfly larvae are  
165 active at night, eggs were incubated and larvae reared under a reversed photoperiod to allow  
166 for observations during normal working hours. They were kept in darkness from 8:00 to 16:00  
167 and all the observations were made under a red light.

168 Experiment 1. The effects of aphids and the density of hoverfly larvae on larval dispersal

169 If mutual interference happens, we expect larvae to become more active and to disperse when  
170 their density relative to prey availability increases. To assess the tendency of larvae to  
171 disperse in the presence of conspecifics and different numbers of prey, a third instar larva (the  
172 “focal larva”) of *E. balteatus*, which had been starved for 2 h prior to the experiment, was  
173 placed at the centre of a 15 cm diameter Petri dish on a 3 cm piece of broad bean stem. Then,  
174 second instar larvae were gently put on the piece of broad bean stem in four treatments  
175 described below and repeated 20 times: 1) two conspecific second instar larvae, 2) two second  
176 instar larvae and 40 pea aphids, 3) eight second instar larvae, and 4) eight second instar larvae  
177 and 40 pea aphids. Larvae of the second instar were used to distinguish the focal larva from  
178 those just there to manipulate the density. Every 30 minutes for 2 hours, we recorded if the  
179 focal larvae were on the broad bean stem or not. The experiment was performed between 8:00  
180 and 16:00 at  $21^\circ\text{C}$ , and under a photoperiod of LD 16:8 h.

181 The data were binary and there was temporal pseudoreplication. We used two Generalised  
182 Linear Mixed Models with binomial errors (package lme4 in R 2.11.1) the first had an  
183 interaction between the two independent variables (numbers of larvae, and presence/absence  
184 of aphids) while there was no interaction in the second. We tested significance by deletion of  
185 the interaction, and compared the change in deviance with a  $\chi^2$  test (Crawley, 2007).

186 Experiment 2. Mutual interference between *E. balteatus* larvae

187 A 3 cm piece of broad bean stem was placed at the centre of a 15 cm diameter Petri dish,  
188 along with 2, 8, 16 or 32 second instar larvae of *E. balteatus*, and 40 similar sized pea aphids.



189 Then, a third instar larva of *E. balteatus* (the “focal larva”) that had been starved for 2h prior  
190 to the experiment was gently put on the stem. The Petri dishes were continuously and  
191 sequentially observed for 30 min and the number of aphids the focal larvae attacked was  
192 recorded. Each treatment was repeated 10 times at 21°C, and under a photoperiod of LD 16:8  
193 h, between 8:00 and 16:00. The same observer carried out three replicates of each treatment  
194 simultaneously. The searching efficiency of third instar larvae (the number of aphids  
195 captured/larva in 30 min) was calculated. The regression of the log of the searching efficiency  
196 on the log of the larval density was calculated. The slope  $m$  is expected to vary from 0 to -1  
197 indicating a growing mutual interference (30).

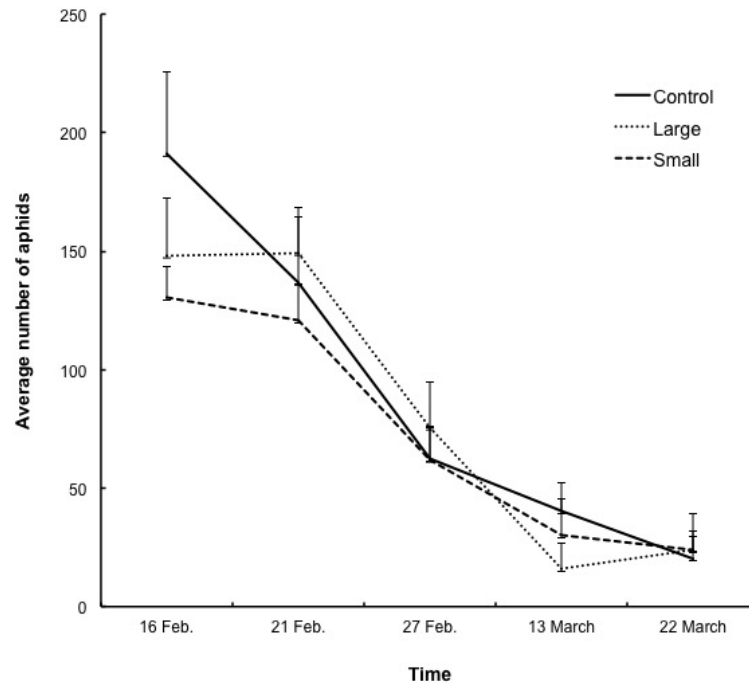
## 198 **Results**

### 199 *Incidence of added floral resources on hoverfly and aphid abundance in the field*

200 We recorded 51,745 lettuce aphids *Nasonovia ribisnigri* (Mosley) and 284 black bean aphids  
201 *Aphis fabae* (Scopoli) on the lettuces throughout the sampling period. We counted 9,257 and  
202 798 hoverfly eggs and larvae respectively. We were not able to assign them to the species but  
203 we only spotted adults of *M. novaezealandiae* and *M. fasciatum*.

204 The mean number of aphids per lettuce was higher at the beginning of the sampling campaign  
205 and declined thereafter (Fig 2). Throughout the sampling period the lettuces hosted similar  
206 numbers of aphids whether they grew in a plot without or with buckwheat (Contrast<sub>Control versus</sub>  
207 Treatment plots: z value=1.240; P=0.215; Contrast<sub>Large versus small plots</sub>: z value=0.510; P=0.610). They  
208 were equally infested on the last date when they reached marketable size (Contrast<sub>Control versus</sub>  
209 Treatment plots: z value=0.459; P=0.646; Contrast<sub>Large versus small plots</sub>: z value=-0.737; P=0.461).

210 Some hoverfly eggs were already recorded on February 16. Over the entire campaign, the  
211 number of eggs on the lettuces of the treatment plots tended to be more abundant than in the  
212 control. However, the difference was not significant (Contrast<sub>Control versus Treatment plots</sub>: Z value=-  
213 1.860; P=0.063; Fig 3a). The lettuces from the plots with the larger area of buckwheat at the  
214 centre had significantly more eggs than those from the plots with the small area of buckwheat  
215 (Contrast<sub>Large versus small plots</sub>: z value=2.803; P=0.005; Fig 3a).

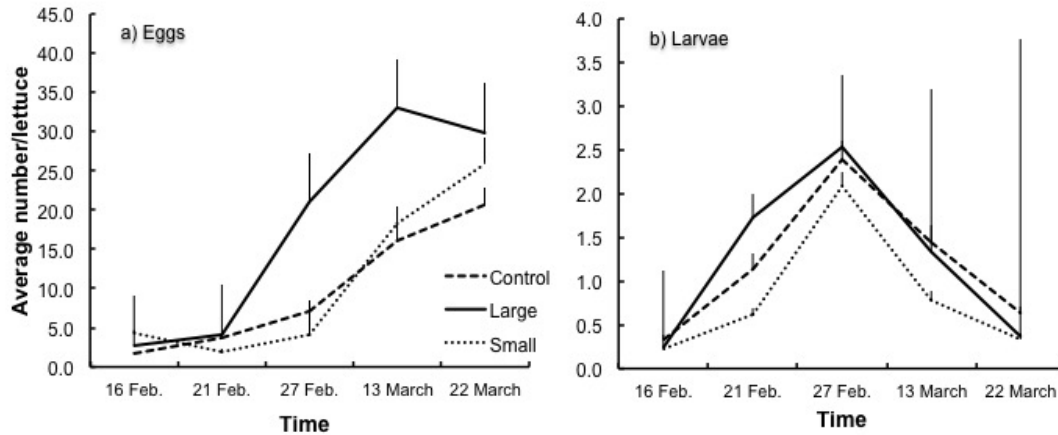


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217 **Fig 2** The average number (SD) of aphids on the lettuces of the experimental plots with a  
218 small (3x3 m) or large (12x12 m) area of buckwheat at the centre, or without buckwheat  
219 (control) at five successive dates. For clarity, one-sided SD are represented.

220 Hoverfly larvae peaked in abundance on February 27, 2006. The number of larvae per lettuce  
221 was on average an order of magnitude smaller than the number of eggs. The average number  
222 of hoverfly larvae per lettuce in the control plots was not significantly different from the  
223 numbers observed in the treatment plots (Fig 3b). However, the large plots had significantly  
224 more larvae than the small plots (Contrast<sub>Control</sub> versus Treatment plots: z value=-1.416; P=0.157;  
225 Contrast<sub>Large</sub> versus small plots: z value=2.170; P=0.030).

226



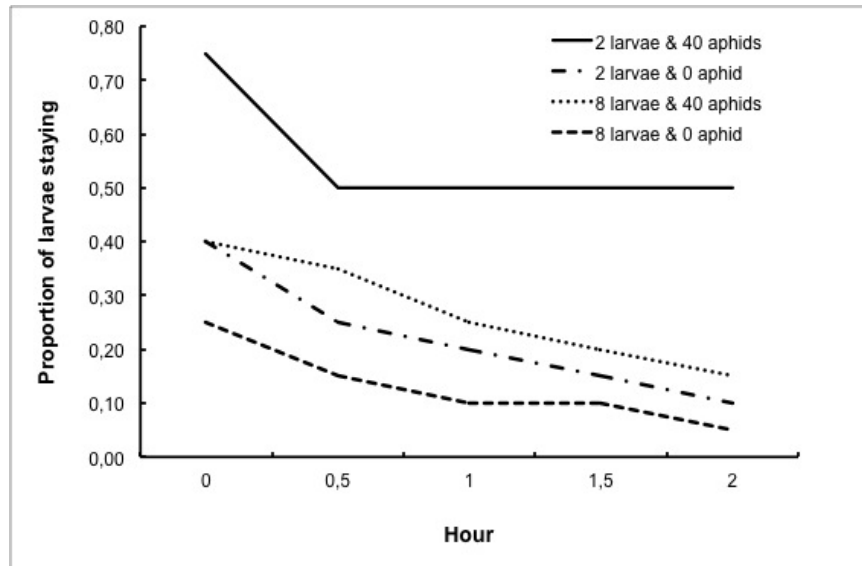
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228 **Fig 3** The average number (SD) of hoverfly eggs (a), and larvae (b) per lettuce in the  
229 experimental plots with a small (3x3 m) or large (12x12 m) area of buckwheat at the centre,  
230 or without buckwheat (control) at five successive dates. For clarity, one-sided SD are  
231 represented.

232 *The behaviour of hoverfly larvae in the laboratory*

233 Experiment 1. The effects of aphids and the density of hoverfly larvae on larval dispersal

234 In the first 30 min of the experiment in which the third instar larva interacted with 2 second-  
235 instar larvae and 40 pea aphids, the proportion of third instar larvae on the broad bean  
236 dropped from 80 to 50%, and then remained at that level for the rest of the experiment. On the  
237 contrary, in the three other treatments, the proportions were much lower in the beginning:  
238 40% and even 25% in the treatment with 8 second-instar larvae and no aphids. Then, it  
239 steadily declined over the course of the experiment. After 2 h, only 5 to 15% of the third  
240 instar larvae, depending on the treatment, still were on the broad bean (Fig 4).



241

242 **Fig 4** The proportions of third-instar larvae of *Episyrrhus balteatus* staying on a piece of  
243 broad bean stem in the presence of 2 second-instar conspecific larvae, 2 second-instar  
244 conspecific larvae and 40 pea aphids, 8 second-instar conspecific larvae or 8 second-instar  
245 conspecific larvae and 40 pea aphids throughout an observation period of 2 hours.

246 The interaction between the presence/absence of aphids and the density of second instar  
247 larvae was not significant (z value=-1.674; P=0.094). The presence of aphids, contrary to the  
248 number of 2<sup>nd</sup> instar larvae, had a significant effect on the number of 3<sup>rd</sup> instar larvae staying  
249 on the broad bean stem (Presence/absence of aphids: z value=2.972; P=0.003; N<sup>r</sup> of 2<sup>nd</sup> instar  
250 larvae: z value=-0.426; P=0.671).

#### 251 Experiment 2. Mutual interference between *E. balteatus* larvae

252 The value of the attack rate of the third-instar larvae gradually declined when the density of  
253 second instar larvae increased (Table 2).

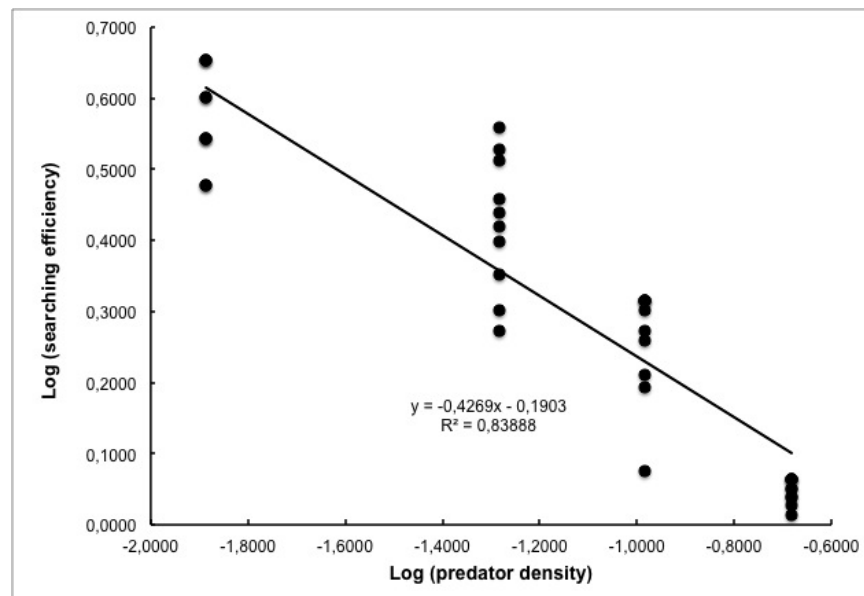
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255 **Table 2** The mean number of aphids eaten, and the attack rate (mean number of aphids  
 256 eaten.larva<sup>-1</sup>.30 min<sup>-1</sup>) by third-instar larva of *Episyrphus balteatus* in the presence of 2, 8, 16  
 257 or 32 second-instar conspecific larvae

Nr of 2 <sup>nd</sup> -instar larvae	Mean nr eaten (min-max)	Attack rate
2	7.6 (6-9)	2.53
8	21.7 (15-29)	2.41
16	29.3 (19-33)	1.72
32	35.7 (33-37)	1.08

258

259 The slope of the relationship between the log of the searching efficiency (the number of  
 260 aphids captured/larva/30 min) and the log of the predator density (Fig 5) is significantly  
 261 different from zero ( $y = -0.4269x - 0.1903$ ;  $F = 47.01$ ;  $df = 38$ ;  $P < 0.05$ ), which indicates the  
 262 existence of mutual interference between larvae.



263

264 **Fig 5** The searching efficiency (aphids captured.unit time<sup>-1</sup>.hoverfly larva<sup>-1</sup>) of third-instar  
265 larvae of *Episyrphus balteatus* as a function of the density of second-instar conspecific larvae

## 266 **Discussion**

267 In our field experiment, we observed more eggs of hoverflies on the lettuces planted around  
268 large floral patches of buckwheat than on the lettuces in the control. There was also a gradient  
269 in the egg numbers from the lowest in the control plots, intermediate in the plots with a small  
270 area of buckwheat to the highest in the plots with the largest area of flowers. Buckwheat is  
271 known to attract several species of hoverflies to which it provides nectar and pollen in  
272 quantity and quality (34, 43). Our results support the practice of planting sweet alyssum  
273 (*Lobularia maritima* (L.) Desv.) in organic lettuce fields to attract hoverflies (44-47). Our  
274 results also confirm that natural enemies respond positively to the provision of additional food  
275 sources in crop and non-crop habitats (21).

276 However, we observe that these higher numbers of eggs did not translate in higher numbers of  
277 larvae throughout the experiment or at the end, when the lettuces were harvestable. An  
278 explanation would be that hoverflies might be limited in the field by predation or cannibalism  
279 in a density-dependent manner (48, 49). Alternatively, mutual interference can be at the origin  
280 of the levelling out in the number of larvae (29).

281 We set up laboratory experiments to see whether hoverfly larvae develop mutual interference  
282 when their density becomes too important. We observed that the larvae of *E. balteatus* were  
283 highly mobile when aphids were rare. They displayed a strong mutual interference that  
284 reduces their searching efficiency for prey. Therefore, if our observations with *E. balteatus*  
285 are representative of the behaviour of the two dominant species recorded in our field  
286 experiment, as would suggest the theory on niche conservatism (Gomez et al. 2010), the  
287 collapse in the numbers of larvae that we observed in the field is likely to be due to the mutual  
288 interference between hoverfly larvae.

289 Finally, aphids were not less abundant on the lettuces around large areas of buckwheat than  
290 on those from the plots with only a small area of it or without buckwheat. The changes in the  
291 numbers of aphids throughout the field experiment were similar in the three treatments. Also,  
292 when the lettuces reached marketable size, the number of aphids per lettuces did not differ  
293 significantly across the three treatments, and was still much higher than the economical

294 threshold of damages (50). Contrary to a field cage experiment (Hogg et al., 2011) and a field  
295 experiment manipulating the number of hoverfly eggs on lettuces (51), our field experiment  
296 shows that an increased abundance of natural enemies in response to the provision of  
297 ecological infrastructures failed to reduce aphid abundance.

298 We did not design our field experiment with an applied perspective in mind. By placing  
299 squares of buckwheat at the centre of plots of lettuces we wanted to disentangle the influence  
300 of the abundance of floral subsidy from the many factors affecting the movement of those  
301 enemies from the locations of the subsidies to the crops throughout the landscape matrix.

302 In conclusion, actions undertaken to attract natural enemies nearby crops do not always  
303 succeed in reducing pest abundance under economic threshold of damage. According to  
304 knowledge and expertise accumulated so far, these actions deliver the expected results in  
305 terms of predator community composition and population abundance (Landis et al. 2000;  
306 Bianchi et al. 2006; Chaplin-Kramer et al. 2011). However, they do not translate in a  
307 predictive way in the biological control of pests because they are curtailed by evolutionary  
308 trade-offs that shape the life history of plants and insects.

309 Recent reviews suggest that predictive and efficient conservation biological control is still out  
310 of reach for two main kinds of reasons: firstly, the lack of understanding in the movements of  
311 natural enemies between the various habitats of agricultural landscape, and secondly the  
312 difficulty in estimating demographic rates of natural enemies in relation to habitat types (3,  
313 10, 27, 52). However, these knowledge gaps do not explicitly refer to the behavioural  
314 decisions made by individual natural enemies searching for preys or hosts. Without clear  
315 insight on the decisions modulating feeding and non-feeding interactions between natural  
316 enemies and their preys/hosts the relationship between the sum of individual behaviour and  
317 population dynamics will remain out of reach (53). From a pest control point of view, it is  
318 probably more important to know how species interact rather than the number and diversity of  
319 species in communities (6). We believe that the absence of a food-web perspective coupled to  
320 behavioural ecology is probably a largely underestimated knowledge gap that affects the  
321 ability to predict the relationship between landscape management and biological control (6,  
322 54). The mismatch between landscape management and the impact of this management for  
323 crop level protection does not mean that biological control is not feasible. It simply indicates  
324 it still is a complex issue (55).

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