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Flowering cover crops in winter increase pest control but not trophic link diversity

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Abstract

1 In agrosystems, the increase in non-crop plant diversity by habitat management in or around
2 arable fields contributes to improved Conservation Biological Control. During winter, plant
3 flower are often used as monospecific ground cover and are expected to die before flowering
4 as a result of recurrent frost events. Decreases in minimal temperature due to climate change
5 offers new possibilities for plants used in such sown cover crops to mature and flowers.
6 Changes in plant phenology thus constitute an important environmental change with expected
7 consequences for ecosystem functioning, such as biological control. In Brittany, where winter
8 agricultural landscape is dominated by a mosaic of cereal and sown cover crops, we assessed
9 the consequences of mustard (*Synapis alba*) flowering cover crops (MFCC) on aphid
10 parasitism and food web structure in plots adjoining cereal crops, in contrast to plots close to
11 spontaneous non-crop plants (SNCP) of the same field. Overall, aphid parasitism rate at the
12 field scale was strong (60-70%), being 13% higher adjacent to the MFCC than closer to
13 SNCP. In addition, there was no change in food web structure between the two distinct zones,
14 enabling us to hypothesize that MFCC mostly constituted an alimentary patch. The positive
15 effect on parasitism rate was significant but weak, as floral nectar of mustard is known to be
16 of poor quality for parasitoids. Results highlight the potential advantages of adapting practices
17 in response to actual changes in agrosystems. Increase floral diversity in sown cover crops
18 could constitute a complementary method in management programs, by providing more
19 alternative food resources, alternative hosts, and climatic refuge to enhance the Conservation
20 Biological Control of parasitoid populations.

21

22 **Key words:** Aphid-Parasitoids trophic system; Biological Control; Sown flowering cover
23 crops; *Synapis alba*; Winter

24 **1. Introduction**

25 The adoption of wide scale agriculture and associated practices by farmers over recent
26 decades has led to drastic changes in both landscape structure and biotic interactions
27 (Redclift, 1989; Singh, 2000; Stoate et al., 2001; Tsiafouli et al., 2015), *e.g.* through the
28 overall decrease in landscape complexity and biodiversity (Flynn et al., 2009; Matson, 1997;
29 Tscharnatke et al., 2005). The increase of cultivated areas over semi-natural habitats (*e.g.*
30 edges, meadows or woods) has resulted in small fragmented non-cropped habitats showing
31 reduced biodiversity, notably across plant communities (Krause et al., 2015; Van Meerbeek et
32 al., 2014; Wesche et al., 2012). This led to low arthropod diversity with modification of
33 trophic interactions between plants and arthropods and/or within arthropod communities
34 (Altieri, 1999; Haddad et al., 2009; Scherber et al., 2010). Such changes have altered, what is
35 referred to as the ‘pest complex system’ (Matson, 1997) and the biocontrol services provided
36 by natural enemies, with an increase in specialist phytophagous agricultural pests, but a
37 reduction in the abundance and diversity of predators and parasitoids (Cardinale et al., 2011;
38 Meehan et al., 2011; Scherber et al., 2010).

39 To counterbalance this trend, habitat management programs in Conservation Biological
40 Control (CBC) aim to enhance natural biodiversity by adaptive management promoting
41 indigenous plant diversity and habitat complexity (Landis et al., 2000; Perović et al., 2017;
42 Tscharnatke et al., 2007). The increase of non-crop plants surrounding arable fields contributes
43 to improved pest regulation by natural enemies at the field scale (Balzan and Moonen, 2014;
44 Tscharnatke et al., 2005; Tschumi et al., 2016a; Wratten et al., 2012). This practice induces an
45 enhanced trophic system stability which reduces the intensity of pest outbreaks (Haddad et al.,
46 2011). Grassy margin vegetation or flowering strips surrounding crops act to support natural
47 enemy communities by constituting complementary patches with additional plants and habitat
48 diversity. Natural enemies then migrate from these semi-natural habitats to the crops. First,

49 these patches can improve natural enemy survival by providing alternative habitats against
50 anthropic crop disturbances (Alignier et al., 2014; Ramsden et al., 2015; Thies et al., 2005). In
51 addition, they can provide additional resources such as pollen, carbohydrates, or alternative
52 prey for predators and hosts for parasitoids, thus improving trophic system complexity and
53 population dynamics in adjoining crops (Wäckers and van Rijn, 2012). Regional spatial scales
54 may also be considered, since increases in the proportion of these patches within the
55 agricultural landscape can act to increase biological control efficiency, notably because they
56 constitute refuges and as a consequence, sources from which natural enemies may emigrate
57 (Alignier et al., 2014).

58 Changes to plant phenology during winter as a result of climate change have been highlighted
59 (Menzel et al., 2006; Parmesan, 2006) at the local and regional scale (Nordli et al., 2008), for
60 example, with advances in bud burst (Badeck et al., 2004) or first flowering date (Fitter,
61 2002). In their study, Uelmen et al., (2016) demonstrated changes in the phenological
62 synchrony between caterpillars and trees in response to warming temperatures during winter.
63 Such changes are likely to produce cascading effects on higher trophic levels and alteration of
64 ecosystem functioning may be expected. However, few studies have focused on plant-
65 arthropod interactions during winter and none in the context of climate change. Therefore,
66 there is a need to unravel the use of semi-natural and cultivated habitats by arthropods during
67 formerly considered unfavorable seasons, such as winter in temperate areas (Gurr et al.,
68 2017), for which warmer temperatures are already observed or predicted (Räisänen et al.,
69 2004). In this context, modifications of plant-insect interactions in agroecosystems may
70 become a new challenge for CBC over seasons.

71 In Brittany (Western Europe), the intensive agricultural landscape during the autumn/winter
72 season is dominated by a mosaic of cereal crops and flowering cover crops. The later are used
73 to prevent soil erosion and to fertilize the soil prior to the planting of corn cultures.

74 Theoretically, these winter sown-cover crops are destroyed by freezing during the winter.
75 However, during the past two decades, winter temperatures have increased and there has been
76 a reduction in the number of days in which temperatures have dropped below 0°C (see Fig1
77 (Andrade et al., 2016). Benefits from sown-cover crops are not documented compared to the
78 benefits of grassy margin vegetation or sown flowering strips (Holland et al., 2016). In
79 addition, the phenology of flower species used in winter sown-cover is impacted by rising
80 temperatures and some species are flowering during the winter, as early as December when
81 there is no frost. Considering the benefits provided by floral resources to natural enemies
82 (Tschumi et al., 2016a, 2016b), such environmental changes may favour their activity and
83 population dynamics resulting in increased early pest regulation.

84 During winter, three aphid species are predominant on cereal crops in the cereal fields of
85 North-Western France (Rabasse et al., 1983): *Rhopalosiphum padi* (Linnaeus), *Sitobion*
86 *avenae* (Fabricius) and *Metopolophium dirhodum* (Walker). The natural enemy guild of aphid
87 pests in cereal crops is composed mainly of Aphidiine parasitoids belonging to the *Aphidius*
88 genus (Krespi et al., 1997), with other aphid predators being in a state of diapause. Oceanic
89 temperate climate allows species involved in this trophic system to remain active during
90 autumn/winter, even at lower activity levels (Andrade et al., 2016, 2015; Dedryver, 1981;
91 Polgar, 1995). Parasitoid communities may benefit from changes in sown-cover plants
92 phenology during this harsh period. Compartmentalization in aphid-parasitoid networks have
93 been shown to be high between crop and non-crop habitats (Derocles et al., 2014; Vialatte et
94 al., 2005), although parasitoids are more prone to foraging in neighbouring crops as opposed
95 to in margin vegetation later in winter (Macfadyen et al., 2015). Sown flowering cover crops
96 may provide carbohydrate, alternative hosts, better climatic refuges for cereal parasitoids, and
97 increase parasitoid activity and/or survival. In addition, according to the diversity-trophic
98 structure hypothesis (Hutchinson, 1959; Knops et al., 1999), each crop, with its own

99 arthropod community, may increase trophic system complexity and improve pest regulation
100 (Haddad et al., 2009). This is due to functional redundancy resulting from greater parasitoid
101 diversity (Peralta et al., 2014; Vos et al., 2001) or as a result of changes to the intra-guild
102 interactions with the presence of alternative hosts and modification of apparent competition
103 (Raymond et al., 2016).

104 Aphid-Parasitoid trophic systems have been used largely as a model system to assess
105 biodiversity change owing to their ecology (Gagic et al., 2011; Roschewitz et al., 2005;
106 Tylianakis et al., 2007). In particular, they are used to evaluate the influence of neighbouring
107 crop habitats (Alignier et al., 2014; Macfadyen et al., 2015; Plečáš et al., 2014). In the current
108 study, we used such pest- enemy complex to assess potential benefits of change in sown
109 covers plant phenology on the biological control service under wintering conditions. In order
110 to evaluate the effects of the earlier flowering time of mustard (*Synapis alba*) flowering cover
111 crops (MFCC hereafter) on aphid pest control by parasitoids, the aphid-parasitoid food web,
112 relative aphid and parasitoid abundances and parasitoid sex ratio were compared between
113 cereal crop plots close to MFCC and close to spontaneous non-crop plants from grassy
114 margins (SNCP hereafter). The following hypotheses were explored to explain change in
115 aphid parasitism: *(i)* The increase of trophic system complexity positively impacts aphid
116 regulation close to MFCC due to functional redundancy or changes in intra-guild interactions.
117 *(ii)* MFCC may result in higher parasitoid relative abundances (higher parasitism rates) and
118 female biased sex ratios (more favorable population dynamics) by providing more favorable
119 environmental conditions than SNCP: two mechanisms are possible, firstly a higher
120 vegetation cover may lead to buffered micro-climatic conditions, or more plants may offer
121 increased floral food, host honeydew and/or host access).

122 **2. Materials and Methods**

123 **2.1 Study area and experimental design**

124 The study was carried out in three different locations near Rennes, France, in the “Zone
125 Atelier Armorique” (Long Term Ecological Research site, see Table 1 for GPS coordinates
126 and crop sizes). Among fifteen cereals crop fields selected in a first approach, only six were
127 retained (five wheat and one barley crops) as the others were not infested by aphids. Sampling
128 was performed on three dates during February 2016 as no aphids were found before the end of
129 January. Cereal crops were sown between September and October 2015 and had reached
130 approximately 20 cm in height (ranging from 10 to 30 cm) at the sampling time. MFCC were
131 sown in October or November in one side of the cereal crop and had reached approximately
132 1-1.20m in height and had been flowering since the beginning of December. SNCP were
133 composed of spontaneous non-crop grassy plants (without shrub or tree) in one of the three
134 remaining sides of the cereal crop.

135 To compare MFCC or SNCP effects on the pest complex system, we compared the
136 community composition and biocontrol services provided by aphid parasitoids using a paired
137 experimental design. For each cereal field and for each date, two plots of 15m² were delimited
138 in the cereal crop when the first aphid was found, respectively near MFCC and near SNCP.
139 New plots were delimited for each sampling and for each date. Samples near SNCP were
140 conducted more than thirty meters away to the MFCC as it has been demonstrated that
141 margins or flowering strips do not affect pest regulation at the field scale above a 20m
142 distance (Lavandero et al., 2005). Since the length of the field is commonly greater than this
143 distance, the comparison of both field margins represents the better compromise. Cereal fields
144 lacking neighbouring MFCC were not taken as control crops because of possible variations in
145 uncontrolled parameters (e.g. agricultural practices, soil characteristics, microclimatic
146 conditions, etc).

147 Due to low aphid density during winter, all living and parasitized aphids (*i.e.* mummies)
148 present on every tillage in delimited wheat plots were collected and brought back to the lab.

149 All live sampled aphids were reared on wheat (*Triticum aestivum* var Ludwig) in plastic cages
150 (L = 10 cm; Ø= 4.5 cm) for 15 days until potential parasitoid metamorphosis for parasitized
151 aphids. During this period, cages containing live aphids were kept in incubators under
152 controlled conditions of 20 ± 1 °C; $70 \pm 20\%$ relative humidity and a 16L:8D photoperiod. All
153 mummies produced from live aphids or directly collected in the field were isolated in gelatine
154 capsules (L = 3cm; Ø = 1 cm) until parasitoid emergence and both parasitized aphids and
155 adult parasitoids were identified to species level. Parasitoid gender was also recorded to
156 calculate the total sex ratio as well as the sex ratio for each species in each sampling plot. This
157 method was performed to obtain the maximum number of emerging parasitoids from the
158 collected aphids to enable better assessment of the winter aphid-parasitoid food web
159 connections and accurately measure parasitism rate (the final number of mummies obtained
160 divided by the total number of collected aphids).

161 **2.2 Statistical analysis**

162 As sampling dates were close in time and there was no significant difference in aphid
163 abundances (LM, $F = 0.63$, $Df = 2$, $P = 0.54$) nor in parasitism rate (LM, $F = 2.5$, $Df = 2$, $P =$
164 0.1) among dates, further analyses were carried out on pooled data for the three sampling
165 dates. Therefore, to compare the benefits from MFCC or SNCP on aphid parasitism in
166 adjacent cereal crop plots accounting for variations between sites, a LMM to compare aphid
167 abundances and GLMM to compare aphid parasitism were performed with *Site* as a random
168 factor (Bolker et al., 2009; Nakagawa and Schielzeth, 2010). As aphid parasitism is under the
169 influence of aphid abundance, this parameter was tested prior to analysing parasitism rate. A
170 Linear Mixed Model (LMM) was performed with aphid abundance in sampling plot as a
171 response variable (after log transformation for count data (Ives, 2015)), the sampling plot as a
172 fixed effect (Close to MFCC vs close to SNCP). To compare aphid parasitism between cereal
173 plots close to MFCC or SNCP, proportion of parasitized and unparasitized aphids in a given

174 plot were also compared by using it as a binomial response variable in a GLMM test with a
175 binomial error and a logit link function, with: aphid abundance in the plot as co-variable to
176 take into account a host abundance effect, sampling plot (close to MFCC vs close to SNCP) as
177 fixed effects. Models were built using *glmer* and *lmer* from *lme4* package (Bates D et al.,
178 2014) and tested using *Anova* functions from *car* package (Fox and Weisberg, 2011).
179 Food webs were built for each of the two cereal plots after pooling the data for each sampling
180 date and site with the *plotweb* function from the *bipartite* package (Dormann et al., 2009,
181 2008). In order to assess changes in trophic system complexity potentially involved in
182 changes to parasitism rate between plots near different vegetation, food webs were compared
183 using specific quantitative and qualitative metrics from the *bipartite* package: such as
184 **Generality**, which is the weighted mean number of aphid species used by each parasitoid
185 species, **Vulnerability**, which is the weighted mean number of parasitoid species attacking
186 each aphid species. A greater value of generality index may show lower competition between
187 parasitoid species as a lower value of vulnerability. Conversely, values of generality are
188 expected to be higher because values of vulnerability are expected to be lower due to
189 increased intra-guild competition. Other indices used included **Connectance**, which is the
190 overall complexity of food webs and the **Interaction evenness** which is **Shannon's evenness**
191 for the food web entries; an indicator of a mean link per species between trophic levels. Such
192 indices quantify food web complexity according to the richness of different trophic level.
193 For each sampled site and cereal plot, data of the three sampled dates were pooled before
194 calculating metrics due to the sample size sensitivity of such metrics and because there was no
195 date effect on population parameters. Each metric was compared between plots close to the
196 two distinct vegetation types using Wilcoxon rank sum test for non-parametric data. Null
197 hypotheses tested were that the means of these metrics did not differ between plots.

198 To determine if the total sex ratio differed between plots, the proportion of males and females
199 were tested and parasitoid gender was coded as follows: 1 for female and 0 for male. A
200 GLMM was performed with sampling plot (close to MFCC or to SNCP), *Species* (to take into
201 account potential parasitoid species effects) and their interactions as fixed effects and *Site* as a
202 random effect (Bolker et al., 2009).

203 For each model set, a full model was first built including all interactions and simple effects.
204 Model simplification was applied by sequentially removing non-significant interactions,
205 starting with the least significant highest order interaction (Zuur et al., 2009). All analyses
206 were carried out in R (R Development Core Team, 2008), using R studio software.

207 **3. Results**

208 Of the 419 parasitized aphids (among 606 sampled aphids), 308 aphid-parasitoid pairwise
209 relationships were obtained after parasitoid emergence with which to build winter food webs
210 and to compare aphid-parasitoid trophic systems between cereal crop plots near MFCC or
211 SNCP. The food web structure and the proportion of aphids and parasitoids were similar in
212 both cases (Fig 1). The dominant aphid species was *Metopolophium dirhodum* (57.23 ± 2.81
213 (\pm SE) and 60.68 ± 2.84 % in plots close to MFCC and plots close to SNCP, respectively),
214 followed by *Rhopalosiphum padi* (22.19 ± 2.36 and 22.37 ± 2.36 %) and *Sitobion avenae*
215 (19.61 ± 2.25 and 13.22 ± 1.97 %). The parasitoid guild was also the same for the two types of
216 plots with a strong dominance of *Aphidius rhopalosiphi* (75.9 ± 3.40 and 80 ± 3.27 % of the
217 parasitoids close to MFCC and SNCP respectively). Three other species from the *Aphidius*
218 genus were identified: *A. matricariae*, *A. ervi* and *A. avenae* which were present in similar
219 proportions between the two different plots with respectively: 8.86 ± 2.26 , 8.23 ± 2.19 and
220 6.96 ± 2.02 % in plots along MFCC, and 9.33 ± 2.38 , 4.00 ± 1.6 , and 6.67 ± 2.04 % in plots
221 along SNCP. No hyper-parasitoids emerged from the mummies (Fig 1).

222 There was no difference in aphid abundance in cereal plots close to MFCC or SNCP ($\chi^2 =$
223 0.067; Df = 1; P = 0.84). By contrast, the parasitism rate was 13% higher ($\chi^2 = 4.05$; Df = 1; P
224 = 0.044) along MFCC than SNCP, with respectively 72.32 ± 3.46 % and 59.45 ± 5.42 % mean
225 parasitized aphids (Fig 2). For both types of zone, there was a significant effect of aphid
226 abundance as co-variable ($\chi^2 = 3.85$; Df = 1; P = 0.049) with increasing aphid parasitism
227 linked to increasing aphid abundance. Factors have an independent effect on the binomial
228 response variable (non-significant interaction: $\chi^2 = 0.60$; Df = 1; P = 0.44), meaning that an
229 increase in aphid parasitism was correlated with an increase in aphid abundance at the field
230 scale (although with the aphid parasitism rate being higher close to MFCC).

231 There was no significant difference between cereal crop plots close to MFCC or SNCP for
232 each of the four food web metrics tested (Table 2). The mean number of aphid species used
233 by each parasitoid (*generality*) did not differ (V = 13; Df = 5; p-value = 0.69), nor was the
234 mean number of parasitoid species attacking each aphid species (*vulnerability*, V = 10; Df =
235 5; p-value = 1). The overall complexity of the trophic system was similar between the two
236 zones as *connectance* values did not differ significantly (V = 12; Df = 5; P = 0.84), nor was
237 the energy flow between trophic levels with similar link ratio between species (*interaction*
238 *evenness*, V = 9; Df = 5; p-value = 0.84).

239 There was no effect of the parasitoid species ($\chi^2 = 6.81$; Df = 3; P = 0.078) nor of the sample
240 plot ($\chi^2 = 0.68$; Df = 1; P = 0.41) and their interaction ($\chi^2 = 1.25$; Df = 3; P = 0.74) on the sex
241 ratio of the parasitoid guild. The sex ratio was 62.66 ± 3.85 % and 67.33 ± 3.83 % female close
242 to MFCC and SNCP respectively.

243 **4. Discussion**

244 Despite the variability in total aphid abundance between sampled fields, mean parasitism rate
245 was high and consistent at the field scale (around 69.14 ± 1.88 % of parasitized aphids). In

246 addition, for a given field, mean aphid density was the same in plots close to MFCC or SNCP.
247 However, mean parasitism rate was significantly higher close to MFCC than along SNCP,
248 suggestive of a greater parasitoid pressure on aphid pests in this part of the cereal crop. Crop
249 colonization by aphids is known to be increased by both the proportion of semi-natural habitat
250 at the landscape scale and margin vegetation in spring, as they act as arthropod sources (Al
251 Hassan et al., 2013; Alignier et al., 2014; Plečáš et al., 2014). In this study, aphid abundance
252 in cereal crops close to the mustard did not increase when compared to aphid populations
253 close to the margin, but parasitism pressure did increase. Such results are consistent with the
254 movement of parasitoids at the field scale reported by (Macfadyen et al., 2015) early in the
255 year when parasitoids are more prone to crossing a crop/crop ecotone rather the crop/margin
256 ecotone. Such observation could be explained by the strong compartmentalization of aphid
257 populations between margins and crops (Derocles et al., 2014; Vialatte et al., 2005) and by the
258 benefits from mustard covers in flower which have allowed the aphid parasitoid guild to be
259 more active in cereal crops close to the mustard rather than close to the margin. We
260 demonstrated that changes in the phenology of mustard cover crops during winter due to
261 rising temperatures had positive cascading effects on the higher trophic level and thus
262 associated biological control services in surrounding crops. The potential mechanisms
263 underlying these benefits on aphid-parasitoid trophic system are discussed below.

264 **4.1 Functional redundancy**

265 According to the “diversity – trophic structure hypothesis” (Haddad et al., 2009; Hutchinson,
266 1959; Knops et al., 1999), both monospecific cereal crops and mustard cover are expected to
267 have their own arthropod community with different degrees of specialization for each trophic
268 level (herbivores and natural enemies). Such situation is expected to modify the structure of
269 the trophic food webs in plots close to the cereal crop with a richer and more complex trophic
270 system along mustard cover crops than compared to grassy margins. A more complex trophic

271 system could explain the enhanced aphid parasitism rate measured (Cardinale et al., 2003) and
272 could contribute to the increase in aphid parasitism observed by the change in food web
273 structure (Gagic et al., 2011; Tylianakis et al., 2007). In the present study, pest complex
274 system was quantitatively and qualitatively identical in cereal crop areas close to MFCC and
275 SNCP. As indicated by the values of the different quantitative food web metrics, parasitoid
276 populations did not differ between plots in species composition or in proportion, nor benefit
277 from additional generalist parasitoid species. Moreover, consistency of *connectance* and
278 *interaction evenness* index confirmed that parasitoid intra-guild interactions were unchanged.
279 Contrary to one of our hypotheses, the increase in aphid parasitism close to the MFCC could
280 not be explained by an increase in diversity of parasitoids and by a potential associated
281 functional redundancy (Macfadyen et al., 2011; Peralta et al., 2014; Vos et al., 2001).

282 **4.2 Decrease in apparent competition.**

283 Another potential explanation of this increased parasitism rate near the MFCC is that some
284 parasitoid species from the cereal crop community use mustard crops aphid species as
285 alternative hosts (e.g. *A. ervi* or *A. matricariae* using *Myzus persicae* as a host; (Desneux et
286 al., 2006; Desneux and Ramirez-Romero, 2009). The use of alternative hosts by generalist
287 parasitoids may decrease apparent competition for cereal aphids and allow a better
288 exploitation by species that are more specialized such as the dominant *A. rhopalosiphi*,
289 resulting in an increase in their population dynamics and increased aphid parasitism as found
290 in this study. Such change in species interaction is expected to modify the trophic system
291 structure resulting in different metric values as *Generality* or *Vulnerability* index (Maunsell et
292 al., 2015; Tylianakis et al., 2007). However, the observed similarity of such metric values
293 between cereal crop plots close to MFCC and close to SNCP in our study indicated that there
294 was no change in intra-guild parasitoid interactions and thus exclude the apparent competition
295 hypothesis (Langer and Hance, 2004; Raymond et al., 2016).

296 **4.3 Improve in micro-climatic conditions**

297 Difference in height between SNCP and MFCC, *i.e.* 20 cm height for spontaneous grass
298 vegetation vs. 100-150 cm for mustard crops, might have improve local micro-climatic
299 conditions *e.g.* reducing wind exposure, and thus have buffered temperatures in close cereal
300 crop plots compared to those along grass margin vegetation. Stressful temperatures, such as
301 prolonged cold exposure, have been demonstrated to induce higher production of male
302 progeny in *Aphidius* parasitoids (Colinet et al., 2006; Ismail et al., 2010). It was then expected
303 that the sex-ratio could be more female biased along MFCC and that the increase in aphid
304 parasitism could result from this higher female proportion. However, our results have shown
305 that the sex-ratio did not differ between the sampled plots close to the MFCC or SNCP and
306 the observed increase in aphid parasitism could therefore not result from the change in sex-
307 ratio.

308 **4.4 Increase in food resource availability**

309 The last hypothesis about the increase in parasitism rate in plots close to MFCC is the
310 potential use of the mustard crops as a food resource for cereal aphid parasitoids. Parasitoids
311 from cereal crops might have benefited from aphid honeydew from aphids inhabiting mustard
312 plants or directly from the nectar of mustard flowers (Tena et al., 2013; Vollhardt et al., 2010;
313 Wäckers, 2001). During winter, few suitable plant species are available and few to none are
314 flowering in grassy margins outside the sown flowering cover in order to provide a
315 carbohydrate source to parasitoids remaining active. This last hypothesis, compared to the
316 three other hypotheses, appears to offer a better explanation according to the results obtained
317 in this study. The increase of only 13% in mean aphid parasitism rate is not an underestimate
318 according to the low standard error obtained for aphid parasitism ($\pm 3.46\%$ close to MFCC
319 and $\pm 5.42\%$ close to SNCP), even when considered in conjunction with the low field sample
320 size. The small effect size may be explained as mustard was shown to be a nectar source with

321 a small impact on parasitoid longevity (Vattala et al., 2006) as a result of its “hexose
322 dominant nectar” (Baker and Baker, 1983). In addition, because nectar production and quality
323 strongly depend on climatic conditions (Nicolson et al., 2007), mustard plants may have
324 produced nectar with lower energetic value during winter (and/or in low quantity). In both
325 cases, food quality provided by new flowering possibilities of plants sown as winter covers
326 might have contributed only over a short distance from the MFCC in the enhancement of
327 aphid parasitism rate through increasing cereal crop parasitoid activity (Lavandero et al.,
328 2005; Tschumi et al., 2016a).

329 **4.5 Conclusion**

330 This study is the first to quantify an aphid-parasitoid trophic system in cereal crops under
331 winter conditions in the study region. In addition to confirming the important role of
332 parasitoids in the biological control of aphids during autumn/winter under temperate climatic
333 conditions, this study provides new knowledge about the response of natural enemy
334 populations to sown flowering cover crops. According to our results, flowering mustard cover
335 crops promote aphid parasitism by cereal parasitoids during unfavorable climatic periods
336 when host and food resources are limited (Wäckers and van Rijn, 2012). Winter sown cover
337 crops may represent an important resource in maintaining the parasitoid guild throughout
338 winter months and, in turn, lead to a reduction in the intensity of spring aphid outbreaks. In
339 addition, the association between winter cereal crops and neighbouring sown flowering cover
340 takes place at a large landscape spatial scale. Parasitoid populations have also been
341 demonstrated to have rapid synchronization at annual temporal and regional spatial scales
342 (Andrade et al., 2015). Such association could substantially contribute to Conservation
343 Biological Control, acting in a similar manner to increasing the proportion of semi natural
344 habitat within an agroecosystem, and ultimately control early season aphid regulation beyond
345 the field scale. Although overall increase in aphid parasitism was low, this study emphasizes

346 the potential benefits for biological control induced by changes in plant phenology. According
347 to predictions on the increase of winter temperatures in northern Europe (Räisänen et al.,
348 2004), changes in organism phenology and in interactions between organisms may be
349 expected. An increase in mean temperature may increase the activity of vectors of diseases,
350 like aphids (Canto et al., 2009; van Baaren et al., 2010) or of their natural enemies (Andrade
351 et al., 2016, 2015). Also shifts in earlier plant phenology may become more and more
352 frequent, which may provide new perspectives for CBC. Indeed, as plant species and their
353 functional traits that compose semi-natural habitats determine the promotion of natural enemy
354 populations in CBC (Balzan et al., 2016; Hatt et al., 2017), modifications in plant phenology
355 may drive new interactions between arthropods inside semi natural habitats and inside the
356 adjacent crops. Moreover, winter covers may have a broader impact than quantified in this
357 study. This is because other natural enemies such as predators may also be more active and
358 could use these habitats for food or refuges and therefore improve the biological control
359 service.

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366 **References**

367 Al Hassan, D., Georgelin, E., Delattre, T., Burel, F., Plantegenest, M., Kindlmann, P., Butet,
368 A., 2013. Does the presence of grassy strips and landscape grain affect the spatial
369 distribution of aphids and their carabid predators? *Agric. For. Entomol.* 15, 24–33.
370 doi:10.1111/j.1461-9563.2012.00587.x

371 Alignier, A., Raymond, L., Deconchat, M., Menozzi, P., Monteil, C., Sarthou, J.-P., Vialatte,
372 A., Ouin, A., 2014. The effect of semi-natural habitats on aphids and their natural
373 enemies across spatial and temporal scales. *Biol. Control* 77, 76–82.
374 doi:10.1016/j.biocontrol.2014.06.006

375 Altieri, M.A., 1999. The ecological role of biodiversity in agroecosystems. *Agric. Ecosyst.*
376 *Environ.* 74, 19–31. doi:10.1016/S0167-8809(99)00028-6

377 Andrade, T.O., Krespi, L., Bonnardot, V., van Baaren, J., Outreman, Y., 2016. Impact of
378 change in winter strategy of one parasitoid species on the diversity and function of a
379 guild of parasitoids. *Oecologia*. doi:10.1007/s00442-015-3502-4

380 Andrade, T.O., Outreman, Y., Krespi, L., Plantegenest, M., Vialatte, A., Gauffre, B., van
381 Baaren, J., 2015. Spatiotemporal variations in aphid-parasitoid relative abundance
382 patterns and food webs in agricultural ecosystems. *Ecosphere* 6, art113.
383 doi:10.1890/ES15-00010.1

384 Badeck, F.-W., Bondeau, A., Bottcher, K., Doktor, D., Lucht, W., Schaber, J., Sitch, S., 2004.
385 Responses of spring phenology to climate change. *New Phytol.* 162, 295–309.
386 doi:10.1111/j.1469-8137.2004.01059.x

387 Baker, H.G., Baker, I., 1983. Floral nectar sugar constituents in relation to pollinator type.
388 *Handb. Exp. Pollinat. Biol.* 117, 141.

389 Balzan, M.V., Bocci, G., Moonen, A.-C., 2016. Utilisation of plant functional diversity in
390 wildflower strips for the delivery of multiple agroecosystem services. *Entomol. Exp.*
391 *Appl.* 158, 304–319. doi:10.1111/eea.12403

392 Balzan, M.V., Moonen, A.-C., 2014. Field margin vegetation enhances biological control and
393 crop damage suppression from multiple pests in organic tomato fields. *Entomol. Exp.*
394 *Appl.* 150, 45–65. doi:10.1111/eea.12142

395 Bates D, Maechler M, Bolker B, Walker S, 2014. lme4: Linear mixed-effects models using
396 Eigen and S4.

397 Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H.,
398 White, J.-S.S., 2009. Generalized linear mixed models: a practical guide for ecology
399 and evolution. *Trends Ecol. Evol.* 24, 127–135. doi:10.1016/j.tree.2008.10.008

400 Canto, T., Aranda, M.A., Fereres, A., 2009. Climate change effects on physiology and
401 population processes of hosts and vectors that influence the spread of hemipteran-
402 borne plant viruses. *Glob. Change Biol.* 15, 1884–1894. doi:10.1111/j.1365-
403 2486.2008.01820.x

404 Cardinale, B.J., Harvey, C.T., Gross, K., Ives, A.R., 2003. Biodiversity and biocontrol:
405 emergent impacts of a multi-enemy assemblage on pest suppression and crop yield in
406 an agroecosystem. *Ecol. Lett.* 6, 857–865. doi:10.1046/j.1461-0248.2003.00508.x

407 Cardinale, B.J., Matulich, K.L., Hooper, D.U., Byrnes, J.E., Duffy, E., Gamfeldt, L.,
408 Balvanera, P., O’Connor, M.I., Gonzalez, A., 2011. The functional role of producer
409 diversity in ecosystems. *Am. J. Bot.* 98, 572–592. doi:10.3732/ajb.1000364

410 Colinet, H., Renault, D., Hance, T., Vernon, P., 2006. The impact of fluctuating thermal
411 regimes on the survival of a cold-exposed parasitic wasp, *Aphidius colemani*. *Physiol.*
412 *Entomol.* 31, 234–240. doi:10.1111/j.1365-3032.2006.00511.x

413 Dedryver, C.A., 1981. Biologie des pucerons des céréales dans l’ouest de la France II.
414 Répartition spatio-temporelle et action limitative de trois espèces
415 d’Entomophthoraceae. *Entomophaga* 26, 381–393. doi:10.1007/BF02374713

416 Derocles, S.A.P., Le Ralec, A., Besson, M.M., Maret, M., Walton, A., Evans, D.M.,
417 Plantegenest, M., 2014. Molecular analysis reveals high compartmentalization in
418 aphid-primary parasitoid networks and low parasitoid sharing between crop and
419 noncrop habitats. *Mol. Ecol.* 23, 3900–3911. doi:10.1111/mec.12701

420 Desneux, N., Rabasse, J.-M., Ballanger, Y., Kaiser, L., 2006. Parasitism of canola aphids in
421 France in autumn. *J. Pest Sci.* 79, 95–102. doi:10.1007/s10340-006-0121-1

422 Desneux, N., Ramirez-Romero, R., 2009. Plant characteristics mediated by growing
423 conditions can impact parasitoid's ability to attack host aphids in winter canola. *J. Pest*
424 *Sci.* 82, 335–342. doi:10.1007/s10340-009-0258-9

425 Dormann, C.F., Fründ, J., Blüthgen, N., Gruber, B., 2009. Indices, graphs and null models:
426 analyzing bipartite ecological networks.

427 Dormann, C.F., Gruber, B., Fründ, J., 2008. Introducing the bipartite package: analysing
428 ecological networks. *interaction* 1, 0.2413793.

429 Fitter, A.H., 2002. Rapid Changes in Flowering Time in British Plants. *Science* 296, 1689–
430 1691. doi:10.1126/science.1071617

431 Flynn, D.F.B., Gogol-Prokurat, M., Nogeire, T., Molinari, N., Richers, B.T., Lin, B.B.,
432 Simpson, N., Mayfield, M.M., DeClerck, F., 2009. Loss of functional diversity under
433 land use intensification across multiple taxa. *Ecol. Lett.* 12, 22–33.
434 doi:10.1111/j.1461-0248.2008.01255.x

435 Fox, J., Weisberg, S., 2011. *An {R} Companion to Applied Regression.*

436 Gagic, V., Tschamntke, T., Dormann, C.F., Gruber, B., Wilstermann, A., Thies, C., 2011. Food
437 web structure and biocontrol in a four-trophic level system across a landscape
438 complexity gradient. *Proc. R. Soc. B Biol. Sci.* 278, 2946–2953.
439 doi:10.1098/rspb.2010.2645

440 Géneau, C.E., Wäckers, F.L., Luka, H., Balmer, O., 2013. Effects of extrafloral and floral
441 nectar of *Centaurea cyanus* on the parasitoid wasp *Microplitis mediator*: Olfactory
442 attractiveness and parasitization rates. *Biol. Control* 66, 16–20.
443 doi:10.1016/j.biocontrol.2013.02.007

444 Gurr, G.M., Wratten, S.D., Landis, D.A., You, M., 2017. Habitat Management to Suppress
445 Pest Populations: Progress and Prospects. *Annu. Rev. Entomol.* 62, 91–109.
446 doi:10.1146/annurev-ento-031616-035050

447 Haddad, N.M., Crutsinger, G.M., Gross, K., Haarstad, J., Knops, J.M.H., Tilman, D., 2009.
448 Plant species loss decreases arthropod diversity and shifts trophic structure. *Ecol. Lett.*
449 12, 1029–1039. doi:10.1111/j.1461-0248.2009.01356.x

450 Haddad, N.M., Crutsinger, G.M., Gross, K., Haarstad, J., Tilman, D., 2011. Plant diversity
451 and the stability of foodwebs: Plant diversity and foodweb stability. *Ecol. Lett.* 14, 42–
452 46. doi:10.1111/j.1461-0248.2010.01548.x

453 Hatt, S., Uyttenbroeck, R., Lopes, T., Mouchon, P., Chen, J., Piqueray, J., Monty, A., Francis,
454 F., 2017. Do flower mixtures with high functional diversity enhance aphid predators in
455 wildflower strips? *Eur. J. Entomol.* 114, 66–76. doi:10.14411/eje.2017.010

456 Holland, J.M., Bianchi, F.J., Entling, M.H., Moonen, A.-C., Smith, B.M., Jeanneret, P., 2016.
457 Structure, function and management of semi-natural habitats for conservation
458 biological control: a review of European studies: Structure, function and management
459 of semi-natural habitats for biological control. *Pest Manag. Sci.* 72, 1638–1651.
460 doi:10.1002/ps.4318

461 Hutchinson, G.E., 1959. Homage to Santa Rosalia or Why Are There So Many Kinds of
462 Animals? *Am. Nat.* 93, 145–159.

463 Ismail, M., Vernon, P., Hance, T., van Baaren, J., 2010. Physiological costs of cold exposure
464 on the parasitoid *Aphidius ervi*, without selection pressure and under constant or
465 fluctuating temperatures. *BioControl* 55, 729–740. doi:10.1007/s10526-010-9303-0

466 Ives, A.R., 2015. For testing the significance of regression coefficients, go ahead and log-
467 transform count data. *Methods Ecol. Evol.* 6, 828–835. doi:10.1111/2041-210X.12386

468 Knops, J.M.H., Tilman, D., Haddad, N.M., Naeem, S., Mitchell, C.E., Haarstad, J., Ritchie,
469 M.E., Howe, K.M., Reich, P.B., Siemann, E., Groth, J., 1999. Effects of plant species
470 richness on invasion dynamics, disease outbreaks, insect abundances and diversity.
471 *Ecol. Lett.* 2, 286–293. doi:10.1046/j.1461-0248.1999.00083.x

472 Krause, B., Culmsee, H., Wesche, K., Leuschner, C., 2015. Historical and recent
473 fragmentation of temperate floodplain grasslands: Do patch size and distance affect
474 the richness of characteristic wet meadow plant species? *Folia Geobot.* 50, 253–266.
475 doi:10.1007/s12224-015-9220-1

476 Krespi, L., Dedryver, C.-A., Creach, V., Rabasse, J.-M., Le Ralec, A., Nenon, J.-P., 1997.
477 Variability in the Development of Cereal Aphid Parasitoids and Hyperparasitoids in
478 Oceanic Regions as a Response to Climate and Abundance of Hosts. *Environ.*
479 *Entomol.* 26, 545–551. doi:10.1093/ee/26.3.545

480 Landis, D.A., Wratten, S.D., Gurr, G.M., 2000. Habitat Management to Conserve Natural
481 Enemies of Arthropod Pests in Agriculture. *Annu. Rev. Entomol.* 45, 175–201.
482 doi:10.1146/annurev.ento.45.1.175

483 Langer, A., Hance, T., 2004. Enhancing parasitism of wheat aphids through apparent
484 competition: a tool for biological control. *Agric. Ecosyst. Environ.* 102, 205–212.
485 doi:10.1016/j.agee.2003.07.005

486 Lavandero, B., Wratten, S., Shishehbor, P., Worner, S., 2005. Enhancing the effectiveness of
487 the parasitoid *Diadegma semiclausum* (Helen): Movement after use of nectar in the
488 field. *Biol. Control* 34, 152–158. doi:10.1016/j.biocontrol.2005.04.013

489 Macfadyen, S., Craze, P.G., Polaszek, A., van Achterberg, K., Memmott, J., 2011. Parasitoid
490 diversity reduces the variability in pest control services across time on farms. *Proc. R.*
491 *Soc. B Biol. Sci.* 278, 3387–3394. doi:10.1098/rspb.2010.2673

492 Macfadyen, S., Hopkinson, J., Parry, H., Neave, M.J., Bianchi, F.J.J.A., Zalucki, M.P.,
493 Schellhorn, N.A., 2015. Early-season movement dynamics of phytophagous pest and
494 natural enemies across a native vegetation-crop ecotone. *Agric. Ecosyst. Environ.* 200,
495 110–118. doi:10.1016/j.agee.2014.11.012

496 Matson, P.A., 1997. Agricultural Intensification and Ecosystem Properties. *Science* 277, 504–
497 509. doi:10.1126/science.277.5325.504

498 Maunsell, S.C., Kitching, R.L., Burwell, C.J., Morris, R.J., 2015. Changes in host-parasitoid
499 food web structure with elevation. *J. Anim. Ecol.* 84, 353–363. doi:10.1111/1365-
500 2656.12285

501 Meehan, T.D., Werling, B.P., Landis, D.A., Gratton, C., 2011. Agricultural landscape
502 simplification and insecticide use in the Midwestern United States. *Proc. Natl. Acad.*
503 *Sci.* 108, 11500–11505. doi:10.1073/pnas.1100751108

504 Menzel, A., Sparks, T.H., Estrella, N., Koch, E., Aasa, A., Ahas, R., Alm-Kübler, K.,
505 Bissolli, P., Braslavská, O., Briede, A., Chmielewski, F.M., Crepinsek, Z., Curnel, Y.,
506 Dahl, Å., SlöG, Defila, C., Donnelly, A., Filella, Y., Jatzcak, K., MåGe, F., Mestre, A.,
507 Nordli, Ø., Yvind, PeñUelas, J., Pirinen, P., RemišOvá, V., Scheifinger, H., Striz, M.,
508 Susnik, A., Van Vliet, A.J.H., Wielgolaski, F.-E., Zach, S., Zust, A., 2006. European
509 phenological response to climate change matches the warming pattern. *Glob. Change*
510 *Biol.* 12, 1969–1976. doi:10.1111/j.1365-2486.2006.01193.x

511 Nakagawa, S., Schielzeth, H., 2010. Repeatability for Gaussian and non-Gaussian data: a
512 practical guide for biologists. *Biol. Rev.* no-no. doi:10.1111/j.1469-
513 185X.2010.00141.x

514 Nicolson, S.W., Nepi, M., Pacini, E. (Eds.), 2007. *Nectaries and nectar*. Springer, Dordrecht.

515 Nordli, Ø., Wielgolaski, F.E., Bakken, A.K., Hjeltnes, S.H., Måge, F., Sivle, A., Skre, O.,
516 2008. Regional trends for bud burst and flowering of woody plants in Norway as

517 related to climate change. *Int. J. Biometeorol.* 52, 625–639. doi:10.1007/s00484-008-
518 0156-5

519 Parmesan, C., 2006. Ecological and Evolutionary Responses to Recent Climate Change.
520 *Annu. Rev. Ecol. Evol. Syst.* 37, 637–669.
521 doi:10.1146/annurev.ecolsys.37.091305.110100

522 Peralta, G., Frost, C.M., Rand, T.A., Didham, R.K., Tylianakis, J.M., 2014. Complementarity
523 and redundancy of interactions enhance attack rates and spatial stability in host–
524 parasitoid food webs. *Ecology* 95, 1888–1896. doi:10.1890/13-1569.1

525 Perović, D.J., Gámez-Virués, S., Landis, D.A., Wäckers, F., Gurr, G.M., Wratten, S.D., You,
526 M.-S., Desneux, N., 2017. Managing biological control services through multi-trophic
527 trait interactions: review and guidelines for implementation at local and landscape
528 scales: Multi-trophic traits & multi-scale filters. *Biol. Rev.* doi:10.1111/brv.12346

529 Plečaš, M., Gagić, V., Janković, M., Petrović-Obradović, O., Kavallieratos, N.G., Tomanović,
530 ž., Thies, C., Tschardt, T., Četković, A., 2014. Landscape composition and
531 configuration influence cereal aphid–parasitoid–hyperparasitoid interactions and
532 biological control differentially across years. *Agric. Ecosyst. Environ.* 183, 1–10.
533 doi:10.1016/j.agee.2013.10.016

534 Polgar, L., 1995. Induction of dormancy in aphid parasitoids: implications for enhancing their
535 field effectiveness. *Agric. Ecosyst. Environ.* 52, 19–23. doi:10.1016/0167-
536 8809(94)09003-P

537 R Development Core Team, 2008. *R: A Language and Environment for Statistical*
538 *Computing.* R Foundation for Statistical Computing, Vienna, Austria.

539 Rabasse, J.-M., Dedryver, C.-A., Gelle, A., Lafont, J.-P., Molinari, J., 1983. *Biologie des*
540 *puçerons des céréales dans l’Ouest de la France. III. Action des hyménoptères*

541 parasites sur les populations de *Sitobion avenae* F., *Metopolophium dirhodum* Wlk. et
542 *Rhopalosiphum padi* L. *Agronomie* 3, 779–790. doi:10.1051/agro:19830809

543 Räsänen, J., Hansson, U., Ullerstig, A., Döschner, R., Graham, L.P., Jones, C., Meier, H.E.M.,
544 Samuelsson, P., Willén, U., 2004. European climate in the late twenty-first century:
545 regional simulations with two driving global models and two forcing scenarios. *Clim.*
546 *Dyn.* 22, 13–31. doi:10.1007/s00382-003-0365-x

547 Ramsden, M.W., Menéndez, R., Leather, S.R., Wäckers, F., 2015. Optimizing field margins
548 for biocontrol services: The relative role of aphid abundance, annual floral resources,
549 and overwinter habitat in enhancing aphid natural enemies. *Agric. Ecosyst. Environ.*
550 199, 94–104. doi:10.1016/j.agee.2014.08.024

551 Raymond, L., Plantegenest, M., Gagic, V., Navasse, Y., Lavandero, B., 2016. Aphid
552 parasitoid generalism: development, assessment, and implications for biocontrol. *J.*
553 *Pest Sci.* 89, 7–20. doi:10.1007/s10340-015-0687-6

554 Redclift, M., 1989. The environmental consequences of Latin America's agricultural
555 development: Some thoughts on the Brundtland Commission report. *World Dev.* 17,
556 365–377. doi:10.1016/0305-750X(89)90210-6

557 Roschewitz, I., Hücker, M., Tschardt, T., Thies, C., 2005. The influence of landscape
558 context and farming practices on parasitism of cereal aphids. *Agric. Ecosyst. Environ.*
559 108, 218–227. doi:10.1016/j.agee.2005.02.005

560 Scherber, C., Eisenhauer, N., Weisser, W.W., Schmid, B., Voigt, W., Fischer, M., Schulze,
561 E.-D., Roscher, C., Weigelt, A., Allan, E., Beßler, H., Bonkowski, M., Buchmann, N.,
562 Buscot, F., Clement, L.W., Ebeling, A., Engels, C., Halle, S., Kertscher, I., Klein, A.-
563 M., Koller, R., König, S., Kowalski, E., Kummer, V., Kuu, A., Lange, M., Lauterbach,
564 D., Middelhoff, C., Migunova, V.D., Milcu, A., Müller, R., Partsch, S., Petermann,
565 J.S., Renker, C., Rottstock, T., Sabais, A., Scheu, S., Schumacher, J., Temperton,

566 V.M., Tschardtke, T., 2010. Bottom-up effects of plant diversity on multitrophic
567 interactions in a biodiversity experiment. *Nature* 468, 553–556.
568 doi:10.1038/nature09492

569 Singh, R., 2000. Environmental consequences of agricultural development: a case study from
570 the Green Revolution state of Haryana, India. *Agric. Ecosyst. Environ.* 82, 97–103.
571 doi:10.1016/S0167-8809(00)00219-X

572 Stoate, C., Boatman, N., Borralho, R., Carvalho, C.R., Snoo, G.R. d., Eden, P., 2001.
573 Ecological impacts of arable intensification in Europe. *J. Environ. Manage.* 63, 337–
574 365. doi:10.1006/jema.2001.0473

575 Tena, A., Pekas, A., WäCkers, F.L., Urbaneja, A., 2013. Energy reserves of parasitoids
576 depend on honeydew from non-hosts: Honeydew feeding by a hymenopteran
577 parasitoid. *Ecol. Entomol.* 38, 278–289. doi:10.1111/een.12018

578 Thies, C., Roschewitz, I., Tschardtke, T., 2005. The landscape context of cereal aphid-
579 parasitoid interactions. *Proc. R. Soc. B Biol. Sci.* 272, 203–210.
580 doi:10.1098/rspb.2004.2902

581 Tschardtke, T., Bommarco, R., Clough, Y., Crist, T.O., Kleijn, D., Rand, T.A., Tylianakis,
582 J.M., Nouhuys, S. van, Vidal, S., 2007. Conservation biological control and enemy
583 diversity on a landscape scale. *Biol. Control* 43, 294–309.
584 doi:10.1016/j.biocontrol.2007.08.006

585 Tschardtke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I., Thies, C., 2005. Landscape
586 perspectives on agricultural intensification and biodiversity – ecosystem service
587 management. *Ecol. Lett.* 8, 857–874. doi:10.1111/j.1461-0248.2005.00782.x

588 Tschumi, M., Albrecht, M., Bärtschi, C., Collatz, J., Entling, M.H., Jacot, K., 2016a.
589 Perennial, species-rich wildflower strips enhance pest control and crop yield. *Agric.*
590 *Ecosyst. Environ.* 220, 97–103. doi:10.1016/j.agee.2016.01.001

591 Tschumi, M., Albrecht, M., Collatz, J., Dubsky, V., Entling, M.H., Najjar-Rodriguez, A.J.,
592 Jacot, K., 2016b. Tailored flower strips promote natural enemy biodiversity and pest
593 control in potato crops. *J. Appl. Ecol.* 53, 1169–1176. doi:10.1111/1365-2664.12653

594 Tsiafouli, M.A., Thébault, E., Sgardelis, S.P., de Ruiter, P.C., van der Putten, W.H.,
595 Birkhofer, K., Hemerik, L., de Vries, F.T., Bardgett, R.D., Brady, M.V., Bjornlund,
596 L., Jørgensen, H.B., Christensen, S., Hertefeldt, T.D., Hotes, S., Gera Hol, W.H.,
597 Frouz, J., Liiri, M., Mortimer, S.R., Setälä, H., Tzanopoulos, J., Uteseny, K., Pižl, V.,
598 Stary, J., Wolters, V., Hedlund, K., 2015. Intensive agriculture reduces soil
599 biodiversity across Europe. *Glob. Change Biol.* 21, 973–985. doi:10.1111/gcb.12752

600 Tylianakis, J.M., Tschardtke, T., Lewis, O.T., 2007. Habitat modification alters the structure
601 of tropical host–parasitoid food webs. *Nature* 445, 202–205. doi:10.1038/nature05429

602 Uelmen, J.A., Lindroth, R.L., Tobin, P.C., Reich, P.B., Schwartzberg, E.G., Raffa, K.F.,
603 2016. Effects of winter temperatures, spring degree-day accumulation, and insect
604 population source on phenological synchrony between forest tent caterpillar and host
605 trees. *For. Ecol. Manag.* 362, 241–250. doi:10.1016/j.foreco.2015.11.045

606 van Baaren, J., Le Lann, C., JM van Alphen, J., 2010. Consequences of Climate Change for
607 Aphid-Based Multi-trophic Systems, in: Kindlmann, P., Dixon, A.F.G., Michaud, J.P.
608 (Eds.), *Aphid Biodiversity under Environmental Change*. Springer Netherlands,
609 Dordrecht, pp. 55–68. doi:10.1007/978-90-481-8601-3_4

610 Van Meerbeek, K., Helsen, K., Hermy, M., 2014. Impact of land-use intensity on the
611 conservation of functional and phylogenetic diversity in temperate semi-natural plant
612 communities. *Biodivers. Conserv.* 23, 2259–2272. doi:10.1007/s10531-014-0720-8

613 Vattala, H.D., Wratten, S.D., Phillips, C.B., Wäckers, F.L., 2006. The influence of flower
614 morphology and nectar quality on the longevity of a parasitoid biological control
615 agent. *Biol. Control* 39, 179–185. doi:10.1016/j.biocontrol.2006.06.003

616 Vialatte, A., Dedryver, C.-A., Simon, J.-C., Galman, M., Plantegenest, M., 2005. Limited
617 genetic exchanges between populations of an insect pest living on uncultivated and
618 related cultivated host plants. *Proc. R. Soc. B Biol. Sci.* 272, 1075–1082.
619 doi:10.1098/rspb.2004.3033

620 Vollhardt, I.M.G., Bianchi, F.J.J.A., Wäckers, F.L., Thies, C., Tschardtke, T., 2010. Spatial
621 distribution of flower vs. honeydew resources in cereal fields may affect aphid
622 parasitism. *Biol. Control* 53, 204–213. doi:10.1016/j.biocontrol.2009.12.011

623 Vos, M., Berrocal, S.M., Karamaouna, F., Hemerik, L., Vet, L.E.M., 2001. Plant-mediated
624 indirect effects and the persistence of parasitoid-herbivore communities. *Ecol. Lett.* 4,
625 38–45. doi:10.1046/j.1461-0248.2001.00191.x

626 Wäckers, F.L., 2001. A comparison of nectar- and honeydew sugars with respect to their
627 utilization by the hymenopteran parasitoid *Cotesia glomerata*. *J. Insect Physiol.* 47,
628 1077–1084. doi:10.1016/S0022-1910(01)00088-9

629 Wäckers, F.L., van Rijn, P.C.J., 2012. Pick and Mix: Selecting Flowering Plants to Meet the
630 Requirements of Target Biological Control Insects, in: Gurr, G.M., Wratten, S.D.,
631 Snyder, W.E., Read, D.M.Y. (Eds.), *Biodiversity and Insect Pests*. John Wiley &
632 Sons, Ltd, Chichester, UK, pp. 139–165.

633 Wesche, K., Krause, B., Culmsee, H., Leuschner, C., 2012. Fifty years of change in Central
634 European grassland vegetation: Large losses in species richness and animal-pollinated
635 plants. *Biol. Conserv.* 150, 76–85. doi:10.1016/j.biocon.2012.02.015

636 Wratten, S.D., Gillespie, M., Decourtye, A., Mader, E., Desneux, N., 2012. Pollinator habitat
637 enhancement: Benefits to other ecosystem services. *Agric. Ecosyst. Environ.* 159,
638 112–122. doi:10.1016/j.agee.2012.06.020

639 Zhang, Y., Yang, N., Wang, J., Wan, F., 2014. Effect of six carbohydrate sources on the
640 longevity of a whitefly parasitoid *Eretmocerus hayati* (Hymenoptera: Aphelinidae). *J.*
641 *Asia-Pac. Entomol.* 17, 723–728. doi:10.1016/j.aspen.2014.07.009

642 Zuur, A.F., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M., 2009. Mixed effects models
643 and extensions in ecology with R, *Statistics for Biology and Health*. Springer New
644 York, New York, NY.

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647 **Table 1: Summary of sample sites** including middle crop GPS coordinates, cereal species
 648 sown, surface of sampled cereal crops, adjoining mustard flowering cover crop (MFCC), and
 649 the sum total of aphids sampled over the three sampling dates.

Site	Latitude	Longitude	Crops	Cereal crops size (Ha)	MFCC size (Ha)	Total aphids sampled
Site 1	48°10'58.8"N	1°40'16.7"W	Barley	6.03	7.75	118
Site 2	48°12'19.2"N	1°40'07.7"W	Wheat	1.53	6.33	74
Site 3	47°58'35.1"N	1°34'49.3"W	Wheat	2.51	1.55	62
Site 4	48°02'24.1"N	1°51'01.3"W	Wheat	8.32	5.77	166
Site 5	48°02'17.1"N	1°51'24.4"W	Wheat	1.61	3.13	113
Site 6	48°02'22.9"N	1°49'01.7"W	Wheat	12.73	13.98	73

650

651 **Table2: Food web metrics for each zone in each sampling site.** Each column name
 652 corresponds to a sampling site (“Sx”) with x, the number of the field and the corresponding
 653 field zone (“MV” for cereal crop plots along spontaneous non-crop plants in margin
 654 vegetation and “MC” for the other plots along the mustard flowering crop cover).

	S1.MV	S1.MC	S2.MV	S2.MC	S3.MV	S3.MC	S4.MV	S4.MC	S5.MV	S5.MC	S6.MV	S6.MC
Generality	2.549	1.934	2.06	2.452	2.239	1.854	1.483	1.748	1.804	1.678	1.26	1.121
Vulnerability	1.754	1.971	1.261	1.419	2.331	1.814	1.258	1.711	2.419	1.543	1.26	1.818
Connectance	0.359	0.39	0.332	0.387	0.381	0.262	0.196	0.247	0.302	0.23	0.315	0.294
Interaction.eveness	0.688	0.759	0.532	0.695	0.795	0.587	0.266	0.459	0.611	0.453	0.334	0.433

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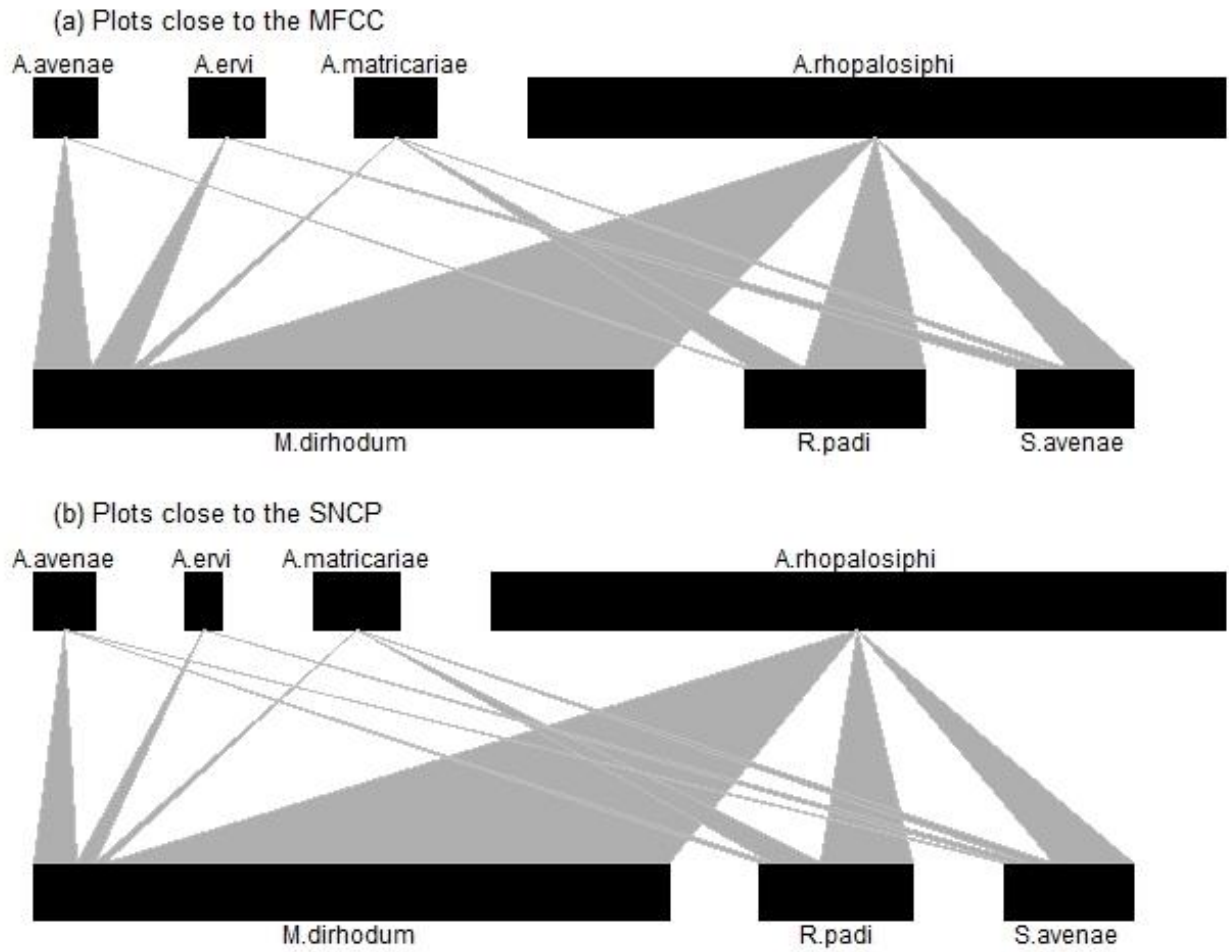
656 **Figure 1: Food web representation of the aphid parasitoid trophic system for cereal crop**
657 **plots, (a) close to the mustard flowering crop covers (MFCC) and (b) away at an opposite**
658 **edge close to spontaneous non-crop plants in grassy margins (SNCP).** For each zone, data
659 from plots of each sampling site and date have been pooled. Species composition are similar
660 between zones with *Metopolophium dirhodum* (M.dirhodum); *Rhopalosiphum padi* (R.padi) and
661 *Sitobion avenae* (S.avenae) for the lower trophic level, and *Aphidius avenae* (A.avenae),
662 *Aphidius ervi* (A.ervi), *Aphidius matricariae* (A.matricariae) and *Aphidius rhopalosiphi*
663 (A.rhopalosiphi) for higher trophic level.

664

665 **Figure 2: Mean aphid parasitism rate in cereal crops close to Mustard flowering covers (MFCC)**
666 **and close to Spontaneous non-crop plants (SNCP). (*: p<0.05)**

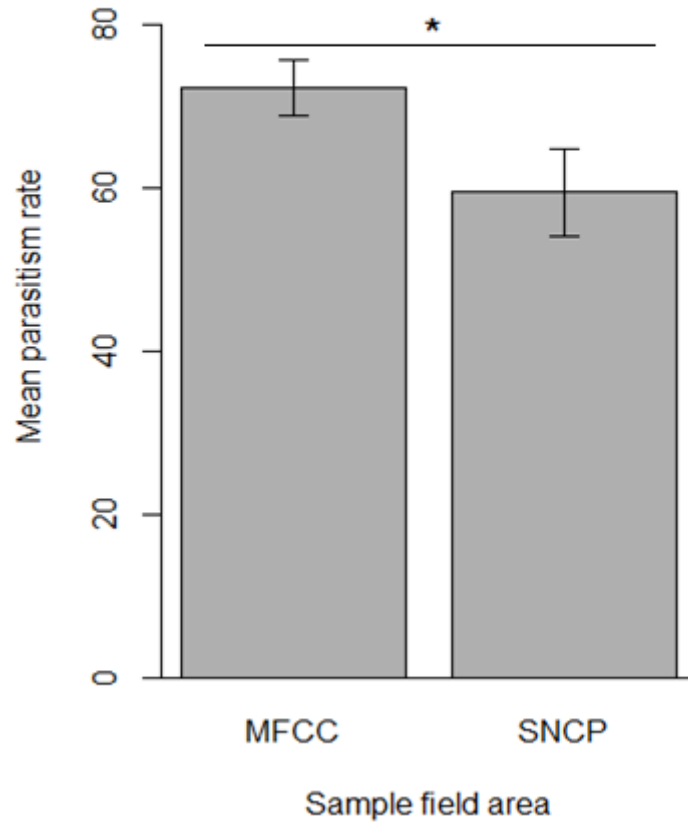
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669

670 **Figure 1: Food web representation of the aphid parasitoid trophic system for cereal**
 671 **crops plots, (a) close to the mustard flowering crop cover (MFCC) and (b) away at an**
 672 **opposite edge close to spontaneous non-crop plants in grassy margins (SNCP).**



673

674 **Figure 2: Mean aphid parasitism rate in cereal crop fields close the Mustard flowering cover**

675 **crops (MFCC) and close to Spontaneous non-crop plants (SNCP) from grassy margins.**