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1 **Natural enemies emerging in cereal fields in spring may contribute to biological**
2 **control**

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18 **Abstract**

19 Biological pest control is known to depend on landscape heterogeneity. However, such
20 relationship shows irregular pattern and seems influenced by local farming practices and natural
21 enemies that overwinter within crop fields. The objective of this study was to assess the
22 contribution of emerging natural enemies in spring to biological control, and their response to
23 the interaction between landscape heterogeneity and farming intensity.

24 We monitored the overwintering insect community using emergence traps and measured the
25 local potential pest predation using prey cards in 30 cereal fields, in spring in France. Study
26 fields were selected along a landscape heterogeneity gradient and farming practices were
27 recorded.

28 None of the ten emerging taxa influenced predation of lepidopteran eggs or weed seeds. On the
29 ground, aphid predation was positively correlated with emerging carabid beetles. In foliage,
30 aphid predation was negatively correlated with emerging parasitoids. Overall, the community
31 of natural enemies that overwinter within crop fields seemed to benefit from landscape-scale
32 lower crop diversity and higher edge density in combination with higher local-scale farming
33 intensities. This suggests that they represent a subset of species adapted to intensified farming
34 systems. This study highlights a broad taxonomic range of emerging natural enemies and their
35 potential contribution to local pest predation.

36 **Keywords: beneficial insects, potential predation, landscape heterogeneity, pesticide, soil**
37 **management, ground compartment, airborne compartment, overwintering**

38 **1. Introduction**

39 The environmental problems caused by modern agriculture calls existing farm production
40 systems into question, particularly their dependence on pesticides and soil management. One
41 of the worldwide agricultural challenges is to reduce the use of chemical inputs while
42 maintaining adequate crop production levels. In addition, farmland biodiversity is decreasing
43 substantially due to the homogenisation and intensification of farming practices (Benton et al.,
44 2003; Fahrig et al., 2011). Farmland biodiversity supports many ecosystem services, including
45 pollination, nutrient cycling and pest control (Garibaldi et al., 2018; Tscharntke et al., 2012). In
46 particular, biological control of agricultural pests by their natural enemies could contribute to
47 agricultural production while enabling reduced pesticide use. Many taxonomic groups,
48 including carabid beetles, hoverflies or wasps, and functional groups, such as generalist
49 predators, specialist seed eaters, or parasitoids, contribute to natural pest control (Labruyere et
50 al., 2018; Raymond et al., 2014, 2015; Schmidt et al., 2003; Sigsgaard & Jacobsen, 2017).

51
52 Conservation biological control (CBC) relies on fostering naturally-occurring enemies, usually
53 arthropod predators and parasitoids (Tscharntke, Klein, et al., 2005), that are already present in
54 both crops and semi-natural habitats (SNH, (Barbosa, 1998; Bianchi et al., 2006; Chaplin-
55 Kramer et al., 2011; Landis et al., 2000). Most natural enemies require different resources to
56 complete their life cycle, including food, shelter, nesting and overwintering sites. Various
57 landscape elements may provide these resources at different time of the year (seasonality,
58 Bertrand et al., 2016; Schellhorn et al., 2015). Such distribution of resources in space and time
59 generate species movements between complementary landscape elements, so-called spill-over,
60 which allow natural enemies to find non-substitutable resources they need (Aviron et al., 2018;
61 Blitzer et al., 2012; Duflot et al., 2017; Dunning et al., 1992). It is now widely accepted that
62 landscape heterogeneity is a strong driver of multitrophic diversity, abundance, and species

63 composition of natural enemies and, therefore, of CBC (Benton et al., 2003; Dainese et al.,
64 2019; Sirami et al., 2019; Tschardt et al., 2012). Hence, effects of landscape heterogeneity
65 are to be considered according multiple trophic levels, which may lead to trade-offs between
66 phytophagous pests, natural enemies and CBC(e.g. Botzas-Coluni et al., 2021).

67

68 The role of SNH in the landscape complementation process, where species use complementary
69 resources from different landscape elements, is well known (Fahrig et al., 2011). SNH, or non-
70 crop habitats, include hedgerows and other field boundary habitats, woodlands, and permanent
71 grasslands. Increased proportion of SNH in a landscape is usually associated with higher species
72 richness and abundance of natural enemies in crop fields due to their seasonal spill-over
73 between SNH, where many species overwinter, and crop fields, where many species find
74 abundant food (Blitzer et al., 2012; Dainese et al., 2019; Tschardt, Rand, et al., 2005). For
75 instance, grassy strips near large arable fields provide perennial vegetation and overwintering
76 sites for natural enemies such as beetles *i.e.* beetle banks (MacLeod et al., 2004; Thomas, 2000).
77 Thus predators disperse more or less far into the crop, depending on the species, and participate
78 to biological control (Anjum-Zubair et al., 2010; Collins et al., 2002; Thomas, 2000). Moreover,
79 complex landscape configuration leading to high density edges between SNH and crop
80 (indicating a relative small field size) promote natural enemies diversity and enhance pest
81 control (Martin et al., 2019).

82

83 Not only SNH but also crop fields can contribute to maintain natural enemies and CBC. On the
84 one hand, the complexity of crop mosaics resulting from the diversity of crop types and field
85 sizes can influence ecological processes such as complementation and spill over (Aviron et al.,
86 2018; Dufлот et al., 2016; Vasseur et al., 2013; Vialatte et al., 2017). Populations of natural
87 enemies may be better supported over the course of a year by a continuous flow of crop-based

88 resources rather than by maintaining nearby semi-natural habitat (Bertrand et al., 2016;
89 Schellhorn et al., 2015; Vasseur et al., 2013). In contrast, crops provide almost unlimited
90 resources for pest populations (Root, 1973) and their continuous presence can support the
91 abundance of specialist pests (Nesme et al., 2016; Root, 1973). On the other hand, some species
92 are able to overwinter in crop fields, which is usually assumed to happen in SNH. For instance,
93 crop fields shelter hoverflies during winter, which significantly contribute to biological control
94 of aphids in autumn (Raymond et al., 2014). In addition, most adults of some species of
95 predatory beetles such as cantharids and carabids, which are generalist predators, emerge from
96 larvae that overwinter in crop fields (Noordhuis et al., 2001). The abundance of these
97 populations varies with field-level characteristics, such as crop type and management, including
98 tillage, fertilisation, and pesticide use (Herzog et al., 2006; Labruyere et al., 2016). For instance,
99 spring tillage of corn fields has negative effects on carabid beetle communities (Purvis & Fadh,
100 2002), and pesticides have lethal or sub-lethal consequences for populations of parasitoids
101 (Roubos et al., 2014; Stapel et al., 2000). Although not fully established, it seems that low-
102 intensity farming practices, in terms of pesticide use and of soil management, may offer better
103 within-field overwintering conditions for different taxa of natural enemies (Vasseur et al.,
104 2013).

105

106 In sum, crop fields may provide more resources for natural enemies than do semi-natural
107 habitats (Rusch, Binet, et al., 2016; Rusch, Chaplin-Kramer, et al., 2016), and local farming
108 practices may control the positive effect of semi-natural habitats on biological control
109 (Labruyere et al., 2016; Ricci et al., 2019). These are two hypotheses that may partly explain
110 the reported irregular response of CBC to landscape heterogeneity (Karp et al., 2018;
111 Tschardt et al., 2016). However, how the properties of the fields themselves influence CBC
112 and interact with landscape context remains poorly quantified. This study investigates for the

113 first time the contribution of a large range of taxa and of the within field overwintering
114 community to CBC.

115

116 The aims of this study were to evaluate (i) the contribution of locally overwintering natural
117 enemies on local CBC in spring and (ii) the effects of farming practices and of the landscape
118 context on the emergence of natural enemies and their own parasitoids or predators in crop
119 fields. We hypothesised that: (i) overwintering natural enemies contribute to biological control
120 early (in spring) because they emerge directly in the fields; (ii) crop fields provide
121 overwintering sites for natural enemies and their parasitoids and predators; (iii) local farming
122 practices interact with the landscape context and influence the abundance of overwintering
123 populations.

124

125 **2. Material and methods**

126 The study was conducted in “*Vallées et Coteaux de Gascogne*”, which is part of the Long-Term
127 Socio-Ecological Research site LTSER ZA PYGAR, a 370 km² hilly area located in south-
128 western France (43°17’N, 0°54’E). The region is dominated by mixed crop-livestock farming
129 systems and is therefore characterized by a fine mosaic of woodlands, grasslands, and crop
130 fields. Thirty conventional winter cereal fields were selected along a gradient of density of the
131 surrounding woodlands (0-30% in a buffer zone with a 563-m radius from the sampling
132 location). Wheat is traditionally grown in this region in a wheat-barley-alfalfa or wheat-wheat-
133 sunflower rotations. Post overwintering emergent arthropods were collected in spring 2017, and
134 at the same time, prey sentinel cards were placed in crop fields to evaluate potential biological
135 control. All the variables calculated and surveyed during this study are presented in appendix
136 A.

137

138 **2.1. Field sampling of overwintering arthropods**

139 Emerging arthropods were caught using emergence traps from the end of winter until the end
140 of spring, covering most of the emergence period of diverse predators and parasitoids. The
141 operating principle of emergence traps is that a specific area of soil is hermetically sealed to
142 collect all the insects that emerge within the area. Traps (surface area: 0.36 m², Soil Emergence
143 trap 96 x 26 mesh, Black, MegaView Science Co., Ltd. Taichung, Taiwan) were placed in
144 agricultural fields at a distance of 50 metres from the field edge. The collection bottle placed
145 on top of the trap collects all the flying insects that emerge from the ground. A pitfall trap was
146 also placed inside the emergence trap to collect emerging ground-dwelling insects. The bottles
147 were filled two thirds full with 70% ethanol and the pitfall traps were filled with a solution of
148 soapy water. The traps were set up in the first half of March and collected every other week
149 from March 15 until the last week in May, *i.e.* a total of six sampling periods.

150 The collected insects were manually sorted, those trapped at the top of the emergence trap were
151 separated from those trapped in the pitfall traps at ground level. The insects were identified to
152 family level and classified in two main functional groups: parasitoids (including
153 hyperparasitoids) and predators. Arthropod families were further classified according to their
154 life history traits into two trophic levels, natural enemies, or hyperparasitoids or parasitoids of
155 natural enemies, and into two compartments of predation/parasitism activity, *i.e.* ground or
156 airborne (Table1). The total abundance of each family was determined in each field.

157

158 **Table 1: Life history traits of overwintering arthropods sampled in the study.** Each taxon
 159 sampled was categorised as predator or parasitoid, and as belonging to the ground or airborne
 160 compartment according to its potential predation activity.

Taxonomic group	Life history traits	Functional group	Compartment of predation/parasitism activity	Mean abundance per field [min;max]
Carabidae	Generalist predator: feeds on eggs, larvae, adults of aphids, slugs, snails and lepidoptera. Some species are also seed predators.	Predator	Ground	9.0 [0; 59.0]
Staphylinidae	Generalist predator: larvae and adults are carnivorous or scavengers. They feed on slugs, underground pests, mites or diptera eggs.	Predator	Ground	202.9 [43.0; 547]
Proctotrupidae	Coleoptera parasite: rove beetles, wireworms, carabid beetles.	Parasitoid of natural enemies	Ground	0.53 [0; 3.0]
Chalcidoidea	Parasitoid of diptera and hemipteran (aphids for instance).	Parasitoid	Airborne	9.7 [1; 31.0]
	Hyperparasitoid: parasites of parasitoids.	Hyperparasitoid of natural enemies	Airborne	2.3 [0; 11.0]
Braconidae	Parasitoid of diptera and aphids.	Parasitoid	Airborne	2.4 [0; 17.0]
Platygasteridae	Parasitoid of diptera (midges).	Parasitoid	Airborne	0.41 [0; 5.0]
Cantharidae	Generalist predator: feed on aphids, caterpillars. Species are polyphagous.	Predator	Airborne	3.5 [0; 19.0]
Diapriidae	Diptera parasite.	Parasitoid of natural enemies	Airborne	2.3 [0; 11.0]

161

162

2.2. Estimation of potential pest biocontrol with sentinel prey cards

Biological control of pests and weeds was evaluated using a standardized protocol based on sentinel prey cards with different types of prey. This method have shown sufficient sensitivity to detect variations in the levels of biological control and the influence of the landscape context (McHugh et al., 2020). The main reason for the massive adoption of monitoring potential predation by sentinel prey cards for 15 years now is that monitoring pest populations is time consuming. Such methodology have known limitations (McHugh et al., 2020; Meyer et al., 2017) but allow collecting standardized data.

Four complementary types of sentinel preys were placed to monitor diverse predation potential at ground and crop level. The prey species were selected according to those used in international devices (e.g. Ricci et al. 2019). The three prey species were selected according to their diversity, their similarity to winter cereal pests, and the diversity of targeted natural enemies, while considering the constraints of rearing (McHugh et al., 2020; Ricci et al., 2019).

Preys were glued to 5 x 5 cm sandpaper cards. Seed predation was measured using 10 *Viola arvensis* seeds exposed on the ground (glue: SADER® WOOD PRO D3 diluted with two-thirds of water). Insect predation was assessed using predation cards on which three adult pea aphids *Acyrtosiphon pisum* were glued (glue: UHU® Twist&Glue solvent-free). The cards were positioned both on the ground and to the top of a crop plant as is commonly done to estimate potential CBC (Karp et al., 2018; Östman, 2004; Ricci et al., 2019). In addition to aphids, predation cards containing clusters of *Ephestia kuehniella* (Lepidoptera) eggs were placed to the top of a crop plant. *Ephestia* eggs are too small to allow precise enumeration so a 5 mm-wide cluster was glued to the card (glue: SADER® all-purpose solvent-free). The glues used were chosen among a set of low toxic glues after practical tests to ensure the prey were just fixed but not mired and that they would not come unstuck during the period of exposure.

187 Sentinel prey cards were either nailed to the ground (“ground level”) or stapled to the top of a
188 crop plant (“crop level”). Aphids were exposed for 24 h to avoid necrophagia, other sentinel
189 preys were exposed for 96 h.

190 In each field, we positioned the four sentinel prey cards in 10 plots evenly distributed along two
191 parallel transects separated by a distance of 10 m. The transects were perpendicular to the field
192 border, with the first card placed 50 m away from the border and the last 100 m away. The
193 transects were also about 20 m away from the emergence trap. The number of preys that remains
194 on the cards at the end of the period of exposure was counted in the field, except for *Ephestia*,
195 which, because of their small size, were counted using a magnifying binocular in the laboratory.

196 Two classes were used for *Ephestia* predation: unconsumed (less than 5% of the eggs missing)
197 or consumed (more than 5%). The predation rate of each type of prey in each field was
198 calculated. Two periods of exposure were used during the crop vegetative growth period: from
199 the 24th to 28th April and from the 29th of May to the 2nd of June 2017. The total size of the
200 dataset was 60 predation rates (30 fields, 2 sessions).

201

202 **2.3. Landscape metrics and farming practices**

203 Using ArcGIS Desktop 10.5.1 software, annual land use maps were drawn for the study sites
204 based on direct field observations. Land cover was digitised from aerial orthophotos (50 cm
205 spatial resolution, BDOrtho®) produced by the French national mapping agency. Landscape
206 metrics were then calculated for a 1 km² circle (*i.e.* inside a circular buffer with a radius of 563
207 m, centred on the middle of ecological measurements). The heterogeneity of the semi-natural
208 habitats and the crop mosaic are described using 13 landscape metrics. First, woodlands,
209 hedgerows and permanent grasslands were grouped to calculate the proportion of semi-natural
210 habitats, their mean patch size, the length of their edges and the length of edges at the interface
211 of semi-natural habitats and crop fields. Second, land-cover categories were used to characterize

212 the heterogeneity of the semi-natural habitats: the proportion of wooded habitats, permanent
213 grasslands, and the total length of hedgerows. To describe crop heterogeneity, land cover was
214 categorised in spring crops, winter crops, and temporary grasslands; and the proportion of each
215 cover was calculated. Winter crops are sown in autumn and harvested in early summer and
216 spring crops are sown in spring and harvested at the end of the summer. Finally, the Shannon
217 diversity index (SHDI) was calculated for the whole landscape based on the proportion of each
218 land cover, while the total length of edges, *i.e.* edge density (all types of edges considered), was
219 calculated to evaluate landscape configuration. The SHDI was also calculated specifically for
220 the crop mosaic (SHDI crop); using detailed crop categories (spring crops and winter crops).
221 Farmers were interviewed during the winter 2017-2018 to collect data on the farming practices
222 used in the sampled fields since the sowing of winter cereal, *i.e.* since the month of October
223 preceding the studied spring. The cumulated tillage depth was used to describe soil management
224 intensity. The quantity of nitrogen provided to the fields was used to describe the fertilisation
225 intensity. The treatment frequency index (TFI) was used to characterize the intensity of
226 pesticide use (Lechenet et al., 2014). The TFI was calculated for each type of pesticides
227 separately (insecticides, fungicides, and herbicides) and all together (TFI total). The total
228 number of operations, *i.e.* the number of times the crop has been visited, was recorded as an
229 overall proxy of farming intensity.

230 Correlations between variables were investigated to identify a limited number of non-correlated
231 variables representative of the landscape context and farming practices, using Pearson's
232 coefficients (Appendix B.1; Appendix B.2). After considering correlations between variables
233 five landscape metrics, and three farming intensity variables were kept for further analyses (
234 Table 2; Appendix C.1).

235

236 **Table 2: Definition of the non-correlated landscape metrics and farming intensity**
 237 **measures used in the study.** See appendix A for the full set of variables.

	Name of variable	Meaning	Mean [Min; Max]
Landscape metrics	SHDI	Shannon diversity of the landscape in 1 km ² buffer zone	1.59 [1.31; 1.83]
	SHDI crop	Shannon diversity of crops	1.37 [0.90; 1.93]
	pSNH	Proportion of semi natural habitats (%)	38.6 [11.2; 68.8]
	pWinterCrop	Proportion of winter crops (%)	21.0 [5.9; 45.1]
	Edge density	Total length of all types of edges (km/ha)	23.2 [13.9; 32.5]
Farming practices	Cumul depth	Cumulated tillage depth (cm)	22.2 [0; 63.0]
	Nqty	Quantity of nitrogen provided in liquid form (kg/ha)	162.4 [46.0; 257.9]
	TFItot	Total treatment frequency index – all types of treatments	4.9 [1; 15.2]

238

239

240 **2.4. Statistical analysis**

241 First, Pearson’s coefficients were calculated between the four types of prey cards to identify
 242 possible redundancies in what they measure, *i.e.* the fact the different types of cards may
 243 characterize the same predation activity.

244 Second, statistical analysis was performed on two sets of pooled data from emergent traps (i)
 245 all six emergence sampling periods, and (ii) the first four sampling periods corresponding to
 246 the beginning of the spring season and that took place before to the first session of predation
 247 measurements. In both cases, we modelled the ground and airborne compartments separately,
 248 which correspond to ground and crop level of the sentinel card exposure, and to the ground and
 249 airborne traps of the emergence sampling set up. These compartments relate to predation and

250 parasitism activity of different arthropod families (Table 1). A generalized linear model (GLM)
251 with a Gaussian distribution was built for each type of prey card, either by considering the
252 whole season using the average of the two predation sessions with all six emergence sampling
253 periods, or by considering only the beginning of the season using the first predation session
254 with the first four emergence sampling periods. To reduce the need for further selection of
255 explanatory variables, following the procedure by Ricci et al. (2019), we included only one
256 landscape variable and one farming intensity variable at a time, and their interaction. This
257 method was appropriate as the pre-selected variables had relatively small covariance. Sixteen
258 models were built for each predation rate to be explained. The first model was a null model that
259 included, for each predation rate, the abundance of corresponding emerged natural enemies, *i.e.*
260 natural enemies in the same ground or airborne compartment. Fifteen other models were then
261 produced from that null model by adding every combination of one landscape variable among
262 the five, and one farming practice variable among the three, and their interactions. The models
263 considered potential spill-over processes and interactive effects between the landscape context
264 and farming practices. Finally, averaged coefficients were calculated across all 16 models using
265 the *model.avg* function of the MuMIn package in R (Ricci et al., 2019).

266 Similarly, the abundance of emerging natural enemies were modelled using GLMs with
267 negative binomial error distribution. We use the negative binomial distribution because of the
268 non-normality and the over-dispersion of data. The null model included the other families of
269 overwintering natural enemies in the compartment considered at the same trophic level and the
270 abundance of their own overwintering enemies, at a higher trophic level. The following models
271 were built from the null model by adding one landscape variable among the five and one
272 farming practice variable among the three and their interactions. Averaged coefficients were
273 calculated across all 16 models. Finally, models of the abundance of hyperparasitoids and
274 parasitoids of natural enemies were built in the same way, as a function of landscape and

275 farming practice variables using a negative binomial error distribution. All analyses were
276 performed with R software version 3.6.2 (R Core Team, 2020).

277

278 **3. Results**

279 Among the identified families, some were natural enemies and others known to be their own
280 parasitoids. Parasitoids were identified at genus level; genera with known parasitic traits could
281 be classified as parasitoids of natural enemies. Different levels of abundance were observed
282 depending on family. A total of 7345 natural enemies were collected, of which 987 from the
283 top of emergence traps and 6358 in the pitfall traps.

284 Carabidae (mean = 9.0; SD = 11.1 individuals per field over the entire sampling period) and
285 Staphylinidae (202.9 ± 113.1) were identified in the ground compartment (Appendix D.1),
286 while, parasitoids belonging to the super-familie of Chalcidoidea (9.7 ± 7.4) and family of
287 Braconidae (2.4 ± 3.7), as well as generalist predators of the Cantharidae family (3.5 ± 5.1)
288 were present in the airborne compartment. Members of the Platygasteridae family (0.41 ± 1.05)
289 also emerged but their abundance was very low (Appendix D.2).

290 We found parasitoids of natural enemies in both compartments. In the ground compartment,
291 individuals belonging to the Proctotrupidae family (0.53 ± 0.82) emerged, but their abundance
292 was low (Appendix D.1). In the airborne compartment, some hyperparasitoids and parasitoids
293 identified as Chalcidoidea (2.3 ± 2.8) and Diapriidae (5.1 ± 3.4) emerged (Appendix D.2). All
294 entomological taxa sampled were considered in this analysis, except for hoverflies that made
295 up, surprisingly compared to Raymond *et al.* (2014), only 4 individuals captured in total.

296 The mean predation rate over the two exposure periods varied depending on the sentinel prey
297 concerned. The highest rate was found for aphids on the ground (0.85 ± 0.12), followed by
298 *Ephestia* eggs in the crop (0.75 ± 0.08) and weed seeds on the ground (0.66 ± 0.17). The lowest
299 rate was found for aphids in the crop, which were about three times less predated than other

300 sentinel preys (0.26 ± 0.12). Predation rates for each of the two sessions are listed in Appendix
301 D.3. Sentinel prey cards exposing aphids did not reveal different predation rates between the
302 two periods, whereas prey cards with *Ephestia* eggs and weed seeds showed higher predation
303 rates in the second period. Correlations between the four types of prey cards ranged between
304 0.03 and 0.52 (Pearson's rho), and were not significant, except between aphids in the crop and
305 aphids on the ground (Appendix C.2).

306 In the following, we first present the results obtained using the complete data set. Second, we
307 describe the differences observed between the complete season and the beginning of the spring
308 season, *i.e.* the first four emergence sampling periods and the first session of sentinel prey cards.

309

310 **3.1. Prey cards and natural enemies in the ground compartment**

311 The predation rate on aphids in the ground compartment was significantly positively influenced
312 by the abundance of emerged carabid beetles, and by the cumulated tillage depth (Fig. 1,
313 Appendix E.1), while the proportion of winter crops had a significant negative effect. The weed
314 seed predation rate was not influenced by any factor considered in this study. The abundance
315 of emerged Staphylinidae did not influence any predation rates measured using the two sentinel
316 prey cards placed on the ground (Fig. 1, Appendix E.1).

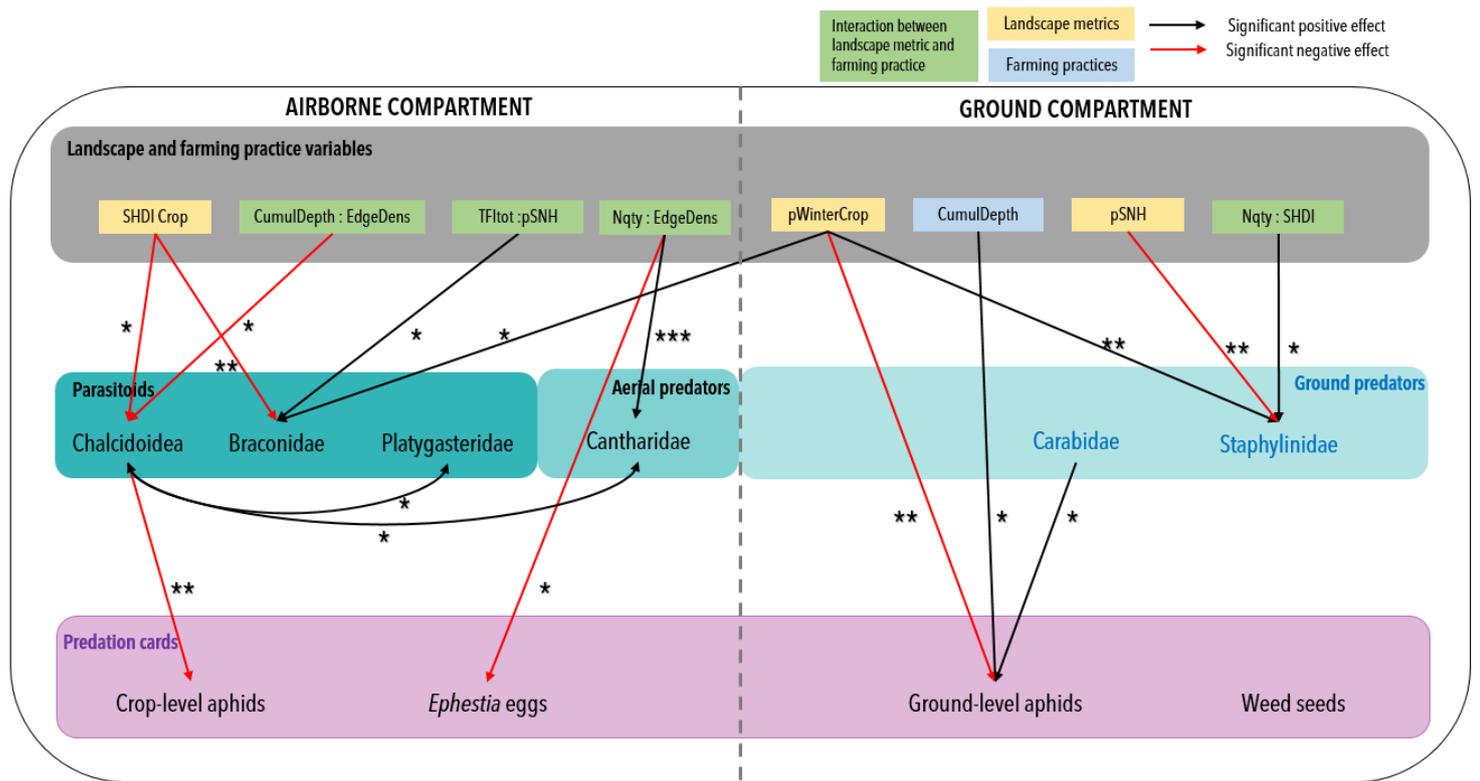


Figure 1: Effects of landscape and farming practices on the abundance of emerged natural enemies and their effects on biological control in the ground and airborne compartments measured using sentinel prey cards. Black arrows represent positive effects of variables or interactions between two variables, and red arrows represent negative effects. All the arrows show a significant effect from multi-model analysis based on GLM. Yellow rectangles correspond to landscape variables; blue rectangles correspond to farming practice variables; green rectangles correspond to interactions between one landscape and one farming practice variable. * p -value < 0.05; ** p -value < 0.01; *** p -value < 0.001. Abbreviations used for explanatory variables are explained in Table 1. See appendix E.1, E.2, F.1 and F.2 for complete results.

317

318 The proportion of semi-natural habitats significantly negatively influenced the abundance of
 319 emerged Staphylinidae (Fig. 1, Appendix E.2). In addition, the proportion of winter crops and
 320 the interaction between the quantity of nitrogen and the SHDI significantly and positively
 321 affected the abundance of emerged Staphylinidae (Fig. 1, Appendix E.2). This interaction
 322 indicates that smaller quantities of nitrogen had a significant positive effect on Staphylinidae
 323 abundance when the SHDI was low. The abundance of emerged Carabidae was not influenced
 324 by any landscape metrics or farming practices considered in this analysis (Fig. 1, Appendix
 325 E.2).

326

3.2. Prey cards and natural enemies in the airborne compartment

The predation rate of aphids present in the crop was significantly and negatively influenced by the abundance of emerged Chalcidoidea parasitoids (Appendix F.2). The predation rate of *Ephestia* eggs was significantly and negatively affected by the interaction between quantity of nitrogen and edge density (Appendix F.2). This interaction indicates that edge density had a positive effect when the quantity of nitrogen in the crop fields was low.

The abundance of emerged Chalcidoidea parasitoids was significantly negatively affected by crop diversity (SHDI crop) and by the interaction between cumulated tillage depth and edge density (Fig. 1, Appendix F.2). This interaction indicates that the edge density had a significant positive effect in the case of low cumulated tillage depth. The abundance of emerged Braconidae was significantly negatively affected by the crop SHDI and positively affected by the proportion of winter crops (Fig. 1, Appendix F.2). There was also a significant interactive effect between the total TFI and the proportion of semi natural habitats, indicating that the proportion of semi natural habitats had a significant positive effect when the total TFI was high.

The last group of parasitoids belonged to the family Platygasteridae and its abundance was not influenced by landscape metrics or farming practices (Fig. 1, Appendix F.2). The only predator group identified in the airborne compartment was the family Cantharidae, which was significantly affected by the interaction between the quantity of nitrogen and edge density, indicating edge density had a significant positive effect when the nitrogen quantity was high (Fig. 1, Appendix F.2).

Relationships between taxa of natural enemies, were significant. Abundances of emerged Chalcidoidea and Platygasteridae were correlated, as were abundances of emerged Chalcidoidea and Cantharidae (Fig. 1, Appendix F.2).

351 **3.3. Hyperparasitoids and parasitoids of natural enemies in both compartments**

352 Whether in the ground or the airborne compartment, the emerged taxonomic groups of
353 hyperparasitoids and parasitoids of natural enemies had no effect on the abundance of emerged
354 natural enemies (Appendix E.2; Appendix F.2).

355 The abundance of hyperparasitoids and parasitoids of groups of natural enemies was
356 significantly influenced by interactions between landscape metrics and farming practices (Fig.
357 2, Appendix G). The interaction between cumulated tillage depth and crop diversity had a
358 significant negative effect on the abundance of emerged Chalcidoidea and a positive effect on
359 Proctotrupidae (Fig. 2, Appendix G). The interaction between cumulated tillage depth and the
360 proportion of winter crops had a significant negative effect on the abundance of emerged
361 Proctotrupidae (Fig. 2, Appendix G). The abundance of emerged Diapriidae was significantly
362 negatively influenced by the interaction between the total TFI and the edge density or the
363 proportion of semi natural habitats. Another positive effect on the abundance of emerged
364 Diapriidae was the interaction between nitrogen quantity and the proportion of winter crops
365 (Fig. 2, Appendix G).

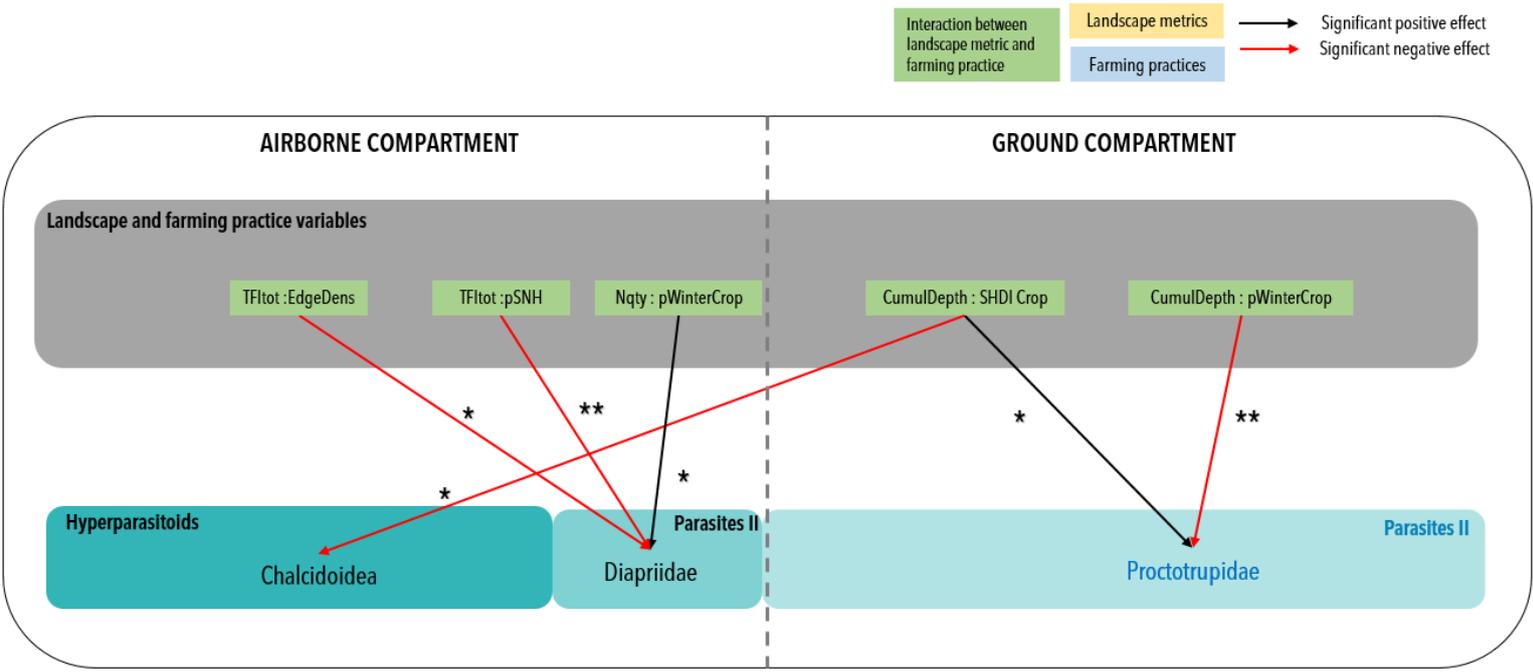


Figure 2: Effects of landscape and farming practices on emerged hyperparasitoids and parasitoids of natural enemies and their influence on the abundance of natural enemies in the ground and airborne compartments. Black arrows represent positive effects of variables or interactions between two variables, and red arrows represent negative effects. All the arrows showed a significant effect in the multi-model analysis based on GLM. Yellow rectangles correspond to landscape variables; blue rectangles correspond to farming practice variables (but none of the landscape or agricultural practice variables had a significant effect alone); green rectangles correspond to interactions between one landscape and one farming practice variable. * *p*-value < 0.05; ** *p*-value < 0.01; *** *p*-value < 0.001. Abbreviations used for the explanatory variables are explained in Table 1. See appendix G for complete results.

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3.4. Comparison between the beginning of the season and the complete season

The analysis carried out using the data from the beginning of the spring season (Appendix H.1, Appendix H.2) did not differ markedly from the analysis of all six sampling periods (Fig. 1, Fig. 2). For instance, in both, ground beetles were found to have a positive effect on aphid predation. A main difference was the positive effect of edge density on weed seed predation not observed in complete season analysis. The general effects of interactions between pairs landscape metrics and farming intensity variables on the different arthropod families remained

376 similar. However, the exact variable involved in these interactions varied. Details concerning
377 these results are presented in appendices E.2 and F.2.

378

379 **4. Discussion**

380 **4.1. Contribution of emerged natural enemies to conservation biological control**

381 Assessing CBC is complex because it involves multiple pests as well as many families of
382 natural enemies. Our results reveal a diversity of responses measured using a set of
383 complementary (non-correlated) sentinel prey cards.

384 One of our main results was that emerged carabid beetles contributed to the biological control
385 of aphids on the ground in spring, whereas staphylinids did not (Fig.1). This result is consistent
386 with several studies that have shown the importance of generalist predators such as carabid
387 beetles for aphid control in cereal fields (Schmidt et al., 2003; Symondson et al., 2002).
388 However, staphylinids feed on many other type of preys, not measured by the sentinel prey
389 cards, including slugs, snails and mites (Birken & Cloyd, 2007; Douglas & Tooker, 2012; Orth
390 et al., 1975), and were, by far, the most abundant natural enemies found in the emergence traps.

391 These results suggest that staphylinids are particularly adapted to living conditions in cereal
392 fields and may greatly contribute to biological pest control. Whether we considered the
393 beginning or the complete spring season, the effect of carabid beetles on aphid cards was still
394 significant (Fig. 1 and Appendix H.1). Therefore, emerging carabids could play an important
395 role as they may already reduce pest populations in early spring and continue predation until
396 the beginning of the summer. The contribution of emerged carabids did not disappear even
397 though their population could have been diluted by incoming carabids due to spill over from
398 semi-natural habitats or other crop fields. Neither agricultural practices nor the landscape
399 context influenced the abundance of emerging ground beetles in our study. The primary role of
400 overwintering carabid for CBC in spring has already been found in earlier studies (Holland et

401 al., 2005; Marrec et al., 2015). Especially, landscape configuration such as edge density and
402 field size have shown positive effects on carabid functional diversity (Gallé et al., 2018, 2019;
403 Gayer et al., 2021). However, landscape composition and the intensity of farming practices may
404 also influence their abundance (Dufлот et al., 2016).

405 The predation rate of weed seeds at the beginning of the season differed from the rate estimated
406 for the complete season (Fig. 1; Appendix H.1). None of the emerging taxa had a significant
407 effect on seed predation but we detected an effect of the landscape based on edge density,
408 suggesting a spill over of seedeaters from outside the fields. However, a subset of the emerging
409 carabid communities may also have contributed. We were unable to test this effect as species
410 level identification is required to identify granivorous species among a community dominated
411 by generalist predators (Trichard et al., 2013). In addition, predation on *Ephestia* eggs was also
412 positively affected by edge density when the quantity of nitrogen was lower, suggesting a
413 potential spill over of natural enemies in small fields with lower fertilization inputs. This
414 influence of fertilization is difficult to interpret in a mechanistic way but give an idea of the
415 influence of the intensity of practices on the studied taxa and on potential pest predation. These
416 results suggest the value of smaller fields to promote biological control by spillover of natural
417 enemies (Martin et al., 2019).

418 The predation of aphids exposed in the crop canopy decreased with an increase in the abundance
419 of emerged Chalcidoidea parasitoids. Parasitoids are considered prey specialists, but parasitism
420 cannot be measured using sentinel prey cards, so we did not measure the biocontrol activity of
421 these taxa. This result may suggest competition between parasitoids and aphid predators in
422 favour of parasitoids as previously found with hoverflies (Almohamad et al., 2008; Vialatte et
423 al., 2017), thus suppressing the effect of predators and resulting in a lower measured predation
424 rate. In addition, the abundance of parasitoids depends on the density of aphids. More
425 parasitoids may be associated with higher aphid abundance in the fields, resulting in a dilution

426 effect of the prey cards, which in this case would be less predated. Measurement of aphid
427 population in field may have uncover this mechanism but was not performed here.

428

429 **4.2. A diversity of natural enemies emerged in cereal fields in spring**

430 This study showed that a diverse range of taxa overwinter in cereal fields as varying abundances
431 of 10 different taxa were observed. A study by Raymond et al. (2014) in the same region
432 highlighted the overwintering of hoverflies (Diptera: Syrphidae), a major predator family
433 involved in pest control, especially aphid control (Schmidt et al., 2003; Tenhumberg &
434 Poehling, 1995). Surprisingly, we observed very few individual Syrphidae (10 in total), maybe
435 because fluctuating meteorological conditions affected their winter survival rate and/or their
436 overwintering strategies (Raymond et al., 2013). Other well-known natural enemies, such as
437 true bugs, lacewings, spiders or ladybird were not found in the emergence traps, showing they
438 most likely do not overwinter in the crop fields (at least in the range of farming practices studied
439 in here).

440 We observed marked variability both in the abundance of emerging taxa and in the seasonality
441 of their emergence (Appendices D.1 and D.2). Individuals belonging to the family
442 Platygasteridae only emerged during the two final sampling periods, *i.e.* in the last two weeks
443 of May, and at a very low rate, whereas most individuals of Cantharidae emerged in early
444 spring (*i.e.* mid-March and the end of April). Differences in the timing of the emergence of the
445 various taxonomic groups sampled is linked to their phenology and life traits. It may be an
446 advantage for the continuity of CBC if several predators of the same pest are present in
447 successive periods.

448 Conversely, the presence of taxa belonging to high trophic levels may be detrimental to the
449 CBC, as the abundance of emerging natural enemies may be reduced by parasitism by their
450 own enemies. Nevertheless, statistical analysis performed in both ground and airborne

451 compartments showed no significant effects of emerging hyperparasitoids or parasitoids on the
452 abundance of emerging natural enemies.

453 In the airborne compartment, different taxa of natural enemies in the same trophic level co-
454 occurred, as the abundance of the Chalcidoidea family was significantly correlated with the
455 abundance of emerged Platygasteridae and Cantharidae (Fig.1). This was not the case in the
456 ground compartment. Such relationships could mean that some natural enemy families may
457 depend on the abundance of the same pest prey in crop fields in autumn, and/or by the same
458 wintering conditions offered by crop fields.

459

460 **4.3. Farming intensity modulates the response of natural enemies to the** 461 **landscape context**

462 Some overwintering natural enemies appear to be particularly adapted to winter crops, favoured
463 by a higher proportion of winter crops in the landscape, mainly cereal fields in the study area,
464 or negatively influenced by the heterogeneity of the crop mosaic characterized by the diversity
465 of crop covers. Such relationships refer to overwintering staphylinids and some parasitoid
466 families, *i.e.* Chalcidoidea and Braconidae. These results suggest that these emerging natural
467 enemies are relatively independent from semi-natural habitats or may even be negatively
468 influenced by them, as was the case for emerging staphylinids (Fig. 1). Chalcidoidea

469 In both compartments, many interactions between landscape elements and farming practices
470 had a significant effect on the abundance of natural enemies. This relate to earlier works
471 showing that, on the one hand, field-scale practices such as soil cultivation and grass cutting
472 have direct and indirect negative effects on generalist predators (Thorbeck & Bilde, 2004).
473 Similarly, soil tillage and pesticide treatment have been found to strongly reduce parasitoid
474 populations during the overwintering period and at emergence (Rusch et al., 2011; Tschardtke
475 et al., 2016). On the other hand, at the landscape scale, surrounding semi-natural elements and

476 diverse crop mosaics provide life support functions for many natural enemies species (Bianchi
477 et al., 2006; Landis et al., 2000; Sirami et al., 2019). In a recent study, Ricci et al. (2019) pointed
478 out that the effects of the landscape context on biological control is modified by the intensity
479 of local pesticide use. Therefore, we expected a negative effect of higher intensity of practices,
480 that would counteract a potential positive effect of landscape heterogeneity on the abundance
481 of emerging natural enemy communities. Surprisingly, we found the opposite trend, with
482 positive interaction between landscape heterogeneity and farming practices intensity. Higher
483 proportion of semi natural habitats or higher crop diversity, combined with more intense
484 farming practices had positive effects on the abundance of several emerging natural enemies.
485 Many taxa of natural enemies are sensitive to farming intensity, as reported in several reviews
486 (e.g. Geiger et al., 2010; Letourneau et al., 2011; Tschardtke, Klein, et al., 2005). However, our
487 result suggests that the natural enemies that overwinter within crop fields may not follow this
488 rule and are adapted to conventional farming practices. They may even benefit from lower inter-
489 specific competition in landscapes where spill over is reduced (positive effect of high intensive
490 practices in complex landscape). The high adaptive potential of natural enemy that overwinter
491 in crop fields does not negate the importance of the spill-over of natural enemies from outside
492 the field for CBC as we found positive effect of edge density on some predation rates in low
493 intensity field.

494

495 **5. Conclusion**

496 The present study highlights the potential contribution of natural enemies that overwinter within
497 crop fields to biological control in spring. Nevertheless, we observed varied responses
498 depending on taxa and the type of the sentinel prey card, which illustrate the complexity of
499 conservation biological control. Considering the trophic chains in two specific compartments

500 (ground and airborne) allowed an overall understanding of natural enemy interactions between
501 each other's, with their own enemies, and their effects on biological pest control.
502 Overwintering natural enemies seem adapted to winter crops and associated intensive farming
503 practices, and relatively independent from semi-natural habitats. These taxa were more
504 abundant when higher crop diversity and edge density at landscape-level was associated with
505 more intense farming practices at field scale. These results suggest a potential trade-off between
506 the community of natural enemies that overwinter within the fields and those arriving from
507 outside the fields (spill-over), with potential consequences on biological control. Further studies
508 using exclusion cages are now required to quantify the contribution of emerging natural
509 enemies to biological pest control relative to spill-over processes.
510 Better qualification of the trophic interactions between the numerous taxa found in crop fields
511 would also facilitate the understanding of biological control mechanisms in the future.
512 Advances in barcoding should enable the specific identification of the different taxa, while
513 metabarcoding would improve the diet analyses of natural enemies; thereby allowing progress
514 in the functional description of arthropod communities found in crop fields.

515

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- Almohamad, R., Verheggen, F. J., Francis, F., Hance, T., & Haubruge, E. (2008). Discrimination of parasitized aphids by a hoverfly predator: Effects on larval performance, foraging, and oviposition behavior. *Entomologia Experimentalis et Applicata*, *128*(1), 73–80. <https://doi.org/10.1111/j.1570-7458.2007.00664.x>
- Anjum-Zubair, M., Schmidt-Entling, M. H., Querner, P., & Frank, T. (2010). Influence of within-field position and adjoining habitat on carabid beetle assemblages in winter wheat. *Agricultural and Forest Entomology*, *12*(3), 301–306. <https://doi.org/10.1111/j.1461-9563.2010.00479.x>
- Aviron, S., Lalechère, E., DufLOT, R., Parisey, N., & Poggi, S. (2018). Connectivity of cropped vs. semi-natural habitats mediates biodiversity: A case study of carabid beetles communities. *Agriculture, Ecosystems & Environment*, *268*, 34–43. <https://doi.org/10.1016/j.agee.2018.08.025>
- Barbosa, P. A. (1998). *Conservation biological control*. Elsevier.
- Benton, T. G., Vickery, J. A., & Wilson, J. D. (2003). Farmland biodiversity: Is habitat heterogeneity the key? *Trends in Ecology & Evolution*, *18*(4), 182–188. [https://doi.org/10.1016/S0169-5347\(03\)00011-9](https://doi.org/10.1016/S0169-5347(03)00011-9)
- Bertrand, C., Burel, F., & Baudry, J. (2016). Spatial and temporal heterogeneity of the crop mosaic influences carabid beetles in agricultural landscapes. *Landscape Ecology*, *31*(2), 451–466. <https://doi.org/10.1007/s10980-015-0259-4>
- Bianchi, F. J. J. A., Booij, C. J. H., & Tscharntke, T. (2006). Sustainable pest regulation in agricultural landscapes: A review on landscape composition, biodiversity and natural pest control. *Proceedings of the Royal Society B: Biological Sciences*, *273*(1595), 1715–1727. <https://doi.org/10.1098/rspb.2006.3530>

- Birken, E. M., & Cloyd, R. A. (2007). Food preference of the rove beetle, *Atheta coriaria* Kraatz (Coleoptera: Staphylinidae) under laboratory conditions. *Insect Science*, *14*(1), 53–56. <https://doi.org/10.1111/j.1744-7917.2007.00125.x>
- Blitzer, E. J., Dormann, C. F., Holzschuh, A., Klein, A.-M., Rand, T. A., & Tschamntke, T. (2012). Spillover of functionally important organisms between managed and natural habitats. *Agriculture, Ecosystems & Environment*, *146*(1), 34–43. <https://doi.org/10.1016/j.agee.2011.09.005>
- Botzas-Coluni, J., Crockett, E. T. H., Rieb, J. T., & Bennett, E. M. (2021). Farmland heterogeneity is associated with gains in some ecosystem services but also potential trade-offs. *Agriculture, Ecosystems & Environment*, *322*, 107661. <https://doi.org/10.1016/j.agee.2021.107661>
- Chaplin-Kramer, R., O'Rourke, M. E., Blitzer, E. J., & Kremen, C. (2011). A meta-analysis of crop pest and natural enemy response to landscape complexity: Pest and natural enemy response to landscape complexity. *Ecology Letters*, *14*(9), 922–932. <https://doi.org/10.1111/j.1461-0248.2011.01642.x>
- Collins, K. L., Boatman, N. D., Wilcox, A., Holland, J. M., & Chaney, K. (2002). Influence of beetle banks on cereal aphid predation in winter wheat. *Agriculture, Ecosystems & Environment*, *93*(1), 337–350. [https://doi.org/10.1016/S0167-8809\(01\)00340-1](https://doi.org/10.1016/S0167-8809(01)00340-1)
- Dainese, M., Martin, E. A., Aizen, M. A., Albrecht, M., Bartomeus, I., Bommarco, R., Carvalheiro, L. G., Chaplin-Kramer, R., Gagic, V., Garibaldi, L. A., Ghazoul, J., Grab, H., Jonsson, M., Karp, D. S., Kennedy, C. M., Kleijn, D., Kremen, C., Landis, D. A., Letourneau, D. K., ... Steffan-Dewenter, I. (2019). A global synthesis reveals biodiversity-mediated benefits for crop production. *Science Advances*, *14*.
- Douglas, M. R., & Tooker, J. F. (2012). Slug (Mollusca: Agriolimacidae, Arionidae) Ecology and Management in No-Till Field Crops, With an Emphasis on the mid-Atlantic Region. *Journal of Integrated Pest Management*, *3*(1), C1–C9. <https://doi.org/10.1603/IPM11023>

- Duflot, R., Ernoult, A., Aviron, S., Fahrig, L., & Burel, F. (2017). Relative effects of landscape composition and configuration on multi-habitat gamma diversity in agricultural landscapes. *Agriculture, Ecosystems & Environment*, *241*, 62–69. <https://doi.org/10.1016/j.agee.2017.02.035>
- Duflot, R., Ernoult, A., Burel, F., & Aviron, S. (2016). Landscape level processes driving carabid crop assemblage in dynamic farmlands. *Population Ecology*, *58*(2), 265–275. <https://doi.org/10.1007/s10144-015-0534-x>
- Dunning, J. B., Danielson, B. J., & Pulliam, H. R. (1992). Ecological processes that affect populations in complex landscapes. *Oikos*, *65*(1), 169. <https://doi.org/10.2307/3544901>
- Fahrig, L., Baudry, J., Brotons, L., Burel, F. G., Crist, T. O., Fuller, R. J., Sirami, C., Siriwardena, G. M., & Martin, J.-L. (2011). Functional landscape heterogeneity and animal biodiversity in agricultural landscapes: Heterogeneity and biodiversity. *Ecology Letters*, *14*(2), 101–112. <https://doi.org/10.1111/j.1461-0248.2010.01559.x>
- Gallé, R., Császár, P., Makra, T., Gallé-Szpisjak, N., Ladányi, Z., Torma, A., Ingle, K., & Szilassi, P. (2018). Small-scale agricultural landscapes promote spider and ground beetle densities by offering suitable overwintering sites. *Landscape Ecology*, *33*(8), 1435–1446. <https://doi.org/10.1007/s10980-018-0677-1>
- Gallé, R., Happe, A.-K., Baillo, A. B., Tschardtke, T., & Batáry, P. (2019). Landscape configuration, organic management, and within-field position drive functional diversity of spiders and carabids. *Journal of Applied Ecology*, *56*(1), 63–72. <https://doi.org/10.1111/1365-2664.13257>
- Garibaldi, L. A., Andersson, G. K. S., Requier, F., Fijen, T. P. M., Hipólito, J., Kleijn, D., Pérez-Méndez, N., & Rollin, O. (2018). Complementarity and synergisms among ecosystem services supporting crop yield. *Global Food Security*, *17*, 38–47. <https://doi.org/10.1016/j.gfs.2018.03.006>
- Gayer, C., Berger, J., Dieterich, M., Gallé, R., Reidl, K., Witty, R., Woodcock, B. A., & Batáry, P. (2021). Flowering fields, organic farming and edge habitats promote diversity of plants and

arthropods on arable land. *Journal of Applied Ecology*, 58(6), 1155–1166.
<https://doi.org/10.1111/1365-2664.13851>

Geiger, F., Bengtsson, J., Berendse, F., Weisser, W. W., Emmerson, M., Morales, M. B., Ceryngier, P., Liira, J., Tschardtke, T., Winqvist, C., Eggers, S., Bommarco, R., Pärt, T., Bretagnolle, V., Plantegenest, M., Clement, L. W., Dennis, C., Palmer, C., Oñate, J. J., ... Inchausti, P. (2010). Persistent negative effects of pesticides on biodiversity and biological control potential on European farmland. *Basic and Applied Ecology*, 11(2), 97–105.
<https://doi.org/10.1016/j.baae.2009.12.001>

Herzog, F., Steiner, B., Bailey, D., Baudry, J., Billeter, R., Bukáček, R., De Blust, G., De Cock, R., Dirksen, J., Dormann, C. F., De Filippi, R., Frossard, E., Liira, J., Schmidt, T., Stöckli, R., Thenail, C., van Wingerden, W., & Bugter, R. (2006). Assessing the intensity of temperate European agriculture at the landscape scale. *European Journal of Agronomy*, 24(2), 165–181.
<https://doi.org/10.1016/j.eja.2005.07.006>

Holland, J. M., Thomas, C. F. G., Birkett, T., Southway, S., & Oaten, H. (2005). Farm-scale spatiotemporal dynamics of predatory beetles in arable crops. *Journal of Applied Ecology*, 42(6), 1140–1152. <https://doi.org/10.1111/j.1365-2664.2005.01083.x>

Karp, D. S., Chaplin-Kramer, R., Meehan, T. D., Martin, E. A., DeClerck, F., Grab, H., Gratton, C., Hunt, L., Larsen, A. E., Martínez-Salinas, A., O'Rourke, M. E., Rusch, A., Poveda, K., Jonsson, M., Rosenheim, J. A., Schellhorn, N. A., Tschardtke, T., Wratten, S. D., Zhang, W., ... Zou, Y. (2018). Crop pests and predators exhibit inconsistent responses to surrounding landscape composition. *Proceedings of the National Academy of Sciences*, 115(33), E7863–E7870. <https://doi.org/10.1073/pnas.1800042115>

Labruyere, S., Petit, S., & Ricci, B. (2018). Annual variation of oilseed rape habitat quality and role of grassy field margins for seed eating carabids in arable mosaics. *Agricultural and Forest Entomology*, 20(2), 234–245. <https://doi.org/10.1111/afe.12250>

- Labruyere, S., Ricci, B., Lubac, A., & Petit, S. (2016). Crop type, crop management and grass margins affect the abundance and the nutritional state of seed-eating carabid species in arable landscapes. *Agriculture, Ecosystems & Environment*, 231, 183–192. <https://doi.org/10.1016/j.agee.2016.06.037>
- Landis, D. A., Wratten, S. D., & Gurr, G. M. (2000). Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annual Review of Entomology*, 45(1), 175–201. <https://doi.org/10.1146/annurev.ento.45.1.175>
- Lechenet, M., Bretagnolle, V., Bockstaller, C., Boissinot, F., Petit, M.-S., Petit, S., & Munier-Jolain, N. M. (2014). Reconciling pesticide reduction with economic and environmental sustainability in arable farming. *PLoS ONE*, 9(6). <https://doi.org/10.1371/journal.pone.0097922>
- Letourneau, D. K., Armbricht, I., Rivera, B. S., Lerma, J. M., Rrez, C. G., Rangel, J. H., Rivera, L., Saavedra, C. A., Torres, A. M., & Trujillo, A. R. (2011). Does plant diversity benefit agroecosystems? A synthetic review. *Ecological Applications*, 21(1), 13.
- MacLeod, A., Wratten, S. D., Sotherton, N. W., & Thomas, M. B. (2004). ‘Beetle banks’ as refuges for beneficial arthropods in farmland: Long-term changes in predator communities and habitat. *Agricultural and Forest Entomology*, 6(2), 147–154. <https://doi.org/10.1111/j.1461-9563.2004.00215.x>
- Marrec, R., Badenhauer, I., Bretagnolle, V., Börger, L., Roncoroni, M., Guillon, N., & Gauffre, B. (2015). Crop succession and habitat preferences drive the distribution and abundance of carabid beetles in an agricultural landscape. *Agriculture, Ecosystems & Environment*, 199, 282–289. <https://doi.org/10.1016/j.agee.2014.10.005>
- Martin, E. A., Dainese, M., Clough, Y., Báldi, A., Bommarco, R., Gagic, V., Garratt, M. P. D., Holzschuh, A., Kleijn, D., Kovács-Hostyánszki, A., Marini, L., Potts, S. G., Smith, H. G., Hassan, D. A., Albrecht, M., Andersson, G. K. S., Asís, J. D., Aviron, S., Balzan, M. V., ... Steffan-Dewenter, I. (2019). The interplay of landscape composition and configuration: New

- pathways to manage functional biodiversity and agroecosystem services across Europe. *Ecology Letters*, 22(7), 1083–1094. <https://doi.org/10.1111/ele.13265>
- McHugh, N. M., Moreby, S., Lof, M. E., Werf, W., & Holland, J. M. (2020). The contribution of semi-natural habitats to biological control is dependent on sentinel prey type. *Journal of Applied Ecology*, 57(5), 914–925. <https://doi.org/10.1111/1365-2664.13596>
- Meyer, S. T., Leidinger, J. L. G., Gossner, M. M., & Weisser, W. W. (2017). *Handbook of field protocols for using REFA methods to approximate ecosystem functions*. 19. <https://doi.org/10.14459/2017MD1400892>
- Nesme, T., Doré, T., Leenhardt, D., & Pellerin, S. (2016). *Agriculture et ressources naturelles: De quoi parlons-nous?* 16.
- Noordhuis, R., Thomas, S. R., & Goulson, D. (2001). Overwintering populations of beetle larvae (Coleoptera) in cereal fields and their contribution to adult populations in the spring. *Pedobiologia*, 45(1), 84–95. <https://doi.org/10.1078/0031-4056-00070>
- Orth, R. E., Moore, I., Fisher, T. W., & Legner, E. F. (1975). A rove beetle, *Ocypus Olens*, with potential for biological control of the brown garden snail, *Helix aspersa*, in California, including a key to the nearctic species of *Ocypus*. *The Canadian Entomologist*, 107(10), 1111–1116. <https://doi.org/10.4039/Ent1071111-10>
- Östman, Ö. (2004). The relative effects of natural enemy abundance and alternative prey abundance on aphid predation rates. *Biological Control*, 30(2), 281–287. <https://doi.org/10.1016/j.biocontrol.2004.01.015>
- Purvis, G., & Fadl, A. (2002). The influence of cropping rotations and soil cultivation practice on the population ecology of carabids (Coleoptera: Carabidae) in arable land. *Pedobiologia*, 46(5), 452–474. <https://doi.org/10.1078/0031-4056-00152>
- Raymond, L., Ortiz-Martínez, S. A., & Lavandero, B. (2015). Temporal variability of aphid biological control in contrasting landscape contexts. *Biological Control*, 90, 148–156. <https://doi.org/10.1016/j.biocontrol.2015.06.011>

- Raymond, L., Plantegenest, M., Gauffre, B., Sarthou, J.-P., & Vialatte, A. (2013). Lack of genetic differentiation between contrasted overwintering strategies of a major pest predator *Episyrphus balteatus* (Diptera: Syrphidae): implications for biocontrol. *PLoS ONE*, *8*(9), e72997. <https://doi.org/10.1371/journal.pone.0072997>
- Raymond, L., Sarthou, J.-P., Plantegenest, M., Gauffre, B., Ladet, S., & Vialatte, A. (2014). Immature hoverflies overwinter in cultivated fields and may significantly control aphid populations in autumn. *Agriculture, Ecosystems & Environment*, *185*, 99–105. <https://doi.org/10.1016/j.agee.2013.12.019>
- Ricci, B., Lavigne, C., Alignier, A., Aviron, S., Biju-Duval, L., Bouvier, J. C., Choisis, J.-P., Franck, P., Joannon, A., Ladet, S., Mezerette, F., Plantegenest, M., Savary, G., Thomas, C., Vialatte, A., & Petit, S. (2019). Local pesticide use intensity conditions landscape effects on biological pest control. *Proceedings of the Royal Society B: Biological Sciences*, *286*(1904), 20182898. <https://doi.org/10.1098/rspb.2018.2898>
- Root, R. B. (1973). Organization of a Plant-Arthropod Association in Simple and Diverse Habitats: The Fauna of Collards (*Brassica Oleracea*). *Ecological Monographs*, *43*(1), 95–124. <https://doi.org/10.2307/1942161>
- Roubos, C. R., Rodriguez-Saona, C., & Isaacs, R. (2014). Mitigating the effects of insecticides on arthropod biological control at field and landscape scales. *Biological Control*, *75*, 28–38. <https://doi.org/10.1016/j.biocontrol.2014.01.006>
- Rusch, A., Binet, D., Delbac, L., & Thiéry, D. (2016). Local and landscape effects of agricultural intensification on Carabid community structure and weed seed predation in a perennial cropping system. *Landscape Ecology*, *31*(9), 2163–2174. <https://doi.org/10.1007/s10980-016-0390-x>
- Rusch, A., Chaplin-Kramer, R., Gardiner, M. M., Hawro, V., Holland, J., Landis, D., Thies, C., Tschamntke, T., Weisser, W. W., Winqvist, C., Woltz, M., & Bommarco, R. (2016). Agricultural landscape simplification reduces natural pest control: A quantitative synthesis.

Agriculture, Ecosystems & Environment, 221, 198–204.

<https://doi.org/10.1016/j.agee.2016.01.039>

Rusch, A., Valantin-Morison, M., Sarthou, J.-P., & Roger-Estrade, J. (2011). Multi-scale effects of landscape complexity and crop management on pollen beetle parasitism rate. *Landscape Ecology*, 26(4), 473–486. <https://doi.org/10.1007/s10980-011-9573-7>

Schellhorn, N. A., Gagic, V., & Bommarco, R. (2015). Time will tell: Resource continuity bolsters ecosystem services. *Trends in Ecology & Evolution*, 30(9), 524–530. <https://doi.org/10.1016/j.tree.2015.06.007>

Schmidt, M. H., Lauer, A., Purtauf, T., Thies, C., Schaefer, M., & Tscharnkte, T. (2003). Relative importance of predators and parasitoids for cereal aphid control. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 270(1527), 1905–1909. <https://doi.org/10.1098/rspb.2003.2469>

Sigsgaard, L., & Jacobsen, S. K. (2017). *Functional agrobiodiversity – a novel approach to optimize pest control in fruit production*. 3.

Sirami, C., Gross, N., Baillod, A. B., Bertrand, C., Carrié, R., Hass, A., Henckel, L., Miguet, P., Vuillot, C., Alignier, A., Girard, J., Batáry, P., Clough, Y., Violle, C., Giralt, D., Bota, G., Badenhauer, I., Lefebvre, G., Gauffre, B., ... Fahrig, L. (2019). Increasing crop heterogeneity enhances multitrophic diversity across agricultural regions. *Proceedings of the National Academy of Sciences*, 116(33), 16442–16447. <https://doi.org/10.1073/pnas.1906419116>

Stapel, J. O., Cortesero, A. M., & Lewis, W. J. (2000). Disruptive sublethal effects of insecticides on biological control: Altered foraging ability and life span of a parasitoid after feeding on extrafloral nectar of cotton treated with systemic insecticides. *Biological Control*, 17(3), 243–249. <https://doi.org/10.1006/bcon.1999.0795>

- Symondson, W. O. C., Sunderland, K. D., & Greenstone, M. H. (2002). Can Generalist Predators be Effective Biocontrol Agents? *Annual Review of Entomology*, 47(1), 561–594. <https://doi.org/10.1146/annurev.ento.47.091201.145240>
- Tenhumberg, B., & Poehling, H.-M. (1995). Syrphids as natural enemies of cereal aphids in Germany: Aspects of their biology and efficacy in different years and regions. *Agriculture, Ecosystems & Environment*, 52(1), 39–43. [https://doi.org/10.1016/0167-8809\(94\)09007-T](https://doi.org/10.1016/0167-8809(94)09007-T)
- Thomas, S. (2000). Progress on beetle banks in UK arable farming. *Pesticide Outlook*, 11(2), 51–53. <https://doi.org/10.1039/b006319n>
- Thorbek, P., & Bilde, T. (2004). Reduced numbers of generalist arthropod predators after crop management. *Journal of Applied Ecology*, 41(3), 526–538. <https://doi.org/10.1111/j.0021-8901.2004.00913.x>
- Trichard, A., Alignier, A., Biju-Duval, L., & Petit, S. (2013). The relative effects of local management and landscape context on weed seed predation and carabid functional groups. *Basic and Applied Ecology*, 14(3), 235–245. <https://doi.org/10.1016/j.baae.2013.02.002>
- Tscharntke, T., Clough, Y., Wanger, T. C., Jackson, L., Motzke, I., Perfecto, I., Vandermeer, J., & Whitbread, A. (2012). Global food security, biodiversity conservation and the future of agricultural intensification. *Biological Conservation*, 151(1), 53–59. <https://doi.org/10.1016/j.biocon.2012.01.068>
- Tscharntke, T., Karp, D. S., Chaplin-Kramer, R., Batáry, P., DeClerck, F., Gratton, C., Hunt, L., Ives, A., Jonsson, M., Larsen, A., Martin, E. A., Martínez-Salinas, A., Meehan, T. D., O'Rourke, M., Poveda, K., Rosenheim, J. A., Rusch, A., Schellhorn, N., Wanger, T. C., ... Zhang, W. (2016). When natural habitat fails to enhance biological pest control – Five hypotheses. *Biological Conservation*, 204, 449–458. <https://doi.org/10.1016/j.biocon.2016.10.001>
- Tscharntke, T., Klein, A. M., Kruess, A., Steffan-Dewenter, I., & Thies, C. (2005). Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. *Ecology Letters*, 8(8), 857–874. <https://doi.org/10.1111/j.1461-0248.2005.00782.x>

- Tscharntke, T., Rand, T. A., & Bianchi, F. J. J. A. (2005). The landscape context of trophic interactions: Insect spillover across the crop–noncrop interface. *Ann. Zool. Fennici*, 42, 12.
- Vasseur, C., Joannon, A., Aviron, S., Burel, F., Meynard, J.-M., & Baudry, J. (2013). The cropping systems mosaic: How does the hidden heterogeneity of agricultural landscapes drive arthropod populations? *Agriculture, Ecosystems & Environment*, 166, 3–14.
<https://doi.org/10.1016/j.agee.2012.08.013>
- Vialatte, A., Tsafack, N., Hassan, D. A., Duflot, R., Plantegenest, M., Ouin, A., Villenave-Chasset, J., & Ernoult, A. (2017). Landscape potential for pollen provisioning for beneficial insects favours biological control in crop fields. *Landscape Ecology*, 32(3), 465–480.
<https://doi.org/10.1007/s10980-016-0481-8>

Appendices

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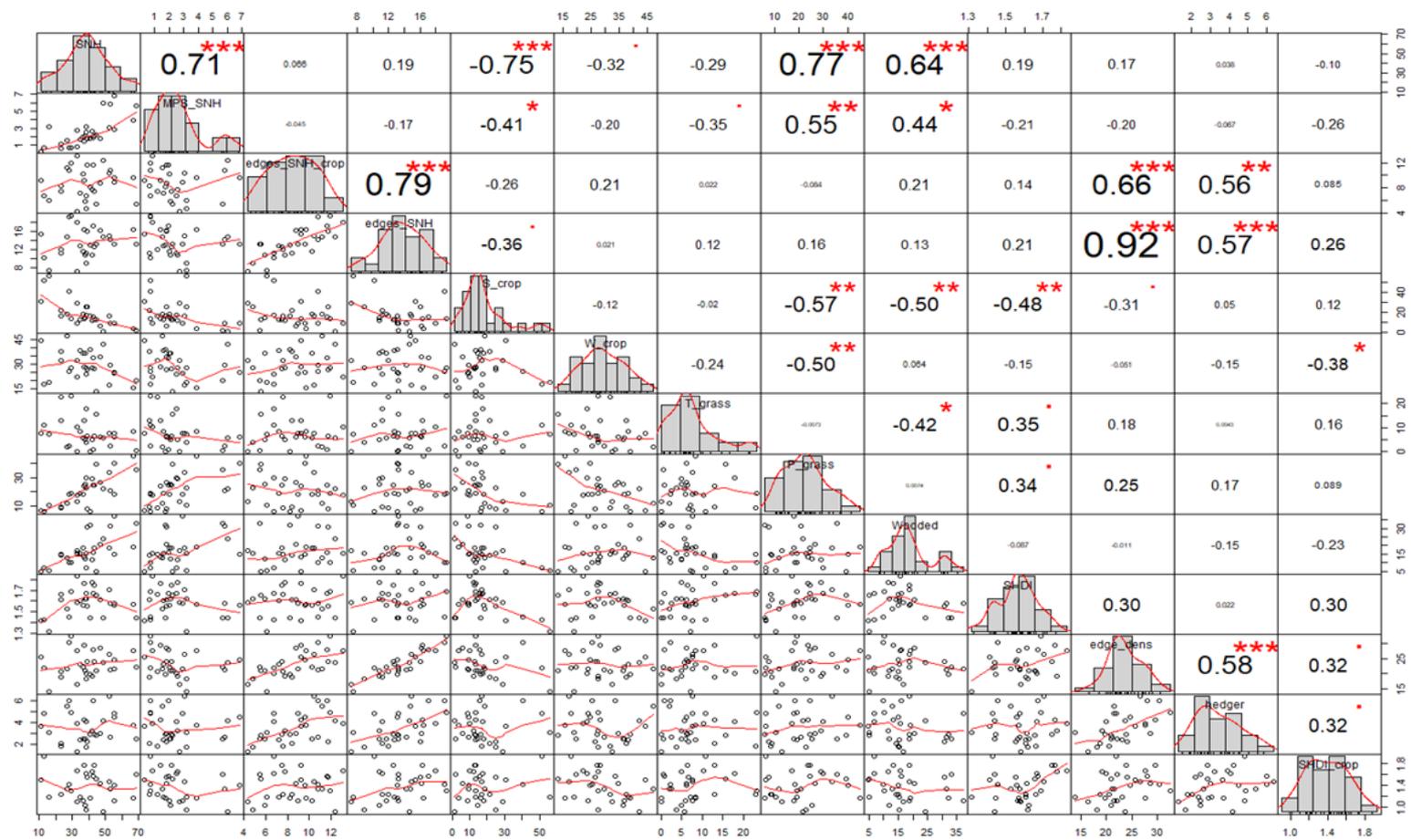
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Appendix H.2: Effects of landscape and farming practices on emerged hyperparasitoids and parasitoids of natural enemies and their consequences for the abundance of natural enemies in the ground and airborne compartments. The results are for the beginning of the spring season. Black arrows represent a positive effect of the variable or the interaction between two variable. Red arrows represent a negative effect. All arrows show a significant effect. Yellow rectangles correspond to a landscape variable; blue rectangles correspond to a farming practice variable; green rectangles correspond to the interaction between one landscape and one farming practice variable. * *p-value* < 0.05; ** *p-value* < 0.01; *** *p-value* < 0.001. Abbreviations for explanatory variables are explained in Table 1. See appendix G for complete results. 2

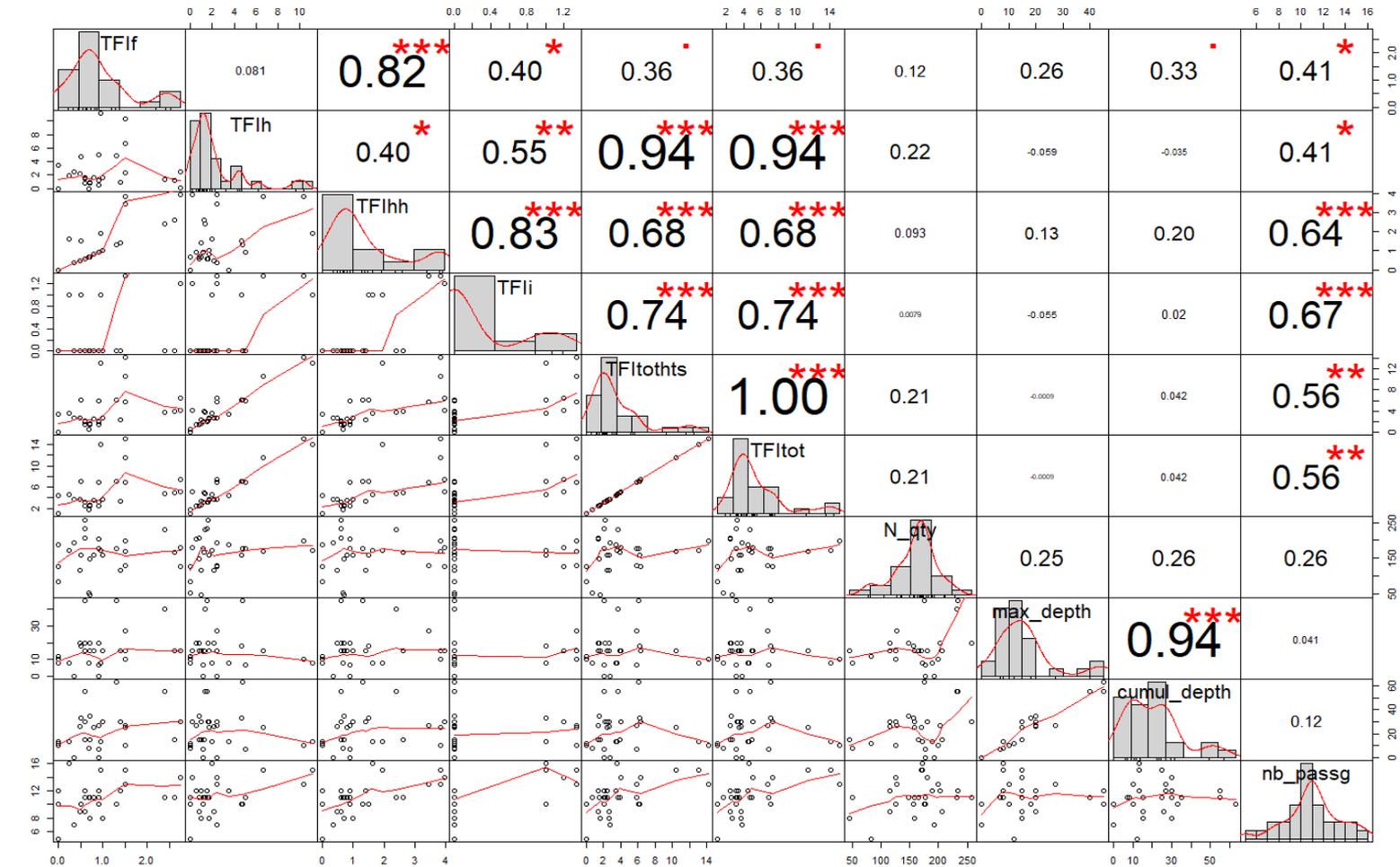
Appendix A: Complete list of variables calculated and surveyed, classified according to the latent variable to which they belong, their unit of measure, and their range of variation.

	Latent variable (LV)	Manifest variable (MV)	Meaning	Unit	Mean [min-max]
	Agricultural production	Crop yield	estimated crop yield	Q/ha	71.4 [34.5;98.1]
AIRBORNE COMPARTMENT	Potential predation	Crop-level aphids	Predation rate of aphids at canopy position	ratio	0.26 [0.02;0.53]
		<i>Ephestia</i> eggs	Predation rate of lepidoptera eggs at canopy position	ratio	0.75 [0.60;0.95]
		Parasitoids	N° of parasitoids emerging	individual	12.1 [3.0;33.0]
		Abundance of Chalcidoidea (parasitoids)	N° of emerging individuals sampled	individual	9.7 [1;31.0]
		Abundance of Braconidae	N° of emerging individuals sampled	individual	2.4 [0;17.0]
		Abundance of Platygasteridae	N° of emerging individuals sampled	individual	0.41 [0 ; 5.0]
		Airborne predators	N° of predators emerging	individual	3.5 [0;19.0]
		Abundance of Cantharidae	N° of emerging individuals sampled	individual	3.5 [0;19.0]
		Airborne (Hyper)parasitoids	N° of hyperparasitoids or parasitoids II sampled	individual	6.0 [0;16.0]
		Abundance of Chalcidoidea (hyperparasitoids)	N° of emerging individuals sampled	individual	2.3 [0;11.0]
		Abundance of Diapriidae	N° of emerging individuals sampled	individual	5.2 [0;12.0]
GROUND COMPARTMENT	Potential predation	Ground-level aphids	Predation rate of aphids on the ground	ratio	0.85 [0.53;1]
		Weed seeds	Predation rate of seeds on the ground	ratio	0.66 [0.24;0.93]
		Predators on the ground	N° of predators emerging	individual	211.9 [48.0;548.0]
		Abundance of Carabidae	N° of emerging individuals sampled	individual	9.0 [0;59.0]
		Abundance of Staphylinidae	N° of emerging individuals sampled	individual	202.9 [43.0;547.0]
		(Hyper)parasitoids II on the ground	N° of hyperparasitoids or parasitoids II on the ground	individual	0.53 [0;3.0]
		Abundance of Proctotrupidae	N° of emerging individuals sampled	individual	0.53 [0;3.0]
	Farming intensity	Cumulated depth	Cumulated tillage depth	cm	22.2 [0;63.0]
		Maximum depth	maximum tillage depth	cm	15.8 [0;45.0]
		TfI.f	Treatment frequency index of fungicides	dose / ha	1.01 [0;2.75]
		TfI.h	Treatment frequency index of herbicides	dose / ha	2.5 [0;11.1]

	TFL.i	Treatment frequency index of insecticides	dose / ha	0.31 [0;1.33]
	TFL.hh	Total treatment frequency index not including herbicides	dose / ha	0.90 [0;3.95]
	TFLtot	Total treatment frequency index including all types of treatments	dose / ha	4.9 [1;15.2]
	Nqty	Quantity of nitrogen provided in liquid form	kg / ha	162.4 [46.0;257.9]
	N° passage	Number of treatments	N°	11.1 [5.0;16.0]
Landscape heterogeneity	% SNH	Proportion of semi-natural habitats	%	38.6 [11.2;68.8]
	MPS SNH	Mean patch size of semi-natural habitats	ha	2.5 [0.3;6.8]
	Edges SNH	Total length of SNH edges	km	13.5 [7.2;19.4]
	Edges SNH-crop	Length of edges between SNH and crops	km	8.7 [4.4;13.1]
	% S. crop	Proportion of spring crops	%	18.1 [1.3;56.0]
	% W. crop	Proportion of winter crops	%	29.1 [13.3;47.2]
	% T. grass	Proportion of temporary grasslands	%	7.7 [0;23.2]
	% P. grass	Proportion of permanent grasslands	%	21.0 [5.9;45.1]
	% Wooded	Proportion of wooded habitats	%	16.9 [4.7;37.3]
	SHDI	Shannon diversity index on % of land cover classes	-	1.6 [1.3;1.8]
	Edge density	Total length of edges – all types of edges types included	km/ha	23.2 [13.9;32.5]
Hedgerows	Total length of hedgerows	km	3.5 [1.3;6.4]	
SHDI crops	Shannon diversity index of crops	-	1.37 [0.90;1.93]	



Appendix B.1: Pairwise Pearson's correlations between landscape variables. * p -value < 0.05; ** p -value < 0.01; *** p -value < 0.001.



Appendix B.2: Pairwise Pearson's correlations between farming practice variables. * p -value < 0.05; ** p -value < 0.01; *** p -value < 0.001.

Appendix C.1: Pairwise Pearson's correlations between the explanatory variables used in the study.

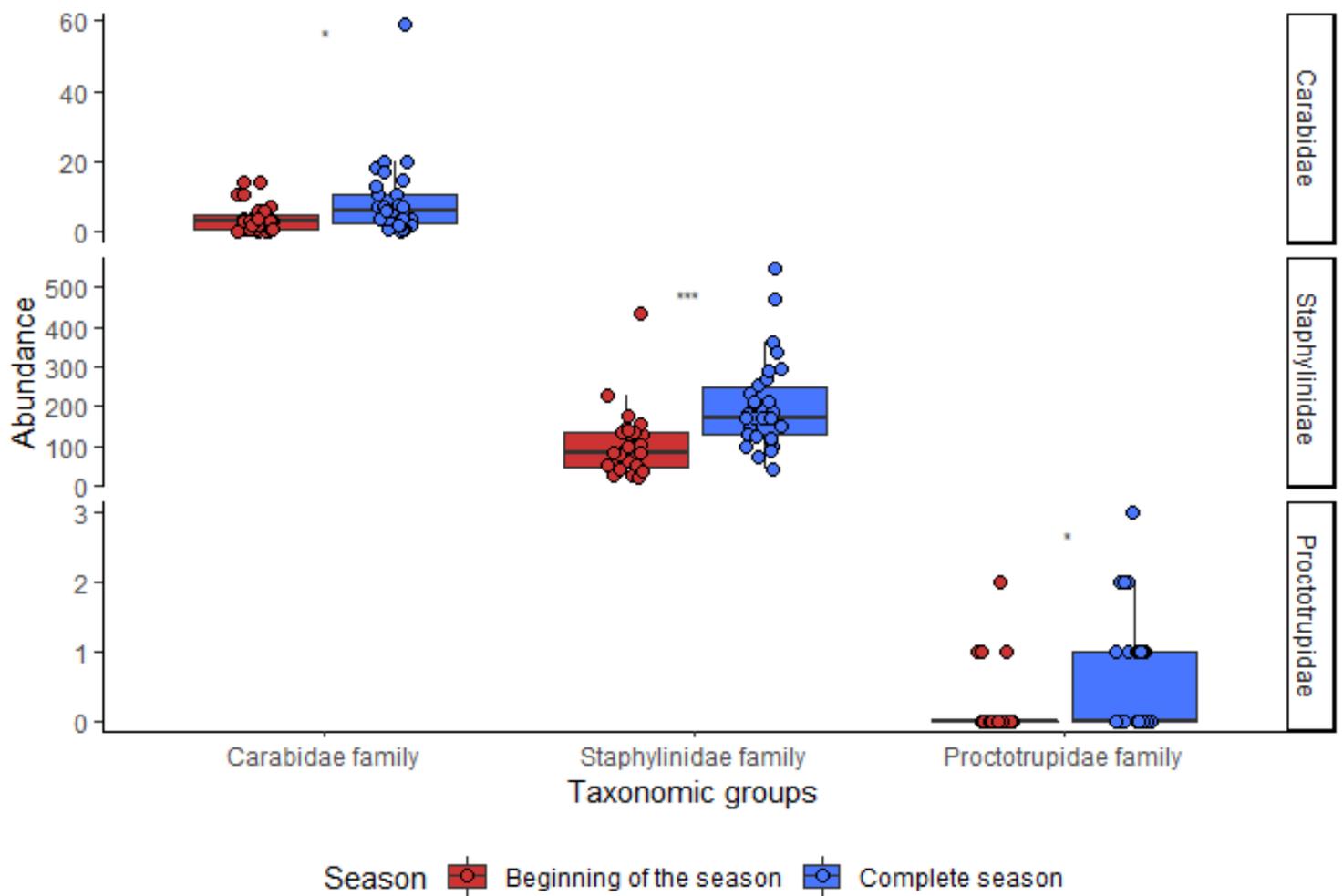
SHDI: Shannon diversity index of landscape in 1km² buffer; SHDI crop: Shannon diversity index of crops; pSNH: proportion of land covered by semi-natural habitats; pWinterCrop: proportion of winter crops similar; Edge dens: total length of edges including all types of edges; Cumul depth: cumulated tillage depth; N qty: quantity of nitrogen provided in liquid form; TFI_{tot}: total treatment frequency index (insecticides, fungicides and herbicides included).

	SHDI	SHDI crop	pSNH	pWinterCrop	Edge dens	Cumul depth	N qty
SHDI crop	0.30						
pSNH	0.19	-0.10					
pWinterCrop	-0.15	-0.38	-0.32				
Edge dens	0.30	0.32	0.17	-0.05			
Cumul depth	-0.05	0.08	-0.004	0.04	0.05		
N qty	-0.16	-0.11	-0.25	0.21	0.02	0.26	
TFI _{tot}	-0.29	-0.42	-0.17	0.46	-0.23	0.04	0.21

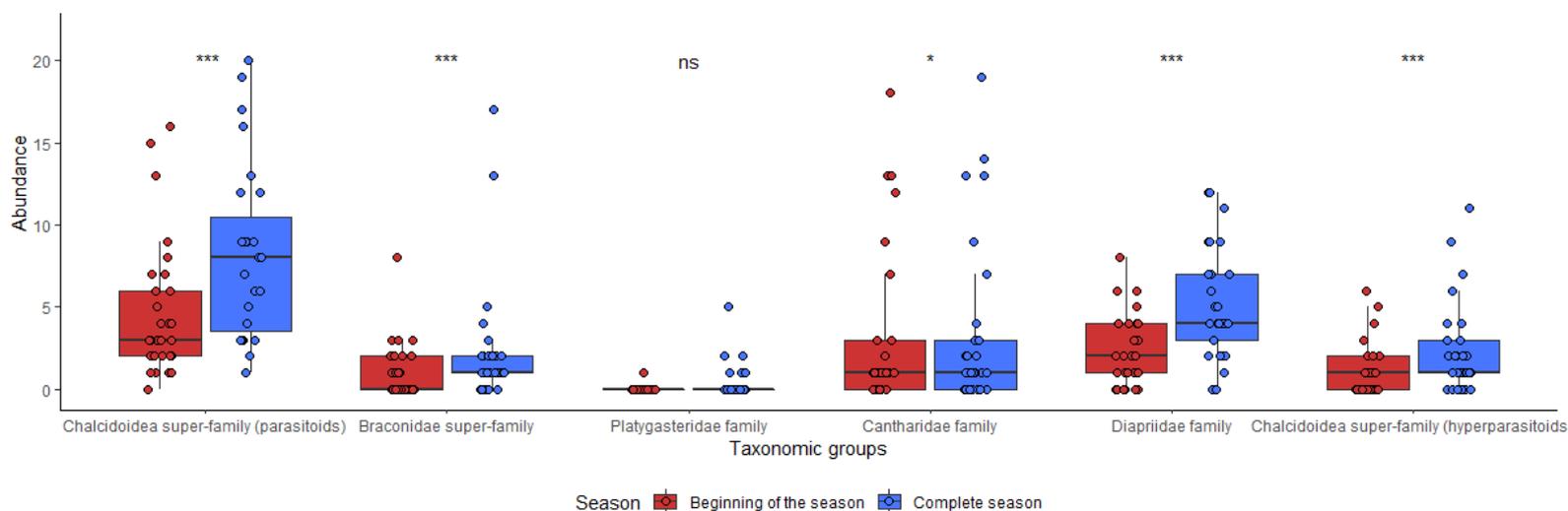
Appendix C.2: Pearson's correlations between predation rates.

Numbers in **bold** correspond to correlations among data for the complete season; numbers in *italics* correspond to the correlations among data for the beginning of the spring season. * *p-value* <0.05; ** *p-value* <0.01; *** *p-value* <0.001.

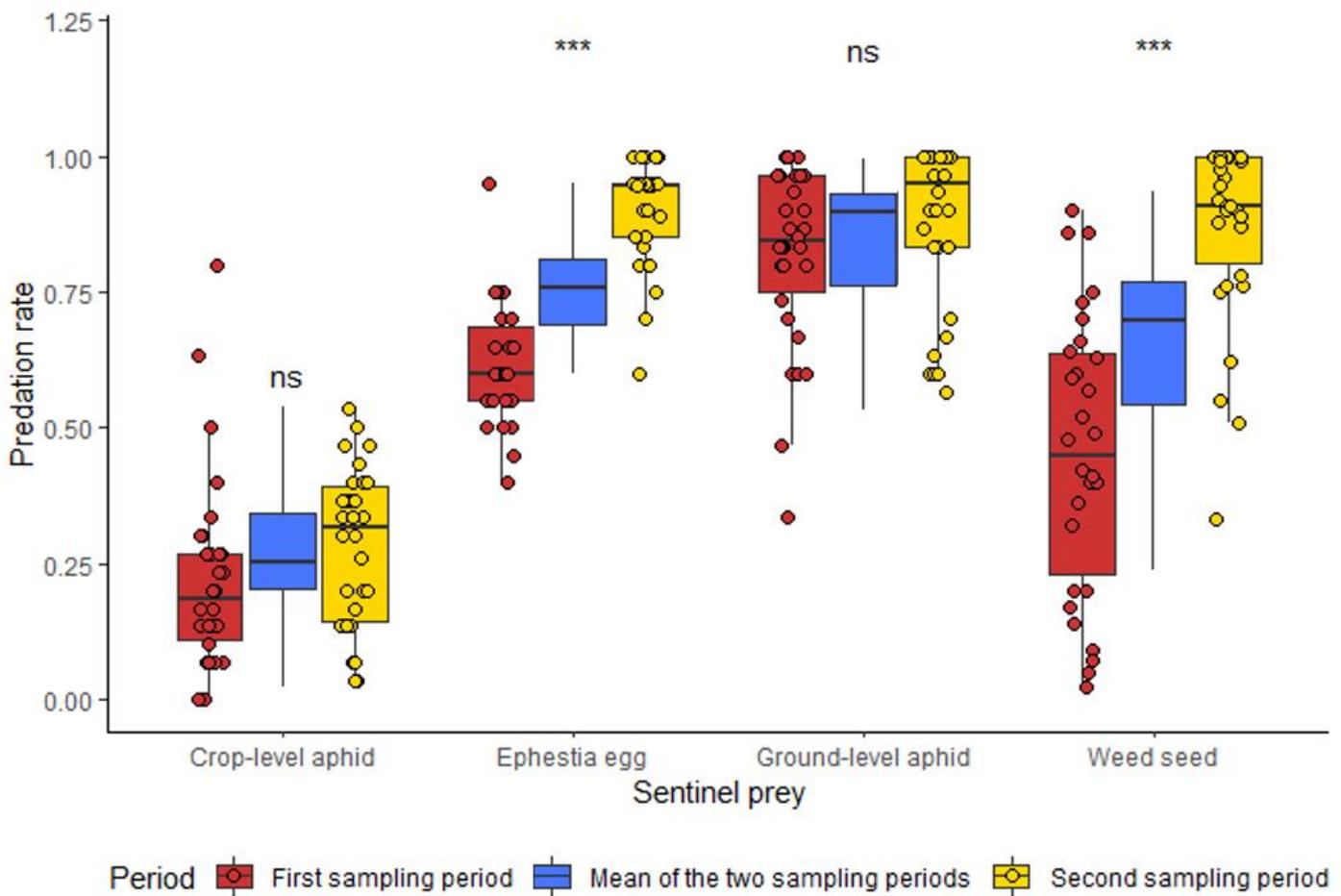
	Crop-level aphids	Epehstia eggs	Ground-level aphids
Epehstia eggs	0.17 <i>0.23</i>		
Ground-level aphids	0.52** <i>0.48**</i>	0.24 <i>0.24</i>	
Weed seeds	0.03 <i>0.25</i>	0.04 <i>0.33</i>	-0.32 <i>-0.021</i>



Appendix D.1: Emerging natural enemies and their own enemies' abundance at the beginning of the season and throughout the season in the ground compartment. The emergence of these taxa at the beginning of the season corresponds to the abundances measured in the first four sampling periods (from the 15th of March to the 26th of April). The emergence of the taxa throughout the season corresponds to all six sampling periods (from the 15th of March to the 23rd of May). The significance of the difference between abundances across spring was tested with a pairwise Wilcoxon's test. * p -value < 0.05; ** p -value < 0.01; *** p -value < 0.001; ns, not significant.



Appendix D.2: Emerging natural enemies of pests and abundance of their own enemies at the beginning of the season and throughout the season in the airborne compartment. The emergence of these taxa at the beginning of the season corresponds to the abundances measured in the first four sampling periods (from the 15th of March to the 26th of April). The emergence of the taxa throughout the season corresponds to all six sampling periods (from the 15th of March to the 23rd of May). The significance of the difference between abundances across spring was tested with a pairwise Wilcoxon's test. * *p-value* < 0.05; ** *p-value* < 0.01; *** *p-value* < 0.001; ns, not significant



Appendix D.3: Predation rates observed on different prey sentinel cards in two sampling periods. The significance of the difference was tested between the predation rates evaluated in the first sampling period (from the 24th to the 28th of April) and in the second sampling period at the end of May (from the 29th of May to the 2nd of June) using a pairwise Wilcoxon's test. * *p*-value < 0.05; ** *p*-value < 0.01; *** *p*-value < 0.001; ns, not significant.

Appendix E.1: Averaged estimated effects of the abundance of overwintering natural enemies, farming practices, landscape variables and their interactions on the two predation rates in the ground compartment. For each explanatory variable or interaction, the averaged coefficient value \pm error standard (s.e.) and its level of significance are given. **Bold** values correspond to averaged estimated effects calculated for the complete season; values in *italics* correspond to those calculated with data at the beginning of the season. * *p-value* < 0.05; ** *p-value* < 0.01; *** *p-value* < 0.001.

Ground compartment				
effect	Weed seed		Ground-level aphid	
	estimate	s.e.	estimate	s.e.
Staphylinidae	0.0003 <i>0.0007</i>	0.0003 <i>0.0006</i>	-0.0008 <i>-0.0005</i>	0.0005 <i>0.0007</i>
Carabidae	0.002 <i>0.010</i>	0.003 <i>0.01</i>	0.009* <i>0.03*</i>	0.004 <i>0.01</i>
TFItot	0.03 <i>0.12</i>	0.04 <i>0.11</i>	-0.05 <i>-0.001</i>	0.07 <i>0.13</i>
CumulDepth	-0.01 <i>0.001</i>	0.03 <i>0.02</i>	0.10* <i>-0.007</i>	0.05 <i>0.03</i>
Nqty	-0.02 <i>-0.003</i>	0.04 <i>0.01</i>	0.05 <i>-0.0003</i>	0.05 <i>0.01</i>
SHDI	0.02 <i>-0.36</i>	0.03 <i>1.63</i>	0.03 <i>-0.15</i>	0.06 <i>1.12</i>
SHDICrop	-0.05 <i>-0.17</i>	0.04 <i>0.59</i>	0.08 <i>-0.06</i>	0.05 <i>0.42</i>
pSNH	0.06 <i>0.01</i>	0.04 <i>0.006</i>	-0.07 <i>0.003</i>	0.05 <i>0.009</i>
pWinterCrop	0.03 <i>-0.008</i>	0.04 <i>0.02</i>	-0.12* <i>-0.01</i>	0.05 <i>0.01</i>
EdgeDens	0.02 <i>0.05*</i>	0.03 <i>0.02</i>	0.08 <i>-0.03</i>	0.05 <i>0.03</i>
TFItot*SHDI	-0.02 <i>-0.09</i>	0.05 <i>0.17</i>	0.009 <i>-0.07</i>	0.07 <i>0.19</i>
TFItot * SHDICrop	0.06 <i>0.008</i>	0.05 <i>0.08</i>	0.08 <i>-0.06</i>	0.07 <i>0.09</i>
TFItot * pSNH	-0.02 <i>-0.001</i>	0.03 <i>0.001</i>	0.03 <i>0.002</i>	0.05 <i>0.001</i>
TFItot * pWinterCrop	0.01 <i>0.003</i>	0.05 <i>0.002</i>	-0.04 <i>-0.0002</i>	0.06 <i>0.003</i>
TFItot *EdgeDens	-0.08 <i>-0.008</i>	0.04 <i>0.004</i>	-0.004 <i>-0.002</i>	0.06 <i>0.005</i>
CumulDepth*SHDI	0.02 <i>-0.005</i>	0.04 <i>0.03</i>	0.03 <i>0.03</i>	0.05 <i>0.03</i>
CumulDepth*SHDICrop	-0.05 <i>-0.005</i>	0.03 <i>0.01</i>	0.05 <i>0.01</i>	0.04 <i>0.01</i>
CumulDepth*pSNH	0.02 <i>-0.0001</i>	0.03 <i>0.0002</i>	0.003 <i>-0.0001</i>	0.04 <i>0.0002</i>
CumulDepth*pWinterCrop	0.03 <i>-0.0001</i>	0.04 <i>0.0005</i>	0.04 <i>-0.0001</i>	0.05 <i>0.0004</i>
CumulDepth*EdgeDens	0.02 <i>0.0005</i>	0.05 <i>0.001</i>	0.10 <i>0.002</i>	0.06 <i>0.001</i>
Nqty*SHDI	0.07 <i>0.01</i>	0.04 <i>0.01</i>	-0.02 <i>-0.01</i>	0.06 <i>0.01</i>
Nqty*SHDICrop	-0.002 <i>0.001</i>	0.04 <i>0.005</i>	0.02 <i>0.002</i>	0.06 <i>0.005</i>
Nqty*pSNH	0.01 <i>-0.00005</i>	0.03 <i>0.0001</i>	-0.01 <i>-0.0001</i>	0.05 <i>0.0001</i>
Nqty*pWinterCrop	0.04 <i>0.0001</i>	0.03 <i>0.0001</i>	-0.04 <i>0.00002</i>	0.04 <i>0.0001</i>
Nqty*EdgeDens	-0.03 <i>-0.0001</i>	0.05 <i>0.0003</i>	0.06 <i>0.0006</i>	0.07 <i>0.0004</i>

Appendix E.2: Averaged estimated effects of emerging natural enemies, farming practices, landscape variables and their interactions on the overwintering beneficials that emerged in the ground compartment. For each explanatory variable or interaction, the averaged coefficient value \pm error standard (s.e.) and its level of significance are given. Numbers in **bold** correspond to averaged estimated effects calculated for the complete season; numbers in *italics* correspond to those calculated for the beginning of the season. * p -value < 0.05; ** p -value < 0.01; *** p -value < 0.001.

Staphylinidae			Carabidae		
effect	estimate	s.e.	effect	estimate	s.e.
Proctotrupidae	0.07 <i>0.07</i>	0.13 <i>0.29</i>	Proctotrupidae	-0.16 <i>0.04</i>	0.22 <i>0.39</i>
Carabidae	0.01 <i>0.0361</i>	0.008 <i>0.0338</i>	Staphylinidae	0.003 <i>0.002</i>	0.002 <i>0.002</i>
TFItot	0.02 <i>0.01</i>	0.12 <i>0.20</i>	TFItot	-0.18 <i>-0.02</i>	0.26 <i>0.27</i>
CumulDepth	-0.04 <i>-0.11</i>	0.09 <i>0.15</i>	CumulDepth	-0.19 <i>-0.36</i>	0.19 <i>0.20</i>
Nqty	0.04 <i>0.18</i>	0.10 <i>0.13</i>	Nqty	-0.10 <i>-0.03</i>	0.18 <i>0.21</i>
SHDI	-0.06 <i>0.09</i>	0.10 <i>0.14</i>	SHDI	0.11 <i>0.02</i>	0.19 <i>0.21</i>
SHDICrop	-0.13 <i>-0.15</i>	0.10 <i>0.14</i>	SHDICrop	0.07 <i>-0.23</i>	0.20 <i>0.20</i>
pSNH	-0.25** <i>-0.19</i>	0.09 <i>0.13</i>	pSNH	0.13 <i>0.13</i>	0.21 <i>0.19</i>
pWinterCrop	0.25** <i>0.09</i>	0.09 <i>0.14</i>	pWinterCrop	-0.25 <i>-0.04</i>	0.21 <i>0.20</i>
EdgeDens	-0.16 <i>-0.26</i>	0.11 <i>0.15</i>	EdgeDens	-0.11 <i>-0.18</i>	0.23 <i>0.22</i>
TFItot*SHDI	0.20 <i>0.38*</i>	0.12 <i>0.16</i>	TFItot*SHDI	-0.30 <i>0.12</i>	0.24 <i>0.27</i>
TFItot*SHDICrop	0.12 <i>0.05</i>	0.14 <i>0.18</i>	TFItot*SHDICrop	-0.11 <i>0.20</i>	0.27 <i>0.28</i>
TFItot*pSNH	-0.15 <i>-0.05</i>	0.09 <i>0.13</i>	TFItot*pSNH	0.19 <i>-0.13</i>	0.20 <i>0.20</i>
TFItot*pWinterCrop	-0.01 <i>-0.33*</i>	0.12 <i>0.17</i>	TFItot*pWinterCrop	-0.15 <i>0.04</i>	0.25 <i>0.28</i>
TFItot*EdgeDens	-0.01 <i>0.07</i>	0.13 <i>0.18</i>	TFItot*EdgeDens	0.11 <i>-0.27</i>	0.25 <i>0.28</i>
CumulDepth*SHDI	0.02 <i>0.04</i>	0.11 <i>0.15</i>	CumulDepth*SHDI	-0.22 <i>-0.17</i>	0.21 <i>0.22</i>
CumulDepth*SHDICrop	-0.11 <i>-0.12</i>	0.11 <i>0.13</i>	CumulDepth*SHDICrop	0.06 <i>0.01</i>	0.21 <i>0.21</i>
CumulDepth*pSNH	-0.09 <i>-0.13</i>	0.08 <i>0.10</i>	CumulDepth*pSNH	-0.10 <i>0.003</i>	0.16 <i>0.17</i>
CumulDepth*pWinterCrop	0.20ns <i>0.17</i>	0.13 <i>0.16</i>	CumulDepth*pWinterCrop	-0.14 <i>0.04</i>	0.28 <i>0.25</i>
CumulDepth*EdgeDens	-0.17 <i>-0.36*</i>	0.12 <i>0.16</i>	CumulDepth*EdgeDens	-0.43 <i>-0.38</i>	0.23 <i>0.25</i>
Nqty*SHDI	0.22* <i>0.13</i>	0.11 <i>0.15</i>	Nqty*SHDI	-0.33 <i>0.68*</i>	0.19 <i>0.30</i>
Nqty*SHDICrop	-0.17 <i>-0.06</i>	0.11 <i>0.15</i>	Nqty*SHDICrop	0.15 <i>0.21</i>	0.21 <i>0.22</i>
Nqty*pSNH	0.01 <i>-0.01</i>	0.09 <i>0.12</i>	Nqty*pSNH	-0.24 <i>0.14</i>	0.17 <i>0.20</i>
Nqty*pWinterCrop	-0.02 <i>-0.02</i>	0.09 <i>0.12</i>	Nqty*pWinterCrop	0.22 <i>-0.05</i>	0.17 <i>0.19</i>
Nqty*EdgeDens	-0.02 <i>0.22</i>	0.14 <i>0.19</i>	Nqty*EdgeDens	0.27 <i>-0.10</i>	0.24 <i>0.30</i>

Appendix F.1: Averaged estimated effects of the abundance of overwintering natural enemies, farming practices, landscape variables and their interactions on the two predation rates at the crop level in the airborne compartment. For each explanatory variable or interaction, the averaged coefficient value \pm error standard (s.e.) and its level of significance are given. Values in **bold** correspond to averaged estimated effects calculated for the complete season; values in *italics* correspond to those calculated with data at the beginning of the spring season.* p -value < 0.05 ; ** p -value < 0.01 ; *** p -value < 0.001 .

Airborne compartment				
effect	<i>Ephestia</i> egg		Crop-level aphid	
	estimate	s.e.	estimate	s.e.
Chalcidoidea	-0.00060 <i>-0.0037</i>	0.003 <i>0.0063</i>	-0.011** <i>-0.018*</i>	0.004 <i>0.009</i>
Braconidae	-0.006 <i>-0.01</i>	0.005 <i>0.015</i>	-0.008 <i>-0.014</i>	0.006 <i>0.021</i>
Platygasteridae	-0.03 <i>-</i>	0.021 <i>-</i>	0.001 <i>-</i>	0.026 <i>-</i>
Cantharidae	0.006 <i>0.008</i>	0.004 <i>0.036</i>	0.005 <i>0.002</i>	0.005 <i>0.008</i>
TFItot	-0.04 <i>-0.02</i>	0.03 <i>0.03</i>	-0.03 <i>-0.03</i>	0.03 <i>0.05</i>
CumulDepth	-0.006 <i>0.02</i>	0.02 <i>0.03</i>	0.0003 <i>0.008</i>	0.03 <i>0.04</i>
Nqty	-0.001 <i>-0.01</i>	0.02 <i>0.03</i>	-0.02 <i>0.002</i>	0.02 <i>0.04</i>
SHDI	0.001 <i>-0.01</i>	0.02 <i>0.03</i>	0.02 <i>0.04</i>	0.02 <i>0.04</i>
SHDICrop	-0.006 <i>-0.04</i>	0.02 <i>0.02</i>	0.02 <i>-0.002</i>	0.03 <i>0.05</i>
pSNH	0.0002 <i>0.02</i>	0.02 <i>0.03</i>	0.0001 <i>0.02</i>	0.03 <i>0.04</i>
pWinterCrop	0.01 <i>-0.02</i>	0.02 <i>0.02</i>	0.002 <i>-0.04</i>	0.03 <i>0.04</i>
EdgeDens	0.009 <i>0.01</i>	0.02 <i>0.03</i>	-0.001 <i>0.001</i>	0.02 <i>0.04</i>
TFItot*SHDI	0.01 <i>0.009</i>	0.02 <i>0.06</i>	-0.05 <i>0.0001</i>	0.03 <i>0.05</i>
TFItot * SHDICrop	0.01 <i>0.04</i>	0.03 <i>0.03</i>	-0.05 <i>0.02</i>	0.04 <i>0.08</i>
TFItot * pSNH	-0.03 <i>-0.03</i>	0.02 <i>0.03</i>	0.02 <i>-0.0004</i>	0.03 <i>0.04</i>
TFItot * pWinterCrop	0.04 <i>0.04</i>	0.02 <i>0.03</i>	0.004 <i>-0.02</i>	0.03 <i>0.05</i>
TFItot *EdgeDens	-0.02 <i>-0.02</i>	0.02 <i>0.03</i>	-0.005 <i>-0.01</i>	0.03 <i>0.05</i>
CumulDepth*SHDI	-0.01 <i>-0.01</i>	0.02 <i>0.03</i>	-0.02 <i>-0.003</i>	0.03 <i>0.04</i>
CumulDepth*SHDICrop	0.01 <i>0.02</i>	0.02 <i>0.02</i>	-0.02 <i>-0.02</i>	0.02 <i>0.04</i>
CumulDepth*pSNH	-0.02 <i>-0.01</i>	0.01 <i>0.02</i>	-0.02 <i>0.01</i>	0.02 <i>0.03</i>
CumulDepth*pWinterCrop	0.01 <i>0.02</i>	0.02 <i>0.04</i>	0.02 <i>0.02</i>	0.03 <i>0.04</i>
CumulDepth*EdgeDens	-0.02 <i>-0.02</i>	0.02 <i>0.03</i>	-0.02 <i>0.02</i>	0.03 <i>0.05</i>
Nqty*SHDI	0.002 <i>0.02</i>	0.02 <i>0.02</i>	-0.005 <i>0.02</i>	0.03 <i>0.04</i>
Nqty*SHDICrop	0.02 <i>0.05</i>	0.02 <i>0.02</i>	0.01 <i>0.03</i>	0.03 <i>0.04</i>
Nqty*pSNH	-0.02 <i>-0.02</i>	0.02 <i>0.03</i>	0.02 <i>0.01</i>	0.02 <i>0.03</i>
Nqty*pWinterCrop	0.02 <i>0.02</i>	0.02 <i>0.03</i>	-0.04 <i>-0.03</i>	0.02 <i>0.03</i>
Nqty*EdgeDens	-0.06* <i>-0.08</i>	0.03 <i>0.006</i>	0.06 <i>0.09</i>	0.04 <i>0.06</i>

Appendix F.2: Averaged estimated effects of hyperparasitoids and parasitoids of natural enemies, farming practices, landscape variables and their interactions on the abundance of overwintering natural enemies in the airborne compartment. For each explanatory variable or interaction, the averaged coefficient value \pm error standard (s.e.) and its level of significance are given. Values in **bold** correspond to averaged estimated effects calculated for the complete season; values in *italics* correspond to those calculated at the beginning of the season.* p -value < 0.05; ** p -value < 0.01; *** p -value < 0.001.

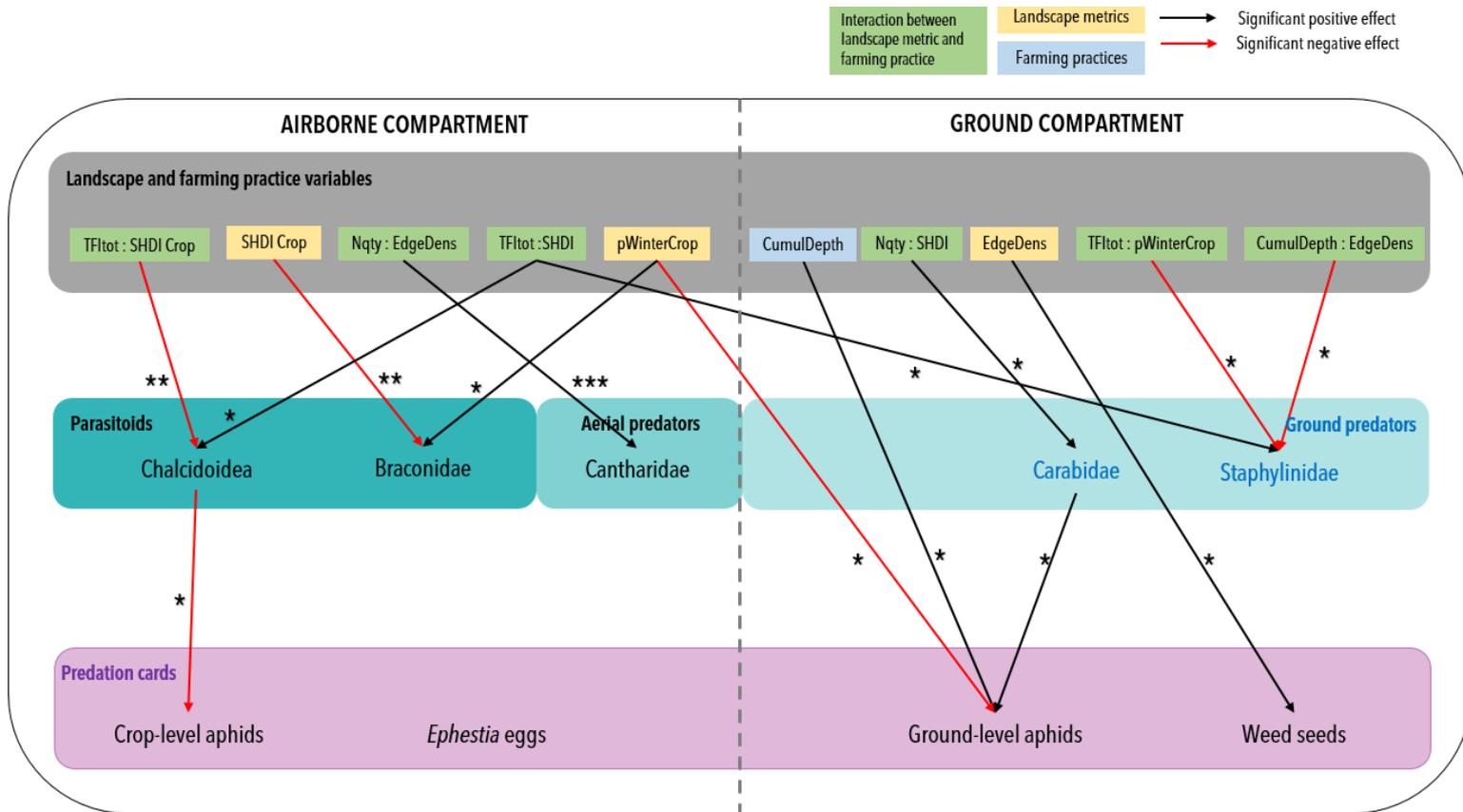
Chalcidoidea (parasitoids)			Braconidae			Platygasteridae			Cantharidae		
effect	estimate	s.e.	effect	estimate	s.e.	effect	estimate	s.e.	effect	estimate	s.e.
Chalcidoidea (Hyperparasitoids)	0.05 <i>0.04</i>	0.04 <i>0.09</i>	Chalcidoidea (Hyperparasitoids)	0.02 <i>-0.01</i>	0.08 <i>0.20</i>	Chalcidoidea (Hyperparasitoids)	0.07 <i>-</i>	0.20 <i>-</i>	Diapriidae	0.02ns <i>0.12ns</i>	0.07 <i>0.12</i>
Braconidae	-0.02 <i>-0.20</i>	0.04 <i>0.11</i>	Chalcidoidea	-0.02 <i>-0.09</i>	0.05 <i>0.11</i>	Chalcidoidea	0.12* <i>-</i>	0.05 <i>-</i>	Braconidae	0.08ns <i>0.20ns</i>	0.06 <i>0.12</i>
Platygasteridae	0.23* <i>-</i>	0.10 <i>-</i>	Platygasteridae	-0.43 <i>-</i>	0.43 <i>-</i>	Braconidae	-0.76 <i>-</i>	0.56 <i>-</i>	Chalcidoidea	0.07ns <i>0.09ns</i>	0.04 <i>0.05</i>
Cantharidae	0.05* <i>0.05</i>	0.02 <i>0.03</i>	Cantharidae	0.02 <i>0.09</i>	0.05 <i>0.06</i>	Cantharidae	0.02 <i>-</i>	0.09 <i>-</i>	Platygasteridae	0.02ns <i>-</i>	0.22 <i>-</i>
TFItot	-0.008 <i>-0.28</i>	0.20 <i>0.22</i>	TFItot	-0.30 <i>-0.13</i>	0.39 <i>0.55</i>	TFItot	0.68 <i>-</i>	1.83 <i>-</i>	TFItot	-0.29ns <i>-0.73ns</i>	0.42 <i>0.46</i>
CumulDepth	0.037 <i>0.06</i>	0.13 <i>0.15</i>	CumulDepth	-0.19 <i>-0.06</i>	0.26 <i>0.28</i>	CumulDepth	-0.66 <i>-</i>	1.14 <i>-</i>	CumulDepth	-0.13ns <i>-0.27ns</i>	0.30 <i>0.31</i>
Nqty	0.02 <i>0.18</i>	0.13 <i>0.16</i>	Nqty	0.21ns <i>-0.03</i>	0.21 <i>0.27</i>	Nqty	-0.29 <i>-</i>	0.80 <i>-</i>	Nqty	-0.22ns <i>-0.41ns</i>	0.22 <i>0.22</i>
SHDI	-0.08 <i>-0.19</i>	0.13 <i>0.15</i>	SHDI	-0.36 <i>-0.35</i>	0.25 <i>0.33</i>	SHDI	1.48 <i>-</i>	1.60 <i>-</i>	SHDI	0.40ns <i>0.40ns</i>	0.29 <i>0.32</i>
SHDICrop	-0.27* <i>-0.49**</i>	0.14 <i>0.15</i>	SHDICrop	-0.74** <i>-1.04**</i>	0.25 <i>0.36</i>	SHDICrop	0.27 <i>-</i>	0.58 <i>-</i>	SHDICrop	-0.09ns <i>0.22ns</i>	0.33 <i>0.32</i>
pSNH	-0.06 <i>-0.05</i>	0.14 <i>0.15</i>	pSNH	0.18 <i>-0.08</i>	0.27 <i>0.32</i>	pSNH	1.31 <i>-</i>	0.80 <i>-</i>	pSNH	0.13ns <i>0.10ns</i>	0.31 <i>0.31</i>
pWinterCrop	0.18 <i>0.03</i>	0.14 <i>0.19</i>	pWinterCrop	0.63* <i>0.64*</i>	0.25 <i>0.30</i>	pWinterCrop	-1.22 <i>-</i>	1.09 <i>-</i>	pWinterCrop	0.20ns <i>0.12ns</i>	0.32 <i>0.35</i>
EdgeDens	-0.04 <i>-0.20</i>	0.12 <i>0.16</i>	EdgeDens	-0.35 <i>-0.37</i>	0.24 <i>0.29</i>	EdgeDens	0.13 <i>-</i>	0.58 <i>-</i>	EdgeDens	0.17ns <i>0.23ns</i>	0.19 <i>0.21</i>
TFItot*SHDI	0.008 <i>0.32*</i>	0.16 <i>0.16</i>	TFItot*SHDI	-0.07 <i>0.29</i>	0.31 <i>0.32</i>	TFItot*SHDI	3.21 <i>-</i>	2.45 <i>-</i>	TFItot*SHDI	-0.47ns <i>-0.31ns</i>	0.35 <i>0.39</i>
TFItot*SHDICrop	-0.32 <i>-0.71**</i>	0.20 <i>0.22</i>	TFItot*SHDICrop	-0.59 <i>-0.77</i>	0.37 <i>0.50</i>	TFItot*SHDICrop	0.35 <i>-</i>	1.18 <i>-</i>	TFItot*SHDICrop	-0.58ns <i>-0.05ns</i>	0.50 <i>0.68</i>
TFItot*pSNH	0.04 <i>0.05</i>	0.14 <i>0.16</i>	TFItot*pSNH	0.55* <i>0.39</i>	0.28 <i>0.29</i>	TFItot*pSNH	1.26 <i>-</i>	1.19 <i>-</i>	TFItot*pSNH	0.21ns <i>-0.15ns</i>	0.36 <i>0.35</i>
TFItot*pWinterCrop	0.06 <i>-0.07</i>	0.17 <i>0.21</i>	TFItot*pWinterCrop	-0.18 <i>-0.47</i>	0.38 <i>0.46</i>	TFItot*pWinterCrop	-0.46 <i>-</i>	1.16 <i>-</i>	TFItot*pWinterCrop	0.27ns <i>0.44ns</i>	0.35 <i>0.37</i>

TFItot*	-0.007	0.15	TFItot*	0.41	0.32	TFItot*	0.45	0.69	TFItot*	-0.14ns	0.41
EdgeDens	<i>0.10</i>	<i>0.20</i>	EdgeDens	<i>0.43</i>	<i>0.37</i>	EdgeDens	-	-	EdgeDens	<i>-0.26ns</i>	<i>0.42</i>
CumulDepth*	0.004	0.14	CumulDepth*	0.08	0.27	CumulDepth*	1.36	0.98	CumulDepth*	0.11ns	0.31
SHDI	<i>-0.09</i>	<i>0.16</i>	SHDI	<i>-0.24</i>	<i>0.32</i>	SHDI	-	-	SHDI	<i>0.36ns</i>	<i>0.34</i>
CumulDepth*	0.05	0.13	CumulDepth*	0.29	0.25	CumulDepth*	0.35	0.62	CumulDepth*	-0.39ns	0.30
SHDICrop	<i>0.13</i>	<i>0.16</i>	SHDICrop	<i>-0.17</i>	<i>0.57</i>	SHDICrop	-	-	SHDICrop	<i>-0.30ns</i>	<i>0.26</i>
CumulDepth*	-0.17	0.1	CumulDepth*	0.10	0.22	CumulDepth*	0.26	0.77	CumulDepth*	0.19ns	0.24
pSNH	<i>-0.23</i>	<i>0.12</i>	pSNH	<i>0.56</i>	<i>0.29</i>	pSNH	-	-	pSNH	<i>-0.14ns</i>	<i>0.23</i>
CumulDepth*	0.06	0.15	CumulDepth*	-0.40	0.25	CumulDepth*	-1.30	1.03	CumulDepth*	-0.16ns	0.33
pWinterCrop	<i>0.04</i>	<i>0.19</i>	pWinterCrop	<i>-0.48</i>	<i>0.30</i>	pWinterCrop	-	-	pWinterCrop	<i>-0.10ns</i>	<i>0.34</i>
CumulDepth*	-0.35*	0.15	CumulDepth*	-0.15	0.32	CumulDepth*	0.32	0.75	CumulDepth*	0.50ns	0.33
EdgeDens	<i>-0.32</i>	<i>0.20</i>	EdgeDens	<i>0.05</i>	<i>0.38</i>	EdgeDens	-	-	EdgeDens	<i>0.50ns</i>	<i>0.34</i>
Nqty*SHDI	-0.02	0.14	Nqty*SHDI	0.03	0.27	Nqty*SHDI	0.23	0.58	Nqty*SHDI	-0.03ns	0.26
	<i>0.009</i>	<i>0.15</i>		<i>0.15</i>	<i>0.31</i>		-	-		<i>0.07ns</i>	<i>0.26</i>
Nqty*	0.08	0.14	Nqty*	-0.47	0.28	Nqty*	-0.20	0.64	Nqty*	-0.40ns	0.32
SHDICrop	<i>0.24</i>	<i>0.17</i>	SHDICrop	<i>-0.51</i>	<i>0.33</i>	SHDICrop	-	-	SHDICrop	<i>-0.44ns</i>	<i>0.30</i>
Nqty*pSNH	-0.09	0.12	Nqty*pSNH	0.33	0.25	Nqty*pSNH	1.06	0.86	Nqty*pSNH	0.08ns	0.25
	<i>-0.10</i>	<i>0.15</i>		<i>0.26</i>	<i>0.33</i>		-	-		<i>-0.10ns</i>	<i>0.25</i>
Nqty*	0.007	0.11	Nqty*	-0.12	0.21	Nqty*	-0.006	0.69	Nqty*	-0.04ns	0.27
pWinterCrop	<i>-0.12</i>	<i>0.15</i>	pWinterCrop	<i>0.07</i>	<i>0.24</i>	pWinterCrop	-	-	pWinterCrop	<i>0.25ns</i>	<i>0.27</i>
Nqty*EdgeDens	-0.30	0.21	Nqty*EdgeDens	-0.26	0.44	Nqty*EdgeDens	-0.30	0.90	Nqty*EdgeDens	1.02***	0.24
	<i>-0.16</i>	<i>0.27</i>		<i>-0.53</i>	<i>0.53</i>		-	-		<i>0.99***</i>	<i>0.26</i>

Appendix G: Averaged estimated effects of farming practices, landscape variables and their interactions on the hyperparasitoids or parasitoids of the natural enemies, which emerged in both ground and airborne compartments. Values in **bold** correspond to averaged estimated effects calculated for the complete season; values in *italics* correspond to those calculated for the beginning of the spring season. * *p*-value < 0.05; ** *p*-value < 0.01; *** *p*-value < 0.001.

Airborne compartment						Ground compartment		
effect	Chalcidoidea (Hyperparasitoids)		effect	Diapriidae		effect	Proctotrupidae	
	estimate	s.e.		estimate	s.e.		estimate	s.e.
TFItot	0.34 <i>0.09</i>	0.30 <i>0.39</i>	TFItot	0.19* <i>0.34**</i>	0.09 <i>0.12</i>	TFItot	-0.49 <i>-0.44</i>	0.50 <i>0.72</i>
CumulDepth	0.56* <i>0.25</i>	0.19 <i>0.27</i>	CumulDepth	-0.19 <i>-0.19</i>	0.14 <i>0.20</i>	CumulDepth	-0.31 <i>-0.14</i>	0.31 <i>0.66</i>
Nqty	-0.06 <i>-0.06</i>	0.24 <i>0.30</i>	Nqty	-0.06 <i>0.18</i>	0.13 <i>0.20</i>	Nqty	0.04 <i>0.32</i>	0.32 <i>0.62</i>
SHDI	0.10 <i>0.39</i>	0.23 <i>0.32</i>	SHDI	0.12 <i>0.20</i>	0.15 <i>0.19</i>	SHDI	-0.11 <i>1.29</i>	0.35 <i>0.81</i>
SHDICrop	-0.15 <i>-0.33</i>	0.19 <i>0.25</i>	SHDICrop	-0.01 <i>-0.009</i>	0.14 <i>0.21</i>	SHDICrop	0.05 <i>-0.14</i>	0.34 <i>0.56</i>
pSNH	0.33 <i>0.50_{ns}</i>	0.22 <i>0.30</i>	pSNH	0.23* <i>0.40**</i>	0.10 <i>0.14</i>	pSNH	-0.37 <i>-0.17</i>	0.31 <i>0.55</i>
pWinterCrop	-0.003 <i>0.05_{ns}</i>	0.23 <i>0.31</i>	pWinterCrop	-0.09 <i>-0.26</i>	0.14 <i>0.21</i>	pWinterCrop	0.05 <i>-0.07</i>	0.33 <i>0.55</i>
EdgeDens	-0.10 <i>-0.08</i>	0.23 <i>0.29</i>	EdgeDens	-0.03 <i>0.03</i>	0.13 <i>0.17</i>	EdgeDens	0.33 <i>0.48</i>	0.31 <i>0.56</i>
TFItot*SHDI	0.22 <i>-0.16</i>	0.28 <i>0.34</i>	TFItot*SHDI	0.06 <i>0.19</i>	0.16 <i>0.20</i>	TFItot*SHDI	0.03 <i>0.42</i>	0.57 <i>1.30</i>
TFItot*SHDICrop	0.10 <i>-0.41</i>	0.32 <i>0.38</i>	TFItot*SHDICrop	-0.06 <i>0.10</i>	0.18 <i>0.25</i>	TFItot*SHDICrop	0.57 <i>0.21</i>	0.65 <i>0.89</i>
TFItot*pSNH	0.12 <i>0.26</i>	0.22 <i>0.31</i>	TFItot*pSNH	-0.24** <i>-0.28**</i>	0.08 <i>0.09</i>	TFItot*pSNH	-0.12 <i>0.38</i>	0.49 <i>0.84</i>
TFItot*pWinterCrop	-0.42 <i>-0.11</i>	0.31 <i>0.40</i>	TFItot*pWinterCrop	0.20 <i>0.10</i>	0.16 <i>0.22</i>	TFItot*pWinterCrop	0.14 <i>-0.45</i>	0.44 <i>0.91</i>
TFItot*EdgeDens	0.20 <i>-0.08</i>	0.30 <i>0.38</i>	TFItot*EdgeDens	-0.35* <i>-0.48*</i>	0.15 <i>0.20</i>	TFItot*EdgeDens	-0.10 <i>-0.90</i>	0.44 <i>0.68</i>
CumulDepth*SHDI	0.03 <i>0.26</i>	0.24 <i>0.34</i>	CumulDepth*SHDI	0.20 <i>0.20</i>	0.16 <i>0.23</i>	CumulDepth*SHDI	-0.37 <i>1.28</i>	0.32 <i>0.76</i>
CumulDepth*SHDICrop	-0.5* <i>-1.10**</i>	0.25 <i>0.41</i>	CumulDepth*SHDICrop	-0.17 <i>-0.10</i>	0.15 <i>0.21</i>	CumulDepth*SHDICrop	0.53* <i>0.10</i>	0.22 <i>0.46</i>
CumulDepth*pSNH	-0.08 <i>0.02</i>	0.16 <i>0.24</i>	CumulDepth*pSNH	0.02 <i>0.10</i>	0.11 <i>0.17</i>	CumulDepth*pSNH	-0.42 <i>0.08</i>	0.29 <i>0.38</i>
CumulDepth*pWinterCrop	0.15 <i>0.02</i>	0.27 <i>0.36</i>	CumulDepth*pWinterCrop	0.09 <i>-0.16</i>	0.17 <i>0.23</i>	CumulDepth*pWinterCrop	-0.83** <i>-0.58</i>	0.27 <i>0.51</i>
CumulDepth*EdgeDens	-0.14 <i>-0.19</i>	0.28 <i>0.38</i>	CumulDepth*EdgeDens	0.004 <i>0.13</i>	0.17 <i>0.24</i>	CumulDepth*EdgeDens	0.02 <i>0.62</i>	0.38 <i>0.59</i>
Nqty*SHDI	0.31 <i>0.24</i>	0.29 <i>0.34</i>	Nqty*SHDI	0.16 <i>0.32</i>	0.15 <i>0.25</i>	Nqty*SHDI	0.27 <i>0.86</i>	0.44 <i>1.04</i>
Nqty*SHDICrop	0.23 <i>0.19</i>	0.26 <i>0.33</i>	Nqty*SHDICrop	-0.15 <i>0.008</i>	0.16 <i>0.22</i>	Nqty*SHDICrop	0.05 <i>0.002</i>	0.35 <i>0.59</i>
Nqty*pSNH	0.35 <i>0.37</i>	0.24 <i>0.32</i>	Nqty*pSNH	-0.13 <i>-0.18</i>	0.12 <i>0.16</i>	Nqty*pSNH	-0.09 <i>0.13</i>	0.29 <i>0.52</i>
Nqty*pWinterCrop	-0.15	0.24	Nqty*pWinterCrop	0.25*	0.11	Nqty*pWinterCrop	-0.38	0.35

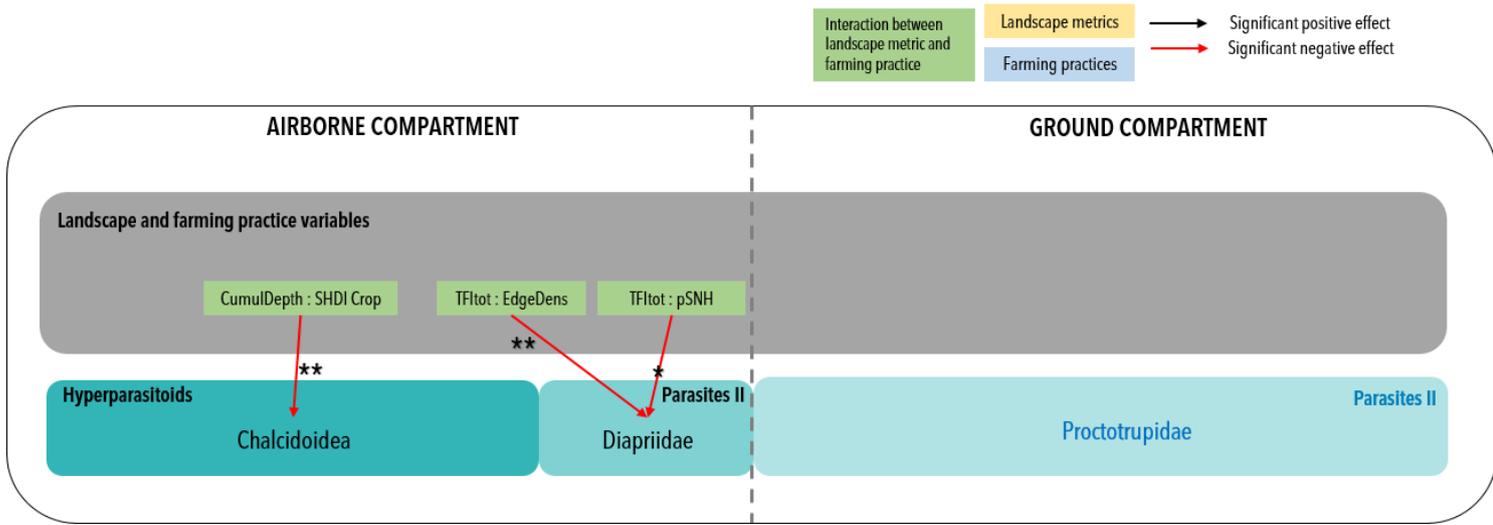
	-0.11	0.29		0.30	0.16		-0.18	0.52
Nqty*EdgeDens	0.01	0.31	Nqty*EdgeDens	-0.13	0.18	Nqty*EdgeDens	0.11	0.38
	0.30	0.39		-0.35	0.26		0.94	0.57



1

2 **Appendix H.1: Effects of landscape and farming practices on the abundance of emerged**
3 **natural enemies and their consequences for biological control in the ground and airborne**
4 **compartments measured using sentinel prey cards.** The results are for the beginning of the
5 spring season. Black arrows represent a positive effect of the variable or the interaction between
6 two variables. Red arrows represent a negative effect. All arrows show a significant effect.
7 Yellow rectangles correspond to a landscape variable; blue rectangles correspond to a farming
8 practice variable; green rectangles correspond to the interaction between one landscape and one
9 farming practice variable. * p-value < 0.05; ** p-value < 0.01; *** p-value < 0.001.
10 Abbreviations for explanatory variables are explained in Table 1. See appendices E.1, E.2, F.1
11 and F.2 for the complete results.

12



15 **Appendix H.2: Effects of landscape and farming practices on emerged hyperparasitoids**
 16 **and parasitoids of natural enemies and their consequences for the abundance of natural**
 17 **enemies in the ground and airborne compartments.** The results are for the beginning of the
 18 spring season. Black arrows represent a positive effect of the variable or the interaction between
 19 two variable. Red arrows represent a negative effect. All arrows show a significant effect.
 20 Yellow rectangles correspond to a landscape variable; blue rectangles correspond to a farming
 21 practice variable; green rectangles correspond to the interaction between one landscape and one
 22 farming practice variable. * *p-value* < 0.05; ** *p-value* < 0.01; *** *p-value* < 0.001.
 23 Abbreviations for explanatory variables are explained in Table 1. See appendix G for complete
 24 results.