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1 **Spontaneous flowering vegetation favours hoverflies and parasitoid wasps in**
2 **apple orchards but has low cascading effects on biological pest control**

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9 **Abstract**

10 Floral resources support several ecosystem services in agroecosystems, such as pollination or
11 biological control. Many beneficial organisms feed on nectar or pollen for an important part of their
12 life cycle. Providing adequate and sufficient floral resources through the conservation of
13 spontaneous flowering vegetation may be a strategy to improve biological pest control. However, the
14 role of spontaneous flowering plant species has mainly been evaluated on the recruitment of natural
15 enemies. Cascading effects on pest regulation and damage reduction are rarely studied.

16 Here we evaluated the effect of spontaneous flowering vegetation on pest regulation in 18
17 Mediterranean apple orchards. We focused on two main apple pests, *Cydia pomonella* and *Dysaphis*
18 *plantaginea*, and on two groups of their natural enemies depending on floral resources: hoverflies
19 and parasitoid wasps. We combined generalised linear mixed models and piecewise structural
20 equation models to test for direct and indirect effects of spontaneous flowering plant species on
21 beneficial insects (hoverflies, parasitoid wasps, wild bees and honeybees) and on pest regulation. We
22 also tested for potential negative interactions between honeybees and hoverflies, parasitoids wasps
23 or wild bees.

24 There was a positive and significant effect of insect-pollinated flowers on hoverflies, parasitoid wasps
25 and bees, but small cascading effects on *D. plantaginea* or *C. pomonella* density and associated
26 damages. There was no evident relationship between honeybees and hoverflies, parasitoid wasps or
27 wild bees. The reduction of *D. plantaginea* infestation was partially mediated by hoverfly abundance.
28 Furthermore, we observed effects of spontaneous flowering vegetation on pest regulation and
29 damage reduction independent of hoverfly and parasitoid wasp abundances. These results highlight
30 the relevance of conserving floral resources to support biological control of apple pests. Further
31 studies are needed to better understand interactions between spontaneous flowering vegetation
32 and crop management practices to promote sustainable pest regulation strategies.

33 **Key-words:** resident vegetation, wildflower, hoverflies, hymenopteran parasitoids, conservation
34 biological control

35 1. Introduction

36 Arthropods are a key component of agroecosystem functioning. Many arthropod species provide
37 important services to agriculture, such as crop pollination or biological pest control (Dainese *et al.*,
38 2019; Requier *et al.*, 2023). However, the current decline of arthropods (Seibold *et al.*, 2019) may
39 compromise such ecosystem services (Zhou *et al.*, 2023). Several causes have been identified to
40 explain arthropod decline and most are related to agricultural intensification (Sánchez-Bayo &
41 Wyckhuys, 2019; Wagner *et al.*, 2021). Thus, there is a clear need for more sustainable farming
42 systems that preserve ecosystem services. Conservation Biological Control (CBC) is an important
43 approach to improve sustainability by providing habitats for natural enemies of pests (Shields *et al.*,
44 2019).

45 Several taxa of natural enemies feed on floral resources such as nectar and pollen during an
46 important part of their life cycle (Lu *et al.*, 2014). Nectar availability is positively related to the
47 longevity of adult parasitoid wasps (Hymenoptera) in general and specifically increases the fecundity
48 of synovigenic parasitoids (Russell *et al.*, 2015; Benelli *et al.*, 2017). The effect of floral resources on
49 predators depends on feeding strategies (He *et al.*, 2021). Hoverflies (Diptera: Syrphidae) and
50 lacewings (Neuroptera: Chrysopidae) are predators at the larval stage, whereas adults feed primarily
51 on floral resources which strongly affect their longevity and fecundity (He *et al.*, 2021). Other
52 predators, such as adult ladybugs (Coleoptera: Coccinellidae), are omnivorous and feed on floral
53 resources when access to other resources is limited (Wolf *et al.*, 2018; He & Sigsgaard, 2019). To
54 promote natural enemies, a common habitat management strategy is to establish flowering plant
55 species within or around crop fields (Landis *et al.*, 2000). Nectar is mainly provided by insect-
56 pollinated plants (Roy *et al.*, 2017). Therefore, insect-pollinated flowers are mainly sought to favour
57 beneficial insects for pest biological control (Albrecht *et al.*, 2021a; Kirmer *et al.*, 2018). Planting such
58 flowering vegetation often improves pest regulation but the increase is highly variable across studies
59 (Albrecht *et al.*, 2021b ; Fountain, 2022).

60 Spontaneous vegetation meaning ruderal and weed vegetation that grow naturally in or around crop
61 fields in field margins or inter-rows of permanent crops can also provide important resources to pest
62 natural enemies. Spontaneous vegetation is usually less costly for farmers to manage, better adapted
63 to local conditions and can be as effective as standard flowering seed mixtures to promote beneficial
64 insects (Blaix et al., 2018 ; Araj *et al.*, 2019). Balfour & Ratnieks (2022) showed that the abundance
65 and diversity of beneficial insects were twice as high on spontaneously occurring weeds than on
66 plant species of a recommended mixture to attract pollinators. Mei *et al.* (2021) also found that the
67 abundance of arthropod predators mainly relied on the cover and diversity of spontaneous flowering
68 plant species in field margins and not on the establishment of flower strips. Yet, the effects of
69 spontaneous flowering vegetation on biological control services are often evaluated based on the
70 recruitment of natural enemies (*e.g.* Blaix & Moonen, 2022; Denis *et al.*, 2021; Rosa García &
71 Miñarro, 2014). The effect of spontaneous flowering vegetation on pest abundance and damage
72 reduction has not always been evaluated or results were inconsistent (Johnson et al., 2020).
73 Cascading effects of floral resource availability on pest regulation and reducing crop damage need to
74 be better understood.

75 Flowering plant species provide resources for different arthropod taxa, also including pests and
76 pollinators that may compete for nectar or pollen (Boetzi et al., 2021). Several studies highlighted
77 competition between honey bees and wild bees to access floral resources (Wojcik et al., 2018).
78 Competition may also occur between pollinators and natural enemies (Campbell et al., 2012; Jeavons
79 et al., 2020) or between natural enemies (Jeavons et al., 2022). However, these interactions remain
80 poorly documented and their effects on biological control services are not well known (Jeavons et al.,
81 2022).

82 Here, we used Mediterranean apple orchards as a model system to study effects of spontaneous
83 vegetation on biological control. Apple is the most harvested and exported fruit in Europe (Eurostat,
84 2017) and apple orchards are the most treated crop in France (Jacquet et al., 2022). Numerous insect

85 pests attack apple trees throughout the growing season. The codling moth (CM), *Cydia pomonella*,
86 Linnaeus 1758 (Lepidoptera: Tortricidae) and the rosy apple aphid (RAA) *Dysaphis plantaginea*,
87 Passerini 1860 (Hemiptera: Aphididae) are the major insect pests, causing high economic losses in
88 apple production. We focused on parasitoid wasps and hoverflies, two groups which include many
89 species that are CM and RAA natural enemies. Several parasitoid species feed on codling moth (CM)
90 at different stages of its development, such as *Ascogaster quadridentata* Wesmael (Hymenoptera:
91 Braconidae), *Pristomerus vulnerator* Panzer (Hymenoptera: Ichneumonidae) or *Trichomma enecator*
92 Rossi (Hymenoptera: Ichneumonidae) (Mills et al., 2005). Other parasitoid species such as *Aphidius*
93 *spp.* and *Ephedrus spp.* (Hymenoptera: Braconidae) attack the rosy apple aphid (RAA) (Dib e al., 2010;
94 Rodriguez-Gasol et al., 2019). Most hoverflies found in crop fields including apple orchards are
95 aphidophagous (Rossi et al., 2006 ; Dib et al., 2010 ; Wojciechowicz-Żytka & Wilk, 2023). Hoverflies
96 and parasitoid wasps arrive early in the season and can therefore control early occurring pest insects
97 (González et al., 2022; Rodríguez-Gasol et al., 2019).

98 In apple orchards, many studies analysed the effects of increased cover and/or diversity of flowering
99 plant species on natural enemy abundance as indicator of biological control. Flowering plantings,
100 such as flower strips or cover crops, have often a positive effect on natural enemies (Herz et al.,
101 2019). In comparison, the effects of spontaneous flowering vegetation are less documented (Herz et
102 al., 2019). Among studies including vegetation effects on pest insects, most of them focused on a
103 single apple pest, often an aphid species (e.g. Rodriguez-Gasol et al., 2019; Gontijo et al., 2013;
104 Santos et al., 2018; Albert et al., 2017). Few studies analysed the integrative effects of non-crop
105 vegetation on the dynamics of different pest species, on fruit damage, and on interactions between
106 natural enemies and pollinators in apple orchards (but see Cahenzli et al., 2019 and Martínez-Sastre
107 et al., 2021).

108 The present study aimed to analyse the effects of spontaneous flowering vegetation on the
109 recruitment of hoverflies, parasitoid wasps and bees and to evaluate cascading effects on CM and

110 RAA infestation and damage. We hypothesised that the cover of resident flowering entomophilous
111 species increases the abundance of these insect groups, whereas anemophilous species do not have
112 a positive effect. We expected that an increase in hoverfly and parasitoid wasp abundances has a
113 negative effect on pest density which in turn reduces the associated damages on apple fruits. We
114 also tested for potential interactions between hoverflies, parasitoid wasps, wild bees and honeybees,
115 which could negatively affect pest regulation. Finally, we combined mixed-effects models and
116 structural equation models to assess complex relationships between spontaneous vegetation, the
117 two natural enemy groups, apple pests and associated damages and to disentangle direct and
118 indirect cascading effects.

119 **2. Material and methods**

120 **2.1 Study sites**

121 The study was conducted in the lower Durance valley (area about 200 km², central point: WGS84:
122 43°8' N, 3°9' E). The study area was an agricultural plain dominated by orchards of which apple
123 production represents 87% of the orchard area. Orchards are bordered by windbreak hedgerows
124 (dominated by cypress or poplar) to protect apple trees against strong north wind often occurring in
125 the study area. Botanical and entomological surveys were conducted in 18 apple orchards for
126 commercial production (Fig. 1): nine orchards were under organic management and the other nine
127 were under integrated pest management (hereafter defined as conventional orchards). Organic and
128 conventional orchards had similar average areas, and surrounding vegetation (Table A.1). The
129 average number of treatments was also similar in organic and in conventional orchards (27.1 ± 4.08
130 and 23.3 ± 6.63 in 2021, respectively), with insecticides representing about one third of the
131 treatments. One or two broad-spectrum insecticides included chlorantraniliprole, pyrethroid or
132 emamectin in conventional orchards and spinosad or neem oil in organic orchards (see Bouvier et al.
133 2022 for detail). Herbicides were applied under apple trees (intra-row) once a year in most

134 conventional orchards. None of the orchards were covered with a protection net against the codling
135 moth.

136 **2.2 Botanical and entomological surveys**

137 Surveys of spontaneous flowering vegetation and some beneficial insects (hoverflies, parasitoid
138 wasps and bees) were carried out in three periods: late March, early May, and early June of 2021.
139 These observation periods coincide with the hatching of RAA eggs laid in the previous autumn (late
140 March to early April), with RAA infestation peak (early May), and with the egg laying of the first CM
141 generation (May and June). In each orchard, two transects of 2 x 10 m along two different rows of
142 apple trees were established (Fig. 1): one transect was in the orchard centre and the other one close
143 to a hedgerow, at the northern edge. The 2 m width was measured from the base of tree trunks and
144 transects covered thus half of the row (below trees) and the inter-row (alley). The rows were usually
145 tilled or treated with herbicides in the beginning of the season. The inter-rows were mown every four
146 to ten weeks. Regrowth in rows resulted in low vegetation cover with a dominance of annual species
147 whereas inter-row vegetation was usually dense and dominated by perennial species of disturbed
148 grasslands. Within orchards, the distance between two transects was on average 20.6 (\pm 10.4) m
149 (Table A.1).

150 *2.2.1 Flower cover and diversity*

151 All flowering plant species were recorded, including grasses, in each transect and at each period. We
152 additionally surveyed the cover of each non-flowering plant species at the June period. For each
153 plant species, we estimated the cover as the vertical projection of above-ground plant organs and
154 the percentage of flowering individuals. Flower cover was then calculated by multiplying total cover
155 by the flowering percentage in each species. All recorded flowering plant species were divided into
156 two main groups: wind-pollinated and insect-pollinated flowers (Table A.2). Insect-pollinated flowers
157 provide nectar whereas wind-pollinated flowers are not nectariferous. We assigned pollination
158 modes using the BiolFlor database (Klotz *et al.*, 2002). For both plant groups, we calculated total

159 flower cover and Shannon diversity, using the relative flower cover of each species in a given
160 transect.

161 2.2.2 Hoverflies, parasitoid wasps and bees

162 We counted hoverflies, parasitoid wasps, wild bees and honeybees on the same day as the botanical
163 surveys using two complementary methods. First, two observers directly recorded all individuals of
164 the four insect groups in each transect for 5 minutes, moving slowly along and taking care not to
165 shade the transect. Insects were recorded when they landed on or hovered over the transect.
166 Second, we used a hand net to collect parasitoid wasps from the vegetation (10 strokes per transect).
167 Netting allowed us to more accurately measure the abundance of parasitoid wasps, which are more
168 difficult to detect by direct observation than hoverflies and bees. Samples were kept in 70° ethanol in
169 8mL tubes and sorted at the laboratory to count all parasitoid wasps without further taxonomic
170 investigation (Goulet *et al.*, 1993). Observations and captures were carried out at days with low wind
171 speed (<15km/h), between 10am and 4pm and temperatures higher than 15°C. Counts from visual
172 observations and net samples collected at the same day were added to estimate the abundances of
173 hoverflies, parasitoid wasps, wild bees and honeybees.

174 2.3. Insect pests and associated damage

175 We focused on two apple pest insects: the rosy apple aphid, *Dysaphis plantaginea* (RAA) and the
176 codling moth, *Cydia pomonella* (CM). RAA infestation was measured by counting the number of
177 infested and active shoots on five trees per row at the three botanical periods. In late June, RAA and
178 CM damage were evaluated on 16 trees per row. We randomly selected 20 apples per tree and
179 measured the proportion of apples with signs of CM damage (*i.e.* feeding holes, stings and frass) or
180 RAA damage (*i.e.* distorted apples). Pest infestation and damage were analysed at medium canopy
181 height at 1.5 m to 2m. In late June, we placed wide corrugated cardboard bands and wrapped them
182 around the trunk of 10 trees per row to capture mature CM larvae. Cardboard traps were removed in
183 October and we counted all diapausing CM larvae.

184 2.4. Statistical analyses

185 All analyses were conducted using R version 4.2.0 (2022-04-22). All models included period and
186 orchard as random factors to account for temporal and spatial autocorrelation (Goulnik et al., 2020).

187 2.4.1. Linear mixed models

188 Vegetation management and disturbance may differ between organic and non-organic orchards and
189 according to the location within the orchard. Therefore, we analysed the effects of orchard
190 management (organic vs conventional) and of the transect location within the apple orchard (centre
191 vs edge) on vegetation cover and diversity using linear mixed models (*lmer*, package: lme4 version
192 1.1-31, Bates *et al.*, 2015). We used five response variables: total vegetation cover, the cover of
193 wind-pollinated flowers, the cover of insect-pollinated flowers, the Shannon index of wind-pollinated
194 flowers and the Shannon index of insect-pollinated flowers. Transect location within orchards and
195 orchard management were considered as fixed factors. Flower cover was square-root transformed
196 for both plant groups to meet assumptions of normality and homoscedasticity. Models were tested
197 using a type II analysis of variance.

198 2.4.2. Generalized linear mixed models

199 Generalized linear mixed models (GLMMs) were used (*glmer*, package: lme4) to assess (i) the effects
200 of vegetation on the abundance of the four groups of beneficial insects and (ii) the effects of
201 hoverflies and parasitoid wasps on pest infestation and damage. In the first set of GLMMs, response
202 variables were the abundance of hoverflies, of parasitoid wasps and of wild bees or honeybees.
203 Explanatory variables were the cover and the diversity of wind-pollinated and insect-pollinated
204 flowers. In the second set of GLMMs, response variables were the number of RAA colonies, the
205 proportion of apples with RAA damage, the proportion of apples with CM damage and the number of
206 diapausing CM larvae. In aphid-related models, explanatory variables were parasitoid wasp
207 abundance and hoverfly abundance (fixed effects). Hoverflies were not included in codling moth-
208 related models. All GLMMs included location and orchard management as fixed factors. We tested

209 for correlation between all variables (Table A.3) and checked for collinearity between explanatory
210 variables using variance inflation factor (VIF) analyses. All VIFs were lower than 2 (Table A.4 and A.5).
211 All GLMMs were built with a Poisson distribution and log-link function. Model fit and over-dispersion
212 were checked graphically (package: DHARMA version 0.4.6, Hartig, 2022). In the case of over-
213 dispersion, an observation-level random factor was added (Harrison, 2014).

214 For each GLMM, we used the *dredge* function (package: MuMIn version 1.47.1, Bartoń, 2022) to
215 obtain all possible subsets of the maximal model and calculated the Akaike weight (w_i) of each
216 model. Then, a model-averaging approach was applied (Grueber *et al.*, 2011). The relative
217 importance of each explanatory variable corresponds to the sum of the weights of all the models in
218 which the variable was included. Explanatory variables were considered significant when their
219 relative importance was greater than 0.6 and when 95% confidence intervals of the estimates did not
220 include zero (Burnham & Anderson, 2002). All explanatory variables were standardized allowing a
221 comparison of size effects among averaged models.

222 2.4.3. Structural equation models

223 We used piecewise structural equation modelling (pSEM), to test for direct and indirect effects of
224 spontaneous vegetation on beneficial insects (hoverflies, parasitoid wasps, wild bees and honeybees)
225 and pest regulation using the *psem* (package: piecewiseSEM version 2.3.0, Lefcheck, 2023) and *glmer*
226 functions. The pSEMs examine multivariate relationships between interrelated variables in a single
227 causal pathway (Lefcheck, 2016). We constructed two separate pSEMs to avoid overparameterization
228 using orchard and period as random factors to account for unexplained variation by the fixed factors.
229 The first pSEM aimed to evaluate potential competition effects between honeybees and the three
230 other insect groups. The second pSEM examined the cascading effects of spontaneous vegetation on
231 CM and RAA regulation and assessed whether these effects were mediated by hoverflies and
232 parasitoid wasps.

233 Both initial pSEMs were *a priori* based on known relationships between flower cover and diversity,
234 hoverflies, parasitoid wasps and pest regulation, and on GLMMs preliminary results (Fig. A.1). Flower
235 cover and diversity of both plant groups were included as exogenous variables not depending on
236 other variables (no paths leading to them). The first pSEM included the four groups of beneficial
237 insects as endogenous variables, and tested for a possible negative effect of honeybees on three
238 other beneficial groups (hoverflies, parasitoid wasps and wild bees). In the second pSEM, we did not
239 include the two bee groups but we added four endogenous variables related to RAA and CM
240 infestations or damages. We expected cascading effects, with nectariferous flowers affecting
241 hoverflies and parasitoid wasps and these natural enemies affecting RAA and CM densities. We
242 hypothesised that the number of RAA colonies in spring would affect the fruit damage caused by RAA
243 in June. Furthermore, we expected that fruit damage caused by the first CM generation measured in
244 June explain the number of CM diapausing larvae collected in October. Significant missing paths in
245 the initial pSEMs were detected by the d-separation test and added to the initial model (Lefcheck *et*
246 *al.*, 2016). The overall model fit was assessed using Fisher's C statistic ($p > 0.05$). Finally, a jack-knife
247 like approach was used to evaluate the robustness of the pSEMs. Eighteen sub-models were built,
248 based on a set of 18 independent orchards by omitting one different orchard in each sub-model. We
249 ran each sub-model separately and identified paths that remained significant in at least 15 out of the
250 18 sub-models (more than 80%).

251 **3. Results**

252 **3.1. Flower cover and diversity**

253 The total cover of spontaneous vegetation was 67.4 (\pm SE: 3.4)% leaving 32.6% of bare soil. The
254 vegetation cover was significantly higher in the centre than at the edge of the orchards (+23.4 %)
255 (Table 1). Over the whole season, the cover of wind-pollinated flowers varied from 1.6% to 20.5%
256 and was on average 9.2 (\pm 1.2)% (Table A.6). It increased during the season and was 1.0 (\pm 0.5)% in
257 late March, 10.7 (\pm 1.7)% in early May and 16.0 (\pm 2.6)% in early June (Fig. A.2). The cover of insect-

258 pollinated flowers per transect varied from 0.0% to 10.5% and was on average 4.6 (± 0.6)% (Table
259 A.6) . It remained constant throughout the season, with a cover of 5.30 (± 1.03)% in late March, 3.5
260 (± 0.7)% in early May and 5.1 (± 1.1)% in early June. Insect-pollinated flower cover was twice as high
261 in the centre of the orchard as in the orchard edge (Table 1). Wind-pollinated flower cover was 2.45
262 times higher in organic orchards than in conventional orchards (Fig. A.3), but we did not find any
263 significant effect of orchard management on the cover of insect-pollinated flowers (Table 1).

264 Over the whole season, we recorded 112 plant species of which 78 were flowering at least at one of
265 the three observation periods. We observed 6.7 (± 0.4) flowering species per transect and per period.
266 In late March, the most frequently flowering species were insect-pollinated plants: *Veronica persica*
267 (Scrophulariaceae), *Taraxacum officinale* (Asteraceae), *Cardamine hirsuta* (Brassicaceae), *Senecio*
268 *vulgaris* (Asteraceae) and *Crepis sancta* (Asteraceae). In early June, the most common flowering
269 plants were wind-pollinated species: *Lolium rigidum* (Poaceae), *Plantago lanceolata*
270 (Plantaginaceae), and *Lolium perenne* (Poaceae). The dominant insect-pollinated species in early June
271 were clover species: *Trifolium repens* and *T. pratense* (Fabaceae). The Shannon index of wind-
272 pollinated flowers increased from March to June. For insect-pollinated flowers, the Shannon index
273 remained constant throughout the season (Fig. A.2). The Shannon index of wind-pollinated species
274 was significantly higher (+ 46%) in organic orchards (Fig. A.4), but we did not find any significant
275 effect of the orchard management on the diversity of insect-pollinated species (Table 1).

276 **3.2. Effects of spontaneous flowering vegetation on hoverflies, parasitoid wasps and bees**

277 Over the whole season, we recorded 423 beneficial insects by combining the two sampling methods
278 (hoverflies: 93, parasitoid wasps: 144, honey bees: 61 and wild bees: 125). We counted 3.9 (± 0.5)
279 insects per transect and per period. Beneficial insect abundance increased throughout the season,
280 with a total of 31 individuals being recorded in late March, 144 in early May and 248 in early June
281 (Table A.7). GLMM results showed that the flower cover of insect-pollinated species had a significant
282 and positive effect on the abundance of all insect groups (Table 2), with the highest effect size for

283 honeybees (Fig. 2). The diversity of insect-pollinated species had only a significant and positive effect
284 on wild bees (Table 2). The cover of wind-pollinated species had a significant and positive effect on
285 the abundance of hoverflies and parasitoid wasps. The diversity of wind-pollinated species also
286 positively affected the abundance of hoverflies and wild bees (Table 2). We did not find a significant
287 effect of location within the orchard or orchard management on either insect group (Fig. 2).
288 Piecewise SEM showed that honeybee abundance did not have a significant effect on any other
289 group of beneficial insects (hoverflies: $p = 0.47$, parasitoid wasps: $p = 0.19$, wild bees: $p = 0.79$; Fig 4.
290 A.). PSEM also confirmed the positive and significant effect of insect-pollinated flower cover on
291 hoverfly and parasitoid wasp abundance (hoverflies: $p = 0.01$; parasitoid wasps: $p < 0.01$; Fig 4. A.).
292 However, nectariferous flower cover explained only a small part of the variation in hoverfly and
293 parasitoid wasp abundances ($R^2_m < 0.15$; Fig. 4).

294 **3.3. Effects of hoverflies and parasitoid wasps on pest regulation**

295 We counted $0.77 (\pm 0.13)$ RAA infested shoots per tree and per period, varying from 0 to 28. The
296 infestation was very low in late March (0.08 ± 0.03) and increased throughout the season (1.05 ± 0.22
297 in early May and 1.22 ± 0.34 in early June). GLMMs showed that hoverfly abundance had a significant
298 negative effect on RAA infestation, and we observed a positive and significant relationship between
299 parasitoid wasp abundance and RAA infestation (Fig. 3 and Table 3). In late June, the proportion of
300 apples with RAA damage was $1.0 (\pm 0.4)$ % and varied from 0 to 8.9 %. None of the tested
301 explanatory variables had a significant effect on RAA fruit damage (Fig. 3 and Table 3). The
302 proportion of apples with CM damage was $5.5 (\pm 2.6)$ %, attaining up to 63.6%, and depended mainly
303 on orchard management (Fig. 3). In October, we collected $0.63 (\pm 1.66)$ CM larvae per tree. A low
304 proportion of small CM larvae was observed (5.7 ± 3.4 % per orchard), indicating parasitism by *A.*
305 *quadridendata* (Table A.6.2). However, we did not observe any significant effect of parasitoid
306 abundance on CM damage or on the number of CM diapausing larvae (Fig. 3 and Table 3).

307 **3.4. Effects of spontaneous flowering vegetation on insect pests and on associated damage**

308 PSEM showed significant effects of spontaneous vegetation on pest infestation and associated
309 damage reduction that were independent of hoverfly and parasitoid wasp abundances (Fig. 4. B). The
310 flower cover of insect-pollinated species had a significant negative effect on the proportion of CM
311 damage ($p < 0.001$). The cover of wind-pollinated flowers was the best predictor of RAA infestation
312 showing a significant negative effect ($p < 0.001$). In contrast, we observed a significant and positive
313 effect of the insect-pollinated plant diversity (Shannon) on RAA infestation ($p < 0.001$). PSEM also
314 showed a negative relationship between RAA infestation recorded in spring and the number of CM
315 larvae collected in autumn ($p = 0.04$). However, this relationship was not robust among the
316 observation sites, being significant in less than 80% of the sub-models (Fig. 4.B).

317 **4. Discussion**

318 We analysed the effects of spontaneous flowering vegetation on the recruitment of hoverflies,
319 parasitoid wasps, wild bees and honeybees in apple orchards and their cascading effects on the
320 regulation of the codling moth and the rosy apple aphid. Our results showed that the cover of insect-
321 pollinated flowers increased the abundances of these four insect groups. The cover of wind-
322 pollinated flowers had also a positive effect on the abundances of hoverflies and parasitoid wasps.
323 We observed a significant negative effect of hoverfly abundance on RAA infestation. The cover of
324 insect-pollinated flowers had a negative effect on CM damage and the cover of wind-pollinated
325 flowers reduced RAA infestation. However, this reduction of RAA infestation was only marginally
326 mediated by hoverfly abundance.

327 The cover of insect-pollinated flowers had a positive effect on hoverflies, parasitoid wasps, wild bees
328 and honeybees, and insect-pollinated flower diversity also had a positive effect on wild bees.

329 Similarly, Bishop *et al.* (2023) found that wildflower cover in apple orchard field margins improved
330 natural enemy richness and abundance and Pollier *et al.* (2018) highlighted the importance of
331 flowering insect-pollinated plants close to wheat and oilseed rape fields. This is likely to be due to an
332 increase in available nectar resources (Mockford *et al.*, 2022). A lack of nectar in early spring is

333 generally observed in farmland (Timberlake *et al.*, 2019), even with the addition of flower strips
334 (Serée *et al.*, 2023). In our study, we observed a constant cover of insect-pollinated flowers
335 throughout the survey periods including early spring. Some flowering plant species predominantly
336 recorded in March (*e.g. Veronica persica, Taraxacum officinale*) are therefore promising candidate
337 species to improve seed mixtures, as they provide accessible nectar for several groups of natural
338 enemies including parasitoid wasps (Gardarin *et al.*, 2021; Serée *et al.*, 2023). We also found positive
339 effects of wind-pollinated species on hoverflies and parasitoid wasps. Although we did not
340 specifically analyse flower visits and pollen consumption, the positive effect on hoverflies may be
341 explained by pollen provisioning. Several studies have reported evidence of hoverflies foraging on
342 grass species (Saunders, 2018; Joseph *et al.*, 2020; Villa *et al.*, 2021). Furthermore, hoverfly and
343 parasitoid females may forage on weeds, searching for alternative prey to lay their eggs (Rodriguez-
344 Gasol *et al.*, 2019). Finally, the high cover of wind-pollinated flowers may indicate low vegetation
345 disturbance (Piqueray *et al.*, 2019), which may also benefit natural enemies (Horton *et al.*, 2003;
346 Meyer *et al.*, 2019).

347 Piecewise SEM showed that spontaneous flowering vegetation explained at most 22% of the
348 variability in beneficial insect abundances and 18% of the variability in pest infestation. This result
349 may be due to the relatively low variability of insect-pollinated flower cover between orchards (0 to
350 10%). Competition between flower visitors may also limit the effect of floral resources on pest
351 biological control (Jeavons *et al.*, 2022), but, we did not observe any relationship between honeybee
352 abundance and that of the three other beneficial insect groups studied here. Effect of spontaneous
353 vegetation on pest biological control may further be limited by other farming practices in apple
354 orchards such as mowing, tillage and pesticide treatment frequencies (McKerchar *et al.*, 2020).
355 However, abundances of hoverflies, parasitoid wasps or bees did not significantly differ between
356 conventional and organic apple orchards in our study. A more detailed description of the farming
357 practices in each apple orchard independently of the organic vs. conventional management typology
358 would help to precise their significance. Landscape composition may also affect natural enemy

359 abundance, in particular the cover of semi-natural habitats, including hedgerows and their proximity
360 to field crops (Maalouly *et al.* 2013; Daelemans *et al.*, 2022; Bishop *et al.*, 2023). The overall
361 abundance of insects (hoverflies, parasitoid wasps and bees) was rather low, which may have limited
362 the strength of observed effects. An increased observation time may be a solution to obtain higher
363 abundances avoiding 0 values that reduce statistical power.

364 Hoverfly abundance had a negative effect on RAA infestation. This confirms the potential of
365 hoverflies to improve aphid biological control (Rodríguez-Gasol *et al.*, 2020). Hoverflies were not
366 identified to species level but previous studies showed that most hoverfly species occurring in apple
367 orchards are aphid predators (Rossi *et al.*, 2006; Dib *et al.*, 2010; Wojciechowicz-Żytka & Wilk, 2023).
368 We did not find a significant relationship between parasitoid wasps collected on spontaneous
369 vegetation and the abundance of codling moth larvae or their associated damage. We also recorded
370 a very low number of small larvae (indicating codling moth parasitism). The RAA infestation was
371 positively related to the abundance of parasitoids sampled in the vegetation. This observation
372 suggests that RAA and parasitoid wasps are influenced by common factors not included in our
373 analysis. The density of hedgerows in the monitored orchards that favours both parasitoid diversity
374 (Bishop *et al.*, 2023) and RAA infestation (Albert *et al.*, 2017) may be such a common factor. We did
375 not distinguish parasitoid wasps (as in Mateos-Fierro *et al.*, 2021; Pollier *et al.*, 2018; Rodríguez-Gasol
376 *et al.*, 2019), assuming that the overall abundance of parasitoids is positively related to the
377 abundance of parasitoid species attacking the apple pests RAA and CM. However, it is possible that
378 parasitoid wasp species collected on spontaneous vegetation were not involved in apple pest
379 regulation. The identification of parasitoid wasps would thus be required to determine whether
380 flowering plants in apple orchards attract parasitoid species that are really involved in pest
381 regulation.

382 Piecewise SEM showed effects of spontaneous flowering vegetation independent of hoverflies or
383 parasitoid wasps. The cover of insect-pollinated flowers negatively affected CM damage, and wind-

384 pollinated flower cover had a negative effect on RAA infestation. These effects may be related to the
385 activity of other groups of natural enemies than parasitoid wasps and hoverflies. Generalist
386 predators such as earwigs (Dermaptera: Forficulidae), spiders (Araneae) highly contribute to RAA and
387 CM regulation (Dib *et al.*, 2020; Unruh *et al.*, 2016). Additionally, ladybirds (Coleoptera: Coccinellidae)
388 or flower bugs (Heteroptera: Anthocoridae) are involved in RAA regulation (Dib *et al.*, 2010). All these
389 predator groups may benefit from spontaneous flowering vegetation without directly consuming
390 floral resources. For example, Mei *et al.* (2021) showed that spiders and ground beetles were
391 positively affected by wildflower cover and diversity even though they do not consume nectar or
392 pollen. Such generalist natural enemies benefit from shelter, favourable microclimate and structural
393 diversity provided by a relatively undisturbed herbaceous layer (Ganser *et al.*, 2019). We also found a
394 small but positive effect of the diversity of insect-pollinated flowers on RAA infestation. This result
395 suggests that both variables, insect-pollinated flower diversity and RAA infestation, were influenced
396 by common drivers not included in our analysis. However, it is also possible that a higher flower
397 diversity may attract a higher number of natural enemy species increasing potential intraguild
398 predation or competition (Daelemans *et al.*, 2022).

399 To conclude, our results demonstrated that spontaneous vegetation rich in insect-pollinated plants
400 improves the recruitment of hoverflies, parasitoid wasps, wild bees and honey bees in apple
401 orchards. Positive effects of spontaneous vegetation on pest regulation and damage reduction were
402 weak but significant. To further increase the regulation of apple pests, the preservation of
403 spontaneous flowering vegetation should be combined with other farming practices, such as sowing
404 plant species within or around orchards that favour apple pest natural enemies. Natural enemy
405 activity generally decreases with increasing distance from such flowering plantings (Albert *et al.*,
406 2017; Santos *et al.*, 2018). Spontaneous vegetation may act as a relay, promoting the movement of
407 hoverflies and parasitoid wasps from field margins within the orchard and should be managed at the
408 whole-field level, rather than only at the edges in agreement with Serée *et al.* (2023). Apple cultivars
409 selected for their low susceptibility to RAA (Alhmedi *et al.*, 2022) or CM (Joshi *et al.*, 2015) and

410 management practices (pruning, irrigation, fertilisation) that reduce tree vigour and RAA infestation
411 (Simon et al., 2007; Rousselin et al., 2018) could additionally reduce apple damages. In order to
412 develop guidelines for farmers, future research should therefore examine interactions between
413 spontaneous flowering vegetation and farming practices to promote sustainable pest regulation.

414 **Authorship contribution statement**

415 LL, AB, FL and PF conceived the ideas and designed the methodology; LL, AB and PF collected the
416 data; LL and RB analysed the data; LL wrote the first draft of the manuscript. All authors contributed
417 critically to the drafts and gave final approval for publication

418 **Declaration of Competing Interest**

419 The authors declare that they have no known competing financial interests or personal relationships
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712 **Figures**

713 Figure 1. Location of the 18 orchards.

714 Figure 2. Effect sizes (mean \pm 95% CI) of flower cover and diversity, location within the orchard, and
715 orchard management on beneficial insect abundance.

716 Figure 3. Effect sizes (mean \pm 95% CI) of natural enemies, location within the orchard, and orchard
717 management on pest infestation and associated damage.

718 Figure 4. Final piecewise structural equation models (pSEM).

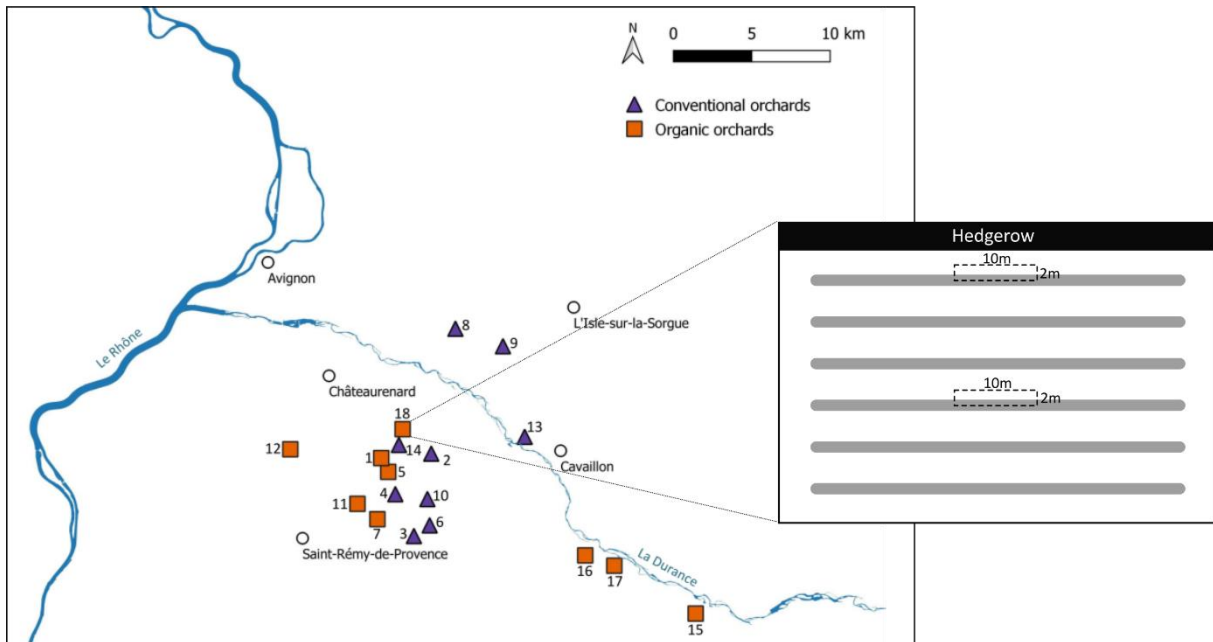
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720 **Tables**

721 Table 1. Results of the Linear Mixed Models (LMM) analysing the effects of location and orchard
722 management on cover and diversity of insect-pollinated flowers and wind-pollinated flowers.

723 Table 2. Averaged estimated effects (GLMM) of spontaneous flowering vegetation on beneficial
724 insect abundance.

725 Table 3. Averaged estimated effects (GLMM) of hoverfly and parasitoid abundances, location and
726 orchard management on pest numbers (RAA infestation and CM larvae) and their damages.



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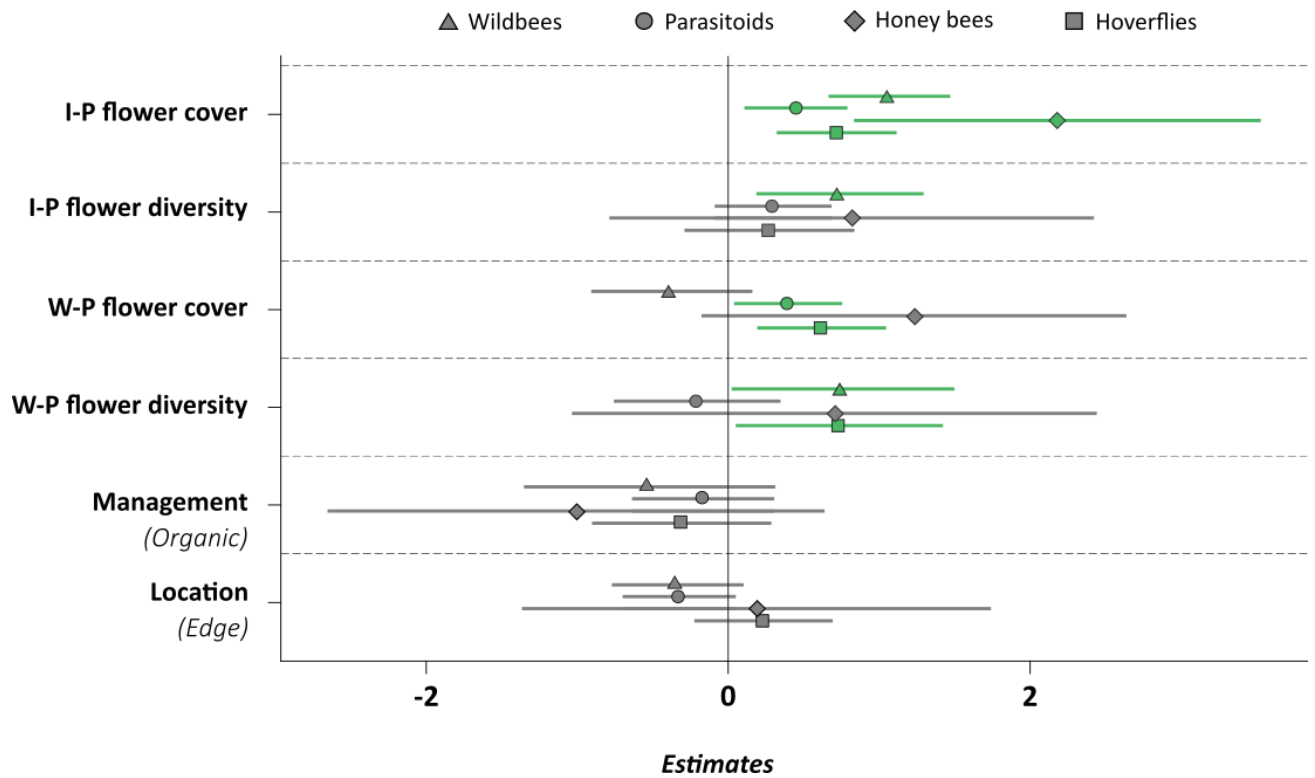
728 **Figure 1. Location of the 18 apple orchards** in south-eastern France within the long-term study zone “Basse
 729 Vallée de la Durance” (<https://site-atelier-basse-vallee-durance.fr>). In each orchard, we defined two transects at
 730 the center and at the edge (2m x 10m) in which we conducted botanical and entomological surveys. Transects
 731 were separated by 20.6 m (± 10.4).

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737 **Figure 2. Effect sizes (mean ± 95% CI) of flower cover and diversity, location within the orchard, and orchard**
738 **management on beneficial insect abundance.** Estimates were obtained by a model averaging approach.
739 Triangles correspond to wild bee abundance, circles to parasitoid abundance, diamonds to hoverfly abundance,
740 and squares to honeybee abundance. Significant positive effects are indicated in green.

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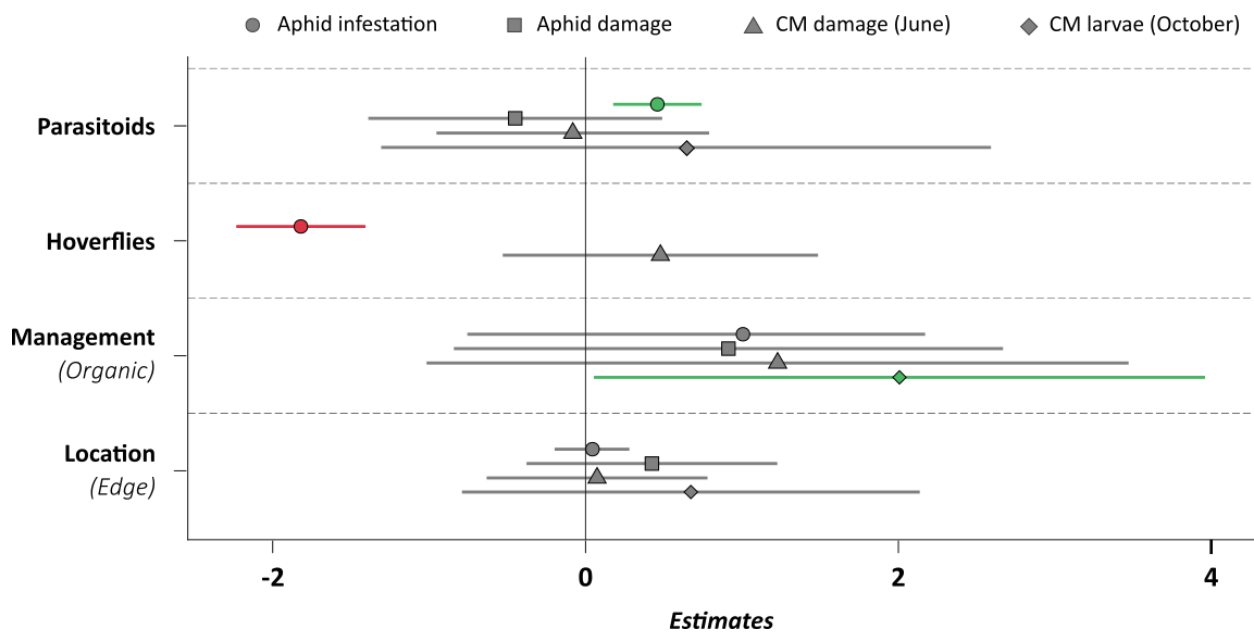
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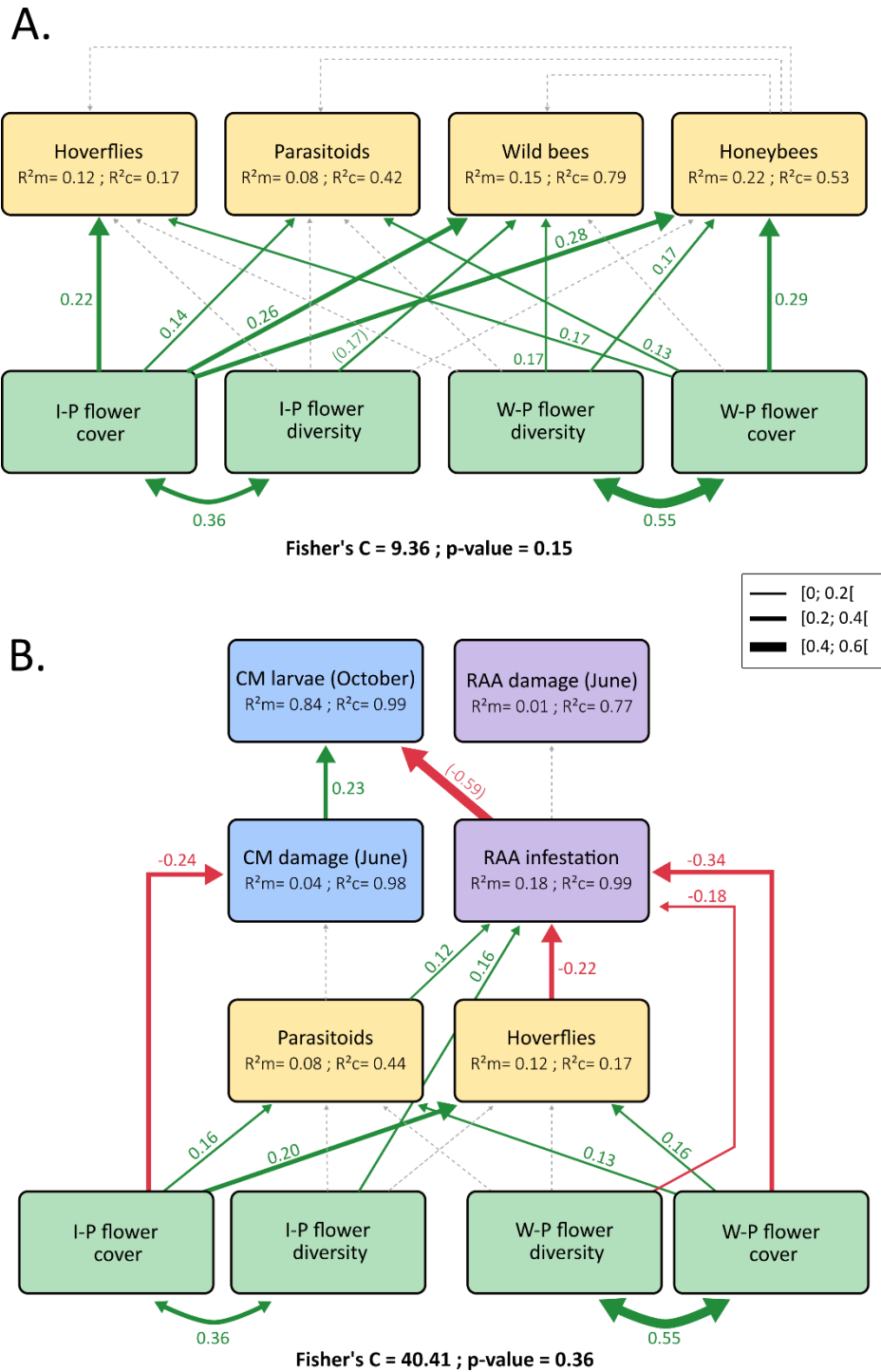
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754 **Figure 3. Effect sizes (mean \pm 95% CI) of natural enemies, location within the orchard, and orchard**
 755 **management on pest infestations and damages.** Estimates were obtained by a model averaging approach.
 756 Circles correspond to rosy apple aphid (RAA) infestation (monitored from April to June), squares to the
 757 proportion of apples with RAA damage (recorded in June), triangles to the proportion of apples with codling
 758 moth (CM) damage (recorded in June), and diamonds to the number of codling moth diapausing larvae
 759 (monitored in October). Positive and negative significant effects are indicated in green and red, respectively.



760

761 **Figure 4. Final piecewise structural equation models (pSEM).** Model **A** shows the effects of spontaneous
 762 flowering vegetation hoverflies, parasitoid wasps, honeybees and wild bees. Model **B** shows the effects of
 763 spontaneous flowering vegetation on natural enemies and cascading effects on pest infestation and associated
 764 damages. I-P flowers: Insect pollinated flowers; W-P flowers: Wind pollinated flowers; RAA: Rosy Apple Aphid;
 765 CM: Codling moth. Green and red arrows represent significant positive and negative pathways, respectively, with
 766 arrow thickness corresponding to standardised path coefficients. Coefficients in parentheses correspond to
 767 pathways significant in less than 80% of sub-models. Dotted grey arrows indicate non-significant paths ($p > 0.05$).
 768 Double-headed arrows illustrate correlated errors. R^2m values show the proportion of variability explained by
 769 fixed effects and R^2c values show the proportion of variability explained by both fixed and random effects. Overall
 770 model fit is indicated using Fisher's C statistic. Summary statistics for the pSEM models are shown in Table A.8
 771 and A.9.

772 **Table 1. Results of the linear mixed models (LMM) analysing the effects of location and orchard**
 773 **management on cover and diversity of insect-pollinated flowers and wind-pollinated flowers.** χ^2 : test
 774 statistic, df: degrees of freedom. Positive estimates for "Location" correspond to an increase towards
 775 "Edge". Positive estimates for "Orchard management" correspond to an increase towards "Organic".

		Location					Orchard management				
		Estimate	SE	χ^2	df	p-value	Estimate	SE	χ^2	df	p-value
Insect-pollinated flower	Cover	-0.66	0.20	10.72	1	<0.001	0.23	0.34	0.46	1	0.50
	Diversity	-0.01	0.08	0.04	1	0.85	0.01	0.14	0.01	1	0.94
Wind-pollinated flower	Cover	-0.42	0.27	2.38	1	0.12	1.11	0.28	16.04	1	<0.001
	Diversity	0.03	0.06	0.19	1	0.67	0.23	0.08	7.89	1	<0.001
Total cover		-0.97	0.37	6.92	1	0.008	0.76	0.50	2.26	1	0.13

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777

778 **Table 2. Averaged estimated effects (generalized linear mixed models, GLMM) of spontaneous**
 779 **flowering vegetation on beneficial insect abundance.** Σw_i : sum of the weights (i.e. relative
 780 importance). Positive estimates for "Location" correspond to an increase towards "Edge". Positive
 781 estimates for "Orchard management" corresponds to an increase towards "Organic". Significant
 782 variables are indicated in bold.

	Explanatory variable	Estimate	Z-value	Σw_i	p-value
Hoverflies	I-P flower cover	0.72 (\pm 0.20)	3.55	0.99	<0.001
	I-P flower diversity	0.27 (\pm 0.29)	0.95	0.34	0.34
	W-P flower cover	0.62 (\pm 0.22)	2.84	0.94	<0.001
	W-P flower diversity	0.74 (\pm 0.35)	2.10	0.73	0.04
	Location	0.23 (\pm 0.23)	1.00	0.35	0.32
	Management	-0.31 (\pm 0.30)	1.02	0.36	0.31
Parasitoids	I-P flower cover	0.45 (\pm 0.17)	2.58	0.85	0.01
	I-P flower diversity	0.30 (\pm 0.20)	1.51	0.51	0.13
	W-P flower cover	0.40 (\pm 0.18)	2.17	0.78	0.03
	W-P flower diversity	-0.21 (\pm 0.28)	0.73	0.30	0.47
	Location	-0.32 (\pm 0.32)	1.69	0.59	0.09
	Management	-0.17 (\pm 0.24)	0.69	0.31	0.49
Wild bees	I-P flower cover	1.07 (\pm 0.21)	5.19	1.00	<0.001
	I-P flower diversity	0.74 (\pm 0.28)	2.62	0.90	0.01
	W-P flower cover	-0.37 (\pm 0.27)	1.37	0.47	0.17
	W-P flower diversity	0.76 (\pm 0.38)	2.02	0.74	0.04
	Location	-0.33 (\pm 0.22)	1.50	0.49	0.13
	Management	-0.52 (\pm 0.42)	1.22	0.41	0.22
Honeybees	I-P flower cover	2.18 (\pm 0.69)	3.17	0.99	<0.001
	I-P flower diversity	0.82 (\pm 0.82)	1.00	0.34	0.32
	W-P flower cover	1.23 (\pm 0.72)	1.71	0.59	0.09
	W-P flower diversity	0.70 (\pm 0.89)	0.79	0.33	0.43
	Location	0.19 (\pm 0.79)	0.24	0.25	0.81
	Management	-1.01 (\pm 0.84)	1.20	0.42	0.23

783

784

785 **Table 3. Averaged estimated effects (generalized linear mixed models, GLMM) of hoverfly and**
786 **parasitoid abundances, location and orchard management on pest numbers (RAA infestation and**
787 **CM larvae) and their damages.** Σw_i : sum of the weights (i.e. relative importance). Positive estimates
788 for "Location" correspond to an increase towards "Edge". Positive estimates for "Orchard
789 management" corresponds to an increase towards "Organic". Significant variables are indicated in
790 bold. RAA: Rosy apple aphid, CM: Codling moth.

	Explanatory variable	Estimate	Z-value	RI	p-value
RAA infestation	Parasitoids	0.46 (\pm 0.14)	3.19	0.98	<0.001
	Hoverflies	-1.82 (\pm 0.21)	8.63	1.00	<0.001
	Management	1.01 (\pm 1.03)	0.97	0.34	0.33
	Location	0.04 (\pm 0.12)	0.34	0.25	0.74
RAA fruit damage	Parasitoids	-0.08 (\pm 0.44)	0.18	0.22	0.85
	Hoverflies	0.48 (\pm 0.51)	0.93	0.31	0.35
	Management	1.23 (\pm 1.14)	1.07	0.34	0.28
	Location	0.07 (\pm 0.36)	0.20	0.22	0.84
CM fruit damage	Parasitoids	0.64 (\pm 0.99)	0.65	0.24	0.52
	Management	2.01 (\pm 1.00)	2.01	0.66	0.04
	Location	0.67 (\pm 0.75)	0.90	0.28	0.37
CM diapausing larvae	Parasitoids	-0.45 (\pm 0.48)	0.94	0.30	0.35
	Management	0.91 (\pm 0.90)	1.02	0.28	0.31
	Location	0.42 (\pm 0.41)	1.04	0.31	0.30

791

792

793 **Appendix**

794 Table A.1. Characteristics of the 18 apple orchards.

795 Table A.2. Assignment of a pollination mode to each recorded flowering plant species.

796

797 Table A.3. Combined Pearson and Spearman correlation matrix.

798

799 Table A.4. Variance inflation factor (VIF) for the GLMM analysing the effects of spontaneous flowering
800 vegetation on beneficial insect abundance.

801

802 Table A.5. Variance inflation factor (VIF) for the GLMM analysing the effects of hoverfly and parasitoid
803 abundances, location and orchard management on pest numbers (RAA infestation and CM larvae) and
804 their damages.

805 Table A.6. Summary statistics for all measured variables.

806

807 Table A.7. Number of recorded hoverflies, parasitoid wasps, wild bees and honeybees.

808

809 Table A.8. Summary statistics of the piecewise structural equation model (pSEM) explaining the effects
810 of spontaneous flowering vegetation on beneficial insect abundance.

811 Table A.9. Summary statistics of the piecewise structural equation model (pSEM) explaining the effects
812 of spontaneous flowering vegetation natural enemies and cascading effects on pest infestation and
813 associated damage.

814 Figure A.1. Initial pSEMs and associated hypotheses.

815

816 Figure A.2. Evolution of flower cover (%), species richness and diversity from March to June.

817 Figure A.3. Comparison of flower cover between organic and conventional orchards and between
818 transect location within the orchard.

819 Figure A.4. Comparison of flower diversity (Shannon index) between organic and conventional
820 orchards and between transect location within the orchard.

Table A.1. Characteristics of the 18 apple orchards.

Orchard ID	Management	Cultivar	Area (ha)	Distance from the edge (first transect)	Distance between transects (m)	Row management	Dominant species in hedgerow
1	Organic	Gala	0.4	2	9	tillage	<i>Cupressus sp.</i>
2	Conventional	Golden	0.5	5	37	herbicide	<i>Cupressus sp.</i>
3	Conventional	Gala	2.8	7	35	tillage	<i>Cupressus sp.</i>
4	Conventional	Golden	1	11	11	herbicide	<i>Cupressus sp.</i>
5	Organic	Reine des reinette	0.5	1,5	15	tillage	<i>Cupressus sp.</i>
6	Conventional	Granny and Gala	1.2	5	24	herbicide	<i>Populus sp.</i>
7	Organic	Golden	1.9	3	46	tillage	<i>Populus sp.</i>
8	Conventional	Golden	0.3	3	15	herbicide	<i>Cupressus sp.</i>
9	Conventional	Early gold	0.5	2	23	herbicide	<i>Cupressus sp.</i>
10	Conventional	Akane	0.2	2	17	herbicide	<i>Cupressus sp.</i>
11	Organic	Golden and Gala	1.2	2	15	none	<i>Populus sp.</i>
12	Organic	Valstar	1.5	4	15	none	<i>Cupressus sp.</i>
13	Conventional	Pink Lady	0.8	3	27	none	<i>Cupressus sp.</i>
14	Conventional	Valstar	0.5	3	10	tillage	<i>Cupressus sp.</i>
15	Organic	Gala	1.9	3	28	none	<i>Cupressus sp.</i>
16	Organic	Early red one	0.6	4	19	none	<i>Cupressus sp.</i>
17	Organic	Chantecler	1.6	4	15	tillage	<i>Populus sp.</i>
18	Organic	Chantecler	0.5	3	10	tillage	<i>Cupressus sp.</i>

Table A.2. Assignment of a pollination mode to each recorded flowering plant species. Flowering phenology was determined from the present study. Pollination mode was determined based on the BioFlor database using information from 'pollen vector' and 'typical pollinator' (Mueller, 1881) traits. For 'self-pollinated' plant species, information from 'typical pollinator' trait were used to assign the species to insect-pollinated or wind-pollinated groups. For plant species not included in the BioFlor database (NA), we used the information available for other species of the same genus to assign a group.

Species	Flowering phenology			Pollination mode in BioFlor		Attribution
	March	May	June	Pollen vector	Typical pollinators	
<i>Allium porrum</i>			■	insects	bees, bumblebees, wasps, bombylides, syrphids	insect-pollinated
<i>Anagallis arvensis</i>		■	■	insects and selfing	short tongued bees, syrphids, flies, beetles	insect-pollinated
<i>Arabidopsis sp.</i>		■		NA	NA	insect-pollinated genus
<i>Arenaria serpyllifolia</i>			■	insects and selfing	syrphids, bees	insect-pollinated
<i>Arrhenatherum elatius</i>			■	wind and selfing	wind flowers	wind-pollinated
<i>Avena barbata</i>		■		wind	wind	wind-pollinated genus
<i>Bellis perennis</i>		■		insects and selfing	bees, bumble bees, wasps, bombylides, syrphids	insect-pollinated
<i>Brachypodium phoenicoides</i>			■	wind	wind	wind-pollinated genus
<i>Brachypodium sylvaticum</i>			■	wind and selfing	wind flowers	wind-pollinated
<i>Bromus catharticus</i>			■	self	wind flowers	wind-pollinated
<i>Bromus diandrus</i>			■	NA	NA	wind-pollinated genus
<i>Bromus hordeaceus</i>		■		wind and selfing	wind flowers	wind-pollinated
<i>Bromus madritensis</i>		■		selfing	wind flowers	wind-pollinated
<i>Bromus rubens</i>			■	wind	wind	wind-pollinated genus
<i>Bromus squarrosus</i>			■	wind, selfing	wind flowers	wind-pollinated
<i>Bromus sterilis</i>		■		wind, selfing	wind flowers	wind-pollinated
<i>Capsella bursa-pastoris</i>	■	■		insects and selfing	syrphids, bees	insect-pollinated
<i>Cardamine hirsuta</i>	■			insects and selfing	syrphids, bees	insect-pollinated
<i>Carduus pycnocephalus</i>			■	insects	NA	insect-pollinated genus
<i>Carex muricata</i>			■	wind	wind flowers	wind-pollinated
<i>Carex sp.</i>		■		wind	wind flowers	wind-pollinated genus
<i>Catapodium rigidum</i>			■	wind and selfing	wind flowers	wind-pollinated
<i>Centaurea aspera</i>			■	insects	NA	insect-pollinated genus
<i>Cerastium fontanum</i>			■	selfing	syrphids, bees	insect-pollinated
<i>Cerastium glomeratum</i>	■	■		selfing	syrphids, bees	insect-pollinated
<i>Convolvulus arvensis</i>			■	insects and selfing	bees, bumblebees, wasps, bombylides, syrphids	insect-pollinated

Table A.2 – continues from previous page

Species	Survey period			Pollination mode in BioFlor		Attribution	
	March	May	June	Pollen vector	Typical pollinators		
<i>Crepis sancta</i>	█	█	█	NA	NA	insect-pollinated	genus
<i>Crepis setosa</i>			█	insects and selfing	bees, bumble bees, wasps, bombylides, syrphids	insect-pollinated	
<i>Crepis vesicaria</i>		█	█	insects and selfing	bees, bumble bees, wasps, bombylides, syrphids	insect-pollinated	
<i>Cynodon dactylon</i>				selfing	wind flowers	wind-pollinated	
<i>Dactylis glomerata</i>	█	█	█	wind and selfing	wind flowers	wind-pollinated	
<i>Ditransectaxis erucooides</i>	█		█	NA	NA	insect-pollinated	genus
<i>Elytrigia repens</i>			█	wind	wind flowers	wind-pollinated	
<i>Epilobium tetragonum</i>			█	self	bees, bumblebees, wasps, bombylides, syrphids	insect-pollinated	
<i>Euphorbia helioscopia</i>	█	█		insects and selfing	beetles, flies, syrphids, wasps, medium tongued bees	insect-pollinated	
<i>Festuca arundinacea</i>		█	█	wind	wind flowers	wind-pollinated	
<i>Festuca pratensis</i>	█	█		wind	wind flowers	wind-pollinated	
<i>Galium aparine</i>		█	█	insects and selfing	beetles, flies, syrphids, wasps, medium tongued bees	insect-pollinated	
<i>Galium mollugo</i>			█	insects and selfing	beetles, flies, syrphids, wasps, medium tongued bees	insect-pollinated	
<i>Geranium dissectum</i>	█			insects and selfing	hymenoptera	insect-pollinated	
<i>Geum urbanum</i>			█	insects and selfing	syrphids, bees	insect-pollinated	
<i>Holcus lanatus</i>		█	█	wind and selfing	wind flowers	wind-pollinated	
<i>Hordeum murinum</i>		█	█	selfing	wind flowers	wind-pollinated	
<i>Hordeum vulgare</i>			█	NA	NA	wind-pollinated	genus
<i>Lamium purpureum</i>	█			insects and selfing	hymenoptera	insect-pollinated	
<i>Lepidium draba</i>		█	█	insects and selfing	syrphids, bees	insect-pollinated	
<i>Lolium perenne</i>		█	█	wind	wind flowers	wind-pollinated	
<i>Lolium rigidum</i>			█	NA	NA	wind-pollinated	genus
<i>Malva sylvestris</i>			█	insects	bees, bumblebees, wasps, bombylides, syrphids	insect-pollinated	
<i>Medicago lupulina</i>		█	█	insects and selfing	hymenoptera	insect-pollinated	
<i>Medicago sativa</i>			█	insects	hymenoptera	insect-pollinated	
<i>Mercurialis annua</i>	█	█		wind	wind flowers	wind-pollinated	
<i>Oxalis corniculata</i>		█		selfing	bees, bumblebees, wasps, bombylides, syrphids	insect-pollinated	
<i>Paspalum dilatatum</i>			█	NA	NA	wind-pollinated	genus
<i>Picris echioides</i>		█	█	insects and selfing	bees, bumble bees, wasps, bombylides, syrphids	insect-pollinated	
<i>Plantago lanceolata</i>		█	█	wind and insect	wind flowers	wind-pollinated	

Table A.2 – continues from previous page

Species	Survey period			Pollination mode in BiolFlor		Attribution
	March	May	June	Pollen vector	Typical pollinators	
<i>Poa annua</i>	■	■	■	wind and selfing	wind flowers	wind-pollinated
<i>Poa pratensis</i>		■	■	wind and selfing	wind flowers	wind-pollinated
<i>Poa trivialis</i>	■	■	■	wind	wind flowers	wind-pollinated
<i>Polygonum aviculare</i>			■	insects and selfing	bees, bumblebees, wasps, bombylides, syrphids	insect-pollinated
<i>Potentilla reptans</i>			■	insects	syrphids, bees	insect-pollinated
<i>Rostraria cristata</i>				NA	NA	wind-pollinated genus
<i>Rumex crispus</i>		■	■	wind	wind flowers	wind-pollinated
<i>Rumex obtusifolius</i>		■	■	NA	NA	wind-pollinated genus
<i>Rumex pulcher</i>		■	■	wind	wind flowers	wind-pollinated
<i>Senecio vulgaris</i>	■	■	■	insects and selfing	bees, bumble bees, wasps, bombylides, syrphids	insect-pollinated
<i>Sisymbrium irio</i>			■	insects and selfing	syrphids, bees	insect-pollinated
<i>Sonchus asper</i>		■	■	insects and selfing	bees, bumble bees, wasps, bombylides, syrphids	insect-pollinated
<i>Sonchus oleraceus</i>		■	■	selfing	bees, bumble bees, wasps, bombylides, syrphids	insect-pollinated
<i>Sorghum halepense</i>			■	selfing	wind flowers	wind-pollinated
<i>Stellaria media</i>	■	■	■	insects and selfing	syrphids, bees	insect-pollinated
<i>Taraxacum officinale</i>	■	■	■	insects	bees, bumble bees, wasps, bombylides, syrphids	insect-pollinated
<i>Torilis arvensis</i>			■	insects and selfing	beetles, flies, syrphids, wasps, medium tongued bees	insect-pollinated
<i>Torilis nodosa</i>			■	insects	beetles, flies, syrphids, wasps, medium tongued bees	insect-pollinated
<i>Trifolium pratense</i>	■	■	■	insects	bumble bees	insect-pollinated
<i>Trifolium repens</i>	■	■	■	insects	bees	insect-pollinated
<i>Veronica arvensis</i>		■	■	insects and selfing	bees, bumblebees, wasps, bombylides, syrphids	insect-pollinated
<i>Veronica persica</i>	■	■	■	insects and selfing	bees, bumblebees, wasps, bombylides, syrphids	insect-pollinated

Table A.3. Combined Pearson and Spearman correlation matrix. The area in grey corresponds to Pearson correlations. Correlation coefficients are indicated (r of Pearson or rho of Spearman) and stars indicate significance level (**: <0.05; ***: <0.01; ****: <0.001).

	I-P flower cover	I-P flower diversity	W-P flower cover	W-P flower diversity	Hoverflies	Parasitoids	Honeybees	Wild bees	RAA infestation	RAA damage	CM damage	CM larvae
I-P flower cover		0.35 ***	0.11	-0.07	0.23*	0.29**	0.37***	0.27**	-0.08	-0.01	0.03	0.30
I-P flower diversity	0.35 ***		0.12	0.13	0.15	0.16	0.23**	0.24**	0.77	-0.02	-0.17	0.01
W-P flower cover	0.11	0.12		0.55***	0.41***	0.50***	0.16	0.40***	0.18	0.23	0.24	0.28
W-P flower diversity	-0.07	0.13	0.55***		0.41***	0.35***	0.11	0.474***	0.23*	-0.11	0.12	0.01
Hoverflies	0.23*	0.15	0.41***	0.41***		0.25**	0.27**	0.36***	-0.02	0.03	0.05	0.10
Parasitoids	0.29**	0.16	0.50***	0.35***	0.25**		0.29**	0.41***	0.13	0.15	0.16	0.13
Honeybees	0.37***	0.23**	0.16	0.11	0.27**	0.29**		0.33***	-0.25*	0.03	-0.003	0.23
Wild bees	0.27**	0.24**	0.40***	0.474***	0.36***	0.41***	0.33***		-0.06	-0.02	-0.06	0.16
RAA infestation	-0.08	0.77	0.18	0.23*	-0.02	0.13	-0.25*	-0.06		0.11	0.03	-0.26
RAA damage	-0.01	-0.02	0.23	-0.11	0.03	0.15	0.03	-0.02	0.11		0.38	0.02
CM damage	0.03	-0.17	0.24	0.12	0.05	0.16	-0.003	-0.06	0.03	0.38		0.33
CM larvae	0.30	0.01	0.28	0.01	0.10	0.13	0.23	0.16	-0.26	0.02	0.33	

Table A.4. Variance inflation factor (VIF) for the GLMM analysing the effects of spontaneous flowering vegetation on beneficial insect abundance.

		VIF
Hoverflies	I-P flowers cover	1.28
	I-P flowers diversity	1.29
	W-P flowers cover	1.39
	W-P flowers diversity	1.51
	Location	1.23
	Management	1.53
Parasitoids	I-P flowers cover	1.25
	I-P flowers diversity	1.15
	W-P flowers cover	1.43
	W-P flowers diversity	1.28
	Location	1.17
	Management	1.56
Wild bees	I-P flowers cover	1.28
	I-P flowers diversity	1.15
	W-P flowers cover	1.34
	W-P flowers diversity	1.30
	Location	1.21
	Management	1.24
Honeybees	I-P flowers cover	1.28
	I-P flowers diversity	1.09
	W-P flowers cover	1.75
	W-P flowers diversity	1.57
	Location	1.16
	Management	1.37

Table A.5. Variance inflation factor (VIF) for the GLMM analysing the effects of hoverfly and parasitoid abundances, location and orchard management on pest numbers (RAA infestation and CM larvae) and their damages.

		VIF
RAA infestation	Parasitoids	1.04
	Hoverflies	1.17
	Management	1.00
	Location	1.16
RAA fruit damage	Parasitoids	1.81
	Hoverflies	1.30
	Management	1.06
	Location	1.80
CM fruit damage	Parasitoids	1.05
	Management	1.03
	Location	1.02
CM diapausing larvae	Parasitoids	1.16
	Management	1.01
	Location	1.17

Table A.6.1 Summary statistics for all measured variables. For the variables related to spontaneous vegetation (flower cover and diversity), given data are means and standard deviation (SD) of the three periods. I-P flower: insect-pollinated flower, W-P flower: wind-pollinated flower.

		Spontaneous vegetation													
		Total cover (%)		Total flower cover (%)				Total flower diversity				I-P flower cover (%)			
ID	Management	Centre	Edge	Centre		Edge		Centre		Edge		Centre		Edge	
		mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD		
1	Organic	70	70	19.71	19.76	21.18	19.15	1.18	0.35	1.43	0.23	2.51	2.23	4.34	1.45
2	Conventional	50	30	25.04	29.25	5.45	6.17	1.45	0.70	0.74	0.73	0.46	0.54	0.19	0.10
3	Conventional	65	70	12.36	13.71	10.38	7.34	1.31	0.03	1.50	0.14	4.34	7.56	1.06	0.64
4	Conventional	65	12	11.69	10.40	10.92	11.75	0.94	0.41	1.06	0.05	3.03	3.40	2.47	3.00
5	Organic	70	25	19.30	15.23	7.74	10.67	1.23	0.28	0.84	0.77	2.27	4.47	0.00	/
6	Conventional	65	60	10.57	9.25	1.25	0.98	1.34	0.31	0.94	0.33	8.06	9.92	5.55	1.48
7	Organic	90	80	7.18	10.94	4.68	5.93	1.41	0.63	1.43	0.44	0.24	0.18	0.28	0.26
8	Conventional	85	75	26.20	21.55	19.97	31.16	1.63	0.89	1.26	0.58	6.35	5.71	5.61	7.04
9	Conventional	85	45	19.59	12.65	18.75	15.20	1.50	0.68	1.42	0.81	1.23	1.17	0.39	0.32
10	Conventional	80	80	14.11	9.70	6.90	4.70	1.26	0.11	1.62	0.60	2.61	3.48	2.23	2.61
11	Organic	90	90	10.08	7.78	8.94	5.87	1.01	0.30	1.01	0.69	5.64	6.76	1.45	1.35
12	Organic	80	75	24.37	21.78	13.97	13.58	0.99	0.73	1.22	0.49	6.13	5.08	3.97	2.64
13	Conventional	85	70	18.06	11.31	6.15	9.70	1.33	0.14	0.97	0.61	4.49	2.87	3.53	0.89
14	Conventional	30	55	26.98	23.71	26.44	16.53	1.10	0.04	1.55	0.18	5.60	4.11	5.11	1.66
15	Organic	90	50	27.08	15.1	13.1	13.33	1.23	0.66	1.17	0.51	10.52	6.97	5.85	4.55
16	Organic	75	40	6.70	4.73	5.39	5.20	0.50	0.44	1.11	0.26	6.86	6.84	2.43	3.62
17	Organic	80	85	9.43	10.73	2.38	0.68	1.06	0.29	1.07	0.76	6.21	5.77	6.57	8.08
18	Organic	80	70	8.82	7.31	17.5	15.18	1.15	0.33	0.82	0.12	6.60	5.87	4.30	4.39

Table A.6.1. Summary statistics for all measured variables. For the variables related to spontaneous vegetation (flower cover and diversity), given data are means and standard deviation (SD) of the three periods. I-P flower: insect-pollinated flower, W-P flower: wind-pollinated flower. – *continues from previous page*

		Spontaneous vegetation											
		I-P flower diversity				W-P flower cover (%)				W-P flower diversity			
		Centre		Edge		Centre		Edge		Centre		Edge	
ID	Management	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD
1	Organic	0.74	0.29	0.98	0.19	17.94	17.88	16.83	20.00	0.80	0.46	0.79	0.13
2	Conventional	0.16	0.26	0.31	0.32	5.58	4.67	5.20	5.10	0.59	0.52	0.76	0.67
3	Conventional	0.61	0.20	0.51	0.24	1.57	1.29	1.32	1.20	0.62	0.52	0.73	0.66
4	Conventional	0.68	0.48	0.46	0.60	10.13	10.61	15.04	14.11	0.43	0.37	0.45	0.43
5	Organic	0.29	0.39	0.00		12.98	17.45	5.45	6.17	0.87	0.77	0.74	0.73
6	Conventional	1.03	0.33	1.07	0.36	3.31	4.67	4.83	6.66	0.40	0.37	0.45	0.39
7	Organic	0.32	0.35	0.20	0.35	11.07	10.01	10.63	11.95	0.67	0.56	0.66	0.57
8	Conventional	0.74	0.41	0.66	0.57	7.17	9.36	2.14	3.70	0.38	0.43	0.22	0.39
9	Conventional	0.62	0.40	0.54	0.37	4.68	6.93	0.87	0.76	0.58	0.55	0.35	0.31
10	Conventional	0.93	0.60	0.85	0.35	3.32	4.52	2.45	3.34	0.60	0.57	0.57	0.71
11	Organic	0.82	0.42	0.63	0.46	17.44	21.33	18.52	29.85	1.02	0.81	0.91	0.79
12	Organic	1.02	0.47	1.26	0.58	13.03	12.99	14.78	15.55	0.98	0.87	0.99	0.99
13	Conventional	1.18	0.33	1.29	0.48	6.02	7.34	3.37	3.94	0.63	0.40	0.70	0.61
14	Conventional	0.52	0.46	0.6	0.33	3.92	4.83	3.83	4.65	0.32	0.35	0.44	0.38
15	Organic	0.85	0.36	0.97	0.17	8.65	11.58	8.12	9.10	0.37	0.57	0.40	0.69
16	Organic	0.60	0.39	0.42	0.20	5.24	5.24	3.72	6.09	0.49	0.44	0.55	0.49
17	Organic	1.07	0.37	1.37	0.25	20.50	18.98	19.88	20.77	0.68	0.60	0.87	0.76
18	Organic	0.85	0.39	0.77	0.38	13.49	16.26	8.80	12.65	0.73	0.61	0.80	0.70

Table A.6.2 Summary statistics for all measured variables. For the variables related to beneficial insects (abundance of each group and Shannon diversity), given data are mean and standard deviation of the three survey periods. – *continues from previous page*

		Beneficial insects																Beneficial insect diversity	
ID	Management	Hoverflies				Parasitoid wasps				Wild bees				Honeybees				Centre	Edge
		Centre		Edge		Centre		Edge		Centre		Edge		Centre		Edge			
		mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD		
1	Organic	0.50	0.84	0.33	0.58	0.67	1.21	1.00	1.73	0.17	0.41	0.33	0.58	0.00		0.00		0.64	0.95
2	Conventional	0.17	0.41	0.33	0.58	1.50	2.35	0.33	0.58	0.17	0.41	0.33	0.58	0.00		0.00		0.00	1.10
3	Conventional	0.33	0.52	0.33	0.58	1.17	1.17	0.67	0.58	1.5	3.21	0.33	0.58	2.00	4.43	0.33	0.58	1.18	1.33
4	Conventional	0.50	0.84	0.00		0.67	1.03	0.67	1.15	0.67	1.63	0.00		0.00		0.00		1.06	0.00
5	Organic	0.50	0.84	0.00		0.67	1.63	0.00		2.5	3.89	1.00	1.73	0.17	0.41	0.00		1.06	0.00
6	Conventional	0.83	1.33	1.00	1.73	1.67	1.75	1.00	1.00	1.5	2.74	0.33	0.58	1.67	2.25	2.33	3.21	1.25	1.20
7	Organic	0.00		0.00	0.00	1.33	1.63	0.67	1.15	0.00		0.00		0.00		0.00		0.00	
8	Conventional	1.00	2.00	1.67	2.89	2.17	2.64	1.00	1.73	2.00	3.16	1.00	1.73	0.50	1.22	0.00		1.13	1.07
9	Conventional	1.17	1.33	1.33	1.15	0.83	0.75	0.33	0.58	0.83	0.75	0.67	0.58	0.17	0.41	0.00		1.29	0.96
10	Conventional	0.67	1.63	0.00		1.33	2.16	1.00	1.73	0.50	0.84	0.67	1.15	0.83	2.04	0.00		1.27	0.67
11	Organic	2.00	3.16	2.67	4.62	1.67	1.86	1.67	2.08	4.33	5.99	1.67	1.15	0.33	0.82	0.00		1.00	1.07
12	Organic	1.17	1.17	1.33	1.53	1.33	1.75	1.00	1.73	0.00		0.00		0.00		0.00		0.66	0.68
13	Conventional	1.50	2.35	2.33	3.21	1.17	1.6	0.67	1.15	1.83	1.83	2.00	2.00	0.00		0.00		1.03	0.99
14	Conventional	0.33	0.82	0.00		0.83	1.17	1.33	1.53	0.67	1.21	0.33	0.58	0.33	0.52	0.33	0.58	1.28	0.87
15	Organic	1.17	1.83	1.33	2.31	2.67	2.16	3.00	2.65	1.67	3.20	2.67	4.62	0.67	1.21	0.33	0.58	1.27	1.18
16	Organic	1.17	2.40	0.33	0.58	1.33	1.21	1.33	1.53	0.67	1.21	0.33	0.58	0.17	0.41	0.00	0.00	1.24	0.87
17	Organic	1.67	1.97	0.00		2.5	2.07	2.67	2.89	1.17	1.60	1.67	2.08	2.33	4.41	3.67	6.35	1.21	1.05
18	Organic	0.83	0.98	1.67	0.58	0.5	0.55	0.33	0.58	0.67	1.63	0.00		1.00	1.67	1.33	2.31	1.04	0.94

Table A.6.2. Summary statistics for all measured variables. For RAA infestation, given data are the mean and standard deviation of the three periods. For damages, given data are proportion recorded in late June. CM larvae corresponds to the number of codling moth diapausing larvae collected in October (sum per transect) – *continues from previous page*

Apple pests and damages													
ID	Management	RAA infestation				RAA damage (%)		CM damage (%)		CM larvae		Small CM larvae	
		Centre		Edge		Centre	Edge	Centre	Edge	Centre	Edge	Centre	Edge
		mean	SD	mean	SD								
1	Organic	2.00	4.43	3.67	6.35	3.06	1.30	2.04	1.30	1	0	0	0
2	Conventional	4.50	3.62	4.00	3.61	0.00	0.00	0.32	0.31	0	10	0	0
3	Conventional	NA	NA	NA	NA	NA	NA	NA	NA	1	0	0	0
4	Conventional	NA	NA	NA	NA	0.00	0.31	0.00	0.31	0	0	0	0
5	Organic	1.17	1.94	2.00	2.65	0.00	0.00	0.00	1.88	5	4	0	0
6	Conventional	0.00		0.00		0.68	0.00	0.68	0.00	1	2	0	0
7	Organic	0.50	1.22	0.00		0.00	0.47	0.00	1.90	18	7	0	0
8	Conventional	0.00		0.00		0.00	0.00	2.19	0.94	NA	23	0	1
9	Conventional	0.33	0.82	0.67	1.15	0.00	0.00	0.00	0.00	0	0	0	0
10	Conventional	4.33	7.92	2.00	2.65	0.00	0.33	0.00	1.64	0	1	0	0
11	Organic	1.33	3.27	0.00		NA	1.69	NA	32.20	NA	NA	NA	NA
12	Organic	26.50	35.40	36.33	50.81	1.05	0.00	2.80	0.00	0	0	0	0
13	Conventional	NA	NA	NA	NA	NA	NA	NA	NA	5	11	0	1
14	Conventional	13.50	23.24	21.33	32.72	1.88	5.04	2.50	0.00	1	NA	0	NA
15	Organic	1.67	3.61	3.00	5.2	0.00	1.66	44.86	63.58	9	33	1	16
16	Organic	0.17	0.41	0.00		0.00	0.00	0.31	6.74	5	24	0	7
17	Organic	6.67	9.05	5.33	8.39	8.86	5.61	0.00	2.80	10	7	0	0
18	Organic	0.50	1.22	0.00		0.00	0.00	0.36	0.00	2	2	0	0

Table A.7. Number of recorded hoverflies, parasitoid wasps, wild bees and honeybees. Mean (\pm SD) corresponds to the mean number of insects recorded per transect and per period.

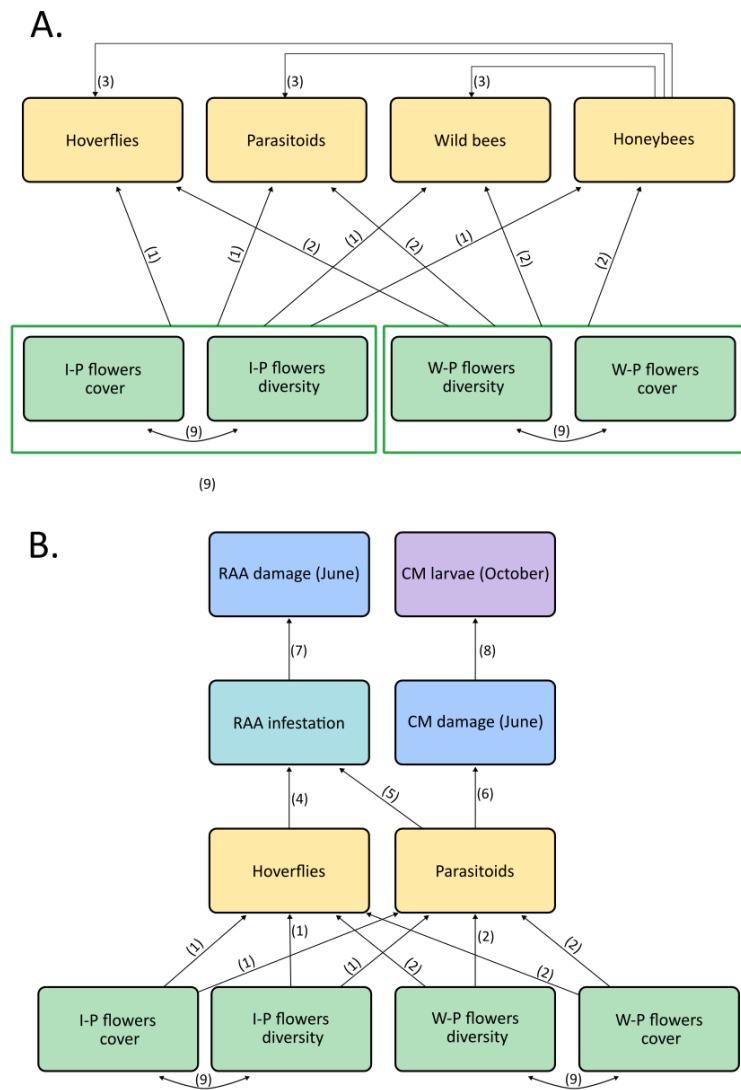
	Late March			Early May			Early June		
	Sum	Mean	SD	Sum	Mean	SD	Sum	Mean	SD
Hoverflies	8	0.22	0.76	40	1.10	1.45	45	1.25	1.96
Parasitoids	12	0.33	0.79	54	1.50	1.56	78	2.17	1.90
Honeybees	9	0.25	0.77	11	0.31	1.12	41	1.14	2.67
Wild bees	2	0.56	0.23	39	1.08	1.89	84	2.33	3.47

Table A.8. Summary statistics of the piecewise structural equation model (pSEM) explaining the effects of spontaneous flowering vegetation on beneficial insect abundance. Each row corresponds to a path in the pSEM. SE: Standard Error; DF: Degree of freedom; Std Estimate: Standardized estimate.

Response	Predictor	Estimate	SE	DF	Crit.Value	Std Estimate	p-value
Parasitoid wasps	I-P flower cover	0.04	0.01	108	2.46	0.14	0.01
Parasitoid wasps	W-P flower cover	0.02	0.01	108	2.36	0.13	0.02
Parasitoid wasps	I-P flower diversity	0.28	0.20	108	1.40	0.09	0.16
Parasitoid wasps	W-P flower diversity	-0.28	0.23	108	-1.20	-0.11	0.23
Parasitoid wasps	Honeybees	0.04	0.03	108	1.31	0.06	0.19
Hoverflies	I-P flower cover	0.06	0.02	108	3.57	0.22	<0.001
Hoverflies	W-P flower cover	0.02	0.01	108	2.65	0.17	0.01
Hoverflies	I-P flower diversity	0.27	0.32	108	0.82	0.07	0.41
Hoverflies	W-P flower diversity	0.51	0.34	108	1.52	0.17	0.13
Hoverflies	Honeybees	-0.04	0.06	108	-0.73	-0.05	0.47
Honeybees	I-P flower cover	0.11	0.02	108	5.04	0.29	<0.001
Honeybees	W-P flower cover	0.05	0.01	108	3.63	0.30	<0.001
Honeybees	I-P flower diversity	0.49	0.53	108	0.92	0.10	0.36
Honeybees	W-P flower diversity	0.93	0.41	108	2.28	0.24	0.02
Wild bees	I-P flower cover	0.10	0.02	108	5.31	0.26	<0.001
Wild bees	W-P flower cover	-0.02	0.01	108	-1.60	-0.09	0.11
Wild bees	I-P flower diversity	0.78	0.29	108	2.67	0.17	0.01
Wild bees	W-P flower diversity	0.66	0.31	108	2.10	0.17	0.04
Wild bees	Honeybees	0.01	0.05	108	0.26	0.01	0.79
~~I-P flower cover	~~I-P flower diversity	0.36	-	106	3.92	0.36	<0.001
~~W-P flower cover	~~W-P flower diversity	0.55	-	106	6.75	0.55	<0.001

Table A.9. Summary statistics of the piecewise structural equation model (pSEM) explaining the effects of spontaneous flowering vegetation on natural enemies and cascading effects on pest infestation and associated damage. Each row corresponds to a path in the pSEM. SE: Standard Error; DF: Degree of freedom; Std Estimate: Standardized estimate.

Response	Predictor	Estimate	SE	DF	Crit.Value	Std Estimate	p-value
Parasitoids wasps	I-P flower cover	0.04	0.01	108	2.95	0.16	<0.001
Parasitoids wasps	W-P flower cover	0.02	0.01	108	2.42	0.13	0.02
Parasitoids wasps	I-P flower diversity	0.30	0.20	108	1.50	0.10	0.13
Parasitoids wasps	W-P flower diversity	-0.28	0.24	108	-1.19	-0.11	0.23
Hoverflies	I-P flower cover	0.06	0.02	108	3.56	0.20	<0.001
Hoverflies	W-P flower cover	0.02	0.01	108	2.62	0.16	0.01
Hoverflies	I-P flower diversity	0.27	0.32	108	0.83	0.07	0.41
Hoverflies	W-P flower diversity	0.52	0.32	108	1.62	0.17	0.1
RAA infestation	Hoverflies	-0.38	0.07	94	-5.48	-0.22	<0.001
RAA infestation	Parasitoids wasps	0.19	0.05	94	4.19	0.12	<0.001
RAA infestation	I-P flower cover	-0.03	0.03	94	-1.02	-0.06	0.31
RAA infestation	W-P flower cover	-0.07	0.01	94	-6.43	-0.34	<0.001
RAA infestation	I-P flower diversity	0.92	0.20	94	4.70	0.16	<0.001
RAA infestation	W-P flower diversity	-0.83	0.24	94	-3.46	-0.18	<0.001
CM damage	Parasitoids wasps	0.00	0.00	13.30	0.32	0.02	0.58
CM damage	I-P flower cover	-0.01	0.00	13.86	13.14	-0.25	<0.001
CM damage	RAA infestation	0.00	0.00	20.58	0.28	0.05	0.60
CM diapausing larvae	CM damage	6.52	1.61	28	4.06	0.23	<0.001
CM diapausing larvae	Parasitoids wasps	-0.08	0.07	28	-1.15	-0.03	0.25
CM diapausing larvae	RAA infestation	-0.20	0.10	28	-2.06	-0.59	0.04
~~I-P flower cover	~~I-P flower diversity	0.36	-	106	3.92	0.36	<0.001
~~W-P flower cover	~~W-P flower diversity	0.55	-	106	6.75	0.55	<0.001



We hypothesized that :

- (1) Insect-pollinated flowers (cover and diversity) improve the abundance of beneficial insects (Kishinevsky et al., 2017; Mei et al., 2021).
 - (2) Wind-pollinated flowers (cover and diversity) can promote beneficial insects, as a source of pollen or potential habitat (Dong et al., 2021 ; Saunders, 2018).
 - (3) Honeybees abundance negatively impacts other beneficial insect groups (Jeavons et al., 2020).
 - (4) Hoverflies have a negative effect on rosy apple aphid infestation (Moerkens et al., 2021; Dib et al., 2011).
 - (5) Parasitoids have a negative effect on rosy apple aphid infestation (Rodriguez-Gasol et al., 2019).
 - (6) Parasitoids observed in spring have a negative impact on the first generation of codling moth (Martinez-Sastre et al., 2021).
 - (7) RAA infestation conducts to distorted apples (i.e. sign of aphid damage) (Blommers, 2004).
 - (8) A high density for the first generation of codling moth conducts to a high number of larvae for the third generation.
 - (9) We observed a correlation between I-P flower cover and diversity as well as between W-P flower cover and diversity.
- Thus, we included correlated errors.

Figure A.1. Initial pSEMs and associated hypotheses. A: Initial pSEM related to interactions between hoverflies, parasitoid wasps, wild bees, honeybees and spontaneous flowering vegetation; B: Initial pSEM related to cascading effects on pest regulation.

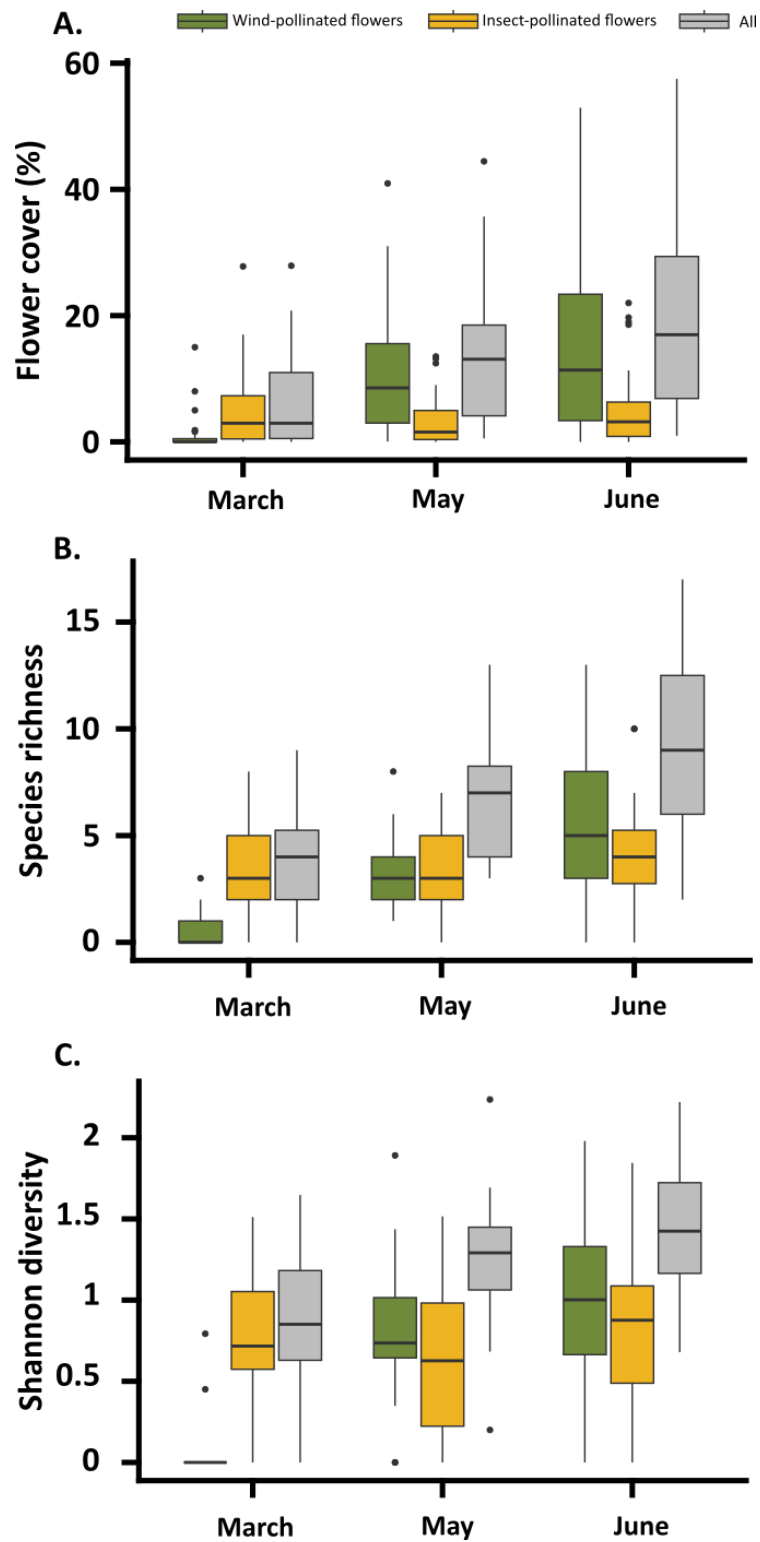


Figure A.2. Temporal dynamics from March to June of the percentage of flower cover (A), specific plant richness (B) and Shannon plant diversity (C).

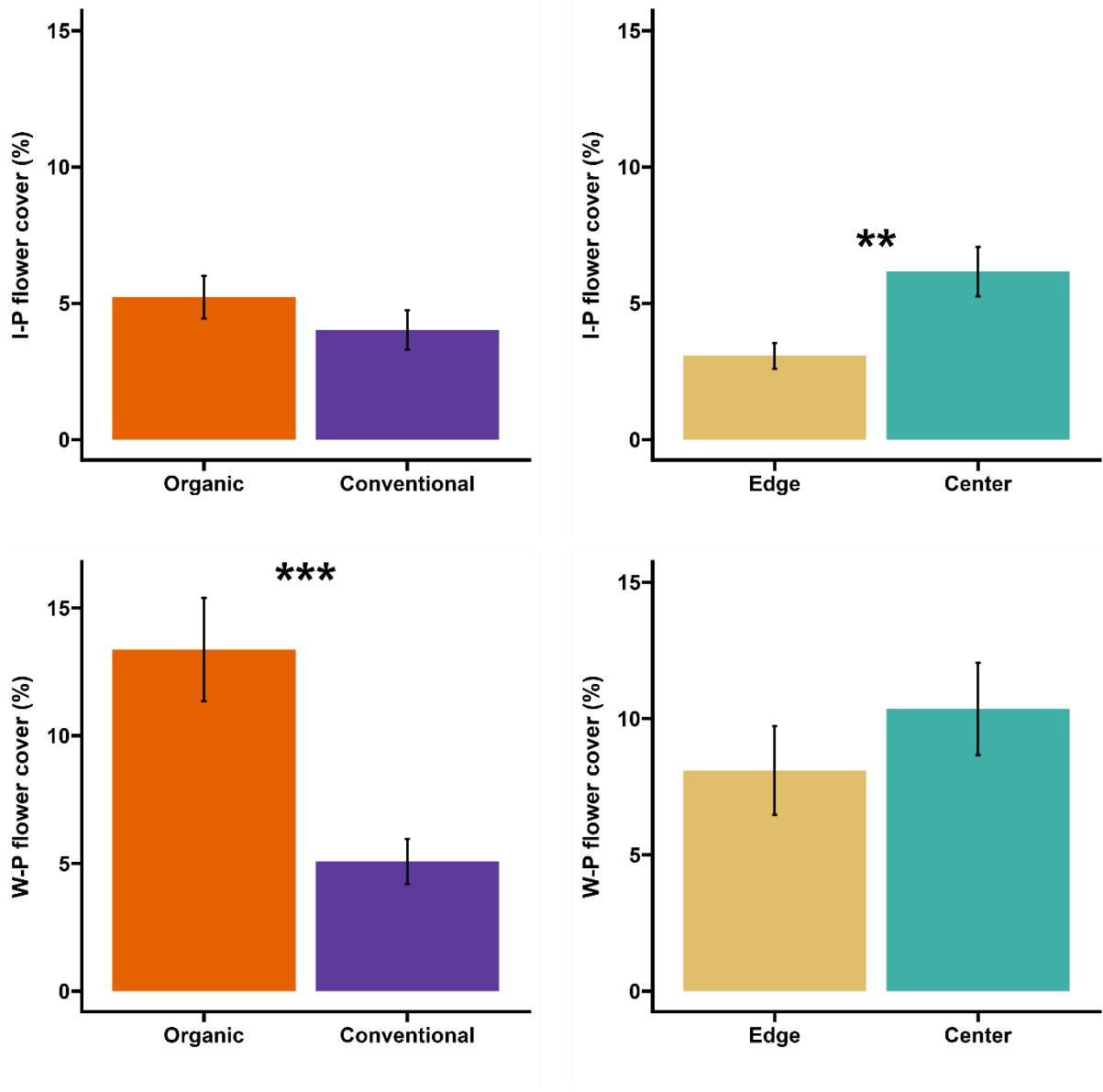


Figure A.3. Comparison of flower cover between organic and conventional orchards and between transect locations within the orchard. Bars indicate standard errors. W-P flower: Wind-pollinated flower and I-P flower: Insect pollinated flower

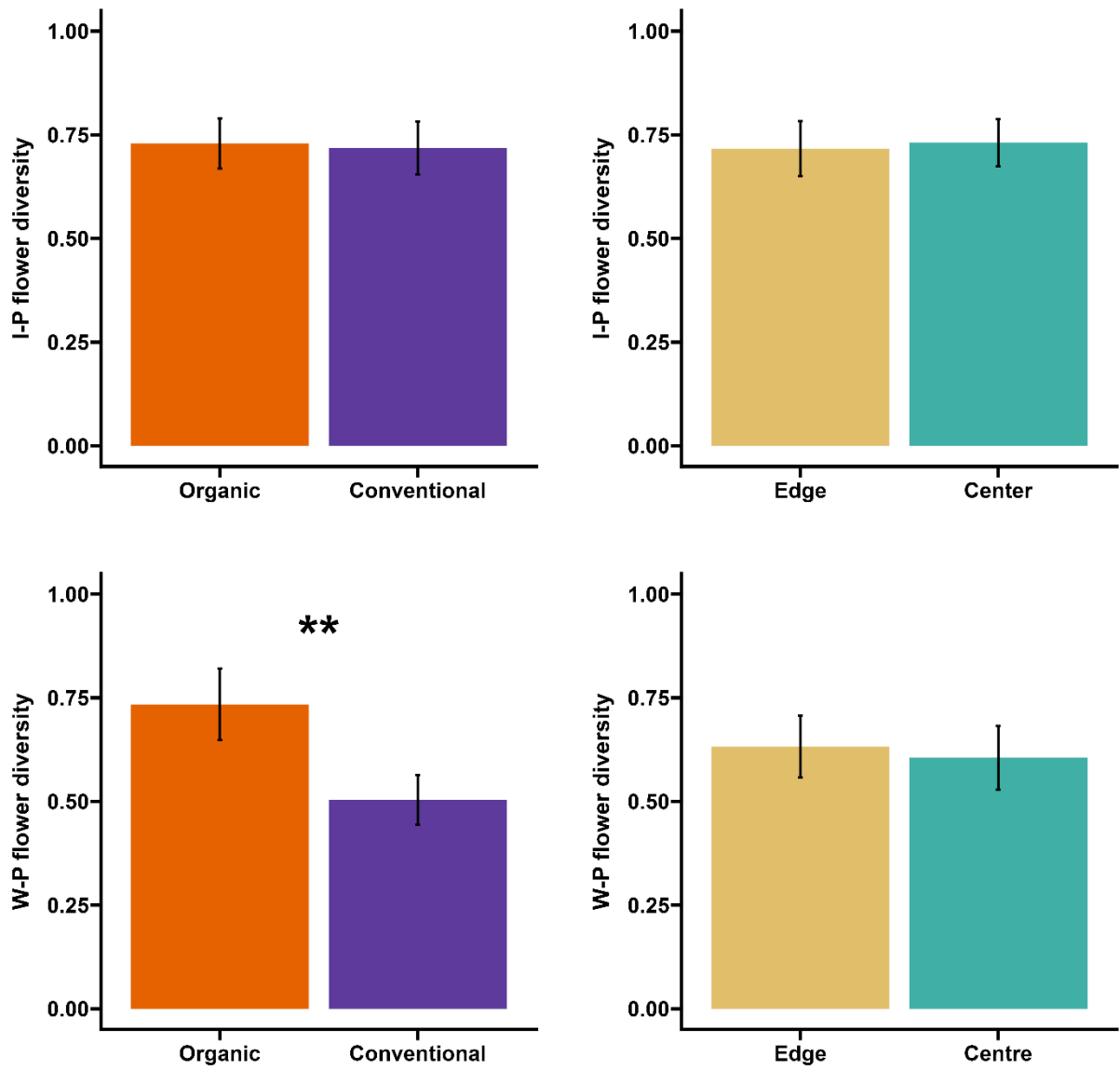


Figure A.4. Comparison of flower diversity (Shannon index) between organic and conventional orchards and between transect location within the orchard. Bars indicate standard errors. W-P flower: Wind-pollinated flower and I-P flower: Insect pollinated flower.

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