

2 **Getting more Power from Your Flowers: Multi-** 3 **Functional Flower Strips Enhance Pollinators and Pest** 4 **Control Agents in Apple Orchards**

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11

12 **Abstract**

13 Flower strips are commonly recommended to boost biodiversity and multiple ecosystem
14 services (e.g. pollination and pest control) on farmland. However, significant knowledge
15 gaps remain regards the extent to which they deliver on these aims. Here, we tested the
16 efficacy of flower strips that targeted different subsets of beneficial arthropods (pollinators
17 and natural enemies) and their ecosystem services in cider apple orchards. Treatments
18 included mixes that specifically targeted: 1) pollinators ('concealed-nectar plants'); 2) natural
19 enemies ('open-nectar plants'); or 3) or both groups concurrently (i.e. 'multi-functional' mix).
20 Flower strips were established in alleyways of four orchards and compared to control
21 alleyways (no flowers). Pollinator (e.g. bees) and natural enemy (e.g. parasitoid wasps,
22 predatory flies and beetles) visitation to flower strips, alongside measures of pest control
23 (aphid colony densities, sentinel prey predation), and fruit production, were monitored in
24 orchards over two consecutive growing seasons. Targeted flower strips attracted either
25 pollinators or natural enemies, whereas mixed flower strips attracted both groups in similar
26 abundance to targeted mixes. Natural enemy densities on apple trees were higher in plots
27 containing open-nectar plants compared to other treatments, but effects were stronger for
28 non-aphidophagous taxa. Predation of sentinel prey was enhanced in all flowering plots
29 compared to controls but pest aphid densities and fruit yield were unaffected by flower
30 strips. We conclude that 'multi-functional' flower strips that contain flowering plant species
31 with opposing floral traits can provide nectar and pollen for both pollinators and natural
32 enemies, but further work is required to understand their potential for improving pest
33 control services and yield in cider apple orchards.

34

35 **Keywords:** agroecology, ecological intensification, agri-environment schemes, floral traits,
36 conservation biological control, ecosystem services, beneficial arthropods

37 **1. Introduction**

38 In the coming decades, agriculture must simultaneously meet the demands of feeding
39 growing human populations whilst reducing its environmental impacts if we are to achieve

40 goals for biodiversity conservation and food security [1]. Yield increases achieved using
41 conventional farming practises (e.g. mechanisation, large field size, agrochemical usage)
42 have come at a great cost to biodiversity [2–4], but also generate negative feedbacks for
43 biodiversity-mediated ecosystem processes that underpin crop yields (e.g. pollination, pest
44 control, nutrient cycling), thus potentially undermining agricultural production [5,6].
45 Consequently, there is growing interest in farming practices that harness the power of
46 ecological functions for crop production (i.e. ‘ecological intensification’), and reduce our
47 reliance on conventional inputs (e.g. pesticides, herbicides, fertilisers), that are increasingly
48 costly and can have negative environmental impacts [7,8].

49 Arthropods provide many important ecosystem services on farmland, including the
50 pollination of crops and control of damaging pest species [9,10]. Pollinators, but also many
51 natural enemies (together termed ‘beneficial arthropods’) depend on flowering plants for
52 essential nutrition (e.g. pollen and nectar) at some point in their life cycle. Consequently,
53 loss and fragmentation of flower-rich habitats (e.g. forest edges, grassland, hedgerows) has
54 had negative effects on their populations in agricultural landscapes [11,12]. These non-crop
55 habitats also provide beneficial arthropods with more general benefits, in terms of shelter,
56 nesting- and overwintering sites, that may be largely absent from modern agricultural
57 systems [13–16].

58 One strategy used to ameliorate the lack of resource-rich habitat for beneficial
59 arthropods on farmland is the establishment of ‘ecological focus areas’ (EFAs) or wildflower
60 strips (here in ‘flower strips’) in field margins or unproductive areas nearby adjacent crops
61 [14,17]. These habitats are often implemented as part of agri-environment schemes (AES),
62 which offer farmers a financial incentive to adopt ‘environmentally-friendly’ management
63 practices [18]. A large body of evidence now exists demonstrating the value of flower strips
64 for beneficial arthropod populations and the provision of ecosystem services in adjacent
65 farmland [19–22]. However, despite apparent synergies in the habitat requirements of
66 pollinators and natural enemies, few studies have investigated effects of flower strips on
67 both groups concurrently [23–25]. Optimising flower strips to support multiple beneficial
68 arthropods is expected to increase their attraction for both policy-makers and farmers [26–
69 28].

70 Where the visitation preferences of pollinators and natural enemies have been
71 compared, there is compelling evidence of a dichotomy in the suitability of flowering plants
72 for these groups, based on morphological incompatibilities between floral structures related
73 to nectar accessibility (e.g. corolla depth, width) and arthropod feeding structures (e.g.
74 tongue length) [25,29]. For example, legume-rich mixtures that are typically dominated by
75 species whose nectar is concealed in deep corollas (e.g. *Trifolium* species), are highly
76 attractive to eusocial bee taxa (e.g. honeybees, bumblebees), but morphologically exclude
77 arthropods with unspecialised mouthparts. These include many important natural enemy
78 groups (e.g. aphidophagous hoverflies, ladybird beetles), but also short-tongued bees [30].
79 Instead, the latter group feed on plant species that present nectar in shallow or ‘open’
80 structures (e.g. umbels, extra-floral nectaries) [29,31]. Therefore, inclusion of flowering plant
81 species with opposing floral morphologies (i.e. ‘concealed’ or ‘open’ species) in seed
82 mixtures could be a simple means of providing floral resources for multiple beneficial
83 arthropod groups. However, few studies have considered the response of both pollinators
84 and natural enemies to different flower mixtures [25,32], and fewer still have investigated

85 effects on ecosystem services [33]. Thus, there is pressing need to examine the efficacy of
86 flower strips to enhance multiple ecosystem services on farmland.

87 Aphids (Hemiptera: Aphididae) are major pests of many crop species, including
88 perennial crops such as apple (*Malus domestica* Borkh.). They cause damage due to both
89 direct effects of aphid feeding (e.g. reduced yield and tree vigour), but also through indirect
90 effects of virus transmission by sap-sucking aphids [34]. Under favourable conditions,
91 aphids in apple orchards are effectively controlled by a diverse range of arthropod natural
92 enemies, many of which depend on floral resources at some point during their life cycles
93 [35–38]. Apple is also extremely dependent on insect pollinators for high fruit set,
94 particularly wild bees, that benefit from the presence of alternative floral resources in
95 orchards [39–42]. However, in conventional orchards, areas between trees (alleyways) are
96 maintained as grass-dominated swards that are frequently mown and offer little in terms of
97 floral resources for beneficial arthropods following apple blossom in spring [15]. Moreover,
98 perennial crops such as apple are well suited to the introduction of flower-rich habitats as
99 the benefits could accrue and transfer across seasons, rather than just be temporarily
100 enhanced within a single growing season [21].

101

102 Here, we used commercial cider apple orchards to examine the effects of perennial
103 flower strips on the abundance and diversity of pollinators (i.e. bees) and natural enemies
104 (i.e. aphidophagous and generalist taxa) in orchards following apple bloom, pest control
105 services (i.e. aphid colony densities, predator-prey ratios, sentinel prey removal), and fruit
106 production in adjacent apple trees. Specifically, we addressed the following questions: 1)
107 Does nectar accessibility determine the diversity and abundance of pollinators and natural
108 enemies visiting flower strips in cider apple orchards? 2) Do patterns in natural enemy
109 abundance and diversity in flower strips correlate with the delivery of pest control services
110 and yield in adjacent apple trees? We discuss our findings in relation to the design of flower-
111 rich AES to boost delivery of arthropod-mediated ecosystem services in apple orchards.

112 2. Materials and Methods

113 2.1. STUDY DESIGN

114 Field experiments were conducted in four cider apple orchards (HP Bulmers Ltd) and
115 located within the same 15 × 15 km square in Herefordshire, South-West England (SO 371
116 434). Orchards were planted with one of three cider apple varieties ('Gilly', 'Hastings' and
117 'Amanda'), and were all within the range of 4.33 – 16.9 ha (mean = 10.45 ha ± 2.39 SEM), of
118 similar age (planted between 2007 and 2009), management (i.e. conventional), and spatial
119 layout (inter-row spacing = 5.5 m; inter-tree = 2.75 m). Alleyways were maintained as a
120 dense sward of fine-leaved grasses and herbs and were mown every other week from May
121 until September each year.

122 2.2. FLOWER STRIPS

123 Based on experience from previous studies and the scientific literature, flowering plant
124 species were selected based on nectar availability as 'concealed' nectar plants (14 species) or

125 'open' nectar plants (11 species) (see Table S1, Supplementary materials). The *concealed nectar*
126 group included those species that hold nectar in deep corollas or spurs (e.g. *Trifolium*
127 species), which require specialised feeding structures (e.g. long proboscis) to access floral
128 resources. The *open nectar* group included plant species that provide food rewards in flowers
129 with short corollas (e.g. Apiaceae), or in extra-floral nectaries. Species selection was biased
130 towards species included in existing AES [20,25,30], or used previously in experimental
131 flower mixtures (Table S1, Supplementary Materials). From these two functional groups, we
132 devised three flower treatments including: concealed-nectar species mix, open-nectar species
133 mix, and a 'multi-functional' or 'mixed' treatment that contained all species, but with half
134 the amount of seed per species by weight.

135 Replicate plots of each flowering treatment and a grass strip control (i.e. alleyways
136 under normal management) were marked out in orchards in April 2011. A single plot
137 encompassed a continuous 40 m length of trees in the same row (= 15 trees), and the pair of
138 alleyways running parallel to the trees. Plots were always located at least 100 m from
139 another, and 50 m from the orchard edge to minimise interactions between treatments and
140 edge effects (Figure S1, Supplementary Materials). In experimental plots, a pair 40 × 1 m
141 flower strips were established down the centre of alleyways (for details on sowing protocol
142 see Appendix A1, Supplementary Materials). Flower strips bloomed sporadically in 2011 but
143 bloomed continuously in the following two years from late May onwards before being cut in
144 September each year using a tractor-mounted mower to prepare alleyways for mechanical
145 harvest. Control plots were mown on a two-weekly rotation from May to September each
146 year.

147 2.3. FLOWER-VISITOR SURVEYS

148 To assess response of pollinators and natural enemies in orchards to different flower
149 mixtures, flower-visitor surveys were carried out in all plots (flower strips and grass strip
150 controls) between June and August in both years (2012 and 2013). We focused our
151 observations on this period as floral resources for beneficial arthropods are more limited
152 during the growing season (June until October) than prior to or during apple blossom [43].
153 Plots were observed 1-3 times per month by an experienced recorder, during which all
154 flower-visiting insects were recorded by walking the full length of both alleyways at an even
155 pace, noting the identity of insect taxa and the plant species being visited. Only taxa that
156 could not be identified on the wing were collected and used to form a reference collection.
157 For control plots, we focused on the central 1 m band of each alleyway to standardise the
158 area considered in all treatments. Observations took place between 10:00 and 17:00 on calm,
159 dry days with minimum temperatures of 13°C if sunny, or 17°C if overcast (in accordance
160 with the UK Butterfly Monitoring Scheme (UKBMS website)). We considered all visiting
161 bees (Hymenoptera: Apoidea; eusocial taxa – *Bombus* spp. and *Apis mellifera*; solitary taxa –
162 Andrenidae, Melittidae, Megachilidae, Halictidae) as pollinators. Other insects contribute
163 little to apple pollination in our study region [40,42]. As focal pests were aphids, natural
164 enemies were separated into known aphidophagous taxa: hoverflies (Diptera: Syrphidae:
165 Syrphinae), ladybird beetles (Coleoptera: Coccinellidae), earwigs (Dermaptera: Forficulidae),
166 and lacewings (Neuroptera: Chrysopidae); and other more generalist or unspecialised taxa,
167 including: non-syrphid flies (Empididae, Scatophagidae, Asilidae and Tachinidae), beetles
168 (Coleoptera: Cantharidae, Staphylinidae), bugs (Hemiptera: Anthocoridae, Miridae), and
169 parasitic wasps (Hymenoptera: Parasitica). Bees were identified to species or aggregate
170 groupings (e.g. *Bombus terrestris* agg.) and natural enemy taxa to at least family level, except
171 parasitoid wasps (super-family).

172 2.4. APPLE TREE SURVEYS

173 To assess effects of flower strips on natural enemies and pest control services in adjacent
174 apple trees, five branches (1 m in length and 1 – 2 m above ground) on ten trees in each plot
175 were intensively sampled for natural enemy taxa (separated into aphidophagous and
176 generalist species) and pest aphid colonies 1-2 times per month (June – August) in 2012 and
177 2013 (five surveys per year). Surveys were performed in warm, sunny conditions and the
178 order in which plots and orchards visited was randomised. We considered an aphid colony
179 to be any aggregation of aphids numbering more than five individuals. We focused on
180 aphids as target pests as they were the only pest group present in all four study orchards.
181 Aphidophagous taxa included hoverflies (egg clutches and larvae), coccinellid beetles (all
182 life stages), earwigs (adults), and lacewings (eggs and larvae). Other natural enemy taxa
183 included non-syrphid flies (adults), cantharid beetles (adults), bugs (nymphs and adults),
184 and parasitoid wasps (adults). Natural enemies and aphid pests were collected using
185 entomological net and aspirator and subsequently stored in 70% ethanol for later
186 identification under a stereomicroscope.

187 2.5. SENTINEL EGG CARDS

188 In addition to tree surveys, batches of sterilised moth eggs (*Ephestia kuehniella*) were
189 used as sentinel cards to measure pest control services in apple trees adjacent to
190 experimental plots. Eggs were mounted onto special monitoring cards from Biobest (Biobest
191 N.V., Ilse Velden 18-2260, Westerlo, Belgium), with each card holding a standardised
192 number of eggs (238 ± 7 (SE) eggs, $n = 20$). Egg cards were put out in plots on five occasions
193 in 2013 only between the 18th of June and 9th of September (1-2 times per month). For each
194 sampling event, four cards were attached to branches on separate trees in plots at a height of
195 1.5 m and left for 48 hours. One card per plot on each sampling date was covered in a fine
196 nylon mesh to exclude arthropods and act as a control ($n = 72$). Cards were recaptured and
197 then scored on a scale from 0 to 1 based on egg loss (0 = no eggs removed; 0.25 = 1 – 25 %;
198 0.50 = 26 – 50 %; 0.75 = 51 – 75 %; 1.00 = 76 – 100 % removed).

199 2.6. FRUIT YIELD

200 To assess the effects of flower strips on fruit production, the number of apples was
201 counted in September (one month prior to harvest) each year on three randomly selected
202 branches in plots (all branches approximately 1 m in length and on separate trees). Unlike in
203 dessert apple orchards, fruit thinning is rarely practiced in cider orchards, as final yield is
204 independent of individual fruit size or appearance. In 2013, up to twenty mature fruits per
205 branch were also weighed using a digital weighing scale and measured at their widest point
206 along their horizontal axis using callipers to assess fruit size.

207 2.7. STATISTICAL ANALYSES

208 Data from different years were analysed separately to account for variation in flowering
209 plant communities and environmental conditions between years. To test effects of flower

210 strips on abundance and richness of flower-visiting pollinators (response variables: eusocial
211 bee abundance, solitary bee abundance; richness) and natural enemies (response variables:
212 aphidophagous taxa abundance; other taxa abundance; overall richness) in orchards,
213 generalised linear mixed effects models (GLMMs) were fitted with negative binomial
214 distributions (log-link function) using the R package ‘glmmADMB’ [44]. Fixed effects
215 included treatment (factor with four levels: grass strip control, concealed nectar mix, open
216 nectar mix, and mixed plots), sampling month (factor with three levels: June, July and
217 August), and the interaction between treatment and sampling month. This allowed testing
218 of continuity of treatment effects over the growing season. Random effects included plots
219 within orchards to account for repeated measures and hierarchical experimental design.

220 To analyse effects of flower strips on aphid densities (response variable: number of
221 colonies per plot – i.e. five branches on 10 trees) and natural enemies (response variables:
222 richness per plot, abundance of aphidophagous taxa and other natural enemy taxa per plot)
223 in adjacent apple trees, we fitted Negative binomial (NB) GLMMs. Fixed effects included
224 treatment, sampling month and the interaction between factors, and plots nested within
225 orchards as random effects to account for hierarchical experimental design and repeated
226 measures. To test effects of flower strips on predation rate of exposed egg cards (excluding
227 negative controls), we fitted a GLMM with binomial errors. Fixed effects included treatment,
228 sampling month (June, July, August and September), and the interaction between predictor
229 variables. Plots were nested within orchard as random effects. Effect of treatment on fruit
230 number in plots was analysed by fitting a NB GLMM with orchard included as a random
231 effect. Effect of treatment on size and weight of harvested apples was analysed using linear
232 mixed effect models (LMM) in the R package ‘nlme’ [45] with individual apples nested
233 within trees, trees nested within plots, and plots within orchards included as random effects.
234 Fruit number per branch was included as an additional covariate to control for effects of
235 resource allocation within trees.

236 Minimum adequate models were selected using a backwards stepwise procedure from
237 the full model and likelihood ratio tests (LRT, fixed effects retained in model when $P < 0.05$).
238 Model assumptions were checked by visually assessing residual plots as recommended in
239 Zuur *et al.* [46]. All statistical analyses were performed in R ver. 3.1.3 [47].

240 3. Results

241 3.1. FLOWER STRIPS

242 Flower abundance was assessed each month in all plots (see Appendix A2,
243 Supplementary materials for details). A total of 16 sown species were recorded in flower in
244 2012 and 2013, but only eight species flowered consistently (*T. hybridum*, *T. pratense*, *T.*
245 *repens*, *L. corniculatus*, *C. montana*, *V. cracca*, *V. sativa* and *D. carota*) (Supplementary Materials,
246 Table 3). Flower spikes of white clover (*T. repens*) were common in control plots, but never in
247 equivalent abundance to flower strips, and other unsown species were rare (<1% of total
248 flower abundance). In either study year, mixed plots contained 60% fewer open-nectar
249 flowers (e.g. *D. carota*) than tailored mixes (i.e. only open-nectar plants), whereas concealed-
250 nectar species (e.g. *Trifolium* species) were found in similar abundance in both tailored and
251 mixed plots. Flower abundance was lower in June each year compared to following months

252 (Mean \pm SE flower number per plot: 2012 - June = 1250 \pm 359; July = 2372 \pm 528, August = 3137
 253 \pm 792; 2013 - June = 570 \pm 139, July = 999 \pm 298, August = 823 \pm 185).

254 3.2. FLOWER-VISITOR SURVEYS

255 Over the two-year study period, 6,533 flower visits by 30 distinct beneficial arthropod
 256 taxa were recorded in the study plots (for species details, see Supplementary Materials Table
 257 S3). Pollinators (bees) and natural enemies, represented 28.3 and 71.7% of visits,
 258 respectively. Pollinators (13 taxa) included eusocial bees (bumblebees - 53.6% of pollinator
 259 visits; and honeybees - 28.9%), and solitary bees (17.5%). Of flower-visiting natural enemies
 260 (17 taxa), 6.7% of visits were by aphidophagous taxa, including adult hoverflies, ladybird
 261 beetles and lacewings, and 93.3% by other natural enemy taxa, including hymenopteran
 262 parasitoids, non-syrphid flies, non-coccinellid beetles, and predatory bugs.

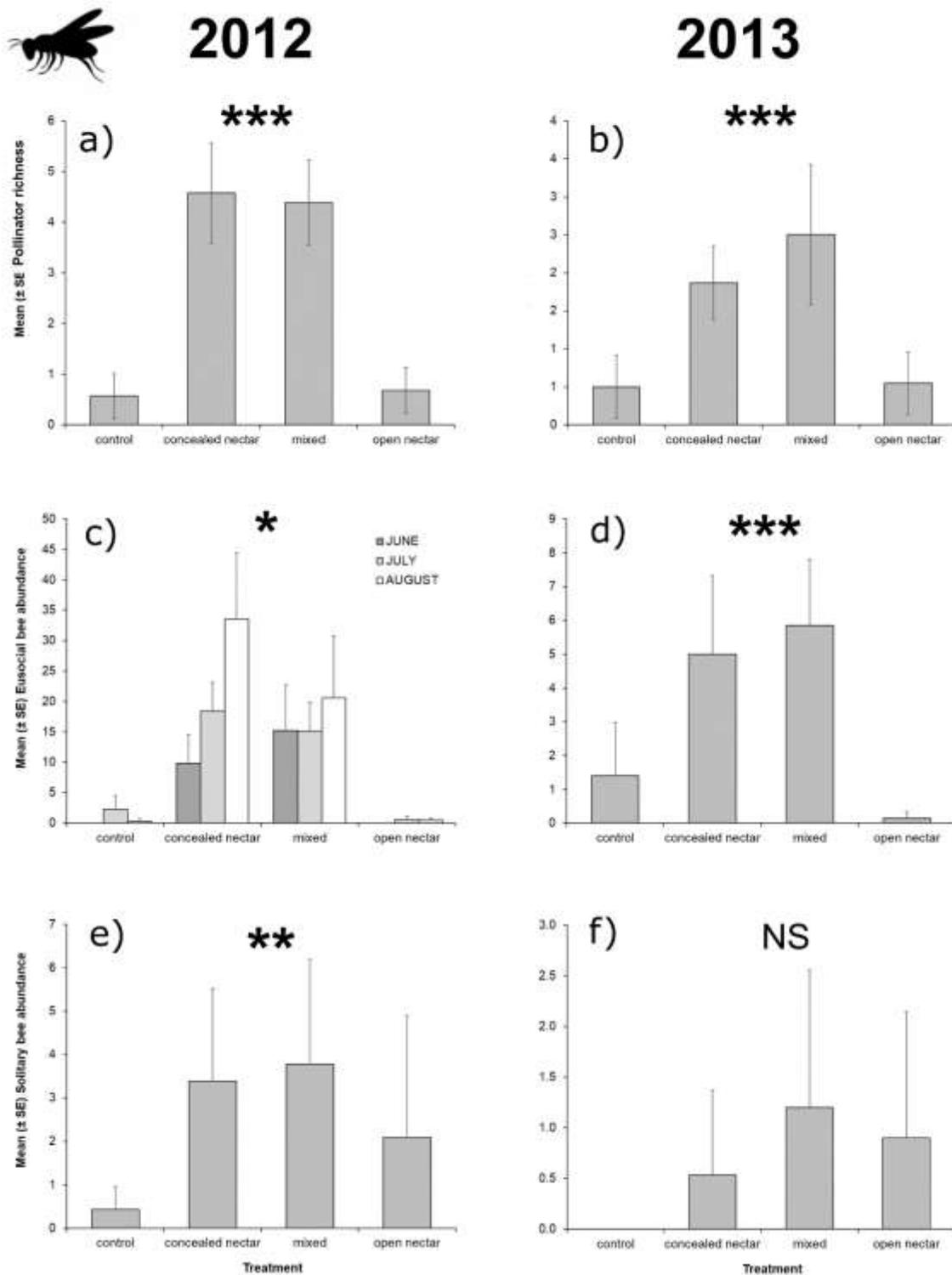
263 Overall, pollinators and natural enemies showed striking differences in flowering plant
 264 visitation patterns, as 92.6% of pollinator visits were to species included in the concealed-
 265 nectar functional group, whereas 97.2% of natural enemy visits were to flowering plants
 266 included in the open-nectar group (including visits to extra-floral nectaries of *V. sativa*).
 267 Although, sub-division of pollinators into eusocial and solitary bee taxa revealed solitary
 268 bees had low preference for either functional group, with 61.7% of visits to concealed-nectar
 269 plants. In both years, pollinator richness was 70% higher in flower strips sown with
 270 concealed-nectar plants compared to control or open-nectar plots (Table 1, Figure 1a & 1b).
 271 Eusocial bee abundance followed similar patterns, however, in 2012 we detected a
 272 significant interaction effect between treatment and sampling period (Table 1), as eusocial
 273 bee visitation to concealed-nectar plots peaked in August that year following intense bloom
 274 of *T. pratense* (Figure 1c). Solitary bees were more abundant in flower strips than controls but
 275 the effect of treatment was only significant in 2012 (Table 1; Figure 1c & d). Total natural
 276 enemy richness and abundance of non-aphidophagous taxa were 90% higher in flower strips
 277 including open-nectar plants compared to other treatments (Table 1, Figure 2a & 2b, Figure
 278 2e & 2f); although, in 2012 the interaction between treatment and sampling month had a
 279 significant effect on natural enemy flower visitation, due to low availability of open nectar
 280 plants in June that year (Figure 2a & c). Aphidophagous taxa were generally more abundant
 281 in treatments containing open-nectar plants, but the effect of treatment was only significant
 282 in 2013 (Table 1, Figure 2c & 2d).

283 **Table 1.** Summary of minimum adequate models selected by inference on likelihood ratio
 284 tests. Effects of treatment (factor with four levels: control, concealed-nectar mix, mixed
 285 plots, and open-nectar mix), sampling month (factor with three levels: June, July and
 286 August), and the interaction between treatment (T) and month (M) on pollinator richness,
 287 pollinator abundance (eusocial bees and solitary bees; flower strips only), aphidophagous
 288 natural enemy abundance, other natural enemy abundance and natural enemy richness in
 289 orchard alleyways. Degrees of freedom (d.f.), test statistics (LRT) and *P*-values from
 290 likelihood ratio tests are shown. *P*-values of fixed effects included in final models are
 291 presented in bold ($P < 0.05$).

Response var.	2012			2013		
	d.f.	LRT	<i>P</i>	d.f.	LRT	<i>P</i>
Pollinators						

Richness

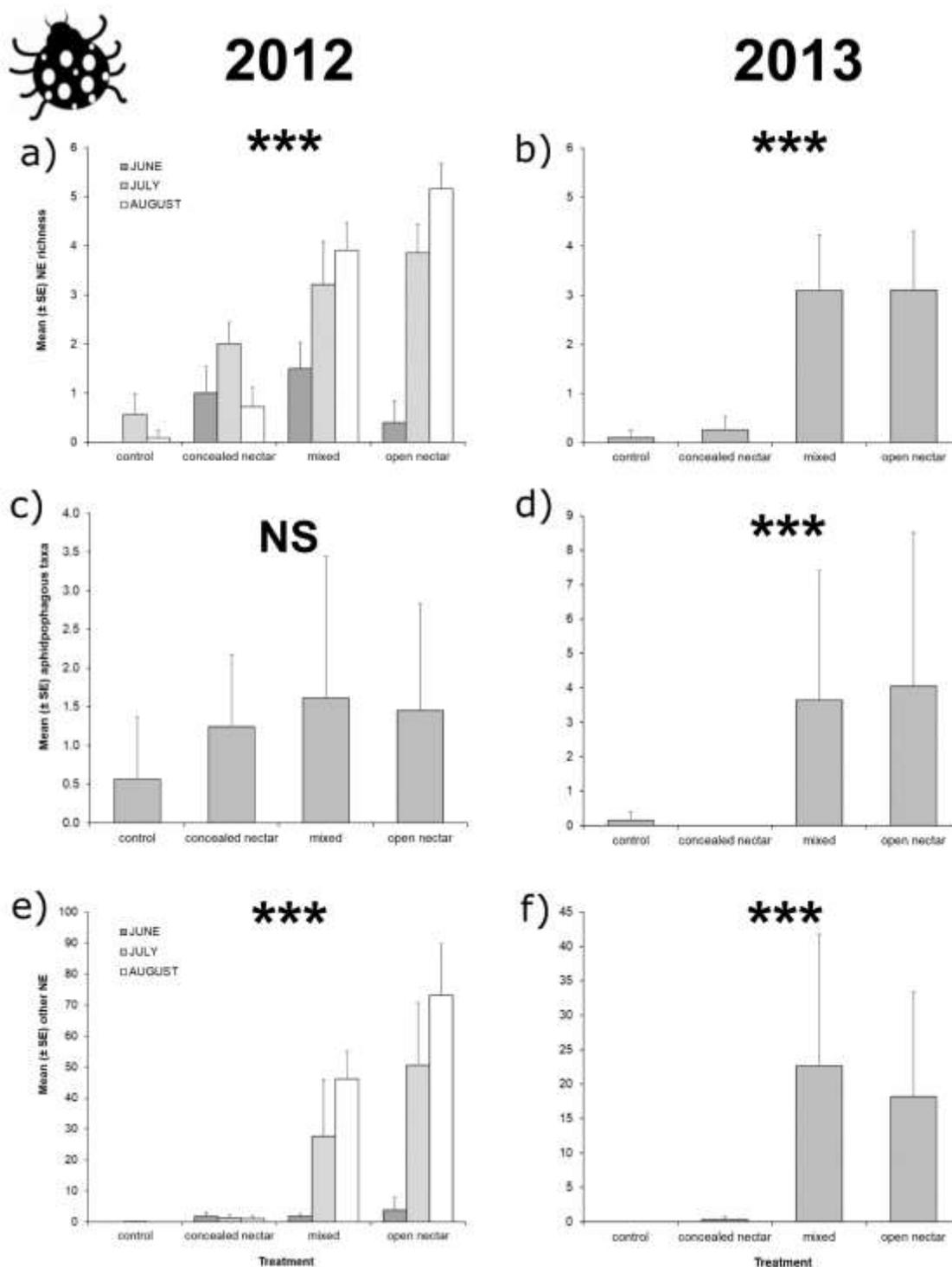
	Treatment	3	34.23	<0.001	3	17.44	0.001
	Month	2	5.63	0.060	2	9.13	0.010
	T x M	6	9.67	0.139	6	7.72	0.259
Eusocial bees							
	Treatment				3	22.51	<0.001
	Month				2	18.37	<0.001
	T x M	6	15.34	0.018	6	6.79	0.341
Solitary bees							
	Treatment	3	13.96	0.003	3	7.02	0.071
	Month	2	8.98	0.011	2	10.79	0.005
	T x M	6	8.49	0.204	6	4.85	0.564
Natural enemies							
Richness							
	Treatment				3	35.22	<0.001
	Month				2	23.14	<0.001
	T x M	6	14.51	0.024	6	3.91	0.689
Aphidophagous taxa							
	Treatment	3	3.27	0.352	3	18.47	<0.001
	Month	2	21.46	<0.001	2	24.82	<0.001
	T x M	6	2.27	0.893	6	9.53	0.146
Other taxa							
	Treatment				3	28.00	<0.001
	Month				2	8.42	0.015
	T x M	6	40.02	<0.001	6	8.74	0.189



293

294 **Figure 1.** Effects of flower strips on flower-visiting pollinators in orchard alleyways.
 295 We detected significant effects of treatment (control, concealed-nectar, mixed, and
 296 open-nectar) on pollinator richness in either study year (a-b); an effect of the
 297 interaction between treatment and sampling month (June, July, and August) on
 298 eusocial bee abundance in 2012 (c), an effect of treatment on eusocial bee abundance
 299 in 2013 (d); and an effect of treatment on solitary bees in 2012 (e), but not 2013 (f).

300 Error bars show standard errors and asterisks show level of significance (* = $P < 0.05$,
 301 ** = $P < 0.01$, *** = $P < 0.001$) reported in LRTs (see Table 1 and main text for details).



302
 303 **Figure 2.** Effects of flower strips on flower-visiting natural enemies in orchard
 304 alleyways. We detected a significant effect of treatment on aphidophagous taxa in
 305 2013 but not in 2012 (c,d). Other natural enemies and overall natural enemy
 306 richness were affected by the interaction between treatment (control, concealed-
 307 nectar, mixed, and open-nectar) and sampling month (June, July, and August) in

2012 (a,e); but by treatment only in 2013 (b,f). Error bars show standard errors and asterisks show level of significance (* = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$) reported in LRTs (see Table 1 and main text for details).

3.3. APPLE TREE SURVEYS

A total of 861 aphid colonies, belonging to three species (*Aphis pomi*, *Dysaphis plantaginea*, and *Eriosoma lanigerum*), and 1,461 natural enemies (all life stages) were recorded on apple trees. Of those arthropods classed as natural enemies, 19% were aphidophagous taxa, including lacewings (eggs and larvae), ladybirds (all life stages), hoverflies (eggs and larvae), and earwigs (adults); and 81% were generalist or unspecialised (other) natural enemies, including hemipteran bugs (nymphs and adults), hymenopteran parasitoids, and non-coccinellid beetles (see Table S4 for species details, Supplementary details).

In both years, aphidophagous and non-aphidophagous natural enemy taxa on apple trees in plots (per fifty branches) showed clear trends for higher abundance in trees adjacent to flower strips sown with open-nectar plants (Figure 3a-d). However, the effect of treatment was only significant ($\alpha=0.05$) for non-aphidophagous taxa (Table 2), and aphid colony densities per plot were unaffected by flower treatment in both years (Table 2; Figure 3e & f). Aphid predator-prey ratios (using mean values) were elevated in apple trees nearby flowering plots containing open-nectar plants compared to other treatments in 2012 (aphidophagous natural enemies per aphid colony: control = 0.35, concealed-nectar = 0.20, mixed = 0.57, open-nectar = 0.71), but were similar in all treatments in 2013 (control = 0.20, concealed-nectar = 0.41, mixed = 0.36, open-nectar = 0.36).

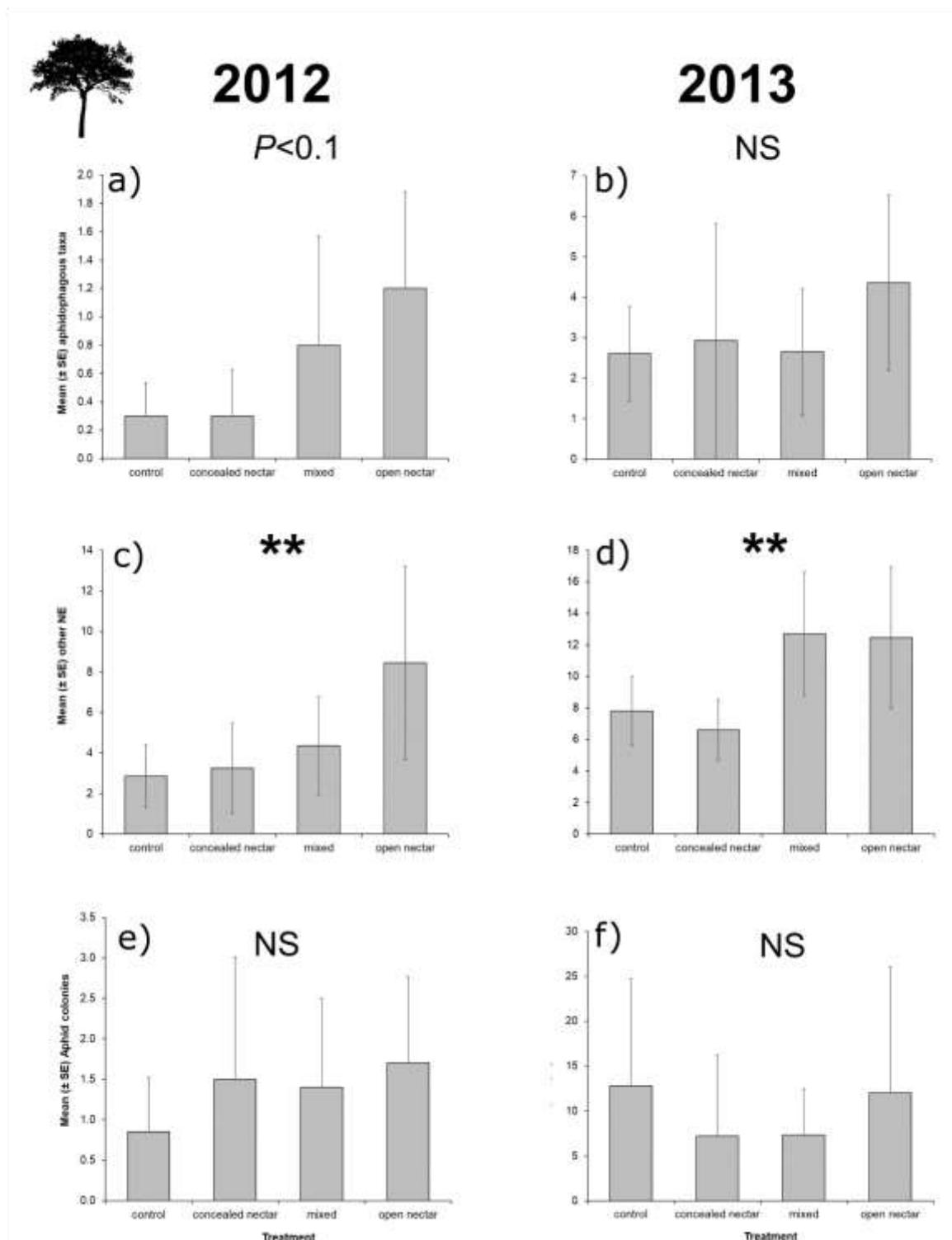
Table 2. Summary of minimum adequate models selected by inference on likelihood ratio tests. Effects of treatment (factor with four levels: control, concealed-nectar mix, mixed plots, and open-nectar mix), sampling month (factor with three levels*: June, July and August), and the interaction between treatment (T) and month (M) on natural enemy richness, abundance of aphidophagous taxa, non-aphidophagous natural enemy taxa, aphid colony densities, and egg card predation within adjacent apple trees in each year. Arthropods sampled on ten trees (five branches per tree) per plot on five separate occasions each year in four orchards. Degrees of freedom (d.f.), test statistics (LRT) and *P*-values from likelihood ratio tests are shown. *P*-values of fixed effects included in final models are presented in bold ($P < 0.05$).

Response var.	2012			2013		
	Within crop			Within crop		
	d.f.	LRT	<i>P</i>	d.f.	LRT	<i>P</i>
Natural enemies						
Richness						
Treatment	3	2.40	0.493	3	2.65	0.449
Month	2	34.80	<0.001	2	0.60	0.742
T × M	6	2.32	0.888	6	1.09	0.982
Aphidophagous taxa						
Treatment	3	6.35	0.096	3	1.93	0.587
Month	2	18.29	<0.001	2	5.61	0.060
T × M	6	6.16	0.406	6	11.25	0.081
Other taxa						

	Treatment	3	13.87	0.003	3	12.77	0.005
	Month	2	83.47	<0.001	2	3.33	0.189
	T x M	6	5.01	0.543	6	7.76	0.256
Pest control							
Aphid colonies							
	Treatment	3	1.54	0.672	3	3.88	0.275
	Month	2	18.97	<0.001	2	55.28	<0.001
	T x M	6	9.37	0.154	6	5.39	0.495
Egg cards							
	Treatment	-	-	-	3	9.54	0.023
	Month*	-	-	-	3	77.71	<0.001
	T x M	-	-	-	9	15.58	0.076

340

341 * Egg card data collected over four months (June – September 2013)



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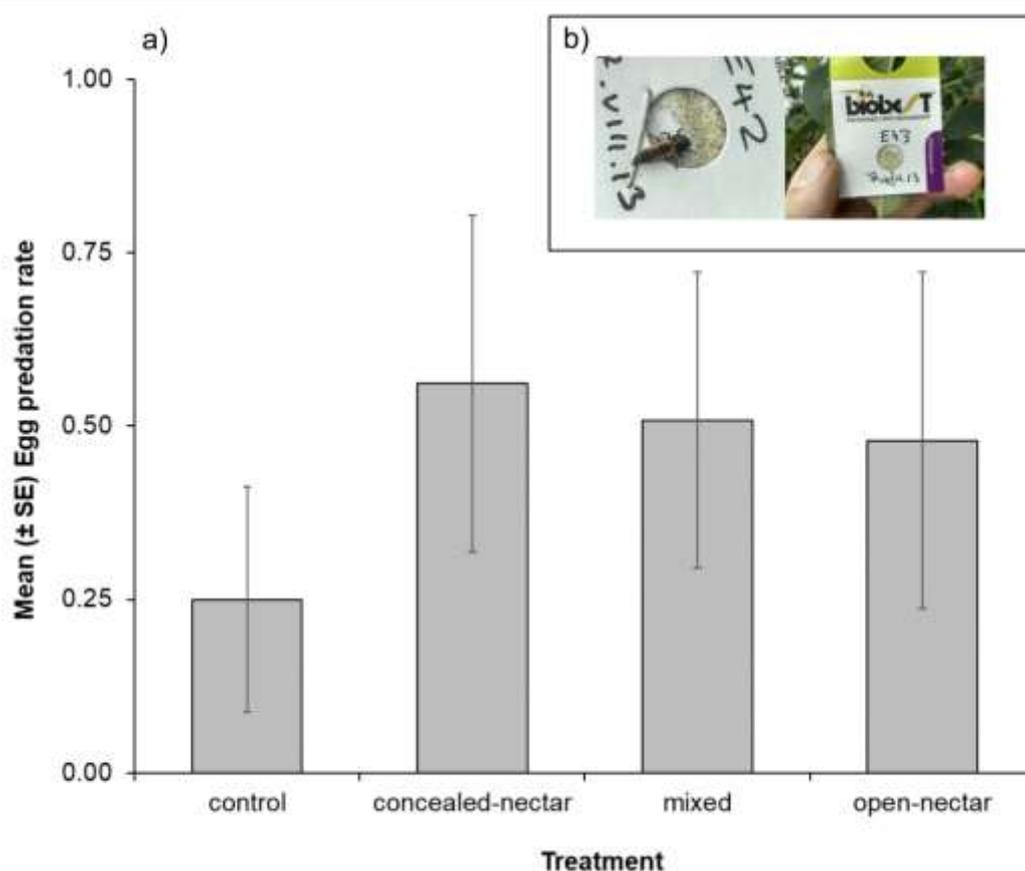
Figure 3. Effects of flower strips on natural enemies and aphid pests in apple trees (number of individuals/colonies per fifty branches). We detected no effect of treatment (control, concealed-nectar, mixed, and open-nectar) on aphidophagous natural enemies (hoverflies, lacewings, earwigs and ladybirds; a,b) or pest aphid densities in either year (e,f), but significant effects of treatment on other natural enemy abundance (non-syrphid flies, parasitoid wasps, bugs and non-coccinellid beetles; c,d). Error bars show standard errors and asterisks show level of

350 significance (* = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$) reported in LRTs (see Table 2
 351 and main text for details).

352

353 3.4. SENTINEL EGG CARDS

354 Several natural enemy taxa were observed attacking exposed egg cards, including
 355 predatory hemipterans, coccinellid adults and larvae, and neuropteran larvae (Figure 4,
 356 inset). Comparison of data from negative controls (natural enemies excluded) confirmed egg
 357 losses were due to arthropod predator activity (Mean \pm SE egg losses: negative controls = 0.03
 358 ± 0.01 , $n = 75$; exposed cards = 0.44 ± 0.03 , $n = 225$). Egg predation was enhanced in all plots
 359 with sown flower strips compared control plots (Table 2; Figure 4), with predation rates
 360 increasing by up to 55% in flowering plots.



361

362 **Figure 4.** Mean (\pm SE) predation rate (0 = no predation and 1 = complete removal) of
 363 sentinel moth eggs in apple trees adjacent to different flower mixtures and control
 364 plots in 2013. Inset photographs (b) show coccinellid larva feeding on eggs and
 365 example of card in apple foliage.

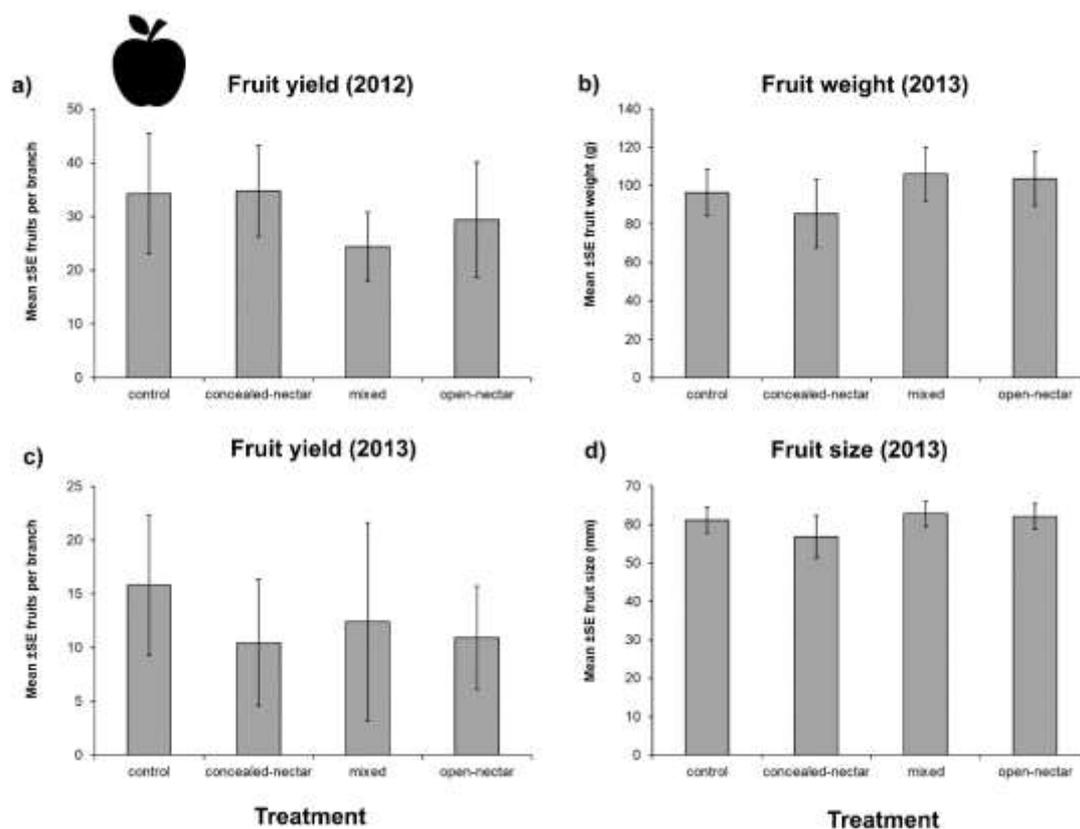
366

367 3.5. FRUIT YIELD

368 Fruit number per branch varied between years, with counts in 2013 around 50%
 369 reduced relative to 2012. Fruit number was not significantly affected by treatment in either
 370 year (Table 3), although, in 2012 the effect of treatment was marginally significant on fruit
 371 number (Table 3), being lowest in mixed plots (Figure 5). We detected no effect of treatment
 372 on either size or weight of harvested fruit in 2013 (Table 3; Figure 5).

373 **Table 3.** Summary of minimum adequate models selected by inference on
 374 likelihood ratio tests. Effect of treatment (factor with four levels: control, concealed-
 375 nectar mix, mixed plots, and open-nectar mix) on fruit number per branch (2012
 376 and 2013; 3 branches per plot, four plots per orchard, $n = 192$), and size (mm) and
 377 weight (g) of harvested fruit (2013) in orchards. Degrees of freedom (d.f.), test
 378 statistics (LRT) and P -values from likelihood ratio tests are shown.

Response variable	Treatment		
	LRT	d.f.	P
2012			
Fruit number	7.01	3	0.071
2013			
Fruit number	4.65	3	0.200
Fruit size (mm)	5.09	3	0.165
Fruit weight (g)	5.94	3	0.114



379
 380 **Figure 5.** Effects of flower strips on fruit yield and fruit quality (size and weight) in
 381 orchards. We detected no effect of treatment (control, concealed-nectar, mixed, and open-
 382 nectar) on fruit yield in either study year (a,c); or on fruit size (b) and weight (d) in 2013.
 383 Error bars show standard errors and asterisks show level of significance (* = $P < 0.05$, ** = P
 384 < 0.01 , *** = $P < 0.001$) reported in LRTs (see Table 2 and main text for details).

385 4. Discussion

386 Flower-rich agri-environment schemes (AES) aim to mitigate biodiversity losses and
 387 improve multiple ecosystem functions on farmland. However, whilst there already exists a
 388 large body of work demonstrating their value for single ecosystem functions [48,49],
 389 evidence on their capacity to support multiple ecosystem services (e.g. pollination and pest
 390 control) in crops remains limited. Here, we demonstrate that careful selection of plant
 391 species based on floral structures that determine nectar accessibility and insect flower
 392 visitation patterns can be used to design flower strips that attract both pollinators and
 393 natural enemies in apple orchards, and enhance natural enemy activity in adjacent apple
 394 trees. However, we found no evidence that enhanced natural enemy communities improved
 395 control of aphid pests or fruit yield in studied orchards. We discuss the implications of our
 396 findings for the design of AES in perennial orchards crops.
 397

398 QUESTION 1 – DO FLORAL TRAITS DETERMINE THE DIVERSITY AND ABUNDANCE
399 OF POLLINATORS AND NATURAL ENEMIES IN CIDER APPLE ORCHARDS?

400 Positive relationships between plant and insect diversity are common in flower-visitor
401 communities [2]. It is now clear that underlying these trends are changes in the diversity of
402 morphological or physiological characteristics of flowering plant species (i.e. functional
403 traits) that act as signals or barriers for feeding by different animal species (e.g. flower
404 colour, shape, volatile profile, resource quantity/quality, bloom period), rather than changes
405 in species diversity *per se* [50]. Thus, plant species that share floral traits are expected to
406 attract similar subsets of flower visitors, and can be considered as a single functional group
407 [25]. In an applied context, this ‘trait-matching’ approach can be used to design ‘tailored’
408 flower strips that target different subsets of beneficial arthropods (e.g. pollinators and
409 natural enemies) and promote the delivery of ecosystem services in adjacent crop plants.

410 Here, in concordance with expectations, we found bees predominantly visited the
411 flowers of plant species included in the concealed-nectar functional group, i.e. species that
412 store nectar in long corollae or spurs and that require specialised mouthparts to access,
413 whereas natural enemies mainly visited plants included in the open-nectar group, i.e.
414 species that present nectar in shallow or open structures. This reflects the fact that many
415 natural enemies have unspecialised (i.e. short) mouthparts that restrict feeding on
416 concealed-nectar plants, the preferred food plants of many bee pollinators [25,29,31]. Thus,
417 when plant functional groups were presented singularly, flower strips were visited either by
418 pollinators or natural enemies, but when mixes were combined (mixed or ‘multi-functional’
419 treatment), they attracted both groups concurrently, and in most cases in similar abundance
420 to preferred targeted mixes. Importantly, these patterns remained consistent over the two-
421 year study period, even though a high rate of turnover in flowering plant species was
422 observed between years, reaffirming the value of a functional trait-based approach to plant
423 species selection in flower strips.

424 In many countries, AES options available to farmers to boost beneficial arthropods
425 comprise of simple mixes of ‘four or five nectar-rich plants’ from the Fabaceae (e.g. England
426 HF4 pollen and nectar mix) [30], analogous to the ‘concealed-nectar’ treatment. Our data
427 suggest that such mixtures provide little in terms of floral resources for pest natural enemies
428 [30], and inclusion of open-nectar plants in mixes offers a simple means to provide floral
429 resources for both pollinators and natural enemies. Although, with the exception of *Trifolium*
430 species specialists (e.g. *Melitta leporina* Panzer), and bivoltine taxa that preferentially visited
431 late season open-nectar plants (e.g. *Andrena minutula* Kirby), solitary bees were infrequent
432 visitors to flower strips compared to eusocial bees (honeybees and bumblebees). This also
433 held for important apple pollinators, such as *Osmia bicornis* L. and large-bodied *Andrena*
434 species, that have short flight periods (March – July) [43,51]. Thus, the selected floral
435 prescriptions, whilst being highly attractive to eusocial bees, may be of limited value for key
436 apple pollinator taxa, because of temporal incompatibilities between flight periods and peak
437 bloom of included plant species. This may explain why these mixtures failed to enhance
438 pollination services in studied orchards when compared to orchards without flower strips
439 [40].

440

441 QUESTION 2 – DOES NATURAL ENEMY VISITATION TO FLOWER STRIPS CORRELATE
442 WITH THE DELIVERY OF PEST CONTROL SERVICES AND YIELD IN ADJACENT
443 APPLE TREES?

444 Flower strips will provide clearest benefit to pest control services if they have positive
445 impacts on the fitness of functionally-important natural enemies, ideally without supporting
446 damaging pest species [29,52]. Therefore, plants selected to support pest control should not
447 only attract flower-feeding natural enemies, but also provide measurable fitness benefits in
448 terms of improved longevity and/or fecundity that leads to increases in their population size
449 and function (i.e. predation) in adjacent crops. Some aphid pests in apple orchards can
450 benefit from flowering vegetation if it includes secondary host plant species (e.g. *Dysaphis*
451 *plantaginea* on *Plantago lanceolata*), but this species was not included in seed mixtures.

452 Although we did not directly measure impacts on natural enemy fitness, we detected
453 clear trends for higher densities of natural enemies in apple trees near those flower strips
454 that contained open-nectar species. This indicates that the inclusion of plants with shallow
455 or open nectaries not only attracted or retained natural enemies, but likely also provided
456 fitness benefits compared to plots without open-nectar plants. Furthermore, reduced natural
457 enemy densities in mixed plots relative to the open-nectar plots suggested that fitness
458 benefits were directly related to densities of accessible flowering plant species, not overall
459 flower abundance in plots [53]. Therefore, increasing the diversity of flower structures in
460 flowering strips may involve trade-offs between ecosystem services, because of the non-
461 overlapping plant-feeding preferences of natural enemies and pollinators [54]. However, we
462 did not detect similar effects on pollinator visitation as concealed-nectar plants were found
463 in equivalent abundance in different treatments, despite 50% reduced seed in mixed plots.

464 In contrast to natural enemy densities, predation of sentinel prey was elevated in all
465 flowering plots relative to controls. Therefore, it is possible that 'non-target' mixes also
466 provided benefits to natural enemies, such as alternate prey or shelter for generalist
467 predators (e.g. anthocorid bugs, earwigs) that have lower dependence on floral resources
468 [37,38,55], but that may have been under sampled during flower-visitor assessments and
469 tree surveys (e.g. small body size or nocturnal activity period). Further, predation on
470 sentinel egg cards remained high up to three weeks after the flowering strips had been
471 mown, which suggested a more permanent, population-level increase in natural enemy
472 densities in alleyways with flower strips, rather than a transient displacement or
473 aggregation of individuals in trees during flowering periods [56].

474 Despite positive effects on natural enemy densities and sentinel prey removal, we found
475 no clear evidence that flower strips affected aphid colony densities, fruit number, or quality
476 of harvested fruit (weight and size) in plots. The absence of a yield effect in studies of flower
477 strips in orchards is not uncommon, as Simon *et al.* (2010) found in a review of 30 studies
478 that just under half showed either no effect, or even negative effects on fruit yields [57].

479 Possible explanations for discrepancies between the responses of natural enemies, pests,
480 and yield to flower strips are numerous. The most obvious explanation for the absence of
481 effect on aphid pest control was that aphidophagous taxa (e.g. lacewings, coccinellids,
482 hoverflies and earwigs) responded weakly to flower strips compared to other natural enemy
483 taxa. This is probably due to lower dependence of some aphidophagous taxa (e.g. coccinellid

484 beetles, earwigs) on flowering plants compared to other natural enemy taxa [15,58].
485 Although, results from sentinel prey assays suggested that natural enemy activity was
486 enhanced in all flowering plots irrespective of plant species composition. However, caution
487 is required as sentinel prey removal rates may not necessarily reflect crop pest control
488 services if species attacking eggs differ from those attacking pest species. Alternatively,
489 natural enemy increases may have come too late to alter pest-yield dynamics in orchards, as
490 many aphid pests attack trees from late spring onwards [59]. Thus, one solution could be to
491 increase the number of early-flowering plants in seed mixtures, particularly species that
492 provide nectar and pollen for hoverflies, as they are highly effective early season aphid
493 predators in apple orchards [36]. Nevertheless, high predator densities at the end of the
494 season can reduce the following year's pest burden through predation of dormant life
495 history stages (e.g. egg masses and pupae) [60], but such effect may only be revealed over
496 longer time periods than considered in the present study [61]. Yet, trees are not only
497 responding to current pest burdens, including other non-aphid pests (e.g. apple sawfly
498 *Hoplocampa testudinea* Klug, apple blossom weevil *Anthonomus pomorum* L., codling moth
499 *Cydia pomonella* L.), that may be poorly controlled by natural enemies, but also pest burdens
500 from previous years, as well as changes in nutrient/water availability, pollination and
501 climate. Therefore, positive effects of enhanced natural enemy communities over a single
502 season may be blurred or rendered inconsequential by other factors that also limit fruit yield
503 in orchards [62–64].

504 Yet, perhaps the most important factor in explaining the lack yield effect was the use of
505 pesticides on studied farms. All farms were sprayed prior to and immediately after blossom
506 to control damaging pest species that are not readily controlled by natural enemies (e.g. *A.*
507 *pomorum* and *H. testudinea*) [15]. Thus, whilst pesticide applications probably ensured that
508 pest densities (including aphids) were indeed kept below economic thresholds, they more
509 than likely decimated emerging natural enemies and limited transfer of benefits from flower
510 strips between growing seasons. Future studies should look at impacts of flower strips
511 across a gradient of agrochemical usage to assess whether natural enemies can replace or
512 improve on ecosystem functions currently provided by agrochemical inputs in orchards
513 under conventional management [8].

514

515 5. CONCLUSION

516 In summary, we show that with careful selection of plant species, flowering strips can
517 provide floral resources for both pollinators and natural enemies in orchards, and enhance
518 predator activity in adjacent apple trees. However, further work is required to optimise the
519 design and management of flowering strips to include a greater number of early-flowering
520 plant species for both efficient apple pollinator taxa (e.g. spring-flying solitary bees) and
521 functionally-important natural enemies of aphids in orchards, and across a gradient of
522 pesticide use to fully examine their potential to replace ecosystem functions presently
523 provided by agrochemical inputs in conventionally-managed orchards. Only through such
524 means can we truly enable an 'ecological intensification' of orchard farming practices, that
525 benefits both biodiversity and fruit production in orchards.

526

527 **Supplementary Materials**

528 Further details on: sowing protocols; calculation of flower abundance; and insect
529 communities in flower strips and adjacent apple trees.

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540 **Author Contributions**

541 All authors contributed extensively to planning and experimental design, AJC completed
542 field and identification of collected arthropods, analysed data and wrote initial draft, and all
543 authors contributed to subsequent revisions and gave final approval for publication.

544 **Conflicts of interest**

545 The authors declare no conflict of interest.

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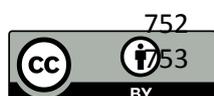
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