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

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Abstract

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

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

1. Introduction

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

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

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

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

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

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].

3. Results

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 ±SE flower number per plot: *2012* - June = 1250 ± 359; July = 2372 ± 528, August = 3137
253 ± 792; *2013* – June = 570 ± 139, July = 999 ± 298, August = 823 ± 185).

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		
	Within flower strip			Within flower strip		
	d.f.	LRT	*P*	d.f.	LRT	*P*
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

292
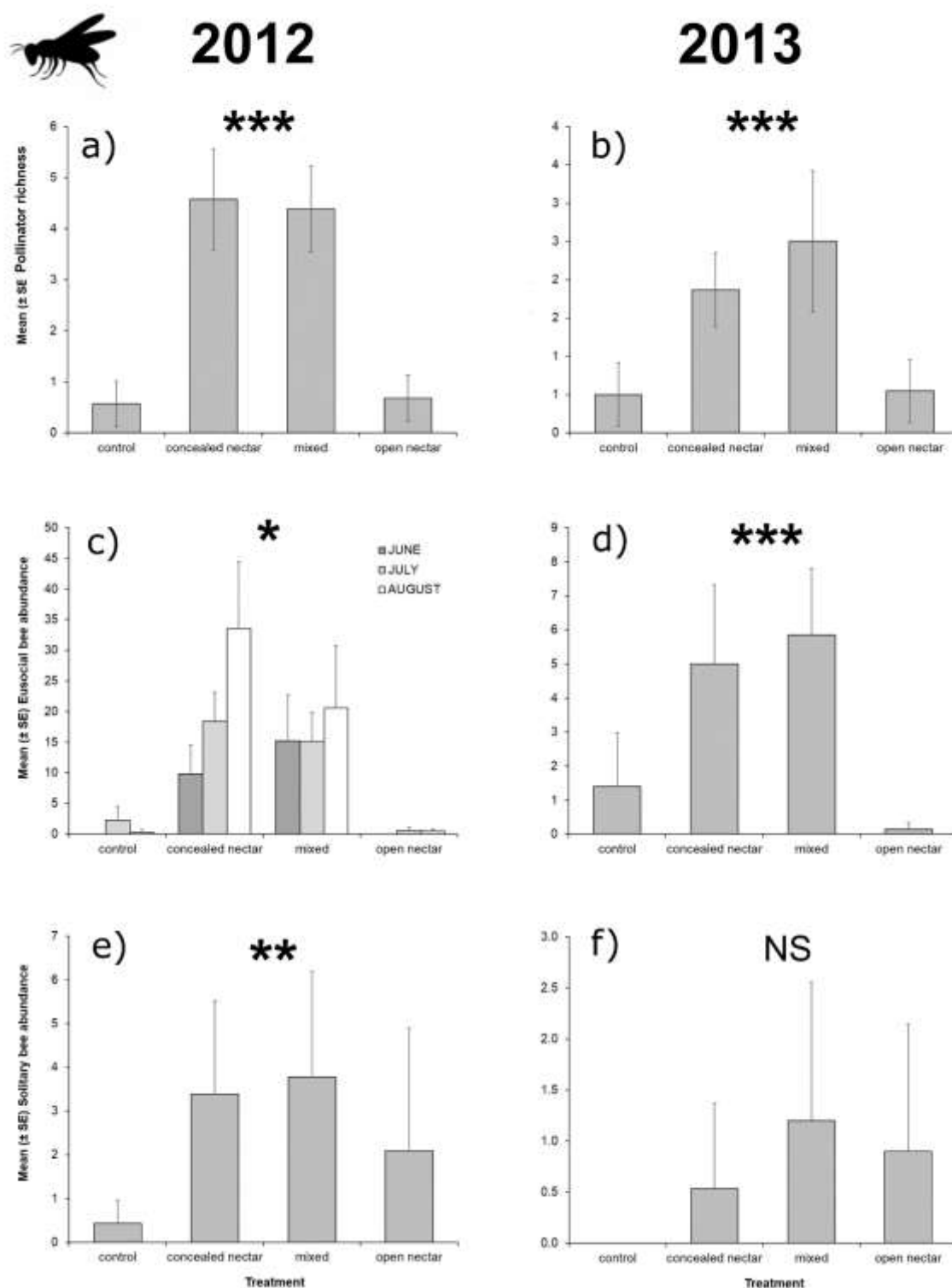
Figure 1. Effects of flower strips on flower-visiting pollinators in orchard alleyways. We detected significant effects of treatment (control, concealed-nectar, mixed, and open-nectar) on pollinator richness in either study year (a-b); an effect of the interaction between treatment and sampling month (June, July, and August) on eusocial bee abundance in 2012 (c), an effect of treatment on eusocial bee abundance 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).
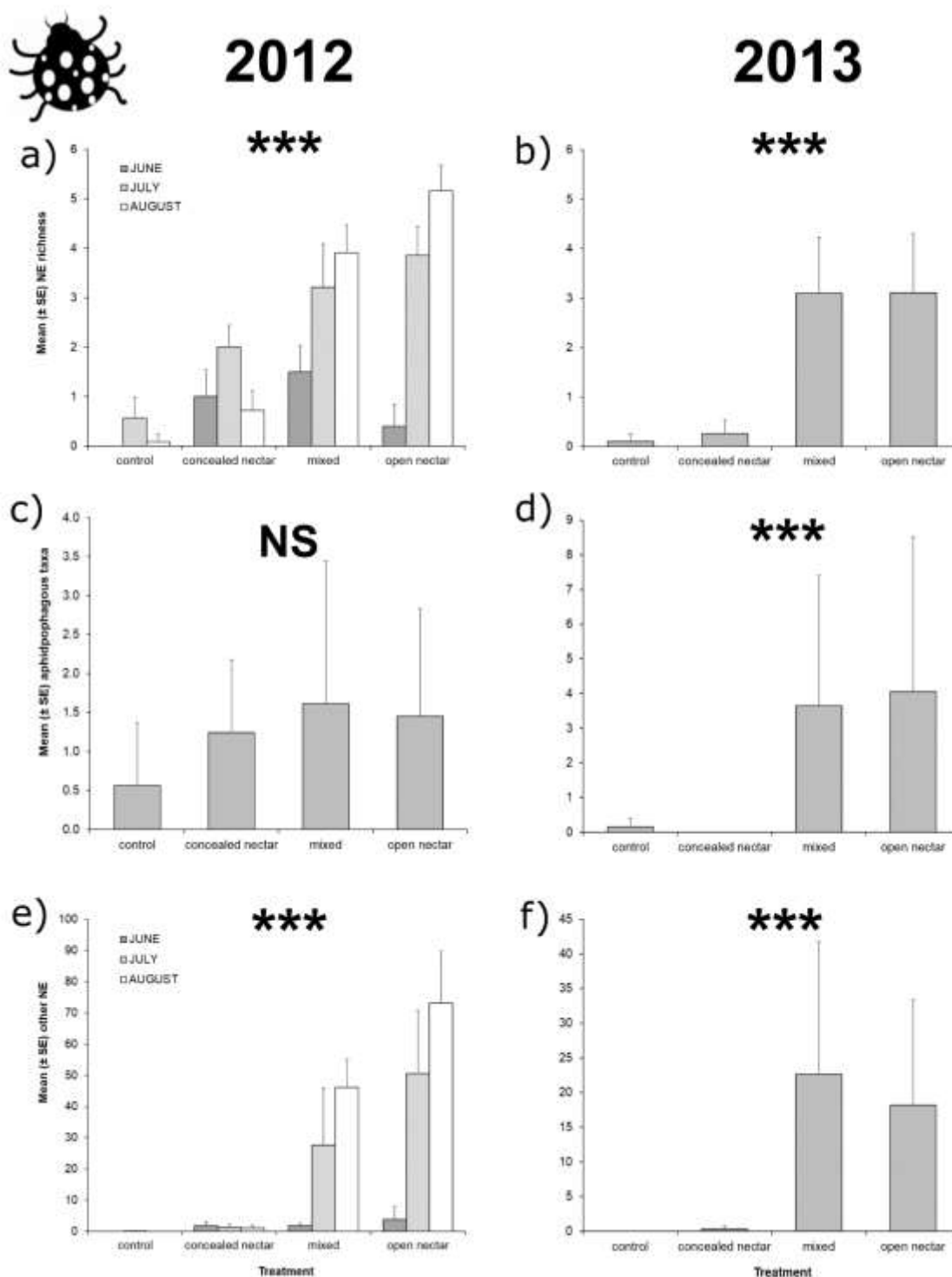
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303   **Figure 2.** Effects of flower strips on flower-visiting natural enemies in orchard
304   alleyways. We detected a significant effect of treatment on aphidophagous taxa in
305   2013 but not in 2012 (c,d). Other natural enemies and overall natural 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

308 2012 (a,e); but by treatment only in 2013 (b,f). Error bars show standard errors and
309 asterisks show level of significance (* = *P* <0.05, ** = *P* <0.01, *** = *P* <0.001) reported
310 in LRTs (see Table 1 and main text for details).
311

312 3.3. APPLE TREE SURVEYS

313 A total of 861 aphid colonies, belonging to three species (*Aphis pomi*, *Dysaphis*
314 *plantaginea*, and *Eriosoma lanigerum*), and 1,461 natural enemies (all life stages) were recorded
315 on apple trees. Of those arthropods classed as natural enemies, 19% were aphidophagous
316 taxa, including lacewings (eggs and larvae), ladybirds (all life stages), hoverflies (eggs and
317 larvae), and earwigs (adults); and 81% were generalist or unspecialised (other) natural
318 enemies, including hemipteran bugs (nymphs and adults), hymenopteran parasitoids, and
319 non-coccinellid beetles (see Table S4 for species details, Supplementary details).
320 In both years, aphidophagous and non-aphidophagous natural enemy taxa on apple
321 trees in plots (per fifty branches) showed clear trends for higher abundance in trees adjacent
322 to flower strips sown with open-nectar plants (Figure 3a-d). However, the effect of treatment
323 was only significant (*α*=0.05) for non-aphidophagous taxa (Table 2), and aphid colony
324 densities per plot were unaffected by flower treatment in both years (Table 2; Figure 3e & f).
325 Aphid predator-prey ratios (using mean values) were elevated in apple trees nearby
326 flowering plots containing open-nectar plants compared to other treatments in 2012
327 (aphidophagous natural enemies per aphid colony: control = 0.35, concealed-nectar = 0.20,
328 mixed = 0.57, open-nectar = 0.71), but were similar in all treatments in 2013 (control = 0.20,
329 concealed-nectar = 0.41, mixed = 0.36, open-nectar = 0.36).

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

		2012 Within crop			2013 Within crop		
Response var.		d.f.	LRT	*P*	d.f.	LRT	*P*
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 x 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 x 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)
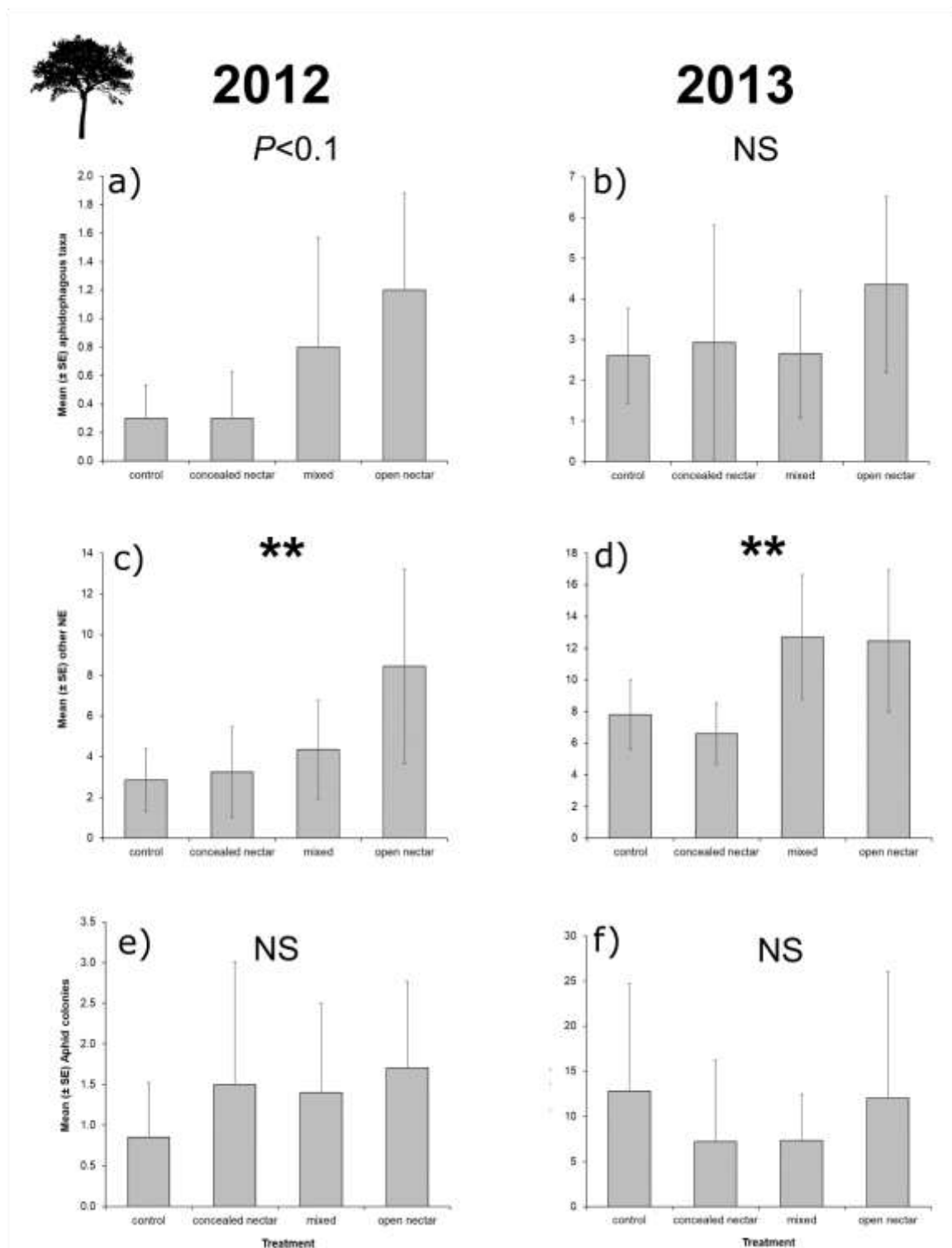
Figure 3. Effects of flower strips on natural enemies and aphid pests in apple trees (number of individuals/colonies per fifty branches). We detected no effect of treatment (control, concealed-nectar, mixed, and open-nectar) on aphidophagous natural enemies (hoverflies, lacewings, earwigs and ladybirds; 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

13

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 ±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.
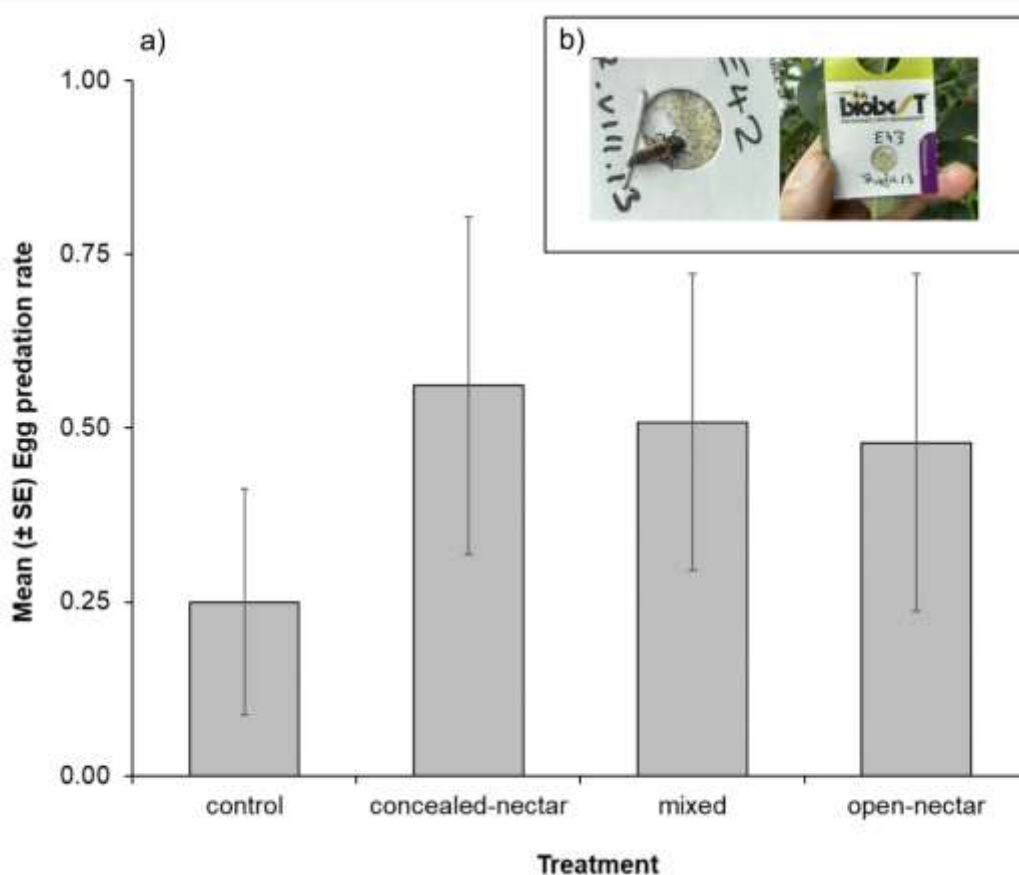
361

362   **Figure 4.** Mean (± 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

14

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.

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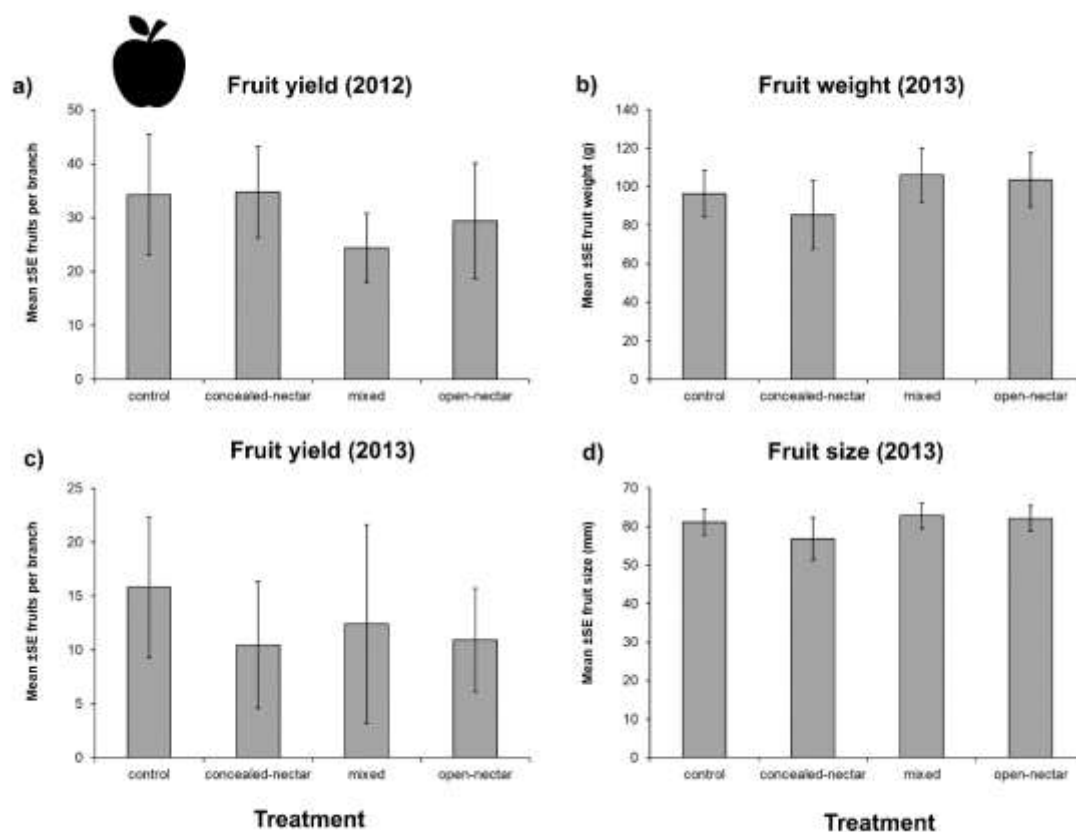
Figure 5. Effects of flower strips on fruit yield and fruit quality (size and weight) in orchards. We detected no effect of treatment (control, concealed-nectar, mixed, and open-nectar) on fruit yield in either study year (a,c); or on fruit size (b) and weight (d) in 2013. Error bars show standard errors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

4. Discussion

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

16

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

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

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

5. CONCLUSION

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

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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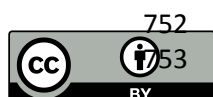
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