

1 **Do sown flower strips boost wild pollinator**
2 **abundance and pollination services in a spring-**
3 **flowering crop? A case study from UK cider**
4 **apple orchards**

5

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18

19 **Abstract**

20 Flower strips are widely recommended as a tool to boost insect pollinators and yield
21 in pollinator-dependent crops. Using UK cider apple orchards (*Malus domestica*
22 Borkhausen) as a model system, we assessed whether flower strips increased
23 pollination services in orchards. Pollinator communities (visual observation) and
24 pollination services (fruit set) were assessed at increasing distance from surrounding
25 semi-natural habitats (0 – 200 m) in eight orchards. In four orchards, perennial flower
26 strips had been established and bloomed in the year before the main experiment. In a
27 separate experiment, insect visits to apple flowers were observed to investigate
28 possible functional mechanisms underpinning pollinator efficacy.

29 The visit rate of wild insects to apple flowers (non-*Apis* bees and flies), but not that of
30 honeybees (*Apis mellifera* L.), increased by 40% in flower strip orchards compared to
31 control orchards, particularly in areas close to semi-natural habitat (<100 m). Wild
32 insect visitation was also positively related to dandelion (*Taraxacum* species)
33 abundance in orchards. Fruit set in orchards was positively related to wild insect
34 richness, and andrenid bee (*Andrena* species) visitation, but neither richness nor
35 andrenid bee visit rate responded positively to flower strips. Wild bees (andrenid bees
36 and bumblebees (*Bombus* species)) contacted apple stigma (95 and 100% of visits)
37 more often than honeybees (81%), but only bumblebees moved frequently between
38 different tree rows, an important trait for transfer of compatible pollen in apples.

39 Our results demonstrate that flower strips enhanced overall wild insect abundance
40 but not pollination services in cider orchards. Positive effects of ground flora on wild
41 insect abundance in orchards suggest that flower mixtures or orchard management
42 could be optimised for andrenid bees, the single most important pollinator taxa, by
43 increasing the availability of early-flowering plants in orchards. Equally, wild insect
44 richness was highest in areas close to semi-natural habitats. Therefore, whilst flower

45 strips can boost abundance of the existing species pool, only large scale preservation
46 of (semi-) natural habitat will maintain pollinator diversity in apple orchards.

47

48 **Key words:** flower strips; *Malus domestica*; pollination; sustainable agriculture; wild
49 bees.

50

51 **1. Introduction**

52 Around 75% of global food crops are to some degree dependent on animal pollination
53 (Klein et al. 2007), with insects being the most important pollinators in both natural
54 and agricultural settings (Kearns et al. 1998). Yet, pollinators are under threat
55 because of several interrelated factors associated with the intensification of
56 agricultural practices (e.g. removal or fragmentation of natural- or semi-natural
57 habitats, agrochemical usage) (Biesmeijer et al. 2006; Park et al. 2015; Potts et al.
58 2010). Historically, many pollinator-dependent crops have been supplemented with
59 domesticated hives of the European honeybee, *Apis mellifera* Linnaeus
60 (Hymenoptera: Apidae), during crop bloom to ensure adequate pollination (Garibaldi
61 et al. 2009). However, in addition to concerns about over-reliance on a single species
62 for global crop pollination services (Breeze et al. 2014), there is a growing body of
63 evidence that the contribution of wild pollinators (e.g. non-*Apis* bees, flies), may be
64 equal to, or even surpass that of honeybees (Garibaldi et al. 2013). As such, there is
65 growing interest in the development of management practices that integrate the
66 needs of wild pollinators into productive landscapes (Bommarco et al. 2013; Dicks et
67 al. 2013; Kleijn et al. 2015).

68 To persist in agricultural habitats, wild pollinators must be able to find suitable nesting
69 sites (if a central-place forager), and collect sufficient food (pollen and nectar) to feed

70 their offspring (Kremen et al. 2004). Changes in agricultural practice that alter the
71 availability of these resources will indirectly affect fitness and population size of wild
72 pollinators (Carvell et al. 2007; Roulston & Goodell 2011). For example, Marini et al.
73 (2012) found wild bee abundance in apple orchards was higher in landscapes
74 dominated by semi-natural habitats (e.g. forest, grassland) compared to orchards in
75 landscapes dominated by apple. They attributed this to semi-natural habitats
76 providing pollinators with a better supply of floral resources, in terms of both temporal
77 availability and abundance, than commercially managed orchards, particularly in
78 periods outside of tree blossom.

79 Although the role of semi-natural habitats in supporting pollinator communities is
80 clear (Carvalho et al. 2010), many farms exist in landscapes already dominated by
81 intensive agriculture (Morandin & Kremen 2013). As an alternative, the restoration of
82 habitat within farms could enable farmers to enhance existing species pools and
83 pollination services (Kremen et al. 2004; Martins et al. 2015). Research effort into
84 within-farm habitat restoration for pollinators has focused on the use of flowering
85 strips, which are typically sown in the marginal areas adjacent to the crop (e.g.
86 headlands, field margins) (Wratten et al. 2012), although the maintenance of existing
87 non-crop flora and the restoration of hedgerows or riparian scrubland habitats have
88 also been investigated (Carvalho et al. 2012; Klein et al. 2012; Morandin & Kremen
89 2013; Rosa García & Miñarro 2014; Sardiñas & Kremen 2015; Saunders et al. 2013).

90 Such flower-rich habitats, if designed effectively, provide pollinators with a greater
91 diversity of pollen and nectar resources, and can increase the availability of nest sites
92 for wild pollinators in crop fields (Carreck & Williams 2002; Pywell et al. 2005; Russo
93 et al. 2013). However, arbitrarily chosen flowering vegetation or naturally regenerated
94 vegetation may be ineffective in supporting key groups of beneficial insects
95 (Campbell et al., 2012; Olson and Wäckers, 2007) and may also generate negative
96 effects, such as increased pest problems (Wäckers et al., 2007; Winkler et al., 2010).

97 For example, incompatibilities between insect feeding structures and floral
98 morphologies, or insufficient temporal overlap between flowering period and insect
99 foraging periods, may limit transfer of fitness benefits to pollinators (Campbell et al.
100 2012; Junker et al. 2013; Russo et al. 2013). Furthermore, plantings at the crop edge
101 may concentrate ambient populations of beneficial insects at field edges and
102 exacerbate pollinator declines in field centres (Kohler et al. 2008; Morandin & Kremen
103 2013). Therefore, establishment of flower-rich areas directly within crop fields may be
104 a more effective means of increasing pollinator visits to crop flowers in large fields,
105 either through facilitative co-pollination (Carvalho et al. 2012), or improved
106 reproductive success of pollinators in crop fields and surrounding habitats (Blaauw &
107 Isaacs 2014).

108 Here, we explore the effects of sown flower strips introduced directly between tree
109 rows in UK cider apple orchards (*Malus domestica* Borkhausen) on pollinator
110 visitation and pollination services. Cider apple orchards are an ideal candidate for
111 such interventions, as apple is regarded as 'greatly dependent' on pollinators for fruit
112 set (Klein et al. 2007), and fruit quality (Garratt et al. 2014), and the semi-permanent
113 nature of orchards allows populations to build across seasons (Shackelford et al.
114 2013; Simon et al. 2010). We also investigate the relative contribution of insects to
115 pollination services in cider apple orchards using insect-exclusion and hand
116 pollination experiments, and identify potential behavioural mechanisms that underpin
117 pollination efficiency of different insect taxa. Specifically, we ask 1) whether perennial
118 flower strips introduced directly into orchards increase pollinator abundance and
119 richness during apple blossom along a gradient of isolation from semi-natural habitat,
120 2) how do changes in pollinator communities (visitor abundance, richness) affect
121 pollination services, and 3) do differences in foraging behaviour among pollinator taxa
122 underpin differences in pollination efficacy?

123

124 **2. Materials and Methods**

125

126 *2.1 Study site details and experimental design*

127 The experiment took place in 2013 during a single growing season in eight cider
128 apple orchards located in Herefordshire, south-west England (52°05' to 52°12' N and
129 2°47' to 2°56' W). All orchards were of similar size, age, crop and sward management
130 practices and separated from each other by a minimum distance of 500 m (Table S1;
131 Figure S1, Supplementary Materials). This distance was considered greater than the
132 average foraging range of most solitary and eusocial bee species found in the study
133 region (Gathmann and Tscharrntke 2002; Zurbuchen et al. 2010). Flower strips had
134 been previously established in four orchards (= 'flower strip orchards'), with the
135 remaining four orchards left unmanipulated (= 'control orchards').

136

137 *2.2 Flower strips*

138 Flower strip orchards were sown with targeted flower mixtures of up to 25 wildflower
139 species in April 2011 (Table S2, Supplementary Materials). Flower mixtures included
140 Fabaceae species attractive to eusocial bee species and commonly included in UK
141 agri-environment schemes (Defra 2013), as well as other plant families (Apiaceae)
142 with short or 'open' corollas to attract short-tongued insects (e.g. solitary bees,
143 hoverflies and parasitoid wasps) (Campbell et al. 2012). Flower strips were divided in
144 three pairs that were randomly distributed among orchard rows and covered a total
145 area of 0.05 ha per orchard. Flower strips bloomed sporadically in the first year
146 following establishment (2011), but flowered consistently in 2012 from early June until
147 August when they were cut to prepare orchards for mechanical fruit harvest. During
148 this period (June – August 2012), insect visitation to flower strips in orchards was

149 recorded on six separate occasions using similar methods (walked transects) to
150 those described below for observations of insect visitors to apple flowers in 2013.

151

152 *2.3 Pollinator sampling*

153 For observations of insects visiting apple blossom in 2013, approximately two weeks
154 prior to the onset of blossom, we marked out four to five plots in study orchards, with
155 each plot consisting of fifteen healthy trees in the same row. To look at effects of
156 flower strips on pollinators in context to the wider landscape, plots in orchards were
157 marked out at 0, 50, 100, 150, and in the four largest orchards, 200 m from an
158 adjacent area of semi-natural habitat (e.g. woodland, grassland or mature hedgerow)
159 (Figure S2, Supplementary Materials). Plots in flower strip orchards bisected flower
160 strips to ensure distance to the nearest flower strip was never more than the
161 maximum distance to semi-natural habitat (range = 8 – 175 m).

162

163 Observations of insect visitation took place in May 2013 during peak bloom in
164 orchards. A single observation consisted of continuously walking alongside trees of a
165 plot for ten minutes. During this period, all insects observed visiting apple flowers
166 within a horizontal band of 0.5 to 2 m above the ground were recorded, only stopping
167 the timer to catch insects that could not be identified on the wing for later
168 identification under a microscope. All bees (Hymenoptera: Apoidea) were identified to
169 species level (except *Andrena* males) and other groups to at least family level.

170 Observations took place only in warm (>13 °C if clear, >17 °C if cloudy), dry
171 conditions with low wind speed (<5 mph) between 10:00 h and 17:00 h. Repeat
172 observations were made on non-consecutive days, with the order in which plots
173 within orchards, and orchards visited, randomised to minimise effects of order. Hives
174 of *A. mellifera* were never directly introduced in orchards, but visiting honeybees were

175 presumed to be from managed hives as feral colonies are expected to be non-
176 existent, or rare in northern Europe (Jaffé et al. 2010).

177 The total number of open apple flowers per plot was estimated for each observation
178 period by counting all visible flowers within the same horizontal band used for insect
179 observations on one side of the same three trees in each plot, and multiplying this by
180 five to give an estimate of apple flowering density for the entire plot. We also counted
181 the number of dandelion (*Taraxacum* spp.) flowerheads in both alleyways that ran
182 parallel to the focal tree row. Dandelions provide wild pollinators with an abundant
183 source of nectar and pollen in orchards during early spring when neither apple trees
184 or flower strips are in bloom (Rosa García & Miñarro 2014). Each plot was observed
185 three to five times over the study period. Solitary bee nest density in plots was
186 estimated once during the study period by counting the number of freshly excavated
187 nest entrances in the areas directly under trees which are kept free of vegetation
188 ('herbicide strip').

189

190 *2.4 Pollination services*

191 Fruit production in orchards was measured as the proportion of flowers on branches
192 that produced fruit (fruit set). Developing flower buds were counted on five branches
193 in each plot approximately two weeks before tree blossom. The number of fruit on
194 branches was then recorded in June, two weeks after petal fall ('initial fruit set'), and
195 again in September ('final fruit set'). Initial fruit set is considered as the best indicator
196 of pollination success, as counts takes place before fruit are lost to pests or naturally
197 abscised by the tree (Klein et al. 2012), but fruit set at harvest (September onwards)
198 is more relevant for orchard managers.

199 To quantify dependence of apple on insect pollination and investigate whether
200 orchards were pollen limited ('pollination deficit'), selected branches were randomly

201 assigned to one of three pollination treatments: 1) wind-pollination (one branch per
202 plot) - where all flying insects were excluded using a wind and rain-splash permeable
203 nylon mesh bag (B & S Entomological Services, Portadown, County Armagh,
204 Northern Ireland); 2) open pollination (three branches per plot) - where branches
205 were left open to be freely visited by insects; or 3) hand-pollination (one branch per
206 plot), where pollen collected from freshly dehisced anthers of the *in situ* polliniser
207 variety was administered to the stigma of receptive flowers (i.e. newly opened) on
208 branches using a fine paintbrush (Garratt et al. 2014). Any 'unreceptive' (e.g. wilted,
209 or brown stigma), or unopened flowers were removed and subtracted from flower
210 counts.

211

212 *2.5 Forager behaviour*

213 In a separate experiment, foraging behaviour of three visitor groups (honeybees,
214 bumblebees and andrenid bees) was observed in flower strip orchards in May 2012.
215 Individual insects were tracked during foraging bouts on apple trees to record
216 foraging behaviour and inter-tree movements. Observations of individual insects were
217 made for up to three minutes or until the observer lost sight of the individual.
218 Observations adhered to the same protocols used in the main experiment regarding
219 insect identification, weather, percentage blossom and temperature. For each insect,
220 we recorded the number of flowers visited per minute, visit duration, resource
221 collected (nectar, pollen or both), and whether contact was made with the stigma. We
222 also noted transfers between trees in the same row, between trees in different rows,
223 as well as visits to other flowering plants (dandelions) in the orchard understory.
224 Individual orchards were evenly sampled (5-7 hr per orchard, 23 hr observation in
225 total).

226

227 *2.6 Statistical methods*

228 For statistical analyses, insect species were pooled into the following groups:
229 honeybees, wild insects (all non-*Apis* bees, flies, beetles), wild bees (bumblebees
230 and solitary bees), and andrenid bees (*Andrena* species). Visits were analysed as
231 visit rates per plot (number of visits per observation divided by number of apple
232 flowers) to account for effects of flower number on insect visitor abundance (Brittain
233 et al. 2013). Wild insect richness was calculated using species and morphospecies
234 level identifications of bees and 15 broader taxonomic groupings for other visitors
235 (e.g. hoverfly genera, non-syrphid fly families; beetle families; Table S4,
236 Supplementary Materials).

237 Visit rates were analysed using linear mixed-effects models (LMMs), and insect
238 richness and solitary bee nest counts were analysed using generalised linear mixed
239 effects models (GLMMs) with Poisson family (R package 'lme4'; Bates et al. 2013).
240 Random effects nested plots within orchards. Fixed effects in all insect models
241 included flower strip presence, distance from orchard edge (0 - 200 m), and
242 dandelion abundance in orchard alleyways. We also included the interaction between
243 flower strips and distance from edge to investigate influence of flower strips on
244 pollinator visitation at increasing distance from bordering semi-natural habitat. Wild
245 insect visitation was also included in honeybee models to investigate potential
246 interactions between wild and managed insects. As orchards were not evenly
247 distributed across the landscape, we additionally tested normalised residuals of
248 insect visitation models where flower strip presence was found to be significant for
249 spatial autocorrelation using Moran's Index (R package 'ape'; Paradis et al. 2004).
250 Effects of pollination treatment (insect exclusion, open or hand pollination), and
251 orchard management (flower strips) on initial and final fruit set, and relationships
252 between insect visitation and fruit production, were analysed in separate binomial

253 GLMMs with plots nested within orchards included as random effects. Where results
254 did not differ between initial and final fruit set, only final fruit set is presented. Apple
255 tree variety, and the interaction between pollination treatment and variety, were
256 included in pollination treatment models to assess whether effects of treatment were
257 consistent among tree varieties studied. Six hand-pollinated branches had to be
258 excluded from analyses as they included fruit set values > 1 , *i.e.* more fruit produced
259 than flowers pollinated by hand, indicating failure of experimental pollination methods.
260 Orchard management models analysed fruit set on open branches only and fixed
261 effects included flower strip presence, distance from edge, dandelion abundance and
262 the interaction between flower strips and distance from edge. To investigate links
263 between pollinator activity and fruit set on open branches, we used mean insect visit
264 rates and richness for each plot and ran separate models to avoid collinearity
265 between insect variables.

266 For observations of foraging behaviour, visit duration and flowers visited per minute
267 were log-transformed prior to analysis to improve model fit and analysed using LMMs
268 with orchard included as a random effect. Fixed effects included visitor group
269 (bumblebee, honeybee or andrenid bee), temperature, and the interaction between
270 visitor group and temperature. Non-parametric rank sums test (Kruskal-Wallis = KW)
271 was used to investigate differences in rates of movement between groups, as data
272 could not be transformed to meet parametric assumptions of normally-distributed
273 residuals. Difference in rate of stigma contact during a single visit among visitor
274 groups was analysed using a binomial general linear model.

275 All statistical models were validated using histograms of normalised residuals, plots
276 of residuals against fitted values, and each explanatory variable to assess model fit
277 and homogeneity of variance amongst factor levels. Significance of explanatory
278 variables in models was determined using a stepwise deletion procedure from the full
279 model combined with likelihood ratio tests, with variables being retained in models

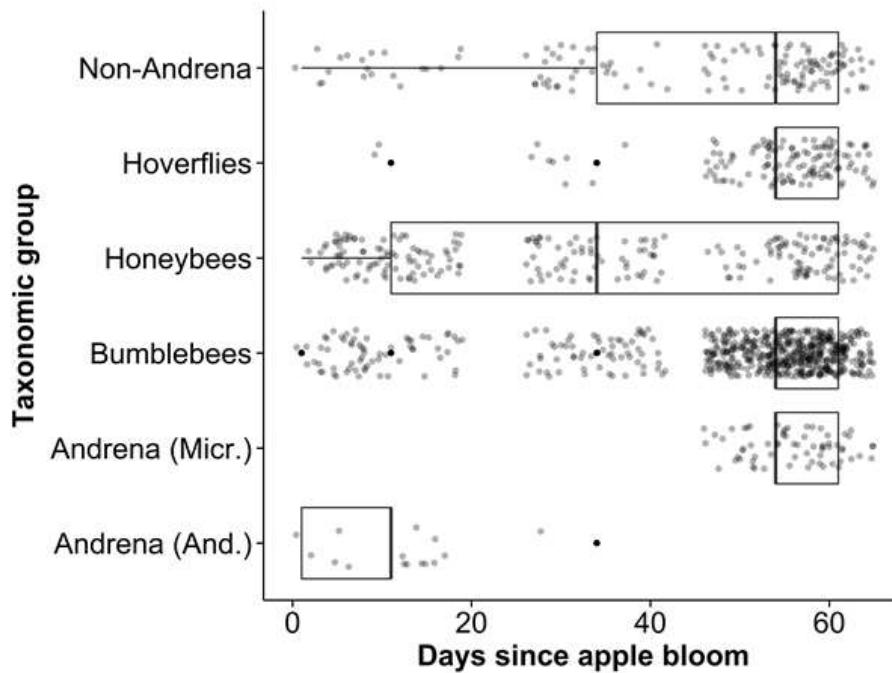
280 where $P < 0.05$ (Crawley 2007, Zuur et al. 2009). All analyses were performed using
281 R software and associated packages (R Development Core Team, 2013, version
282 3.02).

283

284 **3. Results**

285 *3.1 'Potential' apple pollinators in flower strips*

286 Observations of insects in flower strips in the previous summer revealed that 15 of
287 the 25 taxa observed visiting apple flowers in spring 2013 also visited the flower
288 strips (Table S3, Supplementary Materials). The three most frequently visited plant
289 species by these insects were *Trifolium hybridum* (Fabaceae), *Trifolium pratense*
290 and *Trifolium repens*. The most abundant insect visitors were bumblebees (47%),
291 honeybees (34%) and hoverflies (11.5%). Division of visits by andrenid bees
292 (*Andrena* species) into the subgenera *Andrena sensu stricto* (medium-sized species)
293 and *Micrandrena* (small-bodied species), revealed visitation by *Andrena sensu stricto*
294 species ended soon after apple bloom in 2012 (considered first week in June). In
295 contrast, other insect taxa visited flower strips throughout the summer.



296

297 **Figure 1.** Visitation by ‘potential’ apple pollinators to flower strips in the sixty days
 298 following apple bloom in 2012 (start date considered June 9th 2012). ‘Non-Andrena’
 299 includes visits by other solitary bees (Halictidae, Megachilidae, Melittidae). Boxplots
 300 represent median, interquartile range, and maximum and minimum observed values
 301 for each insect group.

302

303 3.2 Insect visitors to apple flowers

304 A total of 475 visits to apple flowers, by 25 distinct insect taxa, were recorded in plots
 305 during timed observations. The most abundant visitor group were andrenid bees
 306 (Hymenoptera: Andrenidae: *Andrena*, six species, 59.8% of visits), followed by
 307 honeybees (Apidae: *Apis mellifera*, 16.8% of visits), bumblebees (Apidae: *Bombus*,
 308 five species, 11.8% of visits) and hoverflies (Diptera: Syrphidae, seven genera, 7.4%
 309 of total visits). In addition to flower visits, a total of 102 freshly-excavated solitary bee

310 nests were recorded in the herbicide strips of experimental plots in 2013, with a mean
311 (\pm SEM) of 2.83 ± 0.47 nests per plot.

312

313

314 *3.2.1 Effects of flower strips on apple flower visitors*

315 Visit rates to apple flowers by wild insects (non-*Apis* bees and flies) and wild bees in
316 flower strip orchards were 40% and 55% higher than visit rates in control orchards,
317 respectively, although effects were marginally significant (Table 1; Figure 2a). Wild
318 insect visit rate and taxonomic richness were higher in plots close to the orchard
319 edge (Table 1, Figure 2d), but visit rates remained high in flower strip orchards up to
320 100 m into the orchard interior (Figure 2b). Visit rates of honeybees (Figure 2a),
321 andrenids (flower strip = 0.68 ± 0.25 visits per 1000 flowers, control = 0.30 ± 0.18),
322 and ground nest densities in plots (flower strip = 3.72 ± 1.72 , control = 1.94 ± 0.92),
323 did not differ between flower strip and control orchards (Table 1). Although, the
324 spatial distribution of honeybees in flower strip and control orchards differed
325 significantly (Table 1), as honeybees were more abundant at the orchard edge in
326 control orchards, but evenly distributed in flower strip orchards. Honeybee visitation
327 was also negatively related to wild insect visitation ($\chi^2 = 10.14$, d.f. = 1, $P = 0.001$).

328 Bumblebees were absent in three of eight orchards, but were more abundant in
329 flower strip orchards (flower strip = 0.12 ± 0.11 visits per 1000 flowers, control = 0.05
330 ± 0.04). Wild insect and andrenid visit rates were positively related to dandelion
331 abundance in orchard alleyways (Figure 2c), although this effect was marginally
332 significant on andrenids (Table 1). Finally, there was no significant effect of spatial
333 autocorrelation between orchards in any models including significant effects of flower
334 strips (Table S4, Supplementary Materials).

335

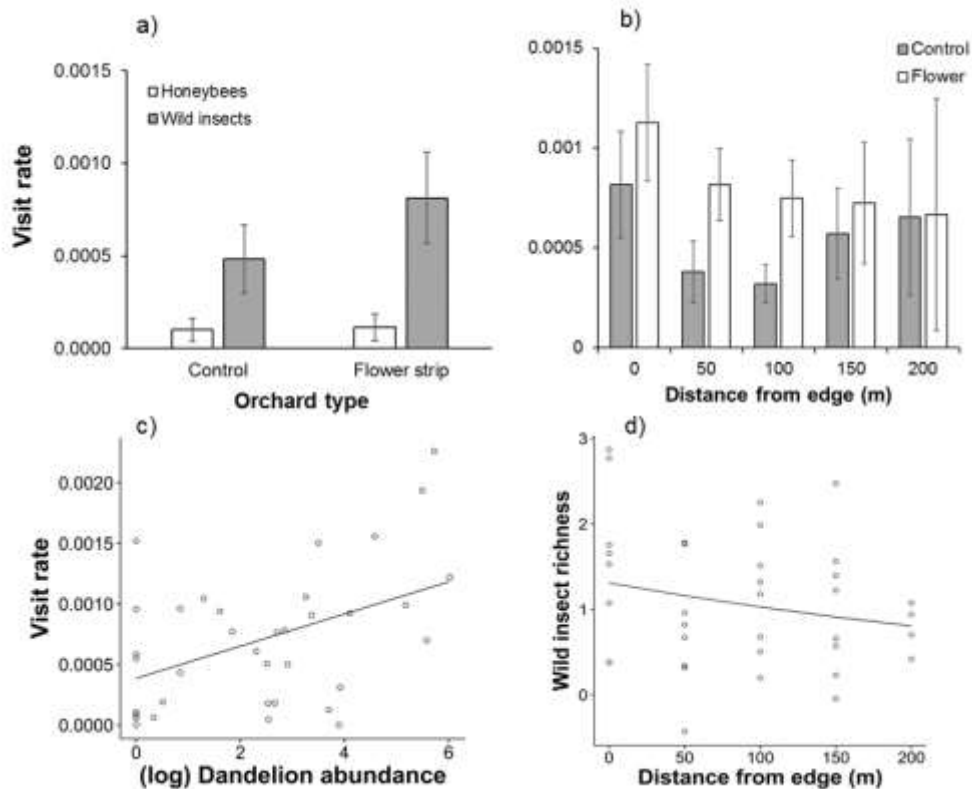
336 **Table 1.** □ Results from LMM and GLMM analyses of insect visit rates and visitor richness
 337 during ten min observation periods in eight apple orchards. The table shows Chi-square
 338 values ($***P < 0.001$, $**P < 0.01$, $*P < 0.05$, ' ' $P < 0.10$; d.f. = 1) from likelihood ratio tests for
 339 all explanatory variables included in minimum models and the direction of relationships.
 340 Blanks represent variables dropped following stepwise deletion from the full model or not
 341 included due to collinearity between explanatory variables.

	Flower strips	Distance from edge (m) [†]	Flower strips x Distance	Dandelion abundance	Wild insects ^{††}
Visit rates					
<i>Honeybees</i>		7.81** (-)	18.22***		10.14** (-)
<i>Wild insects</i>	3.50. (+)			5.27* (+)	
<i>Wild bees</i>	2.81. (+)				
<i>Andrenids</i>				2.70. (+)	
Wild richness		4.27* (-)			
Ground nests			3.12.		

342

343 [†] 200 m plots only present in each of four larger orchards

344 ^{††} Honeybee models only



345

346 **Figure 2.** Flower visit rates (number of visits during ten minutes observation divided by the
 347 number of open flowers per plot) of a) honeybees and wild insects (non-*Apis* bees, flies,
 348 beetles) in flower strip orchards and control orchards, b) wild insects in flower strip and control
 349 orchards at increasing distance from the orchard edge (m); c) Effect of (Log-transformed)
 350 dandelion abundance per plot on wild insect visit rate; and d) effect of distance from edge on
 351 wild insect richness in orchards. Error bars represent standard errors of the mean.

352

353 3.3 Pollination services

354 Open-pollinated branches (final fruit set = 11.7% ± 3.4) set more than double the fruit
 355 of insect-excluded branches (5% ± 1.6), but 64% less fruit than hand-pollinated
 356 branches ($\chi^2 = 728.06$, d.f. = 2, $P < 0.001$) (Figure 3a). Pollen limitation differed
 357 among varieties, as the variety 'Hastings' set significantly fewer fruit under open
 358 pollination than the other two varieties tested (interaction between treatment and
 359 variety: $\chi^2 = 88.28$, d.f. = 4, $P < 0.001$, Figure S3, Supplementary Materials). Initial

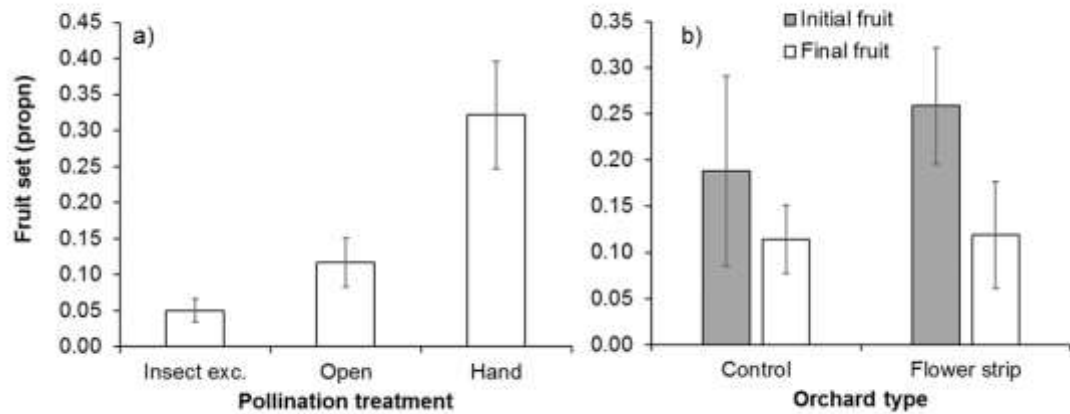
360 fruit set on open branches was higher in flower strip orchards than control orchards,
 361 but this difference was not statistically significant and disappeared at final fruit set
 362 (Figure 3b). Effects of distance from edge and dandelion abundance on fruit set were
 363 not significant. Fruit set was positively related to wild insect richness at both initial
 364 and final fruit set, and andrenid visit rate at final fruit set (Table 2; Figure 4). We also
 365 found a negative relationship with honeybee visit rate at initial fruit set, but this effect
 366 was not significant at final fruit set (Table 2; Figure 4).

367

368 **Table 2.** Results from separate binomial (GLMM) models analysing the effect of insect
 369 visitation rate, richness of wild insects and ground nest densities on initial and final fruit set in
 370 eight cider apple orchards. Visitation rate was considered for honeybees, wild insects, wild
 371 bees and andrenid bees. The table shows Chi-square values ($***P < 0.001$, $**P < 0.01$, $*P <$
 372 0.05 ; d.f. = 1 for all explanatory variables) from likelihood ratio tests with null models for all
 373 explanatory variables and the direction of significant relationships.

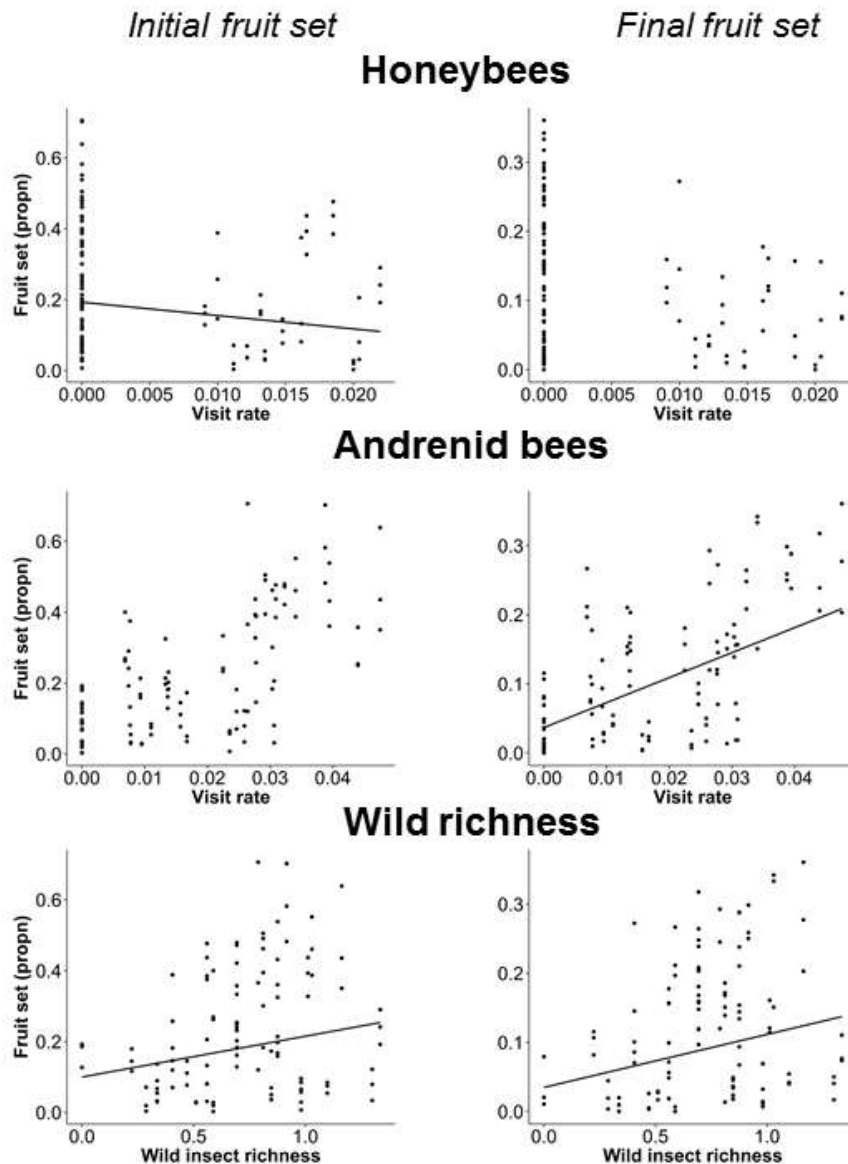
Explanatory variable	Initial fruit set	Final fruit set
Visitation rates		
<i>Honeybees</i>	5.11 * (-)	2.46
<i>Wild insects</i>	0.27	2.77
<i>Wild bees</i>	0.86	3.55
<i>Andrenid bees</i>	2.01	6.42 * (+)
Wild insect richness	3.91 * (+)	5.17 * (+)
Ground nest density	0.00	0.05

374



375

376 **Figure 3.** Fruit set on cider apple trees a) under different pollination treatments
 377 (insect-excluded, open-pollinated (insect + wind) or hand-pollinated (insect + hand +
 378 wind) (final fruit set); b) in flower strip or control orchards (initial and final fruit set).
 379 Error bars represent standard errors of the mean.



380

381 **Figure 4.** Relationship between fruit set (initial and final) and visit rates of honeybees,
 382 andrenid bees, and wild insect richness (each point represents a single tree under
 383 open pollination, $n = 108$).

384

385 3.4 Forager behaviour

386 A total of 1,892 apple flower visits by 224 bumblebees, honeybees and andrenid
 387 bees were recorded during forager observations (Table 3). Visit duration differed
 388 significantly by visitor group ($\chi^2 = 132.42$, d.f. = 2, $P < 0.001$) and was negatively

389 associated with temperature ($\chi^2 = 5.89$, d.f. = 1, $P = 0.015$), with andrenid bees
390 spending up to five times longer per flower than other taxa (Table 3). Accordingly, the
391 number of flowers visited per minute was significantly different between visitor groups
392 ($\chi^2 = 138.94$, d.f. = 2, $P < 0.001$), as honeybees and bumblebees visited two and
393 three times respectively the number of flowers visited per minute by andrenids (Table
394 3). The frequency in which insects moved between trees in the same row (KW =
395 17.99, d.f. = 2, $P < 0.001$), and trees in different rows (KW = 17.99, d.f. = 2, $P <$
396 0.001), differed significantly between visitor groups. Bumblebees and honeybees
397 moved frequently between trees in the same row, but only bumblebees moved
398 frequently between trees in different rows. During flower visits, all taxa collected
399 nectar more often than pollen, but andrenids collected pollen more often than other
400 taxa (Table 3). Bumblebees and andrenids had higher rates of stigma contact than
401 honeybees, but the difference between groups was only marginally significant
402 (binomial GLM: $\chi^2 = 5.22$, d.f. = 2, $P = 0.073$).

403

404 **Table 3.** Total number of observations (individuals and apple flowers visited), mean number of
405 flowers visited per minute (\pm SEM), mean time spent per flower (seconds \pm SEM), mean
406 number of transfers between trees in same row (\pm SEM), mean number of transfers between
407 trees in different rows \pm SEM, proportion of visits for nectar or pollen and proportion of visits
408 where contact was made with apple stigma (number of visits where visitor behaviour could be
409 observed is shown in brackets) for each insect group.

Response	Honeybees	Andrenids	Bumblebees
Individuals (visits)	66 (800)	111 (496)	47 (596)
Flowers visited min ⁻¹	7.44 \pm 0.40	3.35 \pm 0.18	10.20 \pm 0.59
Visit duration (secs)	7.24 \pm 0.80	19.18 \pm 1.63	3.97 \pm 0.29
Transfer to same row tree min ⁻¹	0.20 \pm 0.02	0.03 \pm 0.00	0.31 \pm 0.05
Transfer to different row tree min ⁻¹	0.01 \pm 0.00	0.01 \pm 0.00	0.30 \pm 0.04

Nectar-visits (propn)	0.59 (107)	0.61 (239)	1.00 (28)
Pollen-visits (propn)	0.48 (107)	0.57 (239)	0.00 (28)
Stigma contact (propn)	0.81 (94)	0.95 (215)	1.00 (27)

410

411

412 **4. Discussion**

413 Abundance of wild insects, but not honeybees, was enhanced in flower strip orchards
414 up to 100 m from the orchard edge, suggesting that flower strips enhanced local
415 populations of wild insects (mainly wild bees) in orchards and surrounding natural
416 habitats. However, despite positive trends in wild insect abundance and initial fruit
417 set, flower strips did not significantly increase visitation by andrenid bees, the most
418 important wild pollinator group, or fruit production in orchards. Positive relationships
419 with existing ground flora species (dandelions) and infrequent observations of
420 andrenid bees at flower strips during the latter half of the previous summer suggest
421 that the inclusion of early-flowering plant species in flower mixes, or amendment
422 management practices to encourage bloom of existing ground flora, have great
423 potential to enhance pollination services in cider orchards.

424

425 *4.1 Effects of flower strips on wild insects and managed honeybees*

426 Wild pollinators require access to sufficient nesting and food resources if they are to
427 maintain large populations in agricultural landscapes (Kremen et al. 2004).
428 Conventionally-managed orchards represent partial or sub-optimal habitats for
429 pollinators due to a lack of floral resources in periods outside of crop bloom, or
430 scarcity of nesting opportunities for wild bees (Marini et al. 2012; Martins et al. 2015;
431 Sheffield et al. 2013). Therefore, positive trends observed in wild insect abundance
432 in flower strip orchards are expected to be a result of additional floral resources in the

433 period following crop bloom providing local insect populations with significant fitness
434 benefits relative to populations in control orchards. Our findings add to the growing
435 body of evidence that pollinator-friendly management schemes at local scales can
436 boost wild pollinator populations on farms (Blaauw & Isaacs 2014; Kleijn et al. 2015;
437 Wood et al. 2015a).

438 Wild insect abundance was enhanced up to 100 m into the orchard interior in flower
439 strip orchards relative to controls. Higher wild pollinator densities near adjacent semi-
440 natural habitats is expected as these areas provide wild bees with a greater range of
441 nesting opportunities relative to the orchard interior (Marini et al. 2012; Martins et al.
442 2015; Sheffield et al. 2013). Although, when andrenid bees were considered
443 separately, effects of flower strips, despite positive trends, were not significant.

444 Our study took place in the first spring following full bloom of flower strips. Yet,
445 positive effects of flower strips on wild pollinators take time to materialise, as natural
446 time lags exist in the response of insect populations to changes in resource
447 availability, *i.e.* where current population size reflects resource availability in the
448 previous year (Roulston & Goodell 2011). For example, Blaauw and Isaacs (2014)
449 found that the benefits of flower strips on wild pollinators and pollination services in
450 blueberry plantations only became apparent in the third year following establishment.
451 Alternatively, flower strips may have failed to enhance andrenid bees because they 1)
452 did not provide attractive or accessible floral resources for andrenid bees; or 2) had
453 insufficient overlap with andrenid flight periods to provide a measurable fitness
454 benefit for local populations.

455 Observations from the previous summer revealed that andrenid bees commonly
456 observed on apple flowers (*Andrena sensu stricto*) visited several sown species in
457 flower strips but visitation finished within thirty days of apple bloom ending that year.
458 Yet, sown species visited by andrenids continued to flower until strips were cut in

459 August. Moreover, of the six andrenid species observed visiting apple flowers, only
460 *Andrena nigroaena* and *Micrandrena* species (occasional visitors to apple flowers)
461 are observed on the wing beyond July (Carl Clee, *pers. comm.*). It is therefore likely
462 that a lack of temporal (phenological) overlap between andrenid activity periods and
463 flower strip bloom limited fitness gains received by andrenid bees from flower strips.

464 Alongside effects of flower morphology (Campbell et al. 2012), phenological overlap
465 is regarded as one of the most important factors in structuring insect flower visitor
466 networks, i.e. links between plants and insects, as insects cannot receive fitness
467 benefits from plants that flower outside of their activity periods (Junker et al. 2013).
468 For this reason, effects of flower strips on wild pollinators only became apparent
469 when wild insect species with prolonged flight periods (e.g. bumblebees) were
470 included in our analyses. This finding supports recent evidence suggesting that
471 despite being highly mobile, bumblebee populations can respond to changes in
472 habitat at small spatial scales (Benjamin et al. 2014; Wood et al. 2015a).

473 Unlike wild pollinators, visitation by honeybees was similar in both flower strip and
474 control orchards. As feral colonies are rare in temperate regions (Jaffé et al. 2010),
475 honeybee densities are primarily determined by the number of hives present in the
476 surrounding landscape, rather than the availability of floral resources or nest sites
477 (Blaauw & Isaacs 2014). Furthermore, strips flowered after apple, and so direct
478 effects of flower strips on honeybee foraging on apple flowers (e.g. facilitative
479 pollination), as found in Carvalho et al. (2012), were unlikely. Although, honeybee
480 visitation was negatively correlated with visitation by wild insects. Previous studies
481 have noted that inter-specific competition among flower visitors can lead to shifts in
482 foraging patterns and pollination performance of both wild bees and honeybees
483 (Brittain et al. 2013; Greenleaf & Kremen 2006). However, as we did not
484 experimentally control honeybee densities in orchards, as in Mallinger & Gratton

485 (2014), or observe any competitive interactions between flower visitors, we cannot
486 determine any causality in this interaction.

487

488 *4.2 Pollination services in cider apple orchards*

489 Low fruit set on bagged branches suggested that insect visitation is critical for
490 pollination of apple flowers (Garratt et al. 2014; Mallinger & Gratton 2015). Yet, hand-
491 pollinated branches demonstrated that orchards are pollen limited and suffer from
492 pollination deficits. Therefore, although we did directly not study the contribution of
493 insects on a per visit basis (Vicens & Bosch 2000), positive relationships between
494 fruit set on unmanipulated branches and andrenid bees (final fruit set), and wild
495 insect richness (initial and final fruit set), indicate that wild insect visitation to apple
496 flowers is critical for the closure of pollination deficits and fruit yield in cider orchards.

497 High interaction frequency is an integral component of pollinator effectiveness
498 (Vázquez et al. 2005), and wild insects were observed at much higher visit
499 frequencies (83% of visits to apple flowers) in orchards than honeybees. However,
500 previous studies have found honeybees to be ineffective pollinators of apple flowers
501 even at recommended (high) hive densities (Mallinger & Gratton 2015; Martins et al.
502 2015). One possible explanation is that foraging behaviours of honeybees make them
503 inefficient pollinators of apples (Mallinger & Gratton 2015). Here, we observed that
504 andrenid bees collected pollen more often than other taxa, and alongside
505 bumblebees, had high rates of contact with the stigma during flower visits (95 – 100%
506 of visits). In contrast, honeybees contacted stigma less often (81% of visits), as
507 nectar-foragers can learn to perform lateral visits (known as ‘side-working’) and avoid
508 contact with sexual structures (Thomson & Goodell 2001; Vicens & Bosch 2000).
509 Furthermore, only bumblebees were observed to move frequently between trees in
510 different rows, which may be critical for pollination in orchards where self-

511 incompatible tree varieties are planted in separate rows (Kendall 1973). As a
512 consequence of these behavioural differences, the quantity and quality of pollen
513 being deposited by honeybees per unit time may be reduced relative to the
514 contribution of wild bees. Additionally, recent studies have shown that bumblebees
515 have greater tolerance to cold or unsettled conditions than other insects (Brittain,
516 Kremen & Klein 2013). Together, functional differences in foraging behaviour and
517 tolerance to environmental stresses among wild insect taxa may explain why
518 pollination services were optimal in orchards supporting rich wild insect communities,
519 but unrelated to honeybee visitation. Our results support those from recent studies
520 suggesting wild bees are important pollinators of apple flowers (Garratt et al. 2014;
521 Mallinger & Gratton 2015), and that richer pollinator communities, through greater
522 functional complementarity among pollinator taxa, provide better pollination services
523 than species-poor communities (Blitzer et al. 2016; Martins et al. 2015).

524

525 *4.3 Implications for orchard management and agricultural policy*

526 Flower mixes used here were based in part on seed mixtures commonly deployed in
527 flower-rich UK agri-environment schemes (Defra 2013). These mixtures have been
528 demonstrated to boost bumblebee populations (Wood et al. 2015a), but may be of
529 limited value for other beneficial insects (Campbell et al. 2012; Wood et al. 2015b). In
530 the present study, very few species included in mixes flowered in spring when
531 andrenid bees were actively provisioning their nests. Therefore, such flower mixes
532 are unlikely to support pollination services in apple, or other important crops
533 pollinated by andrenid bees, including sweet cherry (Holzschuh et al. 2012),
534 blueberry (Blaauw & Isaacs 2014), and oilseed rape (Woodcock et al. 2013).

535 Tailoring flower mixes to include a higher number of early-flowering species can
536 maximise benefits for spring-active solitary bees and the pollination services provided

537 by these insects (Russo et al. 2013). Furthermore, positive relationships found here
538 between ground flora community and wild insect visitation to apple flowers show that
539 land managers could also achieve this by enriching existing ground flora in orchards.
540 For example, relaxing mowing regimes and/or reducing herbicide usage in alleyways
541 have been shown previously to enhance native plant and insect communities in
542 orchards (Horton et al. 2003; Saunders et al. 2013). Although we observed andrenids
543 nesting in the areas of bare soil directly beneath tree rows, it is not known to what
544 extent availability of nest sites limits key pollinator species in apple orchards. Future
545 research should focus on identifying what combination of management strategies
546 (e.g. early-season flower strips, reducing agrochemical usage, relaxation of mowing)
547 can bring about the greatest benefits for both orchard biodiversity and crop yield.

548 In addition, pollination services were positively related to wild insect richness in
549 orchards, which was unresponsive to flower strips but higher in plots close to the
550 orchard edge. Although we were unable to demonstrate an effect of distance from
551 semi-natural habitat on fruit production, it is clear from the existing literature that,
552 whilst local management can boost pollinator density, the preservation of surrounding
553 semi-natural habitat is critical for the maintenance of regional species pools and
554 pollinator diversity in orchards (Kennedy et al. 2013). Therefore, scientists and land
555 managers must use a multi-scalar approach to wild pollinator conservation to
556 maintain pollination services in crops.

557

558 *4.4 Conclusion*

559 In summary, flower strips increased wild insect abundance during crop bloom in cider
560 apple orchards, particularly in areas close to bordering semi-natural habitats, and
561 visitation by andrenid bees, the dominant wild insect visitor taxa, was positively
562 related to fruit set. However, in the year following their establishment, flower strips did

563 not enhance fruit production in experimental orchards compared to controls. It is likely
564 that a greater focus on the floral resource needs of key pollinators, wild bees, studied
565 across longer time periods than considered here, would yield a positive effect on
566 apple production. Such within-farm habitat restoration techniques hold great promise
567 because they can simultaneously enhance yields in existing croplands whilst
568 reducing pressure on the remaining natural-, and semi-natural habitat in agricultural
569 landscapes, and thus warrant our attention.

570

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580

581 **Appendix A. Supplementary Materials**

582 Further details on study sites; sown flower mix composition; experimental design;
583 flower visitor species identification; spatial analyses and varietal differences.

584

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586

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