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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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 (Carvalheiro 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 (Carvalheiro 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 (Carvalheiro 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

2. Materials and Methods

2.1 Study site details and experimental design

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

2.2 Flower strips

Flower strip orchards were sown with targeted flower mixtures of up to 25 wildflower species in April 2011 (Table S2, Supplementary Materials). Flower mixtures included Fabaceae species attractive to eusocial bee species and commonly included in UK agri-environment schemes (Defra 2013), as well as other plant families (Apiaceae) with short or 'open' corollas to attract short-tongued insects (e.g. solitary bees, hoverflies and parasitoid wasps) (Campbell et al. 2012). Flower strips were divided in three pairs that were randomly distributed among orchard rows and covered a total area of 0.05 ha per orchard. Flower strips bloomed sporadically in the first year following establishment (2011), but flowered consistently in 2012 from early June until August when they were cut to prepare orchards for mechanical fruit harvest. During 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 ^{o}C if clear, >17 ^{o}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

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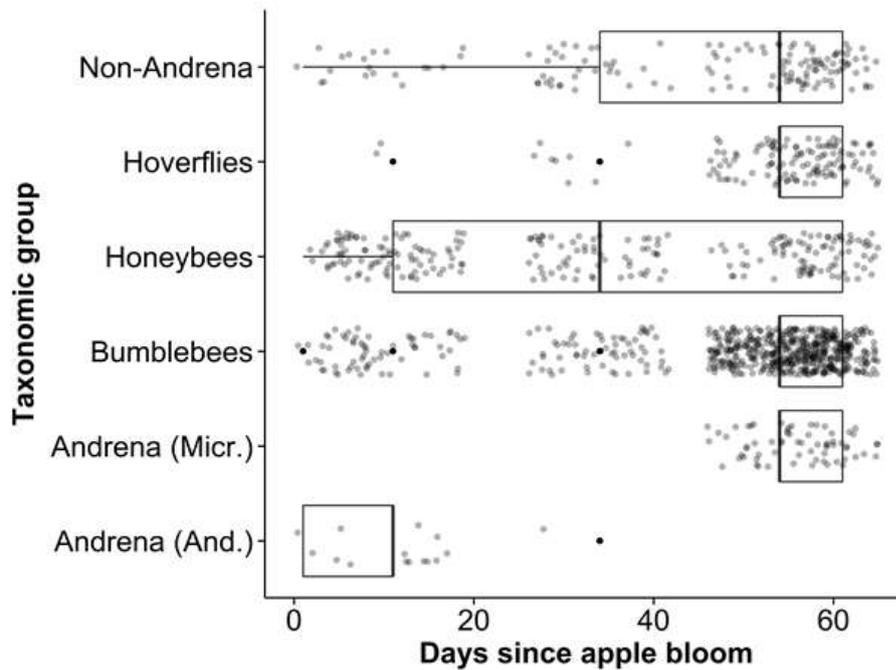
Figure 1. Visitation by 'potential' apple pollinators to flower strips in the sixty days following apple bloom in 2012 (start date considered June 9th 2012). 'Non-Andrena' includes visits by other solitary bees (Halictidae, Megachilidae, Melittidae). Boxplots represent median, interquartile range, and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

3.2 Insect visitors to apple flowers

A total of 475 visits to apple flowers, by 25 distinct insect taxa, were recorded in plots during timed observations. The most abundant visitor group were andrenid bees (Hymenoptera: Andrenidae: *Andrena*, six species, 59.8% of visits), followed by honeybees (Apidae: *Apis mellifera*, 16.8% of visits), bumblebees (Apidae: *Bombus*, five species, 11.8% of visits) and hoverflies (Diptera: Syrphidae, seven genera, 7.4% 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 (± 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

Table 1. ☐Results from LMM and GLMM analyses of insect visit rates and visitor richness

during ten min observation periods in eight apple orchards. The table shows Chi-square

values (***P < 0.001, **P < 0.01, *P < 0.05, '.' *P* < 0.10; d.f. = 1) from likelihood ratio tests for

all explanatory variables included in minimum models and the direction of relationships.

Blanks represent variables dropped following stepwise deletion from the full model or not

included due to collinearity between explanatory variables.

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

342

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

[††] Honeybee models only

345
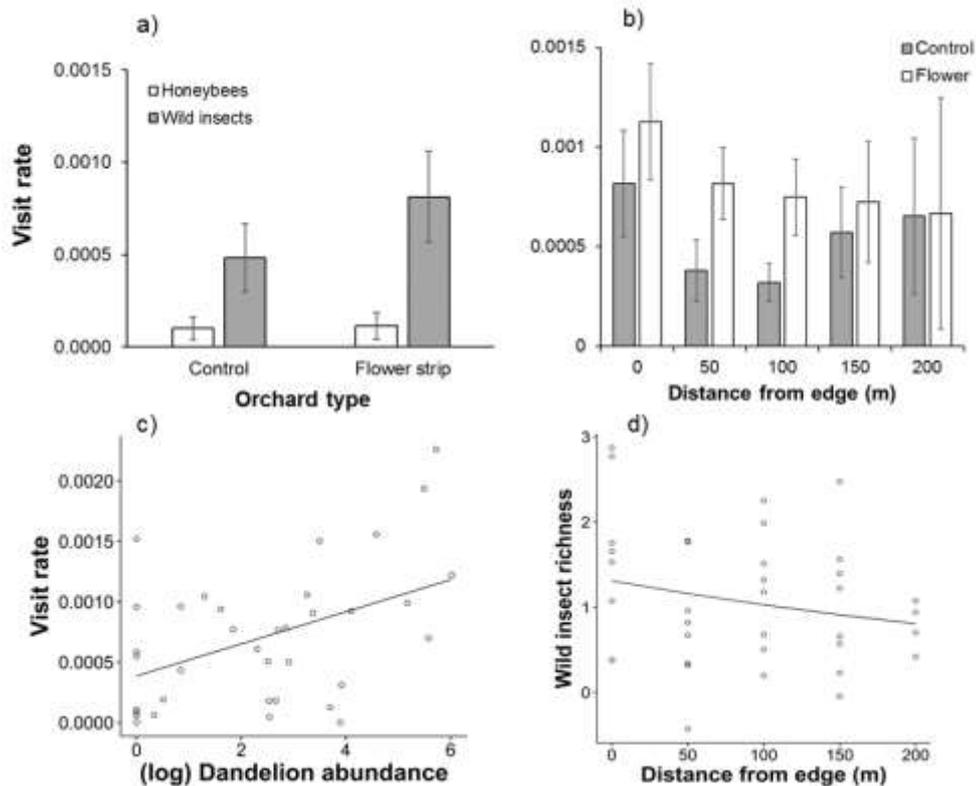
Figure 2. Flower visit rates (number of visits during ten minutes observation divided by the number of open flowers per plot) of a) honeybees and wild insects (non-*Apis* bees, flies, beetles) in flower strip orchards and control orchards, b) wild insects in flower strip and control orchards at increasing distance from the orchard edge (m); c) Effect of (Log-transformed) dandelion abundance per plot on wild insect visit rate; and d) effect of distance from edge on wild insect richness in orchards. Error bars represent standard errors of the mean.

352

3.3 Pollination services

Open-pollinated branches (final fruit set = 11.7% ± 3.4) set more than double the fruit of insect-excluded branches (5% ± 1.6), but 64% less fruit than hand-pollinated branches ($\chi^2 = 728.06$, d.f. = 2, $P < 0.001$) (Figure 3a). Pollen limitation differed among varieties, as the variety 'Hastings' set significantly fewer fruit under open pollination than the other two varieties tested (interaction between treatment and 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		
Honeybees	5.11 * (-)	2.46
Wild insects	0.27	2.77
Wild bees	0.86	3.55
Andrenid bees	2.01	6.42 * (+)
Wild insect richness	3.91 * (+)	5.17 * (+)
Ground nest density	0.00	0.05

374

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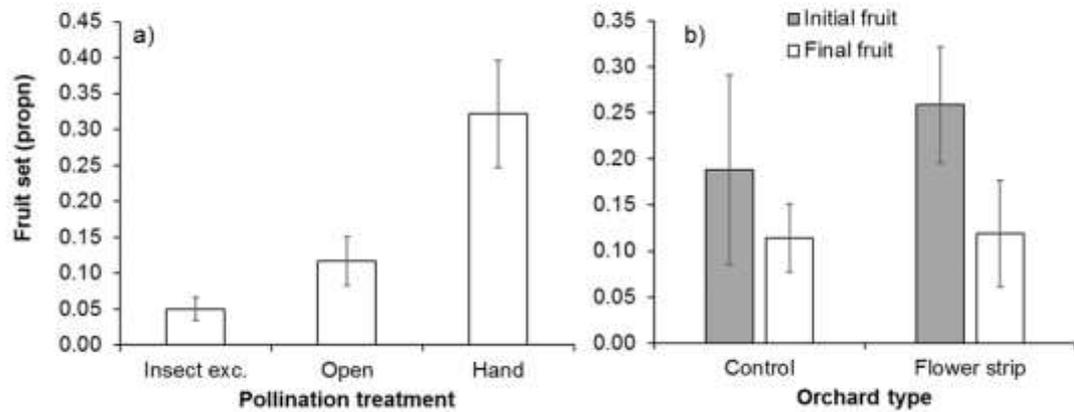
Figure 3. Fruit set on cider apple trees a) under different pollination treatments (insect-excluded, open-pollinated (insect + wind) or hand-pollinated (insect + hand + wind) (final fruit set); b) in flower strip or control orchards (initial and final fruit set). Error bars represent standard errors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

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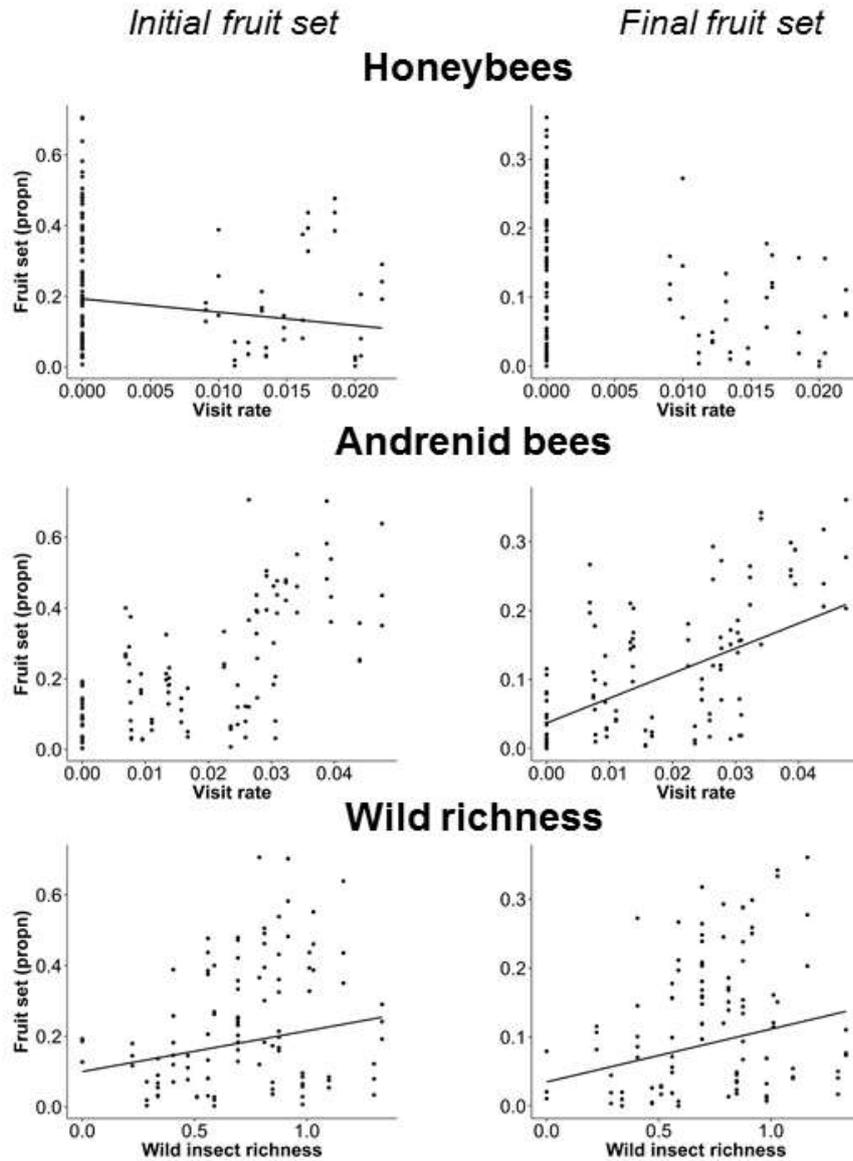
Figure 4. Relationship between fruit set (initial and final) and visit rates of honeybees,

andrenid bees, and wild insect richness (each point represents a single tree under

open pollination, $n = 108$).

3.4 Forager behaviour

A total of 1,892 apple flower visits by 224 bumblebees, honeybees and andrenid

bees were recorded during forager observations (Table 3). Visit duration differed

significantly by visitor group ($\chi^2 = 132.42$, d.f. = 2, $P < 0.001$) and was negatively

389 associated with temperature (χ^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 (χ^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: χ^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 (± SEM), mean time spent per flower (seconds ± SEM), mean

406 number of transfers between trees in same row (± SEM), mean number of transfers between

407 trees in different rows ± 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 ±0.40	3.35 ±0.18	10.20 ±0.59
Visit duration (secs)	7.24 ±0.80	19.18 ±1.63	3.97 ±0.29
Transfer to same row tree min^{-1}	0.20 ±0.02	0.03 ±0.00	0.31 ±0.05
Transfer to different row tree min^{-1}	0.01 ±0.00	0.01 ±0.00	0.30 ±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

4. Discussion

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

4.1 Effects of flower strips on wild insects and managed honeybees

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

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

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

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

Observations from the previous summer revealed that andrenid bees commonly observed on apple flowers (*Andrena sensu stricto*) visited several sown species in flower strips but visitation finished within thirty days of apple bloom ending that year. 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 Carvalheiro 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

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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