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

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ABSTRACT

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

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

Our results demonstrate that flower strips enhanced overall wild insect abundance but not pollination services in cider orchards. Positive effects of ground flora on wild insect abundance in orchards suggest that flower mixtures or orchard management could be optimised for andrenid bees, the single most important pollinator taxa, by increasing the availability of early-flowering plants in orchards. Equally, wild insect richness was highest in areas close to semi-natural habitats. Therefore, whilst flower strips can boost abundance of the existing species pool, only large scale preservation of (semi-) natural habitat will maintain pollinator diversity in apple orchards.

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1. Introduction

Around 75% of global food crops are to some degree dependent on animal pollination (Klein et al., 2007), with insects being the most important pollinators in both natural and agricultural settings (Kearns et al., 1998). Yet, pollinators are under threat because of several interrelated factors associated with the intensification of agricultural practices (e.g. removal or fragmentation of natural- or semi-natural habitats, agrochemical usage) (Biesmeijer et al., 2006; Park et al., 2015; Potts et al., 2010). Historically, many pollinator-dependent crops have been supplemented with domesticated hives of the European honeybee, Apis mellifera Linnaeus (Hymenoptera: Apidae), during crop bloom to ensure adequate pollination (Garibaldi et al., 2009). However, in addition to concerns about over-reliance on a single species for global crop pollination services (Breeze et al., 2014), there is a

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growing body of evidence that the contribution of wild pollinators (*e.g.* non-*Apis* bees, flies), may be equal to, or even surpass that of honeybees (Garibaldi et al., 2013). As such, there is growing interest in the development of management practices that integrate the needs of wild pollinators into productive landscapes (Bommarco et al., 2013; Dicks et al., 2013; Kleijn et al., 2015).

To persist in agricultural habitats, wild pollinators must be able to find suitable nesting sites (if a central-place forager), and collect sufficient food (pollen and nectar) to feed their offspring (Kremen et al., 2004). Changes in agricultural practice that alter the availability of these resources will indirectly affect fitness and population size of wild pollinators (Carvell et al., 2007; Roulston and Goodell, 2011). For example, Marini et al. (2012) found wild bee abundance in apple orchards was higher in landscapes dominated by semi-natural habitats (*e.g.* forest, grassland) compared to orchards in landscapes dominated by apple. They attributed this to semi-natural habitats providing pollinators with a better supply of floral resources, in terms of both temporal availability and abundance, than commercially managed orchards, particularly in periods outside of tree blossom.

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

Such flower-rich habitats, if designed effectively, provide pollinators with a greater diversity of pollen and nectar resources, and can increase the availability of nest sites for wild pollinators in crop fields (Carreck and Williams 2002; Pywell et al., 2005; Russo et al., 2013). However, arbitrarily chosen flowering vegetation or naturally regenerated vegetation may be ineffective in supporting key groups of beneficial insects (Campbell et al., 2012; Olson and Wäckers, 2007) and may also generate negative effects, such as increased pest problems (Wäckers et al., 2007; Winkler et al., 2010). For example, incompatibilities between insect feeding structures and floral morphologies, or insufficient temporal overlap between flowering period and insect foraging periods, may limit transfer of fitness benefits to pollinators (Campbell et al., 2012; Junker et al., 2013; Russo et al., 2013). Furthermore, plantings at the crop edge may concentrate ambient populations of beneficial insects at field edges and exacerbate pollinator declines in field centres (Kohler et al., 2008; Morandin and Kremen, 2013). Therefore, establishment of flower-rich areas directly within crop fields may be a more effective means of increasing pollinator visits to crop flowers in large fields, either through facilitative co-pollination (Carvalheiro et al., 2012), or improved reproductive success of pollinators in crop fields and surrounding habitats (Blaauw and Isaacs, 2014).

Here, we explore the effects of sown flower strips introduced directly between tree rows in UK cider apple orchards (*Malus domestica* Borkhausen) on pollinator visitation and pollination services. Cider apple orchards are an ideal candidate for such interventions, as apple is regarded as 'greatly dependent' on pollinators for fruit set (Klein et al., 2007), and fruit quality (Garratt et al., 2014), and the semi-permanent nature of orchards allows populations to build across seasons (Shackelford et al., 2013; Simon

et al., 2010). We also investigate the relative contribution of insects to pollination services in cider apple orchards using insect-exclusion and hand pollination experiments, and identify potential behavioural mechanisms that underpin pollination efficiency of different insect taxa. Specifically, we ask 1) whether perennial flower strips introduced directly into orchards increase pollinator abundance and richness during apple blossom along a gradient of isolation from semi-natural habitat, 2) how do changes in pollinator communities (visitor abundance, richness) affect pollination services, and 3) do differences in foraging behaviour among pollinator taxa underpin differences in pollination efficacy?

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′–52°12′ N and 2°47′– 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; Fig. 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 recorded on six separate occasions using similar methods (walked transects) to those described below for observations of insect visitors to apple flowers in 2013.

2.3. Pollinator sampling

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

Observations of insect visitation took place in May 2013 during peak bloom in orchards. A single observation consisted of continuously walking alongside trees of a plot for ten minutes. During this period, all insects observed visiting apple flowers

within a horizontal band of 0.5–2 m above the ground were recorded, only stopping the timer to catch insects that could not be identified on the wing for later identification under a microscope. All bees (Hymenoptera: Apoidea) were identified to species level (except *Andrena* males) and other groups to at least family level. Observations took place only in warm (>13 °C if clear, >17 °C if cloudy), dry conditions with low wind speed (<5 mph) between 10:00 h and 17:00 h. Repeat observations were made on non-consecutive days, with the order in which plots within orchards, and orchards visited, randomised to minimise effects of order. Hives of *A. mellifera* were never directly introduced in orchards, but visiting honeybees were presumed to be from managed hives as feral colonies are expected to be non-existent, or rare in northern Europe (Jaffé et al., 2010).

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

2.4. Pollination services

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

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

2.5. Forager behaviour

In a separate experiment, foraging behaviour of three visitor groups (honeybees, bumblebees and andrenid bees) was observed in flower strip orchards in May 2012. Individual insects were tracked during foraging bouts on apple trees to record foraging behaviour and inter-tree movements. Observations of individual

insects were made for up to three minutes or until the observer lost sight of the individual. Observations adhered to the same protocols used in the main experiment regarding insect identification, weather, percentage blossom and temperature. For each insect, we recorded the number of flowers visited per minute, visit duration, resource collected (nectar, pollen or both), and whether contact was made with the stigma. We also noted transfers between trees in the same row, between trees in different rows, as well as visits to other flowering plants (dandelions) in the orchard understory. Individual orchards were evenly sampled (5–7 h per orchard, 23 h observation in total).

2.6. Statistical methods

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

Visit rates were analysed using linear mixed-effects models (LMMs), and insect richness and solitary bee nest counts were analysed using generalised linear mixed effects models (GLMMs) with Poisson family (R package 'lme4'; Bates et al., 2013). Random effects nested plots within orchards. Fixed effects in all insect models included flower strip presence, distance from orchard edge (0–200 m), and dandelion abundance in orchard alleyways. We also included the interaction between flower strips and distance from edge to investigate influence of flower strips on pollinator visitation at increasing distance from bordering semi-natural habitat. Wild insect visitation was also included in honeybee models to investigate potential interactions between wild and managed insects. As orchards were not evenly distributed across the landscape, we additionally tested normalised residuals of insect visitation models where flower strip presence was found to be significant for spatial autocorrelation using Moran's Index (R package 'ape'; Paradis et al., 2004).

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

For observations of foraging behaviour, visit duration and flowers visited per minute were log-transformed prior to analysis to improve model fit and analysed using LMMs with orchard
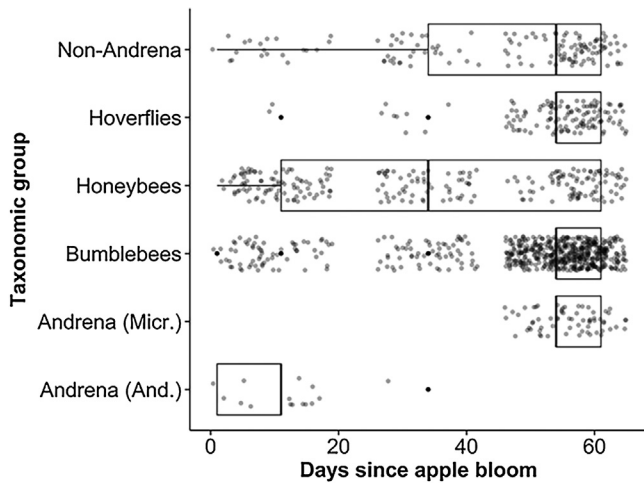
Fig. 1. Visitation by 'potential' apple pollinators to flower strips in the sixty days following apple bloom in 2012 (start date considered June 9th 2012). 'Non-Andrena' includes visits by other solitary bees (Halictidae, Megachilidae, Melittidae). Boxplots represent median, interquartile range, and maximum and minimum observed values for each insect group.

included as a random effect. Fixed effects included visitor group (bumblebee, honeybee or andrenid bee), temperature, and the interaction between visitor group and temperature. Non-parametric rank sums test (Kruskal-Wallis = KW) was used to investigate differences in rates of movement between groups, as data could not be transformed to meet parametric assumptions of normally-distributed residuals. Difference in rate of stigma contact during a single visit among visitor groups was analysed using a binomial general linear model.

All statistical models were validated using histograms of normalised residuals, plots of residuals against fitted values, and each explanatory variable to assess model fit and homogeneity of variance amongst factor levels. Significance of explanatory variables in models was determined using a stepwise deletion procedure from the full model combined with likelihood ratio tests, with variables being retained in models where $P < 0.05$ (Crawley, 2007; Zuur et al., 2009). All analyses were performed using R software and associated packages (R Foundation, 2016).

3. Results

3.1. 'Potential' apple pollinators in flower strips

Observations of insects in flower strips in the previous summer revealed that 15 of the 25 taxa observed visiting apple flowers in spring 2013 also visited the flower strips (Table S3, Supplementary Materials). The three most frequently visited plant species by these

insects were *Trifolium hybridum* (Fabaceae), *Trifolium pratense* and *Trifolium repens*. The most abundant insect visitors were bumblebees (47%), honeybees (34%) and hoverflies (11.5%). Division of visits by andrenid bees (*Andrena* species) into the subgenera *Andrena sensu stricto* (medium-sized species) and *Micrandrena* (small-bodied species), revealed visitation by *Andrena sensu stricto* species ended soon after apple bloom in 2012 (considered first week in June) (Fig. 1). In contrast, other insect taxa visited flower strips throughout the summer.

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

3.2.1. Effects of flower strips on apple flower visitors

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

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

Table 1
Results from LMM and GLMM analyses of insect visit rates and visitor richness during ten minute 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.		

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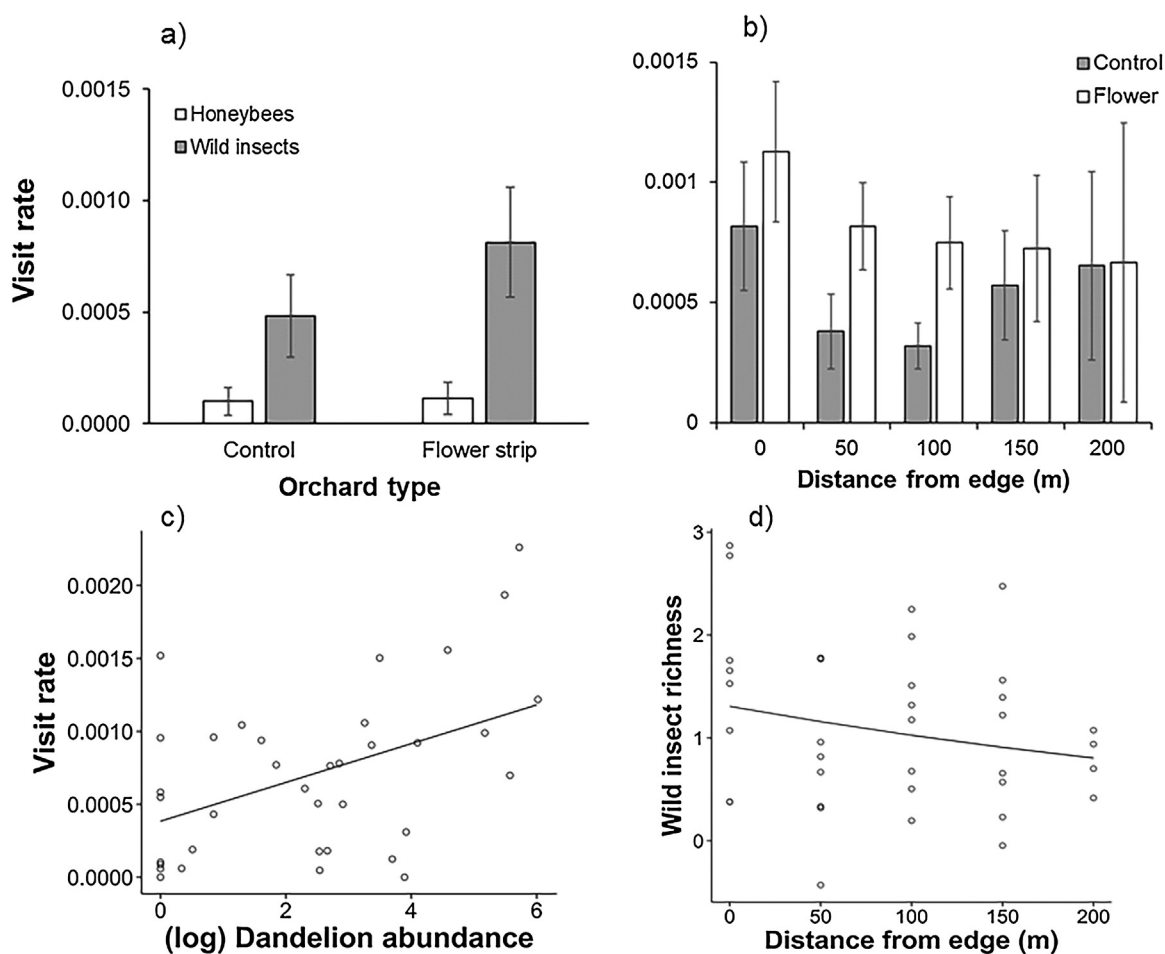[††] Honeybee models only.

Fig. 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.

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, $P < 0.001$) (Fig. 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, $P < 0.001$,

Fig. S3, Supplementary Materials). Initial fruit set on open branches was higher in flower strip orchards than control orchards, but this difference was not statistically significant and disappeared at final fruit set (Fig. 3b). Effects of distance from edge and dandelion abundance on fruit set were not significant. Fruit set was positively related to wild insect richness at both initial and final fruit set, and andrenid visit rate at final fruit set (Table 2; Fig. 4). We also found a negative relationship with honeybee visit rate at initial fruit set, but this effect was not significant at final fruit set (Table 2; Fig. 4).
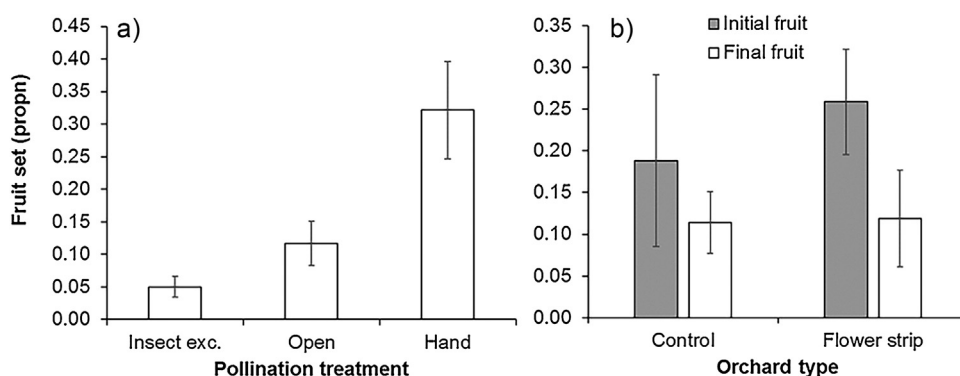

Fig. 3. Fruit set on cider apple trees a) under different pollination treatments (insect-excluded, open-pollinated (insect + wind) or hand-pollinated (insect + hand + wind) (final fruit set); b) in flower strip or control orchards (initial and final fruit set). Error bars represent standard errors of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

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

3.4. Forager behaviour

A total of 1892 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 associated with temperature ($\chi^2 = 5.89$, d.f. = 1, $P = 0.015$), with andrenid bees spending up to five times longer per flower than other taxa (Table 3). Accordingly, the number of flowers visited per minute was significantly different between visitor groups ($\chi^2 = 138.94$, d.f. = 2, $P < 0.001$), as honeybees and bumblebees visited two and three times respectively the number of flowers visited per minute by andrenids (Table 3). The frequency in which insects moved between trees in the same row (KW = 17.99, d.f. = 2,
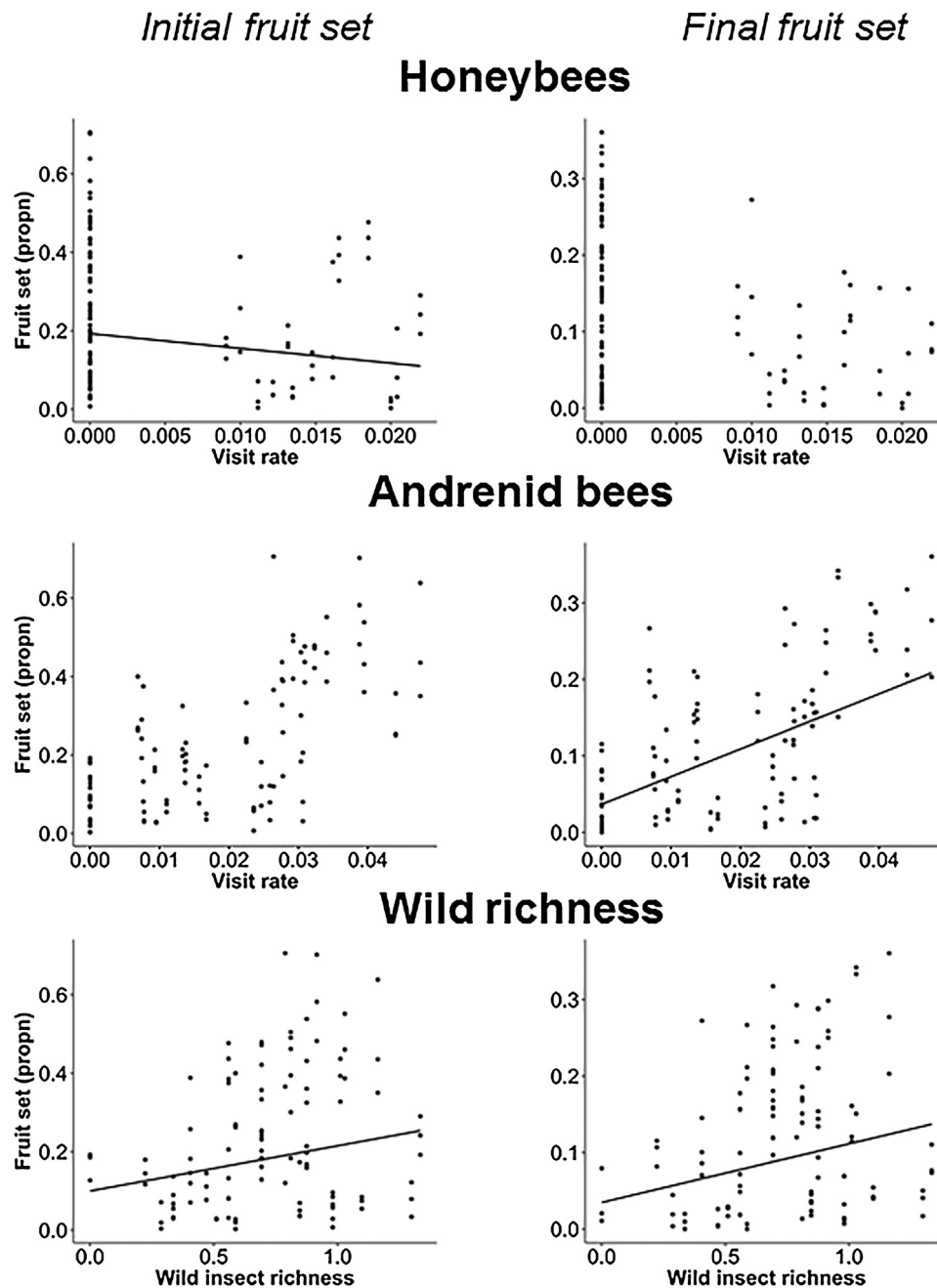

Fig. 4. Relationship between fruit set (initial and final) and visit rates of honeybees, andrenid bees, and wild insect richness (each point represents a single tree under open pollination, *n* = 108).

Table 3
Total number of observations (individuals and apple flowers visited), mean number of flowers visited per minute (±SEM), mean time spent per flower (seconds ± SEM), mean number of transfers between trees in same row (±SEM), mean number of transfers between trees in different rows ± SEM, proportion of visits for nectar or pollen and proportion of visits where contact was made with apple stigma (number of visits where visitor behaviour could be 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)

$P < 0.001$), and trees in different rows (KW = 17.99, d.f. = 2, $P < 0.001$), differed significantly between visitor groups. Bumblebees and honeybees moved frequently between trees in the same row, but only bumblebees moved frequently between trees in different rows. During flower visits, all taxa collected nectar more often than pollen, but andrenids collected pollen more often than other taxa (Table 3). Bumblebees and andrenids had higher rates of stigma contact than honeybees, but the difference between groups was only marginally significant (binomial GLM: $\chi^2 = 5.22$, d.f. = 2, $P = 0.073$).

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

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

Unlike wild pollinators, visitation by honeybees was similar in both flower strip and control orchards. As feral colonies are rare in temperate regions (Jaffé et al., 2010), honeybee densities are primarily determined by the number of hives present in the surrounding landscape, rather than the availability of floral resources or nest sites (Blaauw and Isaacs, 2014). Furthermore, strips flowered after apple, and so direct effects of flower strips on honeybee foraging on apple flowers (*e.g.* facilitative pollination), as found in Carvalheiro et al. (2012), were unlikely. Although, honeybee visitation was negatively correlated with visitation by wild insects. Previous studies have noted that inter-specific competition among flower visitors can lead to shifts in foraging patterns and pollination performance of both wild bees and honeybees (Brittain et al., 2013a, 2013b; Greenleaf and Kremen, 2006). However, as we did not experimentally control honeybee densities in orchards, as in Mallinger and Gratton (2015), or observe any competitive interactions between flower visitors, we cannot determine any causality in this interaction.

4.2. Pollination services in cider apple orchards

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

High interaction frequency is an integral component of pollinator effectiveness (Vázquez et al., 2005), and wild insects were observed at much higher visit frequencies (83% of visits to apple flowers) in orchards than honeybees. However, previous studies have found honeybees to be ineffective pollinators of apple flowers even at recommended (high) hive densities (Mallinger and Gratton, 2015; Martins et al., 2015). One possible explanation is that foraging behaviours of honeybees make them inefficient pollinators of apples (Mallinger and Gratton, 2015). Here, we observed that andrenid bees collected pollen more often than other taxa, and alongside bumblebees, had high rates of contact with the stigma during flower visits (95–100% of visits). In contrast, honeybees contacted stigma less often (81% of visits), as nectar-foragers can learn to perform lateral visits (known as 'side-working') and avoid contact with sexual structures (Thomson and Goodell 2001; Vicens and Bosch, 2000). Furthermore, only bumblebees were observed to move frequently between trees in different rows, which may be critical for pollination in orchards where self-incompatible tree varieties are planted in separate rows (Kendall and Solomon, 1973). As a consequence of these behavioural differences, the quantity and quality of pollen being deposited by honeybees per unit time may be reduced relative to the contribution of wild bees. Additionally, recent studies have shown that bumblebees have greater tolerance to cold or unsettled conditions than other insects (Brittain et al., 2013a, 2013b). Together, functional differences in foraging behaviour and tolerance to environmental stresses among wild insect taxa may explain why pollination services were optimal in orchards supporting rich wild insect communities, but unrelated to honeybee visitation. Our results support those from recent studies suggesting wild bees are important pollinators of apple flowers (Garratt et al., 2014; Mallinger and Gratton, 2015), and that richer pollinator communities, through greater functional complementarity among pollinator taxa, provide better pollination services than species-poor communities (Blitzer et al., 2016; Martins et al., 2015).

4.3. Implications for orchard management and agricultural policy

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

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

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

5. Conclusion

In summary, flower strips increased wild insect abundance during crop bloom in cider apple orchards, particularly in areas close to bordering semi-natural habitats, and visitation by andrenid bees, the dominant wild insect visitor taxa, was positively related to fruit set. However, in the year following their establishment, flower strips did not enhance fruit production in experimental orchards compared to controls. It is likely that a greater focus on the floral resource needs of key pollinators, wild bees, studied across longer time periods than considered here, would yield a positive effect on apple production. Such within-farm habitat restoration techniques hold great promise because they can simultaneously enhance yields in existing croplands whilst reducing pressure on the remaining natural-, and semi-natural habitat in agricultural landscapes, and thus warrant our attention..

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agee.2017.01.005.

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

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