Flower margins support natural enemies adjacent to apple orchards but evidence of spill-over is mixed

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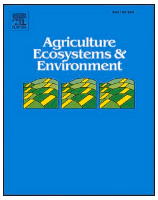

Flower margins support natural enemies adjacent to apple orchards but evidence of spill-over is mixed

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ABSTRACT

Perennial flower margins next to apple orchards can reduce the spread of aphid pests on apple trees and reduce the percentage of trees with fruit damage. To explore the mechanism behind this, we compared the vegetation community in three orchard habitats (flower margins, headlands, and alleyways) to determine whether the presence of a flower margin changed the diversity, abundance, and community of natural enemies of rosy apple aphid (*Dysaphis plantaginea*) in orchard ground vegetation and apple trees. Despite no evident spill-over of plant species into orchards, there was an increased Shannon diversity of natural enemies in the ground vegetation of flower margin orchards compared with controls. This suggests spill-over of natural enemies from the flower margins can reach up to 50 m from the orchard edge. However, we did not find evidence of broad differences between natural enemy taxa abundance, diversity, or community structure on the apple trees themselves. The mechanism behind improved pest control by flower margins is unclear but could be linked to the mobility of certain natural enemy groups or mutualistic relationships with ants. A better understanding of this mechanism would help to optimise the use of flower margins for sustainable pest suppression.

1. Introduction

Insect pests reduce crop quality and yield (Savary et al., 2019). Sustainable long-term crop protection practices are a high priority, in both organic and conventional agriculture, due to issues such as pesticide resistance, secondary pest outbreaks, and harm to beneficial organisms and ecological processes (Bommarco et al., 2013). One practice that can increase the resistance and resilience of crop yields to pest damage is to encourage the abundance and diversity of natural enemies (wild predators and parasites) that can control crop pests (Bommarco et al., 2013; Dainese et al., 2019). To achieve this, natural enemies require year-round vegetative resources for shelter and overwintering, nesting and breeding, and food resources in the form of pollen, nectar, and alternative prey (Gurr et al., 2017). However, continued habitat loss on agricultural land has reduced these resources and their support for beneficial organisms (Emmerson et al., 2016).

One method to increase the amount of semi-natural habitat on farmland is to establish sown or natural flower strips between, or bordering, rows of crop (Herz et al., 2019). Sown perennial flower strips can be designed to contain diverse vegetation with flowering plants blooming across the season year on year (Fountain, 2022). The increased structural complexity and density of diverse plant species can provide food and habitat niches for more species, which in turn can provide more prey for predatory insects ("the natural enemy hypothesis") (Randlkofer et al., 2010; Favarin et al., 2024). Flowering plants provide both pollen and nectar for a range of natural enemies, some life stages of which feed exclusively on these resources, for example adult Syrphidae (Van Emden and Harrington, 2017), and some use supplementally, including Coccinellidae, Araneae, and parasitoid wasps (He and Sigsgaard, 2019: Taylor and Pfannenstiel, 2008: Tylianakis et al., 2004). Flower margins can improve diversity and abundance of arthropods and natural enemies, both within the margins and adjacent crops, and can reduce pest abundance (Crowther et al., 2023). The use of, and spill-over between, flower margins and crop areas by natural enemies can vary between crops, management practices, and natural enemy groups (Fountain, 2022; Macfadyen and Muller, 2013). An increase in

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generalist natural enemies, reduction in crop pests, and reduction in crop damage as a result of flower strips have been recorded up to 50 m into cropped areas (Wyss, 1995; Woodcock et al., 2016; Howard et al., 2024). The relationship between increasing proximity to field edges with natural enemy abundance and pest regulation can vary, from positive through to negative (Boetzl et al., 2024). To encourage implementation of on-farm habitat creation, it is important to understand the value of flower margins as a habitat for natural enemies and whether they spill over into the crop to deliver important pest control services.

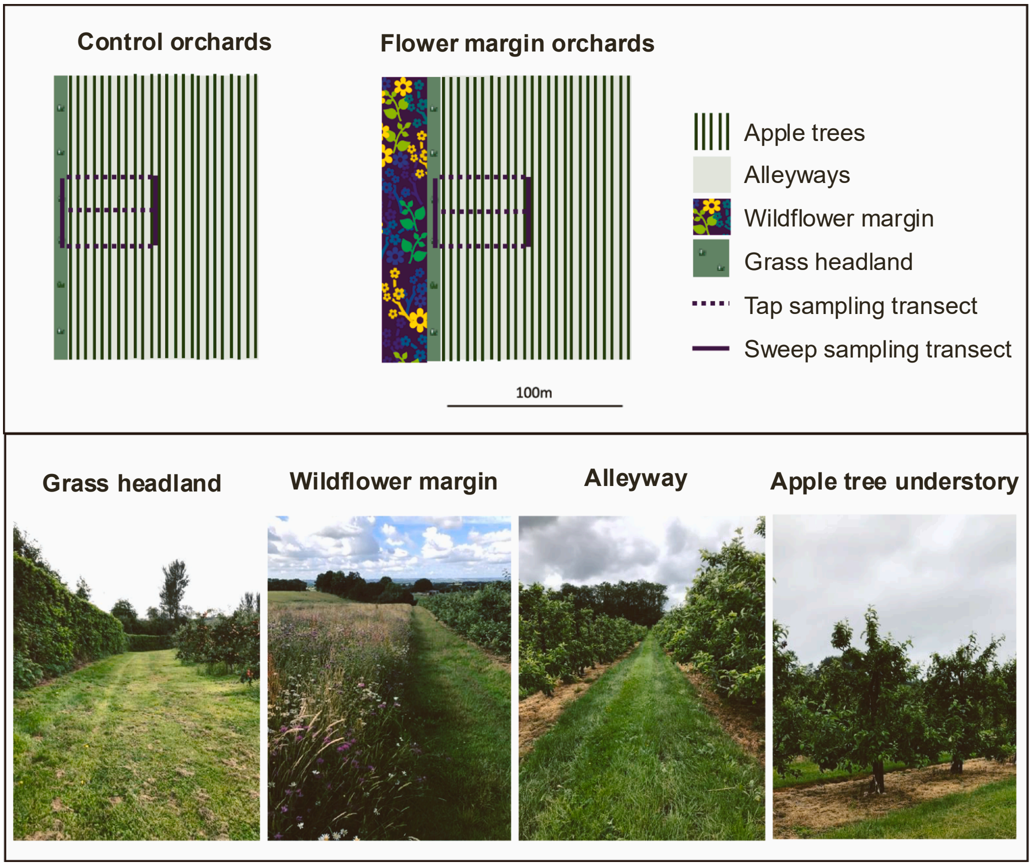
Compared to annual cropping, perennial cropping systems such as orchards can offer a more permanent and stable habitat for natural enemy communities, making them a suitable system for deploying high quality habitats such as perennial flower margins (Cahenzli et al., 2017). One of the main economic pests of apple (*Malus domestica*) in the UK is the rosy apple aphid, *Dysaphis plantaginea* (Passerini). This pest can reduce fruit size and cause malformed fruit, reducing marketable yield (Blommers et al., 2004). *Dysaphis plantaginea* can be suppressed by natural predators (Dib et al., 2010), including generalist predators which eat a wide range of prey, for example, Araneae, Opilliones, and predacious Hemiptera (family: Miridae, Anthocoridae, or Nabidae), and specialist predators which are adapted to consume a narrower range of prey: Coccinellidae, Dermaptera, Syrphidae, and Neuroptera (Campbell et al., 2017) and *Aphidoletes aphidimyza* (Cecidomyiidae). They can also be suppressed by parasitoid wasps (Dib et al., 2010), which reproduce by laying eggs inside the host aphid, killing the aphid upon pupation of the wasp (Le Ralec at el., 2010). A recent global meta-analysis revealed that flower margins in apple orchards increase the abundance of natural enemies without increasing pest populations (Judt et al., 2023). In apple orchards, resident natural enemies and levels of pest control have been shown to respond positively to the introduction of diversified vegetation in the form of flower margins (Herz et al., 2019). These flower margins can provide a refuge from insecticides for non-target organisms and are not extensively mown, which is common practice in orchard alleyways and headlands. The effects of perennial flower strips on apple damage specifically have been investigated with alleyway flower strips and trees in close proximity (up to 3 rows away), but much less is known about the effects of flower margins on trees further into orchards (Cahenzli et al., 2019; Jacobsen et al., 2022; Albert et al., 2017). An improved understanding of the local spatial dynamics of natural enemies is needed to optimise natural regulation of aphids in orchards (Santos et al., 2018).

Howard et al. (2024) found that flower margins next to an apple orchard reduced the spread of *D. plantaginea* on apple trees and reduced the percentage of trees with fruit damage up to 50 m into the crop. To explore the drivers behind this result, we investigated the effects of perennial flower margins on vegetation and natural enemies in conventional commercial apple orchards. This study aimed to compare the vegetation community and structure in the flower margins, orchard headlands and alleyways and to determine whether the presence of a flower margin changed the diversity, abundance, and community structure of natural enemies of *D. plantaginea* in orchard ground vegetation and apple trees. We hypothesised that the diverse vegetation in flower margins would increase the diversity and abundance of natural enemies within the margin, and that this community would spill-over into the orchard.

2. Methods

2.1. Study sites

Study sites have been previously described by Howard et al. (2024).


Control orchards

Flower margin orchards

Grass headland

Wildflower margin

Alleyway

Apple tree understory

Fig. 1. Typical layout of flower margin orchards (n = 5) and control orchards (n = 5) where natural enemies were sampled from apple trees via tap sampling and from ground vegetation via sweep sampling (above), with photographs of each habitat type (below). Vegetation was assessed across the same transects as the sweep sampling.

This study took place within ten commercial dessert apple orchards (Gala var.) located in Kent, UK (Howard et al., 2024, Appendix A). Five orchards, termed "flower margin orchards" were bordered by an established 2–5 year-old sown perennial flower margin, and five "control orchards" had only a permanent 4–5 m wide grass headland typically mown four times per year (Fig. 1). The average width of the flower margins was 15 m (SD = 9.6 m) (Howard et al., 2024, Supplemental Table 1). All orchards were conventionally managed using integrated pest management involving the use of aphicides such as flonicamid, spirotetramat and acetamiprid. The flower margin and control orchards were paired on the same farm so that the use of pesticides, nutrients, and mowing was consistent, and to minimise differences in soil type and aspect. Distances between orchards were 120–410 m. Flower margins were sown with perennial flowering species and grasses designed to offer multiple flowering times and flower shapes, and maximise pollen and nectar resources (as detailed in Carvell et al., 2022). To encourage earlier flowering, and to keep weeds under control, all flower margins were cut to 8–10 cm annually in autumn, and the cuttings removed (Carvell et al., 2022) and no fertilizer or herbicide was applied.

2.2. Orchard vegetation assessment

Percentage cover of each plant group and bare ground was recorded for 3–5 randomly placed 0.25 m^2 quadrats along each sweep transect. The wildflower key (Rose and O'Reilly, 2006) and Pl@ntNet (Joly et al., 2016) were used for plant identification. Vegetation was assessed in three areas: 1) the headland or wildflower margin, 2) the alleyways between apple tree rows (inter-row area) 50 m from the orchard edge, and 3) the understory area immediately beneath the apple trees 50 m from the orchard edge (Fig. 1). Sward height was recorded from the corner of each quadrat using a measuring tape and then averaged. Vegetation assessments were conducted during the summer of June 2021, and July 2022.

2.3. Assessment of natural enemies in ground vegetation

Natural enemies in orchard ground vegetation were surveyed using sweep nets (46 cm diameter, Watkins and Doncaster E679). The net was moved in a figure-of-eight sweeping motion whilst walking at a constant pace. This method was used both in the central alleyway between apple tree rows (50 m from the orchard edge), and also in the flower margins, or equivalent grass headlands (Fig. 1). Specimens were collected from the net using a mechanical pooter (Watkins and Doncaster, E7081). Due to the large volume of specimens collected, the sampling intensity varied from year 1 to year 2 of the study. A 40 m transect was walked whilst sweeping in 2021, and a 2 m transect in 2022. Surveys were carried out when foliage was dry and winds were < 3 (Beaufort scale). All collected specimens were stored in 70 % ethanol. This was repeated four times per growing season in April, May, June, and August to cover the active periods of important natural enemies. Arthropods were identified using a light microscope to the taxonomic levels specified in Table 1.

2.4. Assessment of natural enemies on apple trees

Natural enemies in the orchard trees were surveyed using tap-sampling. For each tree, one randomly chosen horizontal branch was tapped three times consecutively with a stick over a white tray (45 cm×35 cm) to catch dislodged arthropods (McKerchar et al., 2020). Natural enemies of *D. plantaginea* (Table 1) were collected from the tray using a moist paintbrush and stored in 70 % ethanol. Tap sampling was carried out on three adjacent trees, on three transects located perpendicular to the orchard edge at each of the following distances from the orchard edge; 0, 5, 10, 20 and 50 m (45 trees per orchard) (Fig. 1). Foliage was dry and winds were < 3 (Beaufort scale) when sampling was carried out. Assessments were repeated three times per growing season in 2021 (April, June, and August), and four times in 2022 (April, May, June, and August) to cover the most active period of pests and natural enemies. Arthropods were identified to the taxonomic levels specified in Table 1. Natural enemies frequently aggregate in areas of high prey abundance so abundance of *D. plantaginea* was assessed at three-week intervals from April to July in 2021 and 2022 during the apple-growing season using systematic searches of 45 trees per orchard (Howard et al., 2024). Ten areas on one side of each tree were searched for the presence of *D. plantaginea* on buds, flower clusters with leaves, rosettes of leaves, long shoots and fruitlet clusters (tree areas), depending on the phenological stage of the tree (Howard et al., 2024).

Table 1
Taxonomic level of identification of sampled natural enemies of *D. plantaginea* (Dib et al., 2010; Campbell et al., 2017).

Common name	Taxonomic group	Feeding behaviour
Ladybirds	Family: Coccinellidae	Specialist
Earwigs	Order: Dermaptera	Specialist
Hoverfly larvae	Family: Syrphidae	Specialist
Predatory bug adults[a]	Order: Hemiptera, Family: Anthocoridae, Miridae, Nabidae	Generalist
Lacewing larvae	Order: Neuroptera	Specialist
Predatory midge larvae	*Aphidoletes aphidimyza*	Specialist
Solitary and parasitoid wasps	Order: Hymenoptera	Note[b]
Harvestmen	Order: Opiliones	Generalist
Spiders	Order: Araneae	Generalist

[a] Manual identification to these Families is not possible for nymphs. [b] Wasp species can be either parasitic or predatory to aphids and all micro-Hymenoptera were included in the diversity calculations and community analyses as a broad group (Graham, 1989 p13; Boys, 2014; Dib et al., 2010)

2.5. Statistical analysis

Statistical analyses were carried out in R 4.3.0 for Mac (R Core Team, 2023). To compare communities of plants and natural enemies across habitats we used Permutational Multivariate Analysis of Variance (PERMANOVA) based on Bray-Curtis dissimilarity (suited to abundance data with zero values) using the vegan package (Oksanen et al., 2022). To account for repeated measures, vegetation community data were averaged (mean) for each repeat, and sampling years were included as strata. Similarly, for natural enemy communities, data were averaged across distance (tap data), and sampling rounds were included as strata. Data from each sampling year were analysed separately. Pairwise differences between flower margin and control orchards were further explored using pairwise PERMANOVA tests with Holm's adjustment with the devtools and pairwiseAdonis packages (Wickham et al., 2022; Martínez, 2017).

To account for the experimental design of nested repeated measures within a transect, orchard, and pair of orchards, linear mixed models were used with the lme4 package for mixed effect modelling (Bates et al., 2015) (Table 2). For count data, Poisson models were used, or negative binomials in the case of overdispersion. To compare the diversity of natural enemies in different habitats, we used the Shannon diversity index since it can be used to compare the diversity of communities of different sizes (Magurran and McGill, 2010). For diversity index, Gaussian models were used. Natural enemy abundances in the apple trees (tap data) were summed across each of the three trees per transect per distance to improve model fit. The assumptions of the GLMM were tested, including linearity, response distribution, independence, and multicollinearity of predictors. Models were also tested for overdispersion where appropriate. Tukey-adjusted multiple comparisons were used to identify the differences driving significant interactive model terms using the emmeans package (Lenth, 2023). Year was used as a fixed effect where possible, as a random effect where sampling effort was uneven between years, and separate models were created for each

Table 2
Model building specifications, where a ● symbol indicates where fixed and random effects were applied to each response variable (interactive terms are grey). 'Treatment' fixed effect refers to presence or absence of a perennial flower margin. Random effects were nested in the order in which they appear in the table and 'Pair' refers to the experimental design whereby each treatment orchard was paired with a control orchard.

			Fixed Terms							Nested Random Terms		
Response	**Sampling Methods**	**Distribution**	**Treatment**	**Distance**	**Area**	**Year**	**Round**	**Aphid[1] abundance**	**Abundance of group in the margin/ headland**	**Year**	**Pair**	**Orchard**
Diversity of natural enemies in ground vegetation	Sweep	Gaussian	○		○		○			●	●	
Abundance of generalist predators in ground vegetation	Sweep	Negative binomial	○		○		●			●	●	
Abundance of specialist predators in ground vegetation	Sweep	Poisson	○		○		●			●	●	
Abundance of specialist predators in apple trees	Tap	Poisson	○	○		●	●	●			●	●
Abundance of generalist predators in apple trees	Tap	Poisson	○	○		○	○	●			●	●
Diversity of natural enemy taxa in apple trees	Tap	Gaussian	○	○		○	○				●	●
Abundance of specialists in apple trees	Sweep	Poisson	○	●			●	●	○	●	●	
Abundance of generalists in apple trees	Sweep and tap	Poisson	●	●			●		●[2]	●	●	

[1] Total number of aphids per tree was scaled to match the other fixed effects in the model. This was done using a multiplication of 0.01.
[2] Abundance in the margin/headland was scaled and centred (Schielzeth, 2010).

sampling year to aid model convergence where needed (Table 2). The random effect structure was simplified where necessary to avoid over-fitting (Table 2). We modelled generalist and specialist predators separately since specialists rely more heavily on, and are more closely adapted to, aphid prey so are likely to show stronger aphid density dependence (Table 1) (e.g. Campbell et al., 2017).

3. Results

3.1. Orchard vegetation

The plant community composition was significantly different between habitat types ($F = 10.55$, df = 5,49, $P = 0.001$, Fig. 2). The vegetation community in the flower margins was significantly different from the understory areas below the apple trees (Supplemental Table 2). By contrast, in both the flower margin and control orchards, the vegetation community of the understory and alleyway areas of the orchard were similar (Fig. 2, Supplemental Table 2). The vegetation in the alleyway area was similar to that in the headland (Fig. 2, Supplemental Table 2). In the summer, grasses comprised 30.1 % (SD = 35.2) of cover in the flower margins, and 78.1 % (SD = 24.9) of the cover in the headland of control orchards. The alleyways had 81.8 % (SD = 28.3) grass cover in flower margin orchards and 79.7 % (SD = 23.4) in controls. The mean percentage cover of plant groups can be found in Supplemental Table 1. Common flowering species were birds foot trefoil, (*Lotus corniculatus*) and black knapweed, (*Centaurea nigra*) in the flower margin, white clover (*Trifolium repens*) in the headland and alleyway, and broad leaved willow herb (*Epilobium montonum*) and creeping buttercup (*Ranunculus repens*) in the understory. The mean sward height was 13 cm (SD = 5) in alleyways of flower margin orchards, 12 cm (SD

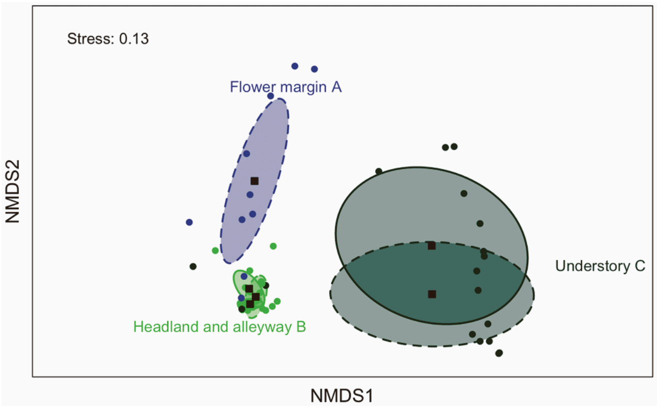


Fig. 2. Non-metric multidimensional scaling ordination of relative abundance of vegetation (summer 2021 and 2022) in orchards with and without flower margins (dotted and solid elipses respectively) across different habitat types (based on Bray-Curtis similarity). Ellipses show one standard deviation region surrounding the centroid (mean of the group), represented by a black square. Greater overlap of ellipses represents greater similarity between communities. Circular points represent the community at that location for each site (n = 5 flower margin orchards, n = 5 controls) and each year (n = 2). Colours and letters A-C denote significant differences between habitats (PERMANOVA).

= 5) in alleyways of control orchards, 10 cm (SD = 6) in headlands, and 72 cm (SD = 26) in flower margins.

3.2. Natural enemies

3.2.1. Diversity of natural enemies in the ground vegetation

In total, 11,922 arthropods were collected from the ground vegetation. In 2021, there were 184 specialist predators of aphids (Coccinellidae, Dermaptera, Syrphidae, and Neuroptera) (12 %), and 1329 generalist predators (Araneae, and predacious Hemiptera) (88 %). In 2022, when sweep-sampling effort was reduced, 10 individuals were specialists (5 %) and 184 were generalists (95 %) (Fig. 3). Shannon diversity of natural enemies in the orchard ground vegetation was significantly higher in orchards with flower margins compared to control orchards ($\chi^2 = 55.846$, df = 1, $P < 0.05$) (Fig. 4). Diversity was also significantly higher in the headland/margin area compared to the central alleyway ($\chi^2 = 13.0$, df = 1, $P < 0.001$) (Fig. 4), and was significantly different between months, highest in June and lowest in April ($\chi^2 = 57.213$, df = 3, $P < 0.001$) (Fig. 4).

3.2.2. Abundance of predators in the ground vegetation

In the ground vegetation, there was a significant interactive effect of presence of a flower margin and habitat type (headland/margin or central alleyway) on abundance of both specialist ($\chi^2 = 12.784$, df = 1, $P < 0.001$) and generalist predators ($\chi^2 = 17.782$, df = 1, $P < 0.0001$). Specifically, there was a significantly higher abundance of both specialist and generalist predators in the flower margin compared to the control headland (mean = 6.6 and 0.7 respectively), yet there was no significant difference in abundance between flower margin and control orchards in the central alleyways (Fig. 5, Supplemental Table 3). There was also a significant effect of sampling round where abundance was highest in June and lowest in April (specialists: $\chi^2 = 196.684$, df = 3, P = 0 < 0.001, generalists: $\chi^2 = 58.824$, df = 4, $P < 0.001$.

3.2.3. Community of natural enemies in the ground vegetation

In 2021, the flower margin had a significantly different natural enemy community composition compared to the headland and the central alleyways in control and treatment orchards (Fig. 6, Supplemental Table 4). In 2022, there was no significant difference between the communities of natural enemy taxa across orchard habitats (Fig. 6, $F = 1.578$, $P = 0.051$).

3.2.4. Diversity of natural enemies in the orchard trees

In total, 2296 natural enemies were collected from the orchard trees. In 2021, 105 of those were specialist predators of aphids (Coccinellidae, Dermaptera, Syrphidae, and Neuroptera) (11 %), and 821 were generalist predators (Araneae, predacious Hemiptera and Opilliones) (89 %). In 2022, 44 were specialists (3 %) and 1326 were generalists (97 %). There was a significant interactive effect of the presence of a flower margin, year, and round on the Shannon diversity of natural enemies in the orchard trees ($\chi^2 = 100.154$, df = 10, $P < 0.001$) where diversity was lower in August 2021 in flower margin orchards compared with controls (Supplemental Table 3). Shannon diversity significantly decreased with increased distance from the orchard edge ($\chi^2 = 19.476$, df = 4, $P < 0.001$).

3.2.5. Abundance of predators in the orchard trees

There was an interactive effect of presence of a flower margin and distance from the orchard edge ($\chi^2 = 12.113$, df = 4, P < 0.05), where there were fewer specialist predators at 10 m in flower margin orchards compared to controls (Supplemental Table 3). Additionally, there were significantly more specialist predators on apple trees where there was a higher number of aphids ($\chi^2 = 8.5194$, df = 1, $P < 0.01$). There were significantly more specialist predators in 2021 than in 2022 ($\chi^2 = 31.028$, df = 1, $P < 0.001$) and increasingly more in each round ($\chi^2 = 94.564$, df = 3, $P < 0.001$).

There was no significant effect of presence of a flower margin or abundance of aphids on the abundance of generalist predators in the apple trees ($\chi^2 = 1.193$, df = 1, P =275; $\chi^2 = 1.836$, df=1, P =0.175, respectively). There were significantly more generalists in 2022 ($\chi^2 = 58.233$, df = 1, P < 0.001) and fewer with increasing distance from the orchard edge ($\chi^2 = 9.540$, df=4, P < 0.05). There was also a significant effect of round, with abundance highest in August and lowest in April ($\chi^2 = 30.040$, df = 3, $P < 0.001$).

3.2.6. Community of natural enemies in the orchard trees

There was no significant difference between the natural enemy communities in the apple trees in flower margin orchards compared with controls in either 2021 ($F = 0.30$, $P > 0.05$) or 2022 ($F = 0.14$, $P > 0.05$) (Fig. 6).

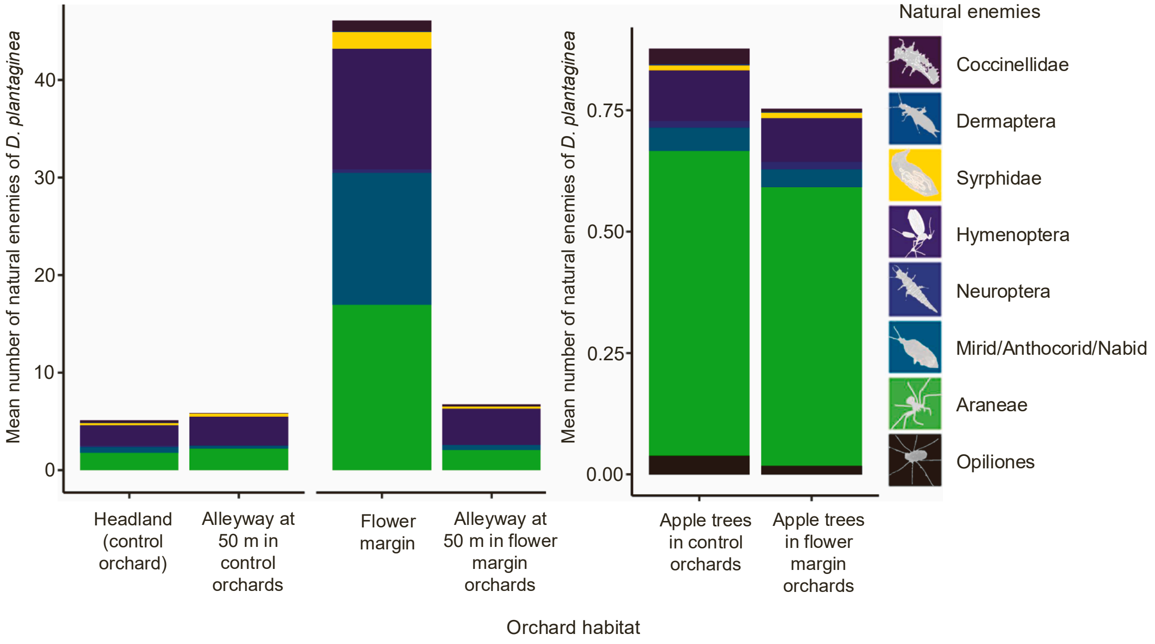


Fig. 3. Mean abundance of groups of natural enemies of *D. plantaginea* collected in different orchard habitats across 4 rounds in both 2021 and 2022.

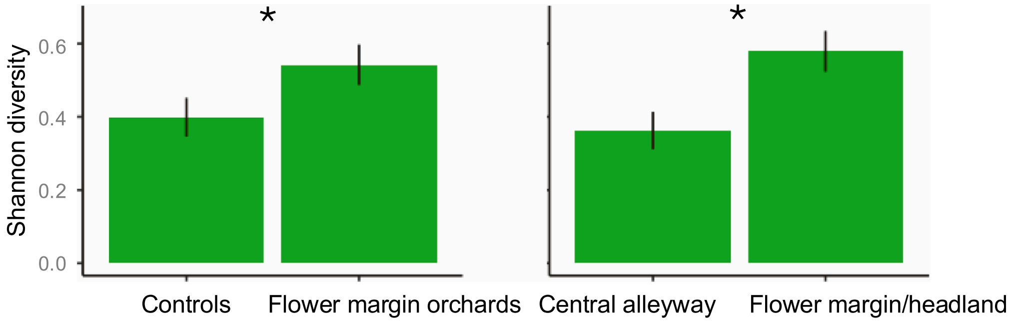


Fig. 4. Shannon diversity index of natural enemies of *D. plantaginea* in flower margin orchards compared with control orchards (left) and in the orchard alleyway compared to the flower margins and control headland (right). Stars denote significance, $P < 0.05$.

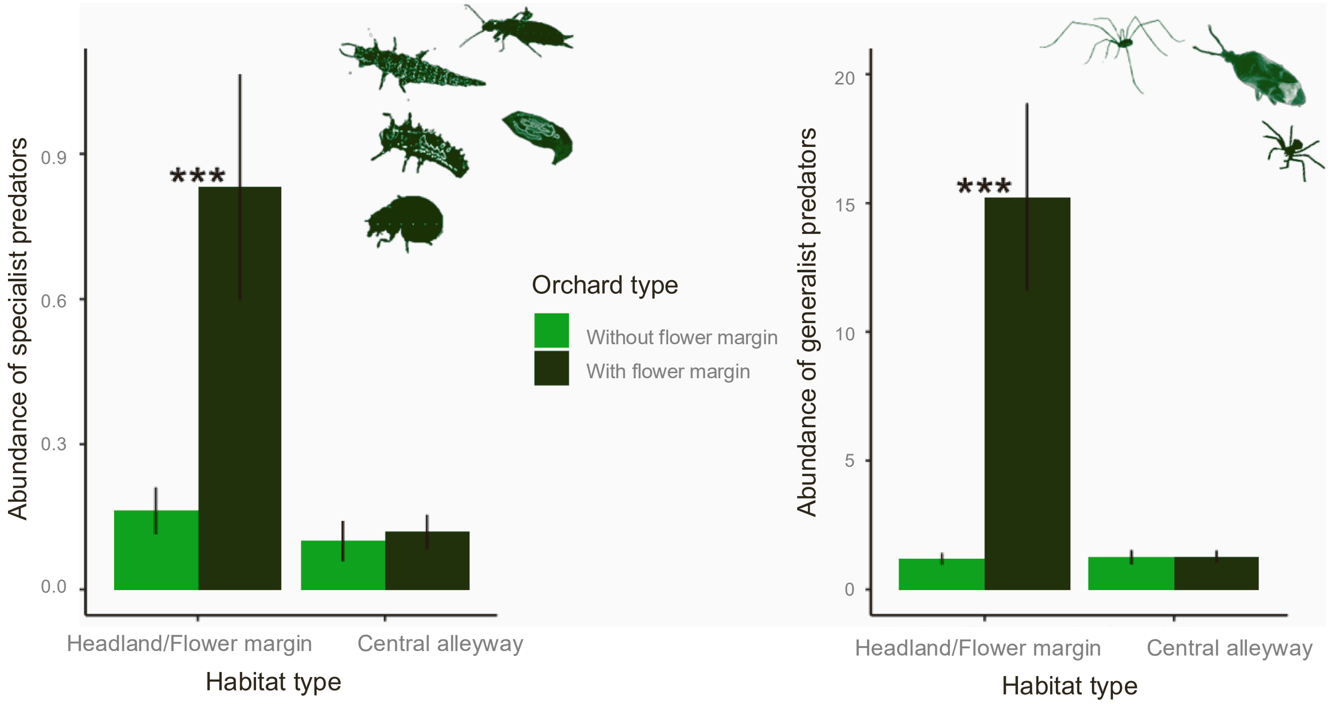


Fig. 5. Mean abundance of specialist (left, n = 194) and generalist (right, n = 1513) predators of *D. plantaginea* in the central alleyways compared to the flower margin or headland in flower margin orchards compared to control orchards across four rounds in 2021 and 2022. Stars denote significance, $P < 0.0001$.

4. Discussion

4.1. Orchard vegetation

The perennial flower margins showed an increased plant species richness compared to the headlands in the control orchards. By contrast, the plant community in the alleyways 50 m from the orchard edge in both types of orchard, and in the headland of the control orchards, were similar. Additionally, the plant communities found in the understory, directly below the trees, were similar in the flower margin and control orchards. This suggests that any effects of the flower margins were from the margins themselves rather than due to spill-over or drift of groups of plants from the flower margins into other orchard habitats. The differences in plant communities between the flower margin, understory, and headland/alleyways are highly likely to be due to the differences in management practices; the margin was sown and was cut once annually, the headlands and alleyways were regularly mown, and the tree understories consisted of spontaneous vegetation and were treated with herbicide 3–4 times across the season having received some of the apple tree nutrient sprays. As previously reported by Pfiffner et al. (2019), the flower strips had a different plant community than the alleyways. In other crop systems, sown flower margins can increase plant species richness, cover, nectar/pollen supply (Schmidt et al., 2022), sward height (Lundin et al., 2023) and structure (Favarin et al., 2024) compared to control borders. Additionally, although the longevity of flower margins is uncertain since few studies have been longer-term (for 3+ years) (Gontijo et al., 2013; Herz et al., 2019; Bostanian et al., 2004; Cahenzli et al., 2017, 2019), our study demonstrates that margins continued to have a rich and different plant community five years post sowing.

4.2. Natural enemies in the flower margin and headland

The flower margins had a significantly different natural enemy community composition compared to the more frequently mown headlands and the central alleyways in 2021. Additionally, there was a significantly greater abundance of both specialist and generalist aphid predators in the flower margin compared to the control headland. We found a 412 % increase in total number of generalists in the flower margin compared to the control headland, and 1183 % increase in specialists. Campbell et al. (2017) in a similar study reported that the total natural enemy richness and abundance of generalist predators were

Fig. 6. Non-metric multidimensional scaling ordination of relative abundance of natural enemies of *D. plantaginea* (in April, May, June/July, and August) for habitats (headland, flower margin, and 50 m alleyway) in orchards with and without flower margins (dotted and solid elipses respectively) (based on Bray-Curtis similarity), sampled from orchard habitats via sweep-netting (top) and tap sampling (bottom). Ellipses show one standard deciation surrounding the centroid (mean of the group), represented by a black square. Greater overlap of ellipses represents greater similarity between communities. Colours and letters A & B denote significant differences (PERMANOVA). Circular points represent the community at that habitat type for each site (n = 5 flower margin orchards, n = 5 controls) and each sampling round (n = 4).

90 % higher in flower strips designed for natural enemies compared to control areas in cider apple orchards (Campbell et al., 2017). These flower strips specifically included nectar-producing species which can be accessed by arthropods without highly specialised nectar-feeding mouthparts, including natural enemies of aphids (Campbell et al., 2017). Hence, the increase in natural enemy abundance could be due to the increase in plant richness since this increases the diversity of physical plant characteristics including flowering phenology and nectar tube depth, catering for a more diverse arthropod fauna (Junker et al., 2013; Favarin et al., 2024). The increased plant richness, forb cover, and sward height in the flower margins also provides arthropods with increased shelter, refuge from pesticides, breeding sites, overwintering sites, moderated microclimate, and different food sources such as pollen, nectar, and alternative prey (Landis et al., 2000; Favarin et al., 2024), and also structure for spider webs (Solomon et al., 2000). Even those natural enemy groups which are considered exclusively predatory can directly use the nectar and pollen provided by flower strips (Herz et al., 2019). Our results suggest that the flower margins were offering resources not provided by the apple trees, alleyways, and headlands, and that both specialist and generalist natural enemies were supported by the flower margins.

4.3. Natural enemies in central alleyways and apple trees

Overall, the Shannon diversity of natural enemies in the ground vegetation was significantly higher in flower margin orchards compared to control orchards, including in the ground vegetation of the central alleyways. Since the central alleyways were 50 m from the orchard edge, this meant the presence of a flower margin had far-reaching effects on the natural enemy community in the orchard. This, along with the reduction in spread of aphids on trees and incidence of fruit damage in these flower margin orchards found in a previous study (Howard et al., 2024), suggests that natural enemies can spill-over from the margin up to 50 m into the crop area. A greater diversity of natural enemies could improve orchard resilience to potential changes in pest pressure from climate change (Oliver et al., 2015).

However, in the apple trees themselves, there was no significant difference between Shannon diversity or total abundance of specialist or generalist predators between flower margin and control orchards except that there were fewer specialist predators at 10 m in flower margin orchards. There was also no significant difference between the natural enemy communities in the apple trees between flower margin and control orchards. Studies to date have often, but not always, found spill-over of beneficial insects from areas of diverse vegetation into the crop. For example, Campbell et al. (2017) found an increased abundance of generalist predators on apple trees with flower strips. Perhaps in our study the identification of natural enemy taxa in apple trees to only nine broad groups was not sufficiently resolved to pick up on differences in natural enemies between habitats, including differences in species richness, diversity or the abundance of particular aphid natural enemies. For example, without species level identification, all predatory Heteroptera were were classified as generalists and as such grouped with other generalists including Araneae. However, some heteropteran species, such as *Anthocoris nemorum* (L.) and *Atractotomus mali* (Meyer-Dur) are more specialised feeders of *D. plantaginea* (Porcel et al., 2018). Campbell et al. (2017) also used broad natural enemy groups and reported higher abundances of generalist enemies in apple trees adjacent to floral alleyway strips. Jacobsen et al. (2022), recording natural enemies found during visual searches for *D. plantaginea,* reported overall increased predator abundance in orchards with a flower margin compared with control orchards, but did not find any differences in diversity despite species-level predator information. Manual identification is labour intensive but molecular identification is becoming more attainable and could aid collection of species-level data in the future (Quandahor et al., 2024).

A recent global meta-analysis revealed that flower margins in apple orchards increase abundance of natural enemies without increasing pest populations (Judt et al., 2023), although the more mobile natural enemies do not always respond directly to habitat management measures such as flower strips and are not always found moving between apple trees and floral strips (Herz et al., 2019), which might also be true in this case, for example, for hoverflies (Howard et al., 2024). In our study, perhaps some natural enemy groups on the trees were under-sampled, for example parasitoid and solitary wasps which may be better sampled using suction sampling or glue traps rather than tap sampling (Hambäck et al., 2020), or Dermaptera which are more active at night rather than in the day (Niedobova et al., 2020). Further studies are needed to improve understanding of the local spatial dynamics of natural enemies to optimise natural regulation of aphids in orchards (Santos et al., 2018), perhaps using a mark-release-recapture study such as that by Zhang et al. (2022) which provided direct evidence of natural enemy movement between flowering plants and apple trees in organic orchards. Another alternative method could perhaps involve close monitoring of marked colonies of aphids at frequent intervals (e.g. weekly) (Dib et al., 2010). This could also include experimental exclusion of the predators via a mesh (Woodcock et al., 2016) to increase the chances of revealing the complex population dynamics and natural enemy activity. It should be noted that ants can form a mutualistic relationship with aphids which can involve protection of the aphids from predators by the ants (Katayama et al., 2013). Artificial provisioning of sucrose solution can significantly reduce *D. plantaginea* populations in apple orchards by reducing ant attendance and increasing enemy pressure (Nagy et al., 2015). As previously discussed by Howard et al. (2024), the potential interaction of ants with aphid predation rates means that the influence of ant mutualisms and how this is affected by the nectar provided by flower margins should be investigated further.

5. Conclusions

Flower margins had a different vegetative community with increased plant richness compared to the other orchard habitats and supported an increased abundance of natural enemies compared to more typical orchard grass borders. This suggests that any effects of the flower margins were from the margins themselves rather than due to spill-over or drift of groups of plants from the flower margins into other orchard habitats. Despite the lack of spill-over of plant species into the central alleyways, there was an increased Shannon diversity of natural enemies in the central alleyways of flower margin orchards compared with controls, which suggests spill-over of natural enemies from the flower margins can reach up to 50 m from the orchard edge. Despite these effects, we did not find evidence of broad differences between natural enemy taxa abundance, diversity, or community structure on the apple trees themselves. However, we know from previous studies that these flower margins reduced pest pressure and incidence of fruit damage by *D. plantaginea* up to 50 m from the orchard edge in a year with high incidence of *D. plantaginea*, but the mechanism behind this is still unclear and could perhaps be linked to the mobility of certain natural enemy groups or mutualistic relationships with ants. A better understanding of this mechanism could help to optimise the use of flower margins for sustainable pest suppression.

CRediT authorship contribution statement

Charlotte Howard: Writing – original draft, Visualization, Formal analysis, Conceptualization. **Michael P.D Garratt:** Writing – review & editing, Funding acquisition, Conceptualization. **Paul J Burgess:** Writing – review & editing, Funding acquisition, Conceptualization. **Claire Brittain:** Writing – review & editing, Funding acquisition, Conceptualization. **Michelle T Fountain:** Writing – review & editing, Funding acquisition, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2024.109327.

Data availability

Data available from the University of Reading Research Data Archive (https://doi.org/10.17864/1947.001355).

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