University of Reading

Evaluating the use of perennial flower margins for sustainable aphid pest control services

Doctor of Philosophy Thesis

Sustainable Land Management

School of Agriculture, Policy and Development

Charlotte Howard

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Declaration

I confirm that this is my own work and the use of all material from other sources has been properly and fully acknowledged.

Charlotte Howard

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Abstract

Apple is a globally important crop that is susceptible to many pests and diseases. Promoting natural pest control could increase crop yield and quality and reduce reliance on harmful pesticides. The addition of nectar and pollen rich floral habitat is a commonly used management practice in agricultural ecosystems. This practice has been demonstrated to increase the abundance of predators and parasites of orchard pests (natural enemies), although there is less evidence of the extent to which this could improve pest control services, yield or profit. This thesis aimed to evaluate the ecological and economic effects of perennial flower margins in UK apple orchards for control of an economically significant global crop pest, *Dysaphis plantaginea*, rosy apple aphid.

Empirical data collected over two years from different locations in commercial orchards, either with or without flower margins, revealed that flower margins provided a distinct plant community, and their presence increased natural enemy diversity in orchard ground vegetation compared to orchards without flower margins. However, there was no evidence of broad differences between natural enemy taxa abundance, diversity, or community structure on the apple trees. Despite this, there was reduced spread of *D. plantaginea* on aphid infested trees in orchards with flower margins*,* and subsequently a reduced number of trees with fruit damage, from 80% to 48%, with effects seen up to 50 m from the flower margin during a year with higher aphid infestation levels. The reduction in the spread of *D. plantaginea,* and percentage of trees with apple damage, varied between the two years and at different distances from the orchard edge. An economic model of these benefits when compared to the costs associated with flower margins, revealed that flower strips bordering the crop area could be a promising economic investment for *D. plantaginea* control if they do not replace apple trees. If non-crop land were not available and apple trees were being replaced by the flowers, establishment of a flower strip in the centre of an orchard instead of the edge, could recoup opportunity costs. The economic model showed that installing a flower strip in the centre of the orchard for 5 years could return £2997 per hectare per year if aphid infestation levels were high. However, the results suggest that this is context-dependent, and a similar flower strip could cost £210 if placed on crop land as a margin instead of in the orchard centre.

This work is the first to demonstrate a reduction in fruit damage by *D. plantaginea* at harvest in orchards with a flower margin compared to a control orchards with mown primarily grass margins, and one of few to evaluate the economic effect. The results highlight the potential for established perennial flower margins to deliver orchard-scale, sustainable, economically viable *D. plantaginea* control benefits, and provides insights into the spill-over distance of the effects. Flower margins could be used as a tool to support more sustainable production in apple orchards. The factors that influence the extent of these potential benefits are discussed.

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1 Introduction

1.1 Apple production

Apple, *Malus domestica*, is the third most widely-produced fruit, globally, of which 96 million tonnes were produced in 2022 (Food and Agricultural Organization, 2024b). Apples are grown in over 90 countries with global production steadily increasing, particularly in China, the biggest producer (Food and Agricultural Organization, 2024a) (Figure 1). In the United Kingdom in 2022, dessert apple trees covered approximately 5900 hectares of the total 32000 hectares of fruit planting area and produced approximately 168,000 tonnes of apples (fresh weight) at a value of £152 Million (DEFRA, 2024).

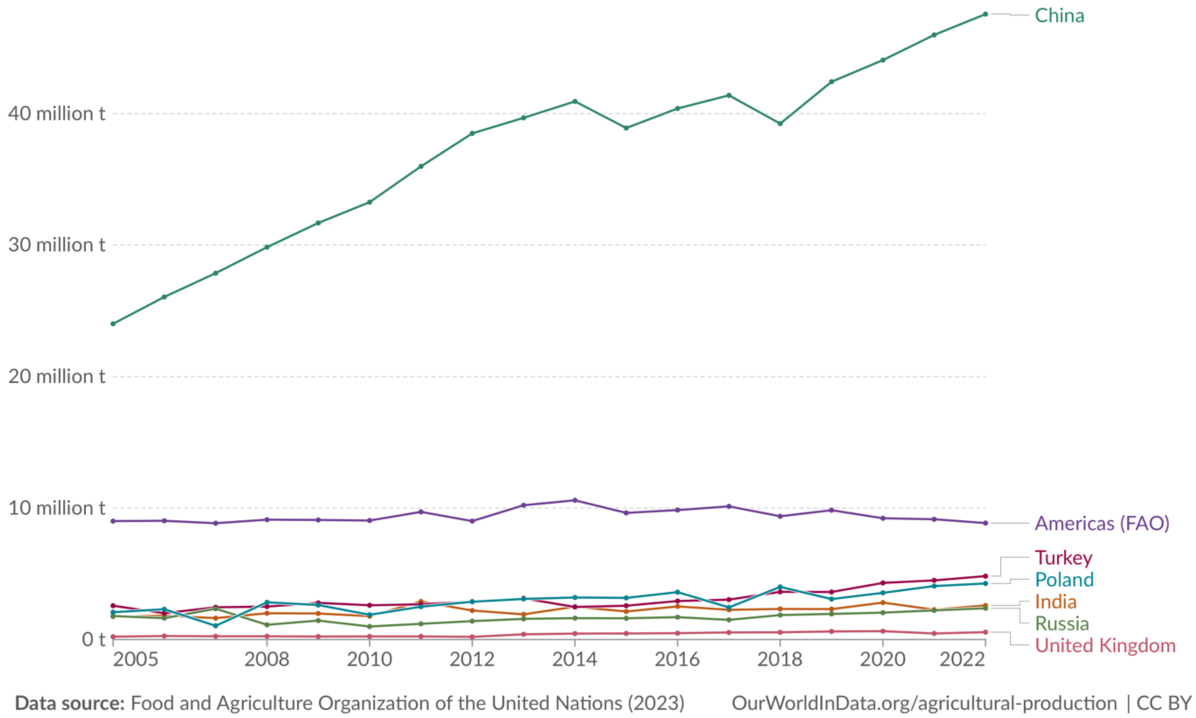

Figure 1: Trends across the top apple production regions and the United Kingdom from 2005-2022 (Food and Agricultural Organization, 2024a).

Over the last 70 years, apple orchards have become higher-density through planting rows, 3.5 to 4 m apart, consisting of dwarf trees trained onto wire with shorter, more numerous branches (Figure 2) to optimise yield and reduce pesticide spray-loss (Damos et al., 2015; Sander et al., 2019). Both conventional and organic apple production require regular use of plant protection products to obtain a reliable and economically viable yield (Daniel et al., 2018) (Section 1.4). Tree fruit production has shifted towards reducing the use of broad-spectrum pesticides, and instead using more selective products in combination with cultural control practices (Shaw et al., 2021) to reduce detrimental environmental and human health effects (Barzman et al., 2015). The challenge with intensive cropping systems will be to sustainably maintain this high productivity to feed a growing population (Connor and Mínguez, 2012) in the face of an increasingly unpredictable climate (Dalhaus et al., 2020).

Figure 2: Photographs showing a typical post and wire production system (left) and typical rows of commercial Gala apple trees in the United Kingdom (right) (taken by author).

1.2 Major apple pests

Furmanczyk et al. (2022) report that there are 11 major arthropod pests of apple in Europe. In a survey of 250 apple and pear growers across 17 European countries it was found that over half of participants gave the following as the most relevant pest species to apple production: *Cydia pomonella* (codling moth), *Dysaphis plantaginea* (rosy apple aphid), *Hoplocampa testudinea* (apple sawfly), and *Eriosoma lanigerum* (woolly aphid) (Figure 3) (Furmanczyk et al., 2022). *Cydia pomonella* and *Hoplocampa testudinea* cause direct damage to apples by burrowing through the fruit (Kadoić Balaško et al., 2020; Blatt and Hiltz, 2021) whereas both aphid species are sap-sucking pests (Blommers et al., 2004;

Sherwani et al., 2016). *Eriosoma lanigerum* lives on the host apple tree for the duration of its life cycle, feeding from both the stem and roots, creating galls, which is most harmful to nursery and young trees (Adhikari, 2022). It can also infest crab apple, almond, hawthorn, pear, and quince (Sherwani et al., 2016). *Eriosoma lanigerum* causes contamination of the fruit with the sugars it excretes ('honeydew'), which can encourage the growth of sooty mould, as is also true for the second most damaging pest, *D. plantaginea* (Warren and Schalau, 2014). *Dysaphis plantaginea* can infest new leaves, causing direct damage to nearby buds and developing fruit (Blommers et al., 2004) (Section 1.3.2).

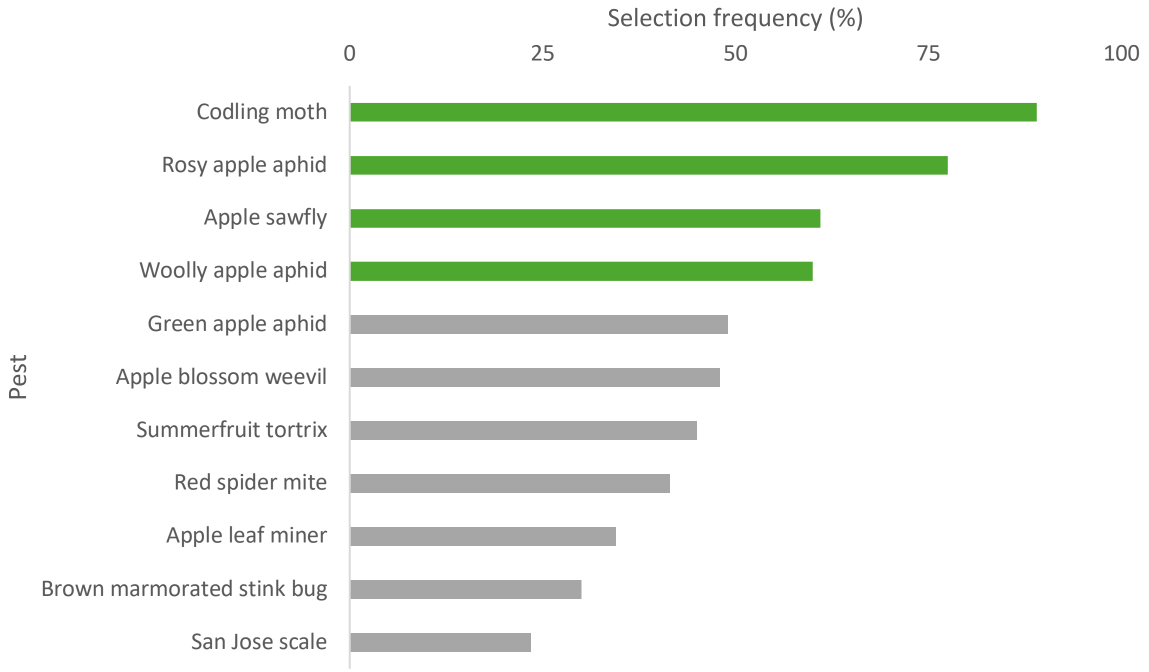

Figure 3: The ranking of pests occurring in apple orchards according to a survey of 250 practitioners across 17 European countries (including 155 apple and pear practitioners with conventional and organic growing experience) (adapted from Furmanczyk et al., 2022).

1.3 Rosy apple aphid, *Dysaphis plantaginea*

1.3.1 Distribution and lifecycle

Dysaphis plantaginea is a global pest of apple with a widespread distribution across temperate regions of the Northern Hemisphere, particularly Europe, North America and Asia (Figure 4). This species reproduces asexually, and sexually, and requires two alternate host plants to complete its lifecycle (Blommers et al., 2004). The eggs hatch in spring on the primary host plant, *Malus domestica* (apple), to give rise to several wingless generations which birth live young (Blommers et al., 2004). Large colonies may form in apple trees from late spring to early summer (NIAB, 2024).

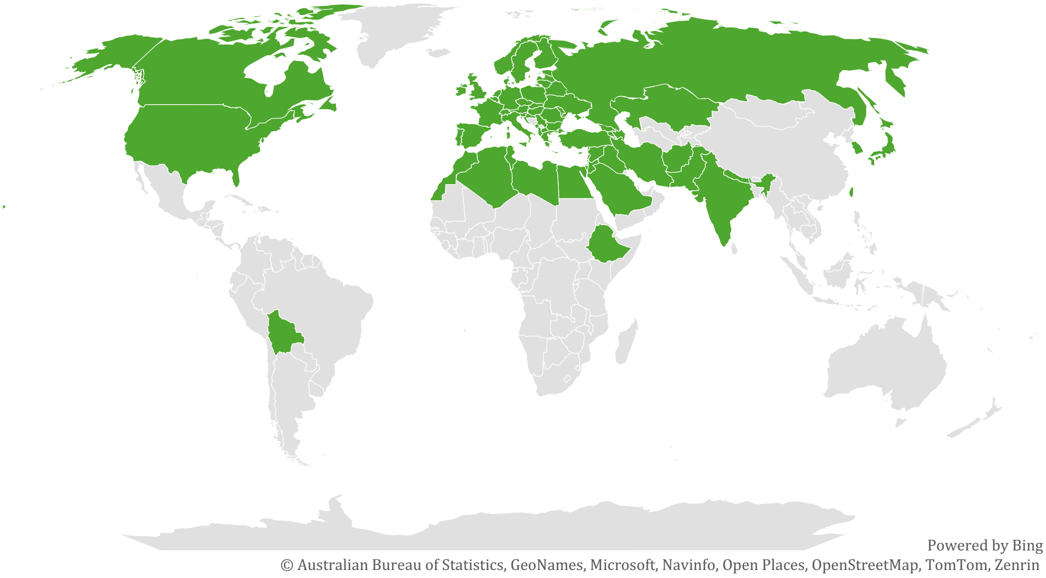

Figure 4: Extant global distribution of *D. plantaginea* (highlighted) (CABI (2024) summary data).

From late June onwards, *D. plantaginea* migrates from apple to the secondary host plant, *Plantago spp* (plantain), to produce further generations (Blommers et al., 2004). When day-length begins to decrease, around apple harvest, sexual reproduction of *D. plantaginea* produces winged females, which followed by males, migrate back to apple to mate and produce fertile eggs which overwinter on the apple tree (Blommers et al., 2004). These sexual morphs do not usually cause damage to the tree.

1.3.2 Damage

Dysaphis plantaginea removes sugars from the sugar transport system of the plant (phloem), causing the leaf to curl and thicken, sometimes turning yellow or brown (Blommers et al., 2004; Qubbaj et al., 2005; NIAB, 2024). This impairs the growth of infested shoots and fruit, leading to unmarketable, malformed fruits of a reduced size (Blommers et al., 2004). These fruits often have uneven, rosy skin and characteristic puckering around the calyx (Figure 5) (NIAB, 2024; M. Fountain Pers. Obs.). Reproduction rates of aphids, and other insect pests, are linked to temperature and precipitation (Senior et al., 2020) and the amount and severity of fruit damage by *D. plantaginea* can vary considerably year-to-year (Blommers et al., 2004; NIAB, 2024).

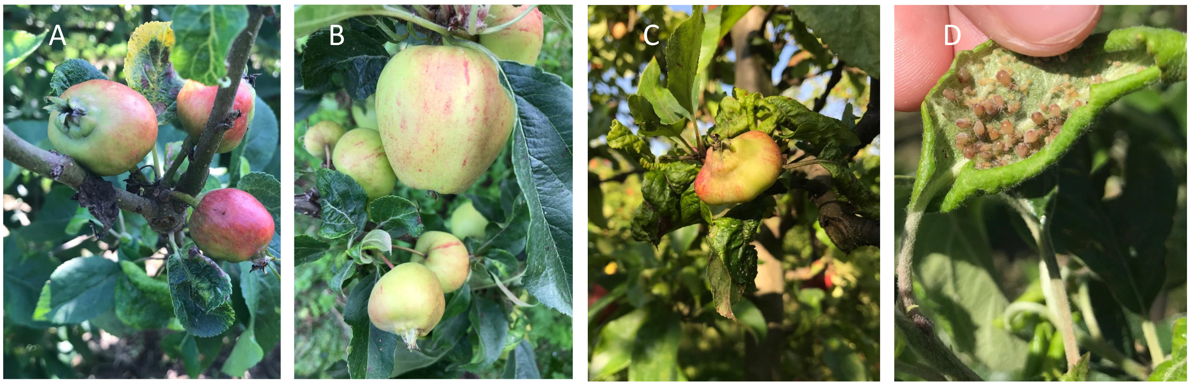

Figure 5: Photographs showing; A) damage to apples by *Dysaphis plantaginea* where fruits are reduced in size and malformed with puckering around the calix and a rosy colour, B) *D. plantaginea*-damaged apples beneath a non-damaged, full-sized apple, C) *D. plantaginea* curled leaves with a damaged apple, and D) *D. plantaginea* on an apple tree (taken by author).

1.4 Pest control

1.4.1 Chemical control

There are currently five main active ingredients for chemical control of *D. plantaginea* in the UK, three of which are broad spectrum (kill of wide range of insects) (Table 1). Three of those active ingredients are also approved to control important non-aphid apple pests such as *Hoplocampa testudinea* (apple sawfly) and *Cydia pomonella* (codling moth) (Table 1). For organic orchards, fatty acids (Table 1) can be used to control *D. plantaginea*, although conventional insecticides are used for the majority of apple production since organic apple orchards cover approximately only 2.5% of the land used for global apple production (Ryalls et al., 2024).

Table 1: Table of the UK chemical control options for *D. plantaginea* (Adapted from The Apple Best Practise Guide (NIAB, 2024)).

Active ingredient	Trade name (examples)	Class	Selectivity	Approved for the control of	Approved in the UK
Acetamiprid	Gazelle	Neonicotinoid	Broad-spectrum, systemic	Aphids	Loss of approval 08/24
Deltamethrin	Decis Forte	Pyrethroid	Broad-spectrum	Aphids, apple sucker, capsids, codling and tortrix moths, sawfly	Yes
Fatty acids	Flipper	Bioinsecticide	Broad-spectrum	Aphids, leafhoppers, mealy bugs, spider mites	Yes
Flonicamid	Mainman	Chlordontonal organ modulator	Selective	Aphids	Yes
Maltodextrin	Eradicoat Max	Polysaccharide	Broad-spectrum	Aphids	Yes
Spirotetramat	Batavia	Tetramic acid derivative	Selective	Sucking insect pests	Yes

Dysaphis plantaginea can be difficult to control with insecticides since they cause leaf-curling which forms a protective gall around the colony (Figure 6) (NIAB, 2024). Resistance of this species to conventional insecticides (ability to withstand the effects) is a significant problem in Italy and Switzerland and is likely a widespread problem in all apple-producing regions of southern/central Europe, although further testing is required to confirm this (NIAB, 2024). There may also be nontarget effects of insecticides on beneficial arthropods, such as natural predators of pests, for example hindering reproduction, predation, development time, and longevity (Schmidt-Jeffris, 2023). In Europe, *D. plantaginea* has developed resistance to carbamates, organophosphates, and pyrethroids (Van Emden and Harrington, 2017). Due to increasing bans and restrictions, the availability of chemical control for apple pests is rapidly changing (Damos et al., 2015; Shaw et al., 2021). Neonicotinoids are increasingly restricted due to their potential harm to pollinators (Cressey, 2017), and there have been recent losses of UK approved conventional pesticides for apple production (Shaw et al., 2021; Ryalls et al., 2024). For example, the following organophosphates, which were previously effective for *D. plantaginea* control, have recently been banned: chlorpyrifos in the EU in 2020 (European Commission, 2020a) and dimethoate in 2019 (European Commission, 2020b). The declining number of available active substances will further favour the emergence of resistance (Barzman et al., 2015). Alternative methods to control apple pests are needed to improve long-term sustainability of apple production by mitigating potential future bans or loss in efficacy of chemical control options and reduce effects on non-target organisms. Conventional chemical insecticides were relied upon for control of most apple pests, including *D. plantaginea* (NIAB, 2024), but other control methods may become more widespread with improved knowledge and development.

1.4.2 Potential alternative control methods

Aside from the chemical controls mentioned above, other potential control methods of *D. plantaginea* can be broadly grouped into the following main categories: crop plant pruning, semiochemicals, physical barriers, biopesticides, augmented biocontrol, and habitat management (Table 2). The potential benefits and drawbacks of these methods for *D. plantaginea* control are summarised in Table 2. Crop plant pruning can reduce aphid pest pressure (Van Emden and Harrington, 2017) for example, by changing the architecture of the crop tree canopy to reduce feeding, establishment, and movement on the tree (Simon et al., 2012; Shaw et al., 2021). Infestation by *D. plantaginea* is higher on long versus short, fruiting versus vegetative, and growing versus non-growing shoots (Simon et al., 2012), and early infestations occur in the lower and middle tree shoots (C. Nagy, unpublished). Pruning excess growth around the central tree zone may reduce areas for *D. plantaginea* to hide from ariel predators, and instead force colonies towards the periphery (Shaw et al., 2021). This pruning technique has been found to reduce foliage damage by 50% compared to an unpruned control (C. Nagy, unpublished) but further testing is required. Complete defoliation in autumn can also be effective (Andreev et al., 2012).

An alternative method is to prune curled leaves containing colonies to halt further damage and spread (Shaw et al., 2021), although this would be time consuming and could be costly.

Another potential control method of apple pests is the use of semiochemicals. These are substances that carry information between organisms, influencing their behaviour, physiology, or development, which can be made synthetically and used to manipulate pests or natural enemies (Damos et al., 2015; Pålsson et al., 2022). For example, laboratory studies by Verheggen et al. (2008) found that an aphid alarm pheromone ((E)-β-farnesene (EβF)) on a *Vicia faba* (broad bean) plants increased attraction and oviposition by an important aphid predator, *Episyrphus balteatus* (marmalade hoverfly) (Verheggen et al., 2008). However, in organic orchards in Sweden, Pålsson et al. (2022) investigated the combined use of semiochemicals tools: sex pheromones for multi-species pest mating disruption, and a blend of herbivory-induced volatiles as a predator attractant, alongside flower strips as a reward for predators, and these tools were effective in reducing lepidopteran pest abundances, but not for reducing artificially established *D. plantaginea* colonies. There are few examples of this method for *D. plantaginea* control, and the effect of semiochemicals is short-lasting so multiple applications would likely be required, and economic costs could be prohibitive (Shaw et al., 2021).

Physical barriers can also be used as a pest control method in apples. Spraying apple trees with inert reflective materials to create a film may disrupt host-plant recognition. For example, autumn treatments of a clay film (Kaolin) can prevent the return of remigrants of *D. plantaginea* (Bürgel et al., 2005; Andreev et al., 2012). For example, in an experimental orchard in Bulgaria, Andreev et al. (2012) found that, whilst single treatments were ineffective, two treatments with kaolin in autumn significantly reduced the number of winter eggs of *D. plantaginea* (as successfully as complete defoliation of apple trees) (Andreev et al., 2012). Conversely, a spring application has been found to increase *D. plantaginea* abundance, perhaps due to disruption of natural enemies such as earwigs and parasitoids (Markó et al., 2008; Van Emden and Harrington, 2017). Whilst these treatments can be washed off easily after harvest, they may need re-applying to the crop after rain (Andreev et al., 2012).

Netting can also be an effective barrier method for lepidopteran apple pests such as *Cydia pomonella* (codling moth) (e.g. Alaphilippe et al., 2016b), but may change natural enemy abundance in apple trees, sometimes detrimentally to *D. plantaginea* control (Dib et al., 2010a; Marshall and Beers, 2022).

An additional alternative control method for *D. plantagniea* is pathogenic biopesticides. For example, entomopathogenic nematodes have been investigated as a living insecticide for *D. plantagniea* using ants to deliver the nematodes inside the curled leaves of the colonies, however, efficacy has been low under field conditions, perhaps due to abiotic factors such as temperature (Bird et al., 2004). Biocontrol through artificial releases of predatory or parasitic insects to kill pests is less suited to open agriculture since they can easily escape (Dib et al., 2016a; Michaud, 2018; Shaw et al., 2021; NIAB, 2024). Dib et al. (2016a) evaluated the potential of early-season releases of *Forficula auricularia* (European earwig) for control of *D. plantaginea* in pesticide-free apple orchards, but this did not reduce *D. plantaginea* populations. However, Tougeron et al. (2023) found that releases of parasitoid wasps, *Aphidius matricariae* and *Ephedrus cerasicola*, can aid *D. plantaginea* control close to the release points, or further away when used in conjunction with habitat management (Section 1.5.2). Whilst these alternative control methods of *D. plantaginea* are understudied, habitat management (Section 1.5.2) has received comparatively more attention.

Table 2: Reported benefits and constraints of potential methods for controlling *Dysaphis plantaginea* in apple orchards.

Method		Mode	Benefits	Constraints	Citation
Crop plant pruning	Removal of curled leaves containing colonies	Halts further damage and spread.	Extremely effective and simple.	Time consuming and potentially costly.	(C. Nagy, unpublished) (Shaw et al., 2021)
	Pruning excess growth around the central area of the tree	Forces colonies to establish on branches accessible to aerial predators, constrains dispersal and reduces feeding resources.	Can reduce *D. plantaginea* damage by up to 50%. May improve ease of visual monitoring of pests for quick detection and action.	Potentially prohibitive labour costs. Few examples in literature.	(Simon et al., 2012; Shaw et al., 2021)
Semiochemicals	Substances for organismal communication e.g. pheromones (sexual, alarm, trail, aggregation)	Can be synthesised and used as attractants (e.g. for mass trapping), disruptors (e.g. mating disruptors),or repellents.	Accurate and localised. Can be more effective than conventional pesticides. Can attract and increase foraging behaviour and oviposition by specialist aphid predators in crop.	Short-lasting (may require multiple applications). Potentially prohibitive economic costs. Few examples in literature.	(Verheggen et al., 2008; Damos et al., 2015; Shaw et al., 2021; Pålsson et al., 2022)
Physical barriers	Spraying crops with inert reflective materials e.g. particle or clay film	Physical barrier e.g. to disrupt host-plant recognition.	Can be easily cleaned from the fruit after harvest.	Potential disruption of earwigs and parasitoids may increase pest numbers. Timing is of high importance. Can wash off in rain and block sunlight.	(Bürgel et al., 2005; Andreev et al., 2012; Rousselin et al., 2017)
	Netting	Insect exclusion netting enclosing the canopy.	Can last 10–15 years. Can reduce pest numbers.	Can be initially time-consuming and costly. Can interfere with machinery. Very fine mesh required. Can affect natural enemy populations.	(Dib et al., 2010a; Shaw et al., 2021; Marshall and Beers, 2022)

Method (continued)		Mode	Benefits	Constraints	Citation
Augmented biocontrol	Augmented natural enemy release	Artificial release of predatory or parasitic insects to kill pests.	Predators and parasitoids of *D. plantaginea* are present in orchards naturally.	Not developed for *D. plantaginea.* Alien species can severely disrupt native ecosystems, but native species can be used. Not well-suited to open agriculture. Little studied.	(Dib et al., 2016a; Michaud, 2018; Shaw et al., 2021; Tougeron et al., 2023; NIAB, 2024)
	Ant feeding with sugar or infested plants	Disrupt mutualistic ant-aphid relationship on the crop.	Can increase likelihood of aphid predation by generalist natural enemies. Can reduce pest numbers.	Further research needed to develop a method that is practical and cost effective.	(Nagy et al., 2015; Pålsson et al., 2020)
Biopesticides	Pathogenic biocontrol	e.g. entomopathogenic nematodes using ants as vectors	Highly specific to pests. Fewer human and environmental risks.	Low efficacy under field conditions.	(Bird et al., 2004; Damos et al., 2015)
Habitat management (Section 1.5.2)	Provision and maintenance of floral resources	Enhance and protect habitat for natural enemies.	Can increase diversity and abundance of natural enemies, including within adjacent crop.	Net economic costs and benefits are uncertain. Can take some cropland out of production. Maintenance costs.	(Shaw et al., 2021; Crowther et al., 2023; Judt et al., 2023; NIAB, 2024)
	Diverse hedgerow establishment and maintenance	Enhance and protect habitat for natural enemies.	Can increase diversity and abundance of natural enemies, including within adjacent crop.	Limited evidence of yield benefits.	(Bishop et al., 2023)

1.4.3 Pest control ecosystem service

Organisms such as native predators, parasitoid wasps, and birds can sustainably reduce pest populations, providing an important ecosystem service(Klinnert et al., 2024). This can be a highly economically valuable ecosystem service for crop production (Zhang et al., 2016; Begg et al., 2017; Zhang et al., 2018), including for apples (Cross et al., 2015). Experiments using exclusion of natural enemies allows for direct comparison between pest numbers with and without natural enemies (Dib et al., 2010b; Marshall and Beers, 2022). For example, a two-year study comparing apple pest, predator, and parasitoid densities in caged and uncaged plots compared to an insecticide free control found that *Eriosoma lanigerum* (woolly aphid) abundance in the caged plots were over 100-fold greater than the uncaged and control plots (Marshall and Beers, 2022). Threats to natural enemies include non-target effects of pesticides, lack of available resources such as food (prey and vegetation), and lack of breeding sites and overwintering sites from loss of natural habitats and monoculture cropping (Gurr et al., 2017). However, natural enemies could be encouraged in apple orchards to increase pest control services (conservation biocontrol), the main methods for which are discussed below.

1.5 Delivering conservation biocontrol

1.5.1 Integrated pest management

Integrated pest management (IPM) aims to control pests and diseases with the least possible disruption to agroecosystems to encourage pest control ecosystem services. This involves the careful consideration of all available crop protection methods, with varied usage rather than reliance on one method. This must be sustainable, both environmentally, and economically (Barzman et al., 2015). Some of the key principles include prevention and suppression of pests to a non-damaging or non-dominant level (Barzman et al., 2015), and the use of selective pesticides, rather than broad spectrum, and as a last resort (Damos et al., 2015). Importantly, a key principle includes consideration of long-term sustainability such as yield stability, and profit over multiple years at the cropping system level, rather than absolute field-level seasonal yield or total absence of pests as measures of success (Barzman et al., 2015).

The current reliance on chemical crop protection means that apple systems offer clear opportunities to implement effective integrated pest management. Ryalls et al. (2024) conducted a meta-analysis of 55 studies from 20 countries to quantify the effects of IPM on beneficial invertebrates, pest pressure, and crop productivity in apple orchards and found that IPM adoption increased the performance of natural enemies, while simultaneously reducing pest and disease pressure overall, although adoption of IPM was associated with lower yield compared to conventional management.

1.5.2 Habitat management

Within IPM, conservation biological control can involve habitat conservation measures to increase the abundance and diversity of natural enemies, with the aim of reducing the need for chemical pest control for crop protection (Begg et al., 2017). For example, this can involve habitat management via the addition of non-crop vegetation (Begg et al., 2017). The protection or addition of non-crop vegetation in agroecosystems can encourage natural pest control and could be employed to promote sustainable crop production (Martin et al., 2019). To design flower strips which are effective for multiple functional groups of arthropods, Favarin et al. (2024) identified plant species richness, composition, and vegetation density as the three important attributes of flower strips since these ensure complementarity of resources and niches, and also ensure sheltering microhabitats and suitable microclimatic conditions.

Habitat management can be tailored to target specific beneficial organisms, maximising their contribution to pest control, for example strips dominated by grass have been shown to benefit beetles (beetle banks) (Collins et al., 2003). Woody perennial features such as diverse hedgerows can increase the abundance and diversity of natural enemies. For example, in a recent study in apple orchards by Bishop et al. (2023), hedgerows were positively related to natural enemy richness and abundance at the field margin, although they found no spill-over into the crop area. Incorporating specific plants into non-cropped areas can also benefit certain natural enemies of target pests. For example, the banker plant method, which includes plants, usually non-crop plants, infested with herbivores as an alternative prey for natural enemies, or carrying other food resources such as nectar. These plants provide food and breeding resources to build populations of natural enemies of crop pests (Huang et al., 2011). For example, in apple an insectary plant, *Cnidium monnieri* (Monnier's snowparsley), increased the abundance of predators compared to controls and reduced the abundance of *Aphis spiraecola* (spirea aphid). Researchers used rubidium as a marker that revealed natural enemies were attracted to the insectary plant before moving onto apple and supressing the aphid pest (Cai et al., 2021).

Similarly, flowering plants in non-crop habitat (flower strips or flower margins) can be particularly beneficial as they provide both pollen and nectar, and can attract a wide range of beneficial organisms (Crowther et al., 2023). For some natural enemies, including Syrphidae and Chrysopidae, floral resources are essential for survival and reproduction (van Rijn et al., 2013; Gonzalez et al., 2016). For some parasitoid wasps, and for natural enemies which are predaceous across life-stages such as Coccinellidae and Araneae, floral food resources can improve fitness (Tylianakis et al., 2004; Taylor and Pfannenstiel, 2008; He and Sigsgaard, 2019; He et al., 2021). Non-crop vegetation can provide a wide range of continuously available resources for beneficial organisms (Pfiffner et al., 2019; Favarin et al., 2024), disturbance is reduced compared with the crop area, and it can act as a refuge from pesticide sprays and a source for alternative hosts/prey (Gurr et al., 2017). Non-crop areas also have higher plant diversity and structural complexity, including microclimatic protection providing shelter for breeding and overwintering (Gurr et al., 2017). The pollen and nectar can increase longevity, fecundity, and predation of natural enemies (He et al., 2021). Among the most widely implemented forms of habitat management in apple orchards are flower strips planted with perennial species (species which return annually rather than die back) (Herz et al., 2019). Sown perennial flower strips can be designed to contain diverse vegetation with flowering plants blooming across the season every year (Carvell et al., 2022). In fruit orchards, they can act as a reservoir for natural enemies year-round, and from year-to-year (Mateos-Fierro et al., 2021; Fountain, 2022).

1.6 Flower strips for *D. plantaginea* control

1.6.1 The effects of flower strips on *D. plantaginea,* natural enemies and fruit damage

Natural enemies of *D. plantaginea* include Coccinellidae (ladybirds), Dermaptera (earwigs), Araneae (spiders), Syrphidae larvae (hover fly), Neuroptera larvae (lacewings), parasitoid wasps, Aphidoletes aphidimyza larvae (predatory midge), Opilliones (harvestmen), Anthocoridae, Miridae, and Nabidae (predatory bugs) (Dib et al., 2010b; Campbell et al., 2017). Studies on flower strips report an increase in the abundance and richness of natural enemies of *D. plantaginea,* but less often report on fruit damage. For example, Wyss et al. (1995) conducted a two-year study in a single orchard in Switzerland in which perennial alleyway flower strips were planted in year one and *D. plantaginea* and natural enemies monitored weekly. There was a higher abundance of *D. plantaginea* predators in the flower strip plot compared to the control plot. There were also fewer *D. plantaginea* colonies, and fewer infested trees, although fruit yield was not reported (Wyss, 1995). Similarly, Albert et al. (2017) monitored aphid and natural enemy populations in pairs of contiguous IPM French cider apple orchards at seven locations for two years. The mean distance to the nearest flower strip was recorded for each orchard, which ranged from 0 m to 14.2 m. Natural enemies, except Araneae, were more abundant closer to perennial flower strips, and aphid abundance decreased, although fruit damage was not assessed (Albert et al., 2017). 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).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). Additionally, studies investigating the effect of flower strips on natural enemies have more often focused on predators. However, parasites are a key natural enemy preventing severe infestations of other apple aphid species, for example *Eriosoma lanigerum* (woolly aphid) and the parasitoid wasp*, Aphelinus mali* (Quarrell et al., 2017). As such, parasites could also be key for *D. plantaginea* control.

Of those studies which have investigated fruit damage by *D. plantaginea,* most have found no effects of flower strips. In a two-year study in Denmark by Jacobsen et al. (2022), row one and row three of apple trees were monitored in five organic orchards with flower margins, and three controls without flower margins. One-year-old perennial strips replaced five-year-old less diverse margins. In the second year of study, more predators were present on the trees in flower strip orchards compared to controls (systematic tap sampling). Predator diversity in apple trees was also positively affected by proximity to a flower strip. Inside *D. plantaginea* colonies, more predators were present in the first row next to the flower margin than in the third row. Despite this, there was no effect of flower strips on the number of curled leaves, or fruit damage caused by *D. plantaginea,* although yield could not be reliably assessed because of severe frost damage (Jacobsen et al., 2022). Additionally, in a three-year study by Cahenzli et al. (2019), perennial flower strips were sown in year one between rows of apple trees (alleyway strips) in nine organic apple orchards across seven European countries (Belgium, Denmark, Italy, Poland, Sweden and Switzerland). There were 23 experimental blocks consisting of seven or eight tree rows with flower strips sown in the alleyways of one half of each block. Organic insecticides were used, although only in exceptional cases of uncontrolled outbreaks. In flower strip plots compared to control plots, visual assessments found higher natural enemy abundance in *D. plantaginea* colonies, and higher counts of Syrphidae, Chrysopidae and generalist predators on trees in the flower strip plots as compared to the controls. Counts of natural enemies in curled leaves were also higher. Whilst there was no effect of flower strips on *D. plantaginea* abundance, or fruit damage at harvest, there was slower colony growth, and reduced fruit damage at second fruit-drop (Cahenzli et al., 2019). Damaged fruits were removed from the trees before harvest (quality fruit thinning) which could explain why there was no effect of the flower strips on fruit damage at harvest. Other potential contributing factors were asynchrony of timing of enemies for pest control, or interaction with ants (Cahenzli et al., 2019). However, fruit damage benefits were found in a six-year study by Cahenzli et al.

(2017). Flower margins were planted between hedgerows and outer-rows of apple trees in an experimental organic orchard in Switzerland. No insecticide was used during the study. Continuous monitoring from two to seven years after flower margin establishment found that autumn abundance of spiders and spider web area both increased. Additionally, fruit damage by *D. plantaginea* was decreased by 10% in the following spring, from 2009–2014 (Cahenzli et al., 2017).

Most recent studies investigating the effect of flower strips on apple pest control (2017 onwards) have been in organic or insecticide-free orchards (for example: (Cahenzli et al., 2019; Jacobsen et al., 2022; Favarin et al., 2024)), with fewer in orchards using IPM (Campbell et al., 2017; McKerchar et al., 2020). The use of conventional pesticides in apple orchards has been suggested to mask effects of flower margins on fruit damage. A two-year study by Campbell et al. (2017), in four commercial IPM cider apple orchards in Southwest England, used orchard plots with alleyway flower strips compared to control plots. There was a higher abundance and richness of natural enemies in trees adjacent to flower strips sown with open-nectar plants, but only generalists. The researchers also recorded a proxy for predation rates using insect eggs as bait by sticking them to cards and hanging them from the apple trees (bait cards). Predation of bait lepidopteran eggs was higher in flower strip plots by up to 55%. The abundance of *D. plantaginea* did not differ between flower margin and control plots. Nor did the predator-prey ratio, and there was no effect on fruit yield (Campbell et al., 2017). It was suggested that the increased natural enemy abundance could have been too late to alter pest and yield dynamics since the damage could have occurred earlier in the season. The use of pesticide was noted as a potentially important factor explaining the lack of yield effects since this may have caused harm to natural enemies (Campbell et al., 2017). Additionally, in a three-year study by McKerchar et al. (2020) in ten orchards in Southeast England, each orchard contained a one-hectare plot with perennial flower alleyways, and a control plot. Tap sampling revealed that there was no effect of flower strips on the total number of aphidophagous predators, or Araneae, in the apple trees. There was no effect on the number of pea aphids eaten from bait cards, nor the number of parasitised *D. plantaginea*, or number of infested trees. There were however interactive effects with cumulative insecticide and acaricide toxicity values for natural enemy groups (Anthocoridae, Chrysopidae, Miridae, parasitoids and predatory mites). This was calculated by summing the treatment frequency index of each pesticide multiplied by the toxicity class of the pesticide (using toxicity classifications from the International Organization for Biological Control). For example, Family richness and diversity of natural enemies were greater in year three in orchards associated with lower toxicity values. The authors suggested that the use of plant protection products could have masked the effects of the flower strips (McKerchar et al., 2020). Further studies in conventionally managed orchards with the pesticides which are currently available are required to determine the strength of *D. plantaginea* control benefits from flower strips. Similarly, previous studies investigating fruit damage effects have often used younger flower strips rather than well-established ones, and older strips may be more effective, but this is yet to be determined (Herz et al., 2019). Additionally, of the studies which considered fruit damage, the effects of perennial flower strips 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).

Flower strips rarely have negative effects (Fountain, 2022), although Vogt and Weigel (1999) found higher *D. plantaginea* infestation and the lowest predator-pest ratio in flower strip plots compared to the control plot. They suggested this could have been caused by higher temperatures and less wind in the flower strips promoting *D. plantaginea* survival, attraction of the pest to the flowers, or improved tree vigour by nitrogen fixing plants in the floral mix (Vogt and Weigel, 1999). Broadly, the effects of flower strips on *D. plantaginea* and natural enemies are variable, typically ranging from neutral to positive. Additional studies are required to determine the strength and spillover of the effects of flower strips for *D. plantaginea* control in apple orchards.

1.6.2 Economic costs and benefits of flower margins for *D. plantaginea* control

Although sown flower strips can provide benefits, they also incur costs. These include the capital costs of establishment including the seed mix and ground preparation. There are also ongoing maintenance costs, although less than establishment costs, which can include one to two cuts per year, preferably with the cuttings removed (Carvell et al., 2022). A second potential cost is the opportunity cost of the land used for the flower strips (potential crop yield that could have been gained from using that same land for agricultural production) (Kleijn et al., 2019). As such, the creation of flower-rich plots on farmland has been subsidised in the UK, EU and USA. Governmental agri-environmental schemes can offer economic incentives for flower-rich plots as part of IPM to support biodiversity (for example, Countryside Stewardship grants and Sustainable Farming Incentives in the UK) (Rural Payments Agency and Natural England, 2024). In addition to governmental schemes, charity and industry-driven incentives might offer economic support or expertise to farmers for habitat creation and environmental improvements, for example by WWF and Air Wick (2021) (e.g. hand collect and drill diverse seed-mix for flower strip establishment), Royal Countryside Fund (2023) (e.g. offer grants, free programmes, and local support), and National Lottery Heritage Fund (2023) (e.g. offer grants). Payments under these schemes can fluctuate year-to-year, and there is no guarantee of continued support, which can create uncertainty for farmers. Although agri-environmental schemes are designed for environmental benefits, some may pay-for-themselves in terms of yield and crop quality benefits, or reduced production costs (Blaauw and Isaacs, 2014; Kleijn et al., 2019). Balancing the costs and benefits of habitat interventions, including flower strips, is a perennial challenge for farmers and land managers, particularly when the full costs and benefits may not be fully characterised (Kleijn et al., 2019).

There is a lack of evidence of economic and yield benefits of flower strips in orchards (Herz et al., 2019; Fountain, 2022), as is true for crops generally (Crowther et al., 2023). When harnessing ecosystem services to enhance yield with minimal environmental damage (ecological intensification), the cost-benefits of these methods are less often studied than the ecological effects (Kleijn et al., 2019). A lack of scientific investigation and knowledge into economic benefits, and direct or opportunity costs, under a range of context-specific scenarios may be limiting uptake of these methods by growers (Kleijn et al., 2019). In other crops, Li et al. (2021) reported that monofloral strips adjacent to aubergine greenhouses led to a reduction in aphid pest pressure and subsequently, led to a reduction in the amount of required insecticide. A cost analysis revealed that this reduction in insecticide use, in combination with the increase in crop value based on environmentally friendly practices, suggested this strategy could be economically viable (~+14,700 RMB or £1,562 per greenhouse) (Li et al., 2021 Supplementary Materials). Similarly, in a 4-year study in rice fields, Gurr et al. (2016) found that growing nectar-producing plants reduced major lepidopteran pest abundance, increased grain yields by 5%, and overall resulted in economic benefits of 7.5% (Gurr et al., 2016). Further studies are needed to understand the strength and spillover of benefits of flower strips for *D. plantaginea* fruit damage. Improved knowledge on how best to implement flower strips in apple orchards could improve uptake by growers.

1.7 Aims, objectives and structure

The aim of this thesis was to evaluate the ecological and economic impact of perennial flower margins for control of *D. plantaginea* in UK apple orchards considering effects on natural enemy populations, predation rate, and fruit damage and how this is influenced by location and from year to year.

To address this aim, the thesis had the following objectives:

1. To determine the effects of flower margins on *D. plantaginea* infestation and subsequent fruit damage, quantifying how far effects reach into orchards and exploring seasonal variability (Chapter 2).
2. To compare the vegetation community and structure in flower margins, orchard headlands and alleyways, and determine if and how flower margins change the diversity, abundance, and community structure of natural enemies of *D. plantaginea* in orchards across seasons (Chapter 3).

3. To establish whether presence of established perennial flower margins increased parasitism of *D. plantaginea* by parasitoid wasps, and how this is affected by distance from the flower margin (Chapter 4).
4. To assess the economic costs and benefits of flower margins in terms of aphid pest control and how this is influenced by flower margin location and aphid infestation level (Chapter 5).

2 Perennial flower margins reduce orchard fruit damage by rosy apple aphid, *Dysaphis plantaginea*

This chapter is derived from the following publication:

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Author Contributions

Charlotte Howard: Conceptualization, Formal analysis, Writing - Original Draft, Visualization. **Michelle T Fountain**: Conceptualization, Writing - Review & Editing, Funding acquisition. **Claire Brittain**: Conceptualization, Writing - Review & Editing, Funding acquisition. **Paul J. Burgess**: Conceptualization, Writing - Review & Editing, Funding acquisition. **Michael Garratt**: Conceptualization, Writing - Review & Editing, Supervision, Funding acquisition.

2.1 Abstract

Sown or natural flower strips are a commonly used management practice in agroecosystems and have been demonstrated to increase the abundance of predators of orchard pests. There is less evidence of the extent to which such strips can reduce pest damage in orchards. Here I examined the effect of managed, perennial flower margins on fruit damage by an economically significant crop pest, *Dysaphis plantaginea,* rosy apple aphid, in conventional apple orchards over two years compared to orchards without flower margins. This study found that orchard flower margins reduced the percentage of apple trees with fruit damage by *D. plantaginea,* from 80% to 48%. In 2021, a period of severe infestation (65% of trees had fruit damage), there was reduced spread of *D. plantaginea* on infested apple trees and the number of trees with fruit damage was significantly reduced up to 50 m into orchards. During 2022, a period of lower infestation (25% of trees damaged), fruit damage was significantly reduced up to 10 m from the flower margin. A significant reduction in predation of aphids from bait cards in flower margin compared with control orchards suggests specialists, rather than generalist predators, may be driving the positive effects of the margin on pest pressure. There was no significant effect of flower margins on abundance of important aphid predators, including Syrphidae (hoverflies) and Coccinellidae (ladybirds). To my knowledge, this study is the first to detect a reduction in fruit damage by pests at harvest in orchards with a flower margin. This study highlights the potential for established perennial flower margins to deliver measurable, sustainable, *D. plantaginea* control benefits and provide insights into the optimal spatial arrangement of flower strips in orchards.

2.2 Introduction

Loss of key resources and habitats in agricultural landscapes can have negative impacts on biodiversity and species beneficial to ecosystem services (Emmerson et al. 2016). Sown or natural flower strips are one of the more commonly used management practices designed to support the natural predators and parasites of crop pests (natural enemies) (Herz et al., 2019). They can be sown within the crop or border the crop as a margin. It has been reported that a mix of perennial wildflowers, in particular, can provide beneficial insects with breeding and/or food resources year-round, and from year to year (Fountain 2022 and references therein). A recent meta-analysis exploring the use of flower margins found they lead to increased abundance and diversity of arthropod and natural enemy communities within the margin and in adjacent crops (Crowther et al., 2023). The same analysis also showed that sown margins, and to a lesser extent, spontaneous vegetation, reduced pest abundance in comparison to grass control margins (Crowther et al., 2023). Supporting natural enemies through such approaches can reduce reliance on chemical pest control (Dib et al., 2016c; Cahenzli et al., 2017; Judt et al. 2023).

Apple is one of the most widely grown fruits in the world, with 93 million tonnes harvested in 2021 (Food and Agricultural Organization, 2023). In 2020, the UK produced 200 thousand tonnes of dessert apples with a value of £158 million (DEFRA, 2020a). Dessert apple production requires intensive management typically involving high inputs of pesticides and fertiliser (Simon et al., 2011a; Simon et al., 2011b; Herz et al., 2019). Even organic production requires regular use of biological and organic plant protection products to obtain a reliable and economically viable yield (Daniel et al., 2018). Hence, there is particular interest in the use of flower margins as a biocontrol strategy.

Rosy apple aphid, *Dysaphis plantaginea* (Passerini), is an important apple pest which can cause significant economic damage, even at low population levels, such as leaf curling, reduction of fruit size, and fruit deformation (Blommers et al., 2004). If untreated, *D. plantaginea* infestation can lead to economic losses of up to 80% (C. Schulz, 2003, pers. comm. in Qubbaj et al., 2005), and hence aphid infestations in fruit orchards are typically treated using insecticides (Dib et al., 2010b; Penvern et al., 2010). Whilst insecticides can be an affordable and effective part of integrated pest management (IPM), the drawbacks can include pesticide resistance (Dunley and Welter, 2000; Pretty et al., 2018) and biodiversity loss (Katayama et al., 2019), including negative effects on non-target organisms such as pollinators (Goulson et al., 2015) and natural enemies (Fountain and Harris, 2015). The use and availability of pesticides changes over time (McKerchar et al., 2020), and recent pesticide withdrawals are leaving fruit growers with fewer effective products (Cressey, 2017). Studies have demonstrated that aphids can be suppressed by natural enemies (Dib et al., 2010b) including generalist predators, such as earwigs and spiders (Dib et al., 2010b; Diehl et al., 2013) and specialists including Syrphidae larvae (hoverfly), Coccinellidae (ladybirds), Chryopsidae larvae (lacewings) and parasitoid wasps (Order: Hymenoptera) (Graham, 1989; Solomon et al., 2000; Dib et al., 2010b). Predacious bugs (Anthocoridae, Miridae, and Nabidae) and predacious beetles (Cantharidae and Staphylinidae) are also aphidophagous (Dib et al., 2010b; Dib et al., 2016b). Additionally, Formicidae (ants) can predate aphids, but in the absence of sugar resources such as nectar, they form mutualisms whereby they protect aphids from predators in return for the sugars they excrete (Nagy et al., 2015). These natural enemy groups often rely on floral resources for food during various life-stages, or scarcity of aphid prey (Wyss, 1995; Markó et al., 2013).

Whilst there is evidence for increased abundance and diversity of natural enemies in apple orchards with flower strips, there is a lack of investigation into evidence of increased pest control services such as increased yield (Herz et al., 2019; Fountain 2022), as is true for crops generally (Crowther et al., 2023). For example, only a few studies have investigated apple damage, most finding no effect (Cahenzli et al., 2019; Jacobsen et al., 2022; Campbell et al., 2017). Additionally, many recent studies have been in organic or insecticide-free orchards, with fewer in orchards using Integrated Pest Management (Fountain 2022).

The spatial extent of the effect of flower strips to control pests into orchards (spill-over) is also uncertain. Benefits have been found only in close proximity, such as the row of apples neighbouring the flowers (Cahenzli et al., 2019; Jacobsen et al., 2022; Albert et al., 2017). Studies for crops in general, apples included, suggest that positive effects can extend to 50 m for generalist natural enemies (Wyss et al., 1995; Woodcock et al., 2016) with the effects decreasing with increasing distance from the flower strip (Collins et al., 2002; Tylianakis et al., 2004; Gontijo et al., 2013; Albert et al., 2017; Mei et al., 2021). The effects of perennial flower strips on fruit damage specifically have more often been investigated with alleyway flower strips and trees in close proximity (up to 3 rows away) rather than investigating the effects of flower margins on more distant trees. More knowledge on the spill-over effects of well-established flower margins in orchards is needed for fruit growers designing orchards and landscapes for more effective ecosystem service delivery.

This study aimed to examine the spatial effect of established perennial flower margins on pest pressure and fruit damage by *D. plantaginea*. The objectives were to 1) determine whether flower margins can suppress *D. plantaginea* and subsequent fruit damage in conventionally managed apple orchards; 2) establish whether this is driven by the abundance and activity of natural enemies in the orchard trees; and 3) quantify the distance of spill-over from flower margins into orchards. I hypothesised that predator abundance and predation would be increased in orchards with adjacent flower margins, leading to overall reduced aphid pressure and fruit damage, particularly close to the flower margin.

2.3 Methods

2.3.1 Study sites

Gala is the most widespread variety of dessert apple grown in the UK (DEFRA, 2020b). This study took place in ten commercial dessert apple orchards (Gala var.) located in Kent, UK. Five orchards, termed “flower margin orchards” were bordered by an established sown perennial flower margin (2-5 years), and five “control orchards” had only a permanent grass headland 4-5 m wide, typically mown four times a year (Figure 1, Supplemental Figure 2.1). The average width of the flower margins was 15 m (SD = 9.6 m) (Supplemental Table 2.1). All orchards were conventionally managed, involving 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, with a distance of 120-410 m between treatments to minimise co-use by the same invertebrates and differences in soil type and aspect.

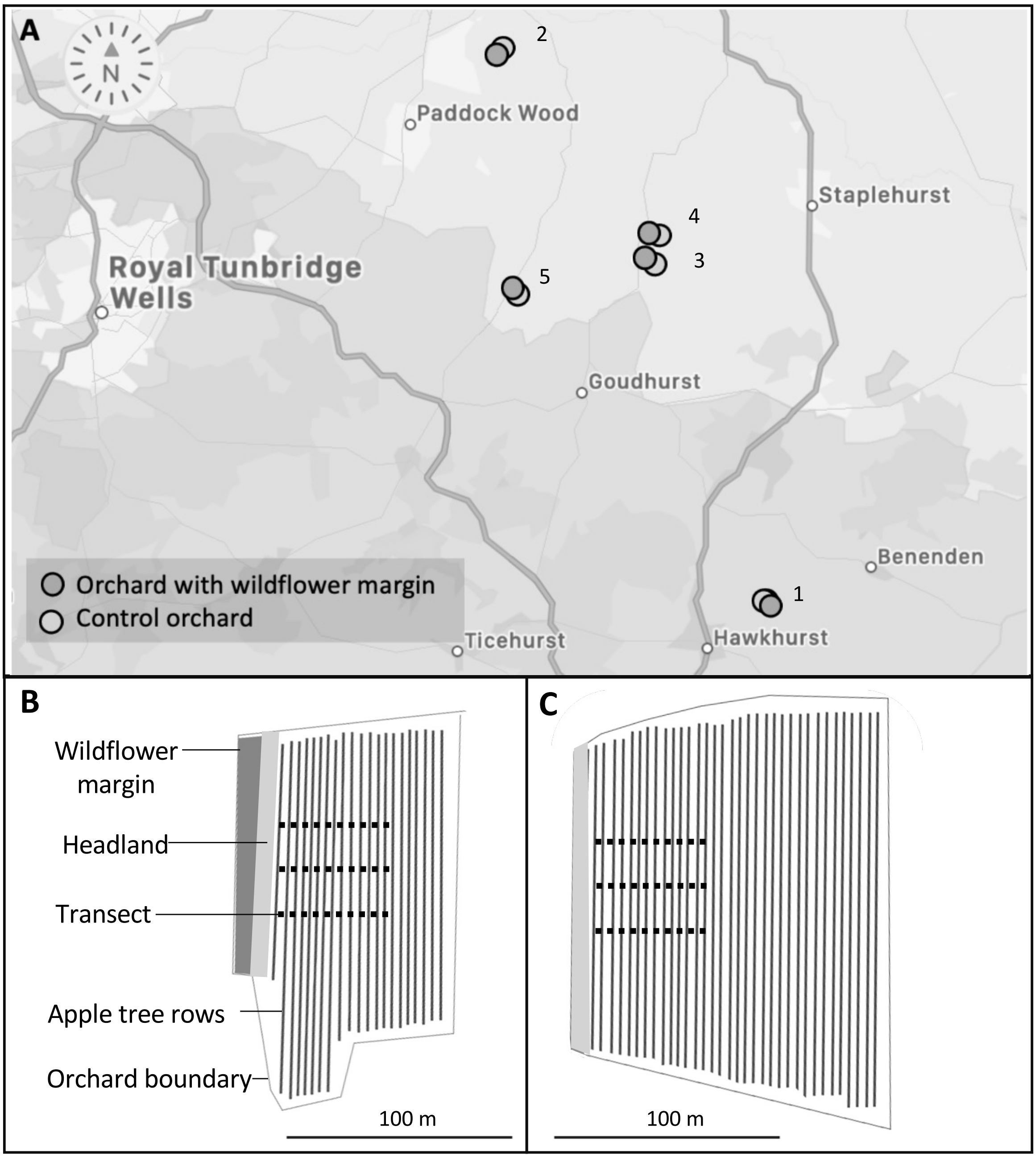

Figure 1. Map showing locations of the 10 study orchards in Kent, South East England, UK, numbered according to orchard pair (A) (Taken from Apple Maps), typical layout of an orchard with a flower margin (B) and without (control) (C) (Adapted from Carvell et al. (2022)).

2.3.2 Flower margins

Four of the flower margins were sown in 2017 with four low-growing fine grass species and 15 perennial flowering species designed to offer multiple flowering times, flower shapes, and maximise pollen and nectar resources (Supplemental Table 2.2) (Carvell et al., 2022). At the fifth site, the margin was sown in 2019 with a different perennial seed mix with some overlap of the plant species

(Supplemental Table 2.2). 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). They did not receive fertilizer or herbicide treatments.

2.3.3 Sampling design

Data were collected along three 50 m transects extending from the flower margin or control edge to the centre of each orchard. Transects were 20 m apart, and to reduce edge effects, at least 20 m from the perpendicular field edge (Figure1). Flower margin and control edges were matched for adjacent habitat types, ordinal direction, and tree row direction where possible. Where it was not possible to meet all criteria, priority was given to matching the adjacent habitat (including type of crop and type of semi-natural habitat). In the narrowest orchard, 50 m was the furthest into the orchard that could be sampled before becoming closer to the opposite edge and so was set as the maximum distance. Five distances along each transect were chosen for sampling: 0, 5, 10, 20, and 50 m. Generally, a distance of 5 m and 10 m from the edge corresponded with tree rows 2 and 4 respectively, so for consistency, data were collected from these rows in each orchard and then from a row at least 20 m, and 50 m from the orchard edge.

2.3.4 Aphid assessments

Abundance of *D. plantaginea* was assessed at three-week intervals from April to July in 2021 and 2022 during the apple-growing season, after which *D. plantaginea* typically migrates to a secondary host, *Plantago spp.* (plantain). This included a pre-bloom assessment in April, an assessment during bloom in May, and post-bloom assessments during the fruitlet and fruit stages in July and August. For each of the three transects, three trees were surveyed at each of the five distances (45 trees per orchard). 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 (Cahenzli et al., 2019) (Figure 2). To cover a range of areas on the tree, areas were searched systematically, starting next to the trunk on the lowest branch on the right, and finishing with the highest reachable branch on the left (up to 2 m), and searching areas in-between in an arc across the tree (Figure 2), alternating the position of the branch between proximal, distal, and intermediate distance from the trunk. Curled leaves were uncurled to search inside. The number of *D. plantaginea* colonies were counted and the number of aphids in each was estimated. Natural enemy taxa including ants and aphid mummies (host to a pupated parasitoid wasp) were recorded. The active predatory stage of most predators of *D. plantaginea* are not highly dispersing, and as such, systematic visual searches were well-suited to sampling these groups (Araneae, predatory Hemiptera, Opilliones, Coccinellidae, Dermaptera, Syrphidae larvae, and Neuroptera larvae). When present, natural enemies were identified in the field. Assessments and sampling were carried out between 08:00 and 18:30. Paired orchards were surveyed on the same day to minimise weather effects. The order of visits to each site was randomised.

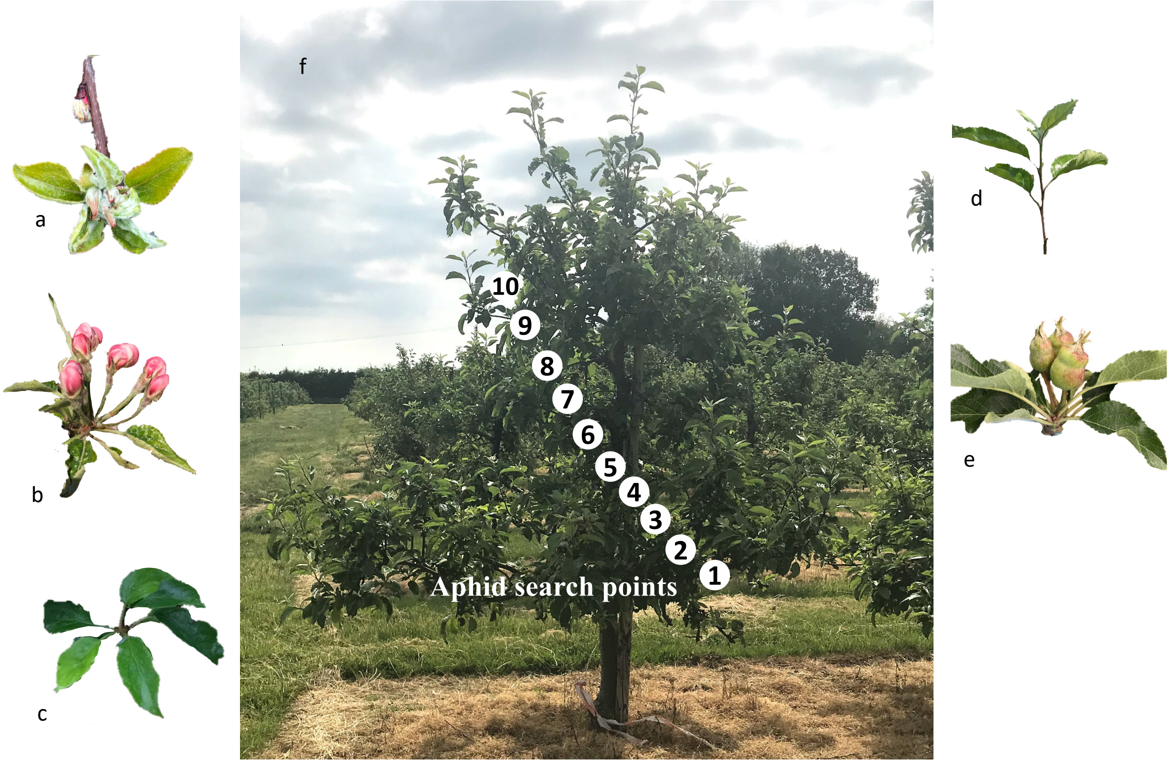

Figure 2. Areas (a-e) and positions (f) on commercial apple trees selected for visual searches for rosy apple aphids. Areas include a) buds, b) flower clusters with leaves, c) rosettes of leaves, d) long shoots and, e) fruit clusters.

2.3.5 Aphid fruit damage assessment

The same three trees used for *D. plantaginea* assessments were assessed for pre-harvest fruit damage on each of the three transects, at each of the five transect distances. The total number of fruit and number of fruit with *D. plantaginea* damage were counted on each tree. Rosy apple aphid damaged fruit was identified by reduced size, malformed shape, often with puckering around the calix (Figure 3), and/or a coating of aphid honeydew which can lead to sooty mould (Warren and Schalau, 2014). A pre-harvest thinning of fruit was carried out a few days before the fruit damage assessment in one of the five orchard pairs. In that case, pest-damaged fruits which had been removed from the tree and dropped to the ground below, were included in the calculation of total fruit number.

Figure 3. Damage to apples by *Dysaphis plantaginea*, where fruits are reduced in size and malformed, with puckering around the calix (left) and *D. plantaginea* damaged apples beneath a non-damaged, full-sized apple (right).

2.3.6 Sentinel bait experiment

Sentinel bait cards (Boetzl et al., 2020) were deployed to assess predator activity in the trees in 2021. Since rosy apple aphids are not commercially available, a culture of *Acyrthosiphon pisum* (pea aphid) was obtained from Dartfrog (http://www.dartfrog.co.uk). Aphids were reared *in vitro* at room temperature on *Pisum sativum* (pea) and *Vicia faba* (broad bean) in cages (44.5 cm^3) of fine nylon mesh (160 µm mesh). Ten adult and late-stage *A. pisum* nymphs were euthanised in a freezer and then glued to a polyvinyl chloride card (Mateos-Fierro et al., 2021) (Figure 4) which was hung adjacent to the trunk from the lowest branch of three apple trees at each of the five transect distances. The percentage of aphids depleted by predators and scavengers was recorded, where possible, every 48 hours for five days in May, six days in July and eight days in September, after deployment (Figure 7). This study did not require ethical approval, licenses or permits.

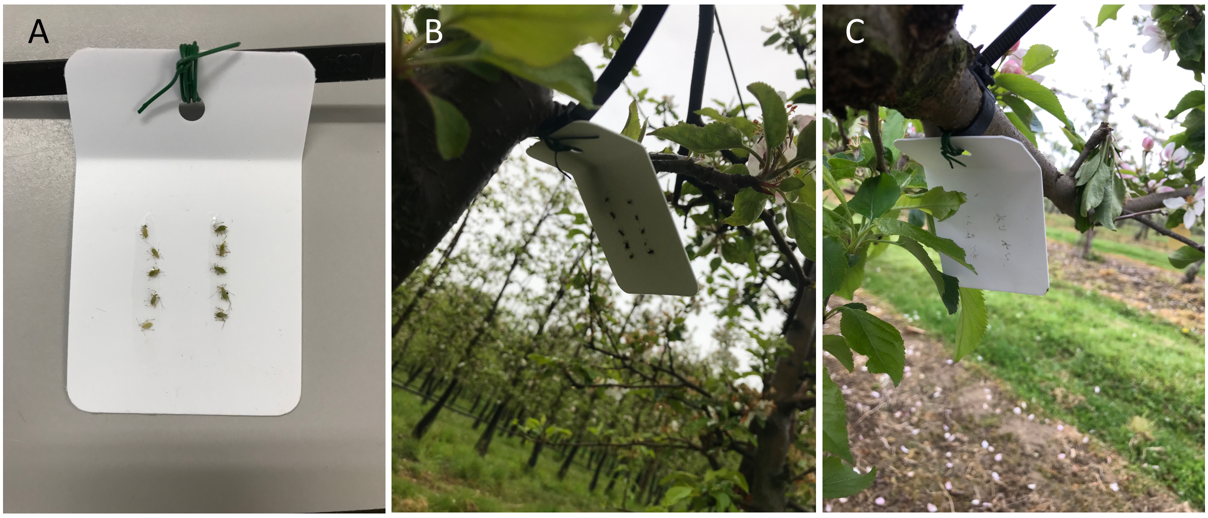

Figure 4. Sentinel bait card of A) ten adult and late-stage *Acyrthosiphon pisum* nymphs glued to a pvc card (as in Mateos-Fierro et al., 2021), B) hung at approximately 1.5 m in the lowest apple tree branch, and C) depleted by predators and scavengers.

2.3.7 Statistical analyses

Statistical analyses were carried out in R 4.2.2 for Mac (R Core Team, 2022), using the lme4 package for mixed effect modelling (Bates et al., 2015). To account for the experimental design of nested repeated measures within a transect, orchard, and pair of orchards, generalised linear mixed models

(GLMM) were used. Binomial models were used for proportional data, and Poisson models (or negative binomials in the case of overdispersion) were used for other data. The assumptions of the GLMM were tested, including linearity, response distribution, independence, and multicollinearity of predictors. Models were also tested for overdispersion where appropriate. Aphid densities can be uneven due to their natural distribution, leading to data analysis issues such as overdispersion and zero-inflation. To account for this, colony metrics, fruit damage and enemy abundance data were modelled using a hurdle (zero-adjusted) model (e.g. Sampaio et al., 2017), a two-step approach which evaluates the zero values using a binomial linear regression, and then uses truncated linear regression for the positive values. Therefore, the data are considered first on a presence-absence basis (e.g. are trees aphid-infested or not), and then the counts are assessed (e.g. abundance of aphids on infested trees) (Zuur et al., 2011). 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, but separate models were created for each sampling year to aid model convergence where needed (Table 1). Similarly, sampling 'round' was included as a fixed effect where possible, but values were averaged across the year if needed (Table 1). The random effect structure had to be simplified in some cases to avoid over-fitting (Table 1). Total fruits per meter squared was modelled to compare productivity between flower margin and control orchards, accounting for differences in fruits per tree due to varying production systems affecting intra-row tree spacing and tree height.

Table 1. Model building specifications, where a ● symbol indicates where fixed and random effects were applied to each response variable for a) 2-part hurdle (zero-adjusted) models, and b) non-hurdle models. 'Treatment' fixed effect refers to presence or absence of a perennial flower margin. 'Pair' fixed effect refers to the experimental design whereby each treatment orchard is paired with a control orchard. Random effects were nested in the order in which they apear in the table.

				Fixed Terms					**Random Terms**			**Weights**
Response	**Data**	**Sampling Methods**	**Distribution**	**Treatment**	**Distance**	**Year**	**Round**	**Aphid[1] abundance**	**Pair**	**Orchard**	**Transect**	**No. aphids deployed[2]**
a) Fruit damage by Rosy apple aphids												
Presence/absence	All trees	Pre-harvest fruit damage assessment	Binomial	●	●	●			●	●		
Percentage (damaged&undamaged)	Affected trees	Pre-harvest fruit damage assessment	Binomial	●	●	●			●	●	●	
Apples per meter squared	All trees	Visual aphid assessments across the season	Negative binomial	●	●	●			●	●	●	
Aphid metrics in 2021 (averaged by round)												
Presence/absence	All trees	Visual aphid assessments across the season	Binomial	●	●				●			
Spread	Aphid-infested trees	Visual aphid assessments across the season	Binomial	●	●				●			
Abundance	Aphid-infested trees	Visual aphid assessments across the season	Poisson	●	●				●	●	●	
Syrphidae metrics during peak aphid abudance, June 2021												
Presence/absence	All trees	Visual aphid assessments across the season	Binomial	●	●			●	●	●		
Abudance	Aphid-infested trees	Visual aphid assessments across the season	Negative binomial	●	●			●	●			
Coccinellidae metrics during peak aphid abudance, June 2021												
Presence/absence	All trees	Visual aphid assessments across the season	Binomial	●	●			●	●	●	●	
Ant presence/absence, 2021	All trees	Visual aphid assessments across the season	Binomial	●			●	●	●	●		
b) Percentage predation from bait cards after 5 to 8 days from deployment	All trees	Bait cards	Binomial	●	●		●		●	●	●	●

[1] The total number of aphids per tree was appropriately scaled to match the other fixed effects in the model. This was done using a multiplication of 0.01.

[2] The model was weighted according to number of aphids deployed to account for occasional cards with fewer than 10 aphids, for example if one fell off during transit.

2.4 Results

2.4.1 Aphids

Between April and July 2021, *D. plantaginea* were present on 23% of 450 surveyed trees. Peak abundance was in June, with an average of 71 aphids per tree (all trees) (SD = 305 aphids). Across the 2021 season, there was no significant effect of presence of a flower margin on the percentage of trees with *D. plantaginea* ($\chi^2 = 5.165$, df = 4, $P > 0.05$). However, infested trees had fewer aphid-infested areas in flower margin orchards compared with controls (Figure 5A) ($\chi^2 = 17.924$, df = 1, $P < 0.001$). Overall, *D. plantaginea* presence was significantly reduced with increased distance from the orchard edge ($\chi^2 = 25.454$, df = 4, $P < 0.001$). There was also a significant interaction between distance and presence of a flower margin ($\chi^2 = 12.188$, df = 4, $P < 0.01$), which meant that the flower margin was associated with fewer aphids per infested tree at 10 m into the orchard (Z ratio = 2.286, $P < 0.05$) (Figure 5B), but not at other distances.

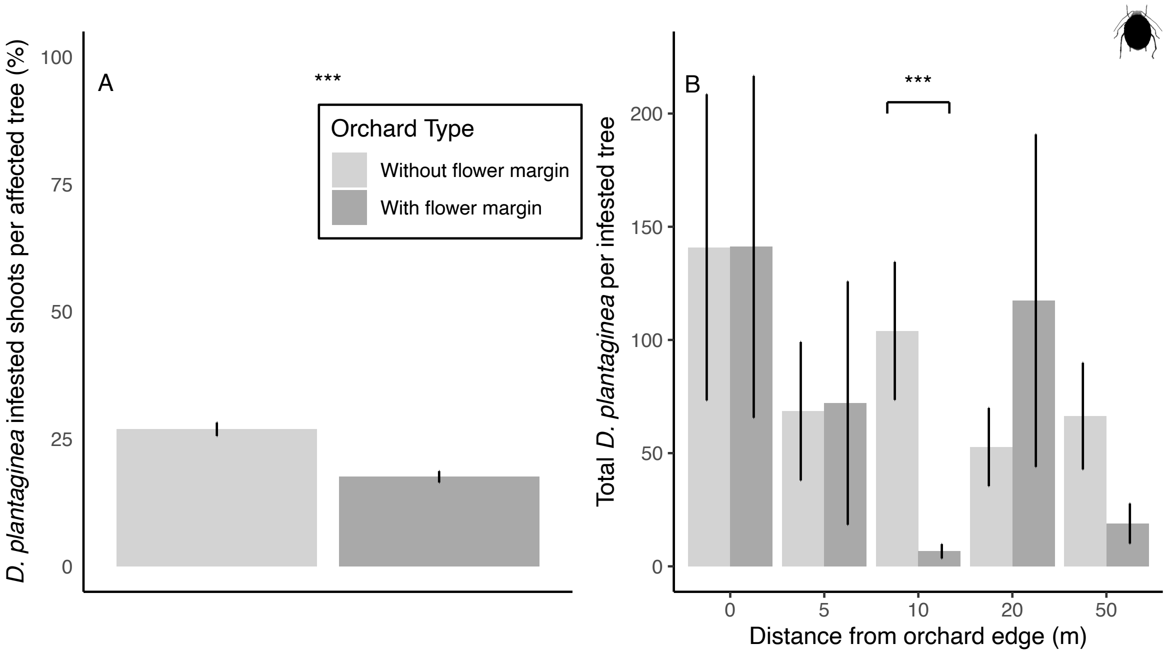

Figure 5. Effect of presence/absence of a flower margin on A) the mean percentage of infested shoots per infested tree in 2021 and B) the mean total number of *D. plantaginea* on apple trees in 2021 at distances from the orchard edge. Lines show standard error. Stars denote significance of treatment; *P < 0.05, **P < 0.01, ***P < 0.001.

In 2022, *D. plantaginea* was only on 4.5% of 1799 tree searches across the season with a mean of 6% in flower margin and 3% in control orchards, although I could not test for significance. Only two aphid mummies were found across both seasons. In both cases, numbers were too low for detailed statistical analysis.

2.4.2 Aphid fruit damage

The percentage of trees with *D. plantaginea*-damaged fruit varied with year. The mean percentage of trees with *D. plantaginea*-damaged fruit was 65% in 2021 and 25% in 2022. There were significant interactions between treatment, distance from the orchard edge, and year, on the probability of fruit damage on a tree (spread of damage within the orchard) (Figure 6) (χ^2 = 35.996, df = 13, P < 0.001). Additionally, on those trees with damaged fruit, there were significant interactions between treatment, distance from the orchard edge, and year, on the percentage of damaged fruit (intensity of damage on affected trees), detailed below (Figure 6) (χ^2 = 137.65, df = 13, P < 0.001).

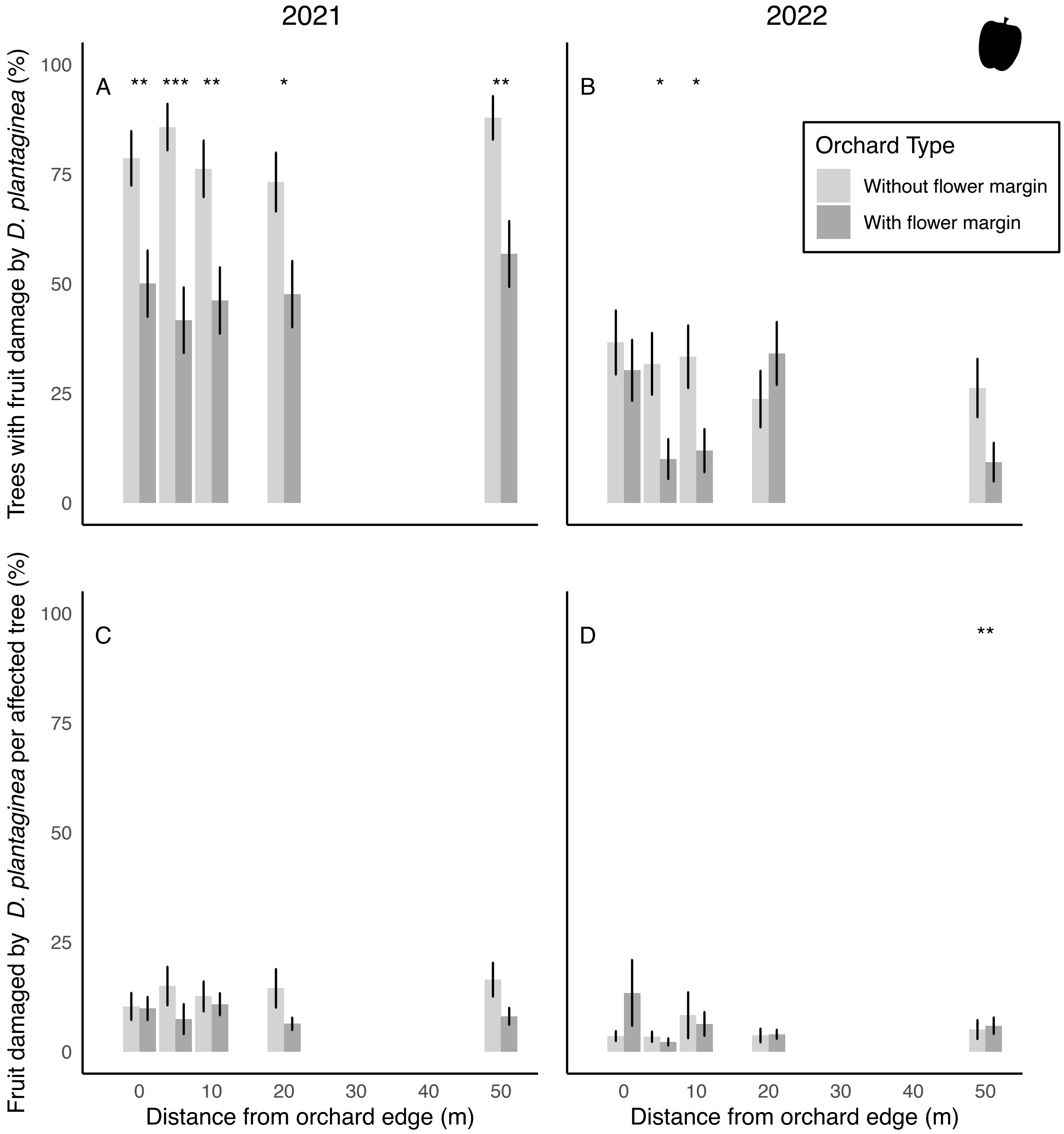

Figure 6. Mean percentage of trees with *D. plantaginea* damaged apples in A) 2021, and B) 2022, and the number of *D. plantaginea* damaged apples on trees with damage present in C) 2021, and D) 2022. Lines show standard error. Stars denote significant effect of treatment at that distance from the orchard edge; *: P < 0.05, **: P < 0.01, ***: P < 0.001.

In 2021, there was a mean of 93 (SD = 73) apples per tree across all 10 orchards. In 2021, orchards with flower margins had significantly fewer trees with fruit damage by *D. plantaginea* (48%) than control orchards (80%) overall (SD = 3) (Figure 6A, Supplementary Table 2.3). Orchards with flower margins had significantly fewer trees with fruit damage at all measured distances from the orchard edge (0 – 50 m) (Figure 6C, Supplementary Table 2.3). The mean percentage of *D. plantaginea*-damaged fruit on affected trees was 4.1% in the flower margins and 11.1% in the control orchards, although the effect was not significantly different (Supplemental Table 2.3).

In 2022, there was, again, a mean of 93 (SD = 76) apples per tree across all 10 orchards. Orchards with a flower margin had significantly fewer trees with *D. plantaginea*-damaged fruit than control orchards, this time at 5 m and 10 m from the orchard edge (Figure 6B, Supplemental Table 2.3). In general in 2022, the mean percentage of *D. plantaginea*-damaged fruit on affected trees was similar in the flower margin (1.4%) and control orchards (1.5%), however only 1.5% of apples on affected trees were damaged (Figure 6D). In 2022, orchards with a flower margin had significantly higher percentage of *D. plantaginea*-damaged fruit on affected trees than control orchards at 50 m from the orchard edge.

Irrespective of fruit damage, across both years, there was no significant difference in total number of apples per square metre between flower margin and control orchards, year, or distance from the orchard edge ($\chi^2 = 0.557$, df = 1, $P > 0.05$, and $\chi^2 = 3.631$, df = 1, $P > 0.05$, and $\chi^2 = 4.112$, df = 4, $P > 0.05$, respectively).

2.4.3 Sentinel bait cards

Depletion of *A. pisum* from bait cards was significantly lower in flower margin orchards compared with controls at 10, 20 and 50 m from the orchard edge in May, at 10 and 20 m in July, and at 50 m in September 2021, and was significantly higher in flower margin orchards compared to controls at 0 m from the orchard edge in September (Figure 7, Supplemental Table 2.5) (interaction: $\chi^2 = 19153$, df = 22, $P < 0.001$).

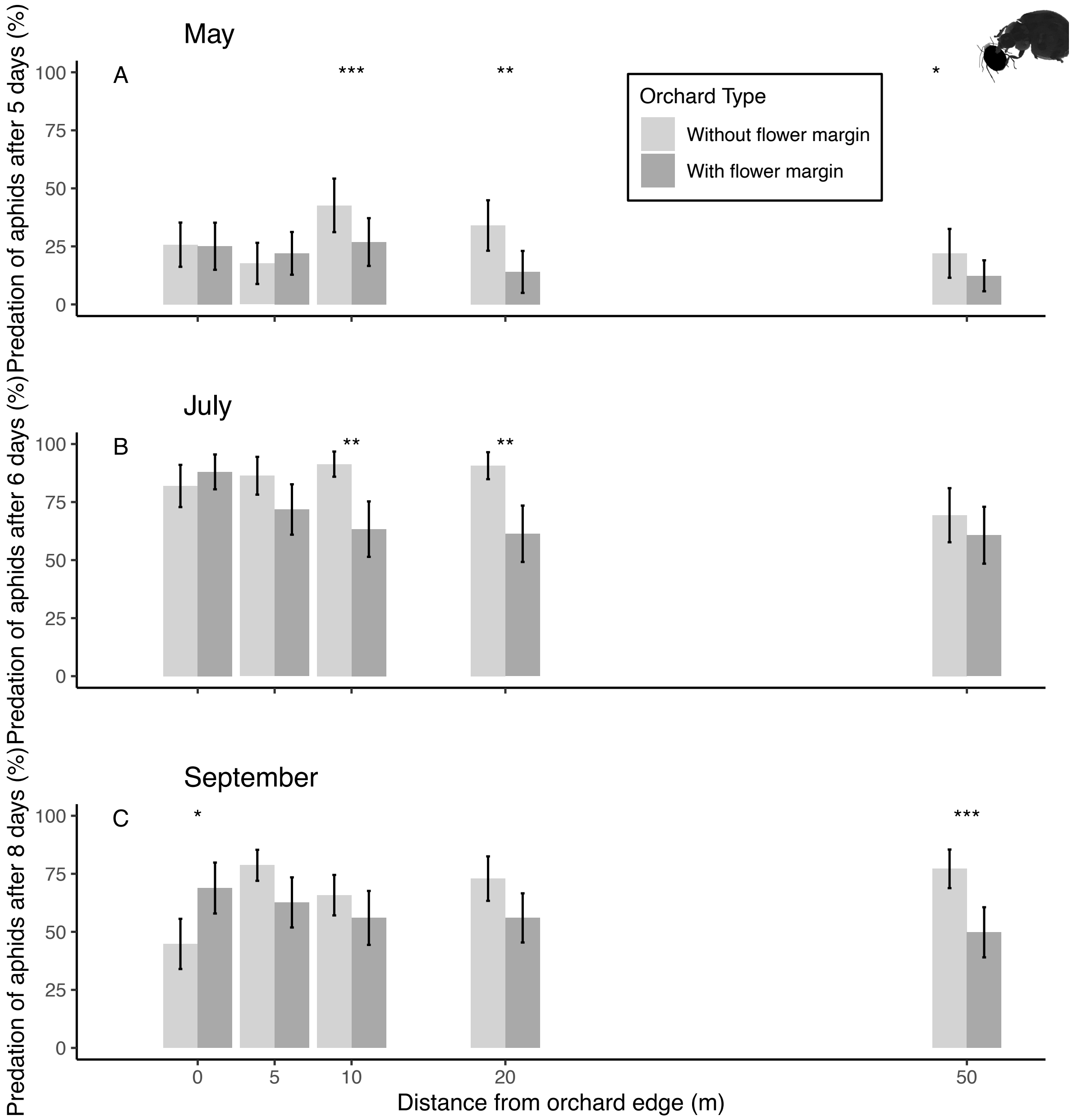

Figure 7: Depletion of aphids from bait cards in A) May, B) Early July, and C) Early September, 2021. Lines show standard error. Stars denote significant effect of treatment at that distance from the orchard edge; *: $P < 0.05$, **: $P < 0.01$, ***: $P < 0.001$.

2.4.4 Predators associated with *Dysaphis plantaginea* surveys

Combined across 2021 and 2022 aphid surveys, 668 natural enemies were counted in the apple trees, of which 61% were found in 2021 when *D. plantaginea* infestation was high. The following predator groups were recorded; Araneae (45%), Syrphidae (27%), Coccinellidae (21%), Heteroptera (10%), Forficulidae (1%), Chrysopidae (< 1%), Opiliones (< 1%) and *Aphidoletes aphidimyza* (Cecidomyiidae)

(1%). The most abundant group, Araneae, comprising spiders, a generalist predator, was found across most sampling rounds albeit in consistently low numbers (too low for statistical modelling) (n=298, mean = 0.08 , SD = 0.33). In 2021, the mean number of spiders was one for every 20 trees and 25 trees (SD = 5 trees) in flower margin orchards and control orchards, respectively. In 2022, the mean number of spiders was one for every 10 (SD = 4) trees in orchards with and without a flower margin. Araneae and predator groups which represent 10% or less of the abundance of the total number of natural enemies were not considered for the subsequent statistical analyses.

The second most abundant natural enemy group was Syrphidae (hoverfly) larvae (n = 182). In June 2021, during peak *D. plantaginea* abundance, 150 Syrphidae were observed. The mean number of Syrphidae was 2 and 1 (SD = 3 and 2) per aphid-infested tree in flower margin and control orchards respectively. There was no significant effect of treatment, or distance from the orchard edge, on Syrphidae abundance on trees ($\chi^2 = 0.022$, df = 1, P > 0.05, and $\chi^2 = 0.121$, df = 1, P > 0.05, respectively) or the likelihood of Syrphidae presence on trees ($\chi^2 = 0.658$, df = 1, P > 0.05, and $\chi^2 = 0.0001$, df = 1, P > 0.05, respectively). However, the likelihood of Syrphidae presence and abundance was significantly and positively associated with increased *D. plantaginea* abundance per tree ($\chi^2 = 28.391$, df = 1, P < 0.001, and $\chi^2 = 7.541$, df = 1, P < 0.001, respectively).

The third most abundant group was Coccinellidae (ladybird) larvae and adults (n = 137). In June 2021, during peak *D. plantaginea* abundance, 116 Coccinellidae were recorded. There was 1 (SD = 3) Coccinellidae per tree in control orchards, and 1 (SD = 1) every 3 trees in orchards with a flower margin. Likelihood of Coccinellidae presence was significantly and positively associated with increased *D. plantaginea* abundance per tree ($\chi^2 = 16.808$, df = 1, P < 0.01). Additionally, there was a significant negative effect of increased distance from the orchard edge on likelihood of coccinellid presence ($\chi^2 = 4.282$, df = 1, P < 0.05), but there was no significant effect of flower margins on likelihood of Coccinellidae presence ($\chi^2 = 0.983$, df = 1, P > 0.05).

In 2021, 437 ants were found during *D. plantaginea* surveys. There was a significantly higher probability of Formicidae presence with increased *D. plantaginea* abundance ($\chi^2 = 21.851$, df = 1, P > 0.001). There was a significant interactive effect of sampling round, and presence of a flower margin on the number of trees with Formicidae present ($\chi^2 = 19.993$, df = 3, P < 0.001). There were significantly fewer trees with ants present in flower margin compared with control orchards in April and August, but not in May or June (Figure 8, Supplemental Table 2.4). Formicidae numbers were too low in 2022 for statistical analysis.

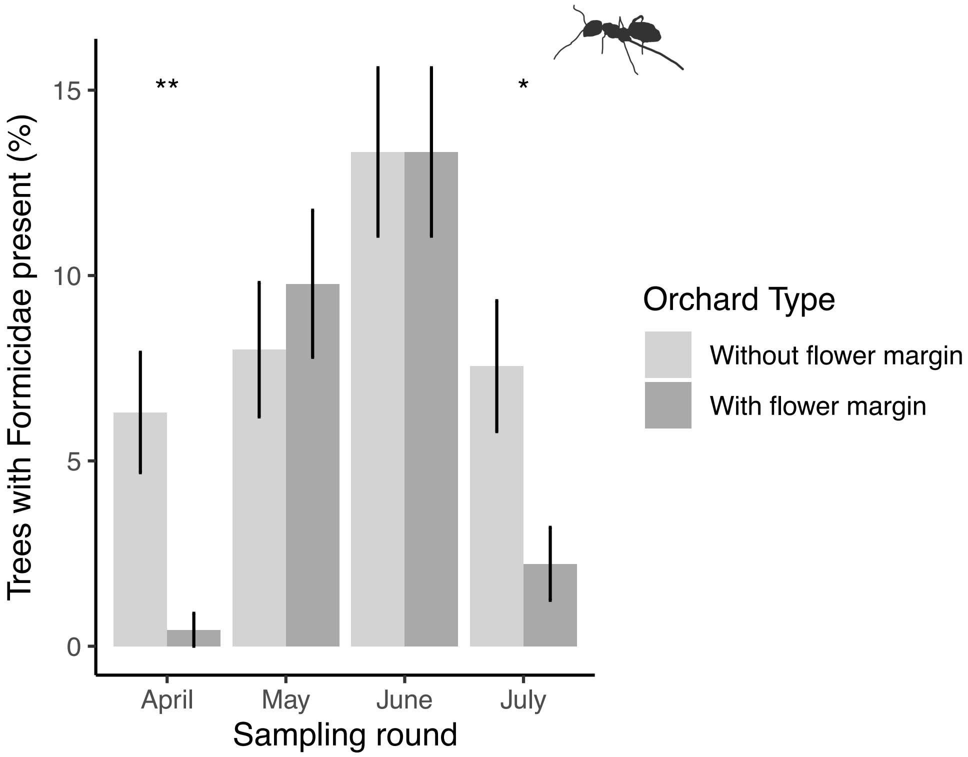

Figure 8: Percentage of orchard trees with Formicidae (ants) present in 2021. Lines show standard error. Stars denote significant effect of presence/absence of flower margins *: P < 0.05, **: P < 0.01.

2.5 Discussion

2.5.1 *Dysaphis plantaginea*

It is common for aphid pest pressure to vary widely by year as demonstrated in the study with 65% of trees infested in 2021 and 25% of trees infested in 2022. Senior et al. (2020) related the temporal variation in pests, at least in part, to changes in temperature and precipitation. For example, perhaps in this case the mild, wet winter proceeding the 2021 apple-growing season (Met Office 2023) led to higher levels of infestation. Changes in pest numbers can both be caused by, and be a cause of, changes in the abundance of natural enemies, which might explain why there were double the number of trees with spiders in 2021 compared to 2022. Whilst abundance of *D. plantaginea* was too low in 2022 for detailed analysis, in 2021, a year with high levels of infestation, there were significantly fewer areas of the apple trees were infested with *D. plantaginea* in flower margin compared to control orchards. This study also found a significant decrease in *D. plantaginea* abundance at 10 m from the orchard edge in flower margin orchards compared to 10 m in control orchards. Previous studies have provided some evidence that perennial flower strips can slow the growth of *D. plantaginea* colonies compared with control plots by increasing natural enemy populations (Cahenzli et al., 2019). The abundance, likelihood, and duration of presence of *D. plantaginea* can decrease with proximity to flower strips (Albert et al., 2017). The reduced number of areas on the apple trees infested by *D. plantaginea* in flower margin orchards would have reduced the number of buds or fruit clusters in close proximity to a colony. This could have reduced the likelihood of a tree having any damaged fruit at harvest since an aphid colony feeding on or near to buds and fruit is what causes fruit damage. As such, the reduced spread of aphid colonies in the trees could have been a driving factor behind the reduction in number of trees with damaged fruits. Of those infested trees, the number of damaged fruits was not significantly different in flower margin and treatment orchards, perhaps suggesting that there could have been a reduction in colony establishment rather than a difference in colony growth rates, although this was not directly measured.

2.5.2 *D. plantaginea* fruit damage

During 2021 when there were high levels of *D. plantaginea* infestation, the proportion of trees with apple damage was significantly reduced, from 80% in control orchards compared to only 48% of trees in flower margin orchards. Assuming that 4.1% and 11.1% of fruit was damaged by *D. plantaginea* on affected trees in the flower margin and control orchards respectively, and a marketable apple yield of 35,000 kg/ha for Gala orchards in the UK in 2021 (DEFRA, 2023), the flower margins could result in an additional 2420 kg/ha of undamaged fruit (Supplemental Table 2.6). To my knowledge, this is the first study to find a significant reduction in incidence of fruit damage at harvest in orchards provisioned with flower margins compared with control orchards. Only a few studies have investigated the effects of flower strips on fruit damage by *D. plantaginea*. For example, Campbell et al. (2017) measured the effect of flower margins in apple orchards and found no impact on yield, despite finding positive effects on natural enemy communities, as did Jacobsen et al. (2022). Similarly, a large-scale pan-European study found reductions in fruit damage by *D. plantaginea* after second fruit drop, but not at harvest, perhaps due to quality thinning practices (Cahenzli et al., 2019). These studies assessed newly established flower strips (although Jacobsen et al. replaced 5-year-old, less-diverse strips). A review by Herz et al. (2019) indicated that older flower strips may be more effective, as in other crops (Blaauw and Isaacs, 2015), although, in apple orchards, only a minority of previous studies have investigated well-established strips (Albert et al., 2017; Cahenzli et al., 2017; Cahenzli et al., 2019). In a recent agroforestry study in a farm using 6-year-old sown flower strips there was a reduced percentage of apples lost to *D. plantaginea* for trees with spontaneous flowering understories compared with both mown herbage and arable crop (Staton et al., 2021). In the study, and that of Staton et al. (2021), perhaps the maturity of the flower strips led to more effective reduction of fruit damage caused by *D. plantaginea*. The observation in this study that wildflower margins significantly reduce the incidence of fruit damage at harvest in orchards, compared to control orchards, raises useful opportunities for orchard managers. It suggests that flower margins can help to control crop damage in the face of varying pest-pressure resulting from crop management and climate variation. To my knowledge, this is the first study to demonstrate reduced *D. plantaginea* damage in conventionally managed fruit orchards with floral margins. A similar study in conventional orchards found no effect of inter-row flower strips on pest regulation services, which was suggested to be due to detrimental impacts on natural enemies by the plant protection products which were used at the time (McKerchar et al., 2020). To put fruit damage results into an economic context relevant for growers, future studies could investigate the economic significance of fruit damage, and perhaps the net economic benefits of flower strips as a tool for pest suppression. Whilst this study focuses on *D. plantaginea*, there are many other insect pests of apple which have the potential to be controlled by natural enemies, for example tortricids or codling moth (Bostanian et al., 2004; Fountain, 2022).

2.5.3 Spill-over of *D. plantaginea* control

During 2021, when there were high levels of *D. plantaginea* infestation, spill-over of beneficial effects of flower margins, i.e. reduced spread and fruit damage by *D. plantaginea*, reached up to 50 m from the orchard edge, which was the maximum distance measured. By contrast, in 2022, with low levels of infestation, the positive impact of the flower margin was detected up to 10 m away from the orchard edge. To find a significant effect on incidence of fruit damage from marginal flower strips up to 50 m into apple orchards suggests that mobile predators are key drivers of aphid control. For example, aphidophagous hoverflies can travel 50-250 m from a pollen source (Harwood *et al.* 1994; Wratten *et al.* 2003), and Miliczky and Horton (2005) report that flower margins could affect the abundance of natural enemies up to 40 m into orchards. The exact extent of the effect in any particular year is also likely to be affected by climate and crop management (Fountain, 2022). The average length of the orchards, perpendicular to the flower margin, was 130 m. As such, the finding that incidence of trees with fruit damage can be significantly, and consistently, reduced up to 50 m away, and nearing the centre of the orchards, indicates that for *D. plantaginea* control, flower margins may offer a practical alternative to interrow flower strips (which may interfere with farm machinery).

2.5.4 Predators

The most abundant specialist predator groups found in *D. plantaginea* surveys were Syrphidae, and Coccinellidae, consistent with many previous studies (Albert et al., 2017; Santos et al., 2018; Cahenzli et al., 2019; Rodríguez-Gasol et al., 2019). However, there were no effects of flower margins on abundance or likelihood of presence for either group, suggesting that they are highly motivated to search for and attack *D. plantaginea* colonies. Other studies have generally found similar or neutral effects of flower strips (Santos et al., 2018; Jacobsen et al., 2022), or found significantly increased abundance of generalists, and specialist predators including Syrphidae and Chrysopidae (Albert et al., 2017; Cahenzli et al., 2019). These authors also identified an increased likelihood of Syrphidae and Coccinellidae within *D. plantaginea* colonies on orchard trees where flower strips were provided (Albert et al., 2017). Jacobsen et al. (2022) found no difference in the proportion of aphid colonies containing predators during visual searches for *D. plantaginea* between orchards with and without flower strips. The current study found that Coccinellidae abundance and likelihood of Syrphidae presence on trees increased with higher abundance of *D. plantaginea* on trees, as was found by Albert et al. (2017). Natural enemies frequently aggregate in areas of high prey abundance. For specialist predators of aphids such as Syrphidae, Coccinellidae, and Chrysopidae, it is not surprising that there is a positive response to aphid abundance (Miñarro et al., 2005; Albert et al., 2017; Cahenzli et al., 2019). Some hoverfly species are aphid density-dependent, i.e. they lay more eggs where there is increased size of aphid colonies (Graham, 1989), to meet the needs of their larvae. For example, *Episyrphus balteatus*, considered an important enemy of *D. plantaginea* (Dib et al., 2010b), exhibits highly density-dependent egg-laying compared with other aphid predators (Sutherland et al., 2001). This species also avoids laying eggs in proximity to conspecific eggs, mummified aphids, other predators (Dib et al., 2011), or attending ants (Nagy *et al.* 2015). Perhaps, in the study, these behaviours masked effects of flower margins on Syrphidae and their pest-control services. Visual searches as a survey method could be less effective at recording faster-moving predators, for example predatory Hemiptera. To sample these groups, a method such as tap sampling would reduce the opportunity for these predators to flee upon any disruption of the tree branches or leaves. Tap sampling however does not allow for the curled leaves surrounding a *D. plantaginea* colony to be uncurled.

There were significantly fewer trees with ants present in flower margin compared to control orchards in April and July 2021. Ants prefer to obtain sugar from floral resources when aphid colonies are small, but as colonies grow and produce more honeydew, ants attend aphids protecting them from predators in exchange for the sugar (Katayama et al*.,* 2013) resulting in aphid populations growing more rapidly due to reduced predator pressure (Stewart-Jones et al., 2008; Nagy et al., 2015). In the study, the reduction in ant presence in flower margin orchards, particularly early in the season, could have contributed to the reduced spread of infestation by *D. plantaginea*, and reduced abundance at 10 m, in flower margin compared with 10 m in control orchards. These results provide preliminary evidence to suggest that ant attendance may be reduced by a flower margin in the early and late season, which should be investigated further.

2.5.5 Predation

Although the results demonstrated reduced *D. plantaginea* pressure in flower margin orchards, more *A. pisum* aphids were removed by predators from bait cards in the control orchards. During the assessments, the following groups were observed feeding from the cards; Formicidae (ants), Heteroptera (bugs), Chrysopidae larvae (lacewing), Coccinellidae larvae (ladybird), and adult midges. Bait cards were used as a proxy for predation, and are particularly useful when there are time, resource, or logistical limitations associated with the use of more elaborate methods of recording predation of live animals (Boetzl et al., 2020). Cahenzli et al. (2019) also found no significant increase in the activity of natural enemies, using aphid bait cards in flower strip compared to control orchards. Nevertheless, predation from bait cards was increased up to 55% in conventional apple orchards with flower strips as compared with control orchards in similar experiments by Campbell et al. (2017), despite finding no effects on aphid densities or natural enemies. Perhaps this was because sterilised moth eggs were used as bait instead of dead aphids, or due to the difference in location (Herefordshire, SW England). Other issues with the bait cards include dead compared to live aphids and the use of a different species, both potentially changing the interaction with natural enemies. Additionally, this method is less likely to reflect predation by some groups, for example Syrphidae larvae. Bait cards are suggested to provide a proxy for predation by generalists rather than specialists (Lövei and Ferrante, 2017), which could suggest that generalists are not the main group driving *D. plantaginea* control here, although this remains unknown.

2.5.6 Parasitism

Only two *D. plantaginea* mummies were found during the sampling seasons. Similar studies have also reported absences or low levels of evidence of parasitism of *D. plantaginea* (Miñarro et al., 2005; Brown and Mathews, 2014; Albert et al., 2017). Parasitism rates can be higher in organic orchards (Rodríguez-Gasol et al., 2019; Dib et al., 2010b), and insecticide-free orchards (Santos et al., 2018), but not in every case (Albert et al., 2017), and a lack of observed parasitism may be driven by the high sensitivity of parasitoid wasps to plant protection products (Albert et al., 2017).

2.5.7 Conclusions

To my knowledge, this is the first study to detect a reduction in crop pest-damage at harvest when a flower strip is present compared with a control. This is one of few studies to investigate flower strips in conventionally-managed crop. This study found an agronomically significant reduction in crop damage and yield-loss by a globally important pest at far-reaching distances into the crop area. Positive effects of flower margins were stronger and extended further into the crop during a year with higher pest pressure. The results show perennial flower strips as a realistic tool to support pest control services for sustainable production in the future, for example by buffering effects of pest pressure related to climate variation and change.

2.5.8 Data Availability

Data available from the University of Reading Research Data Archive at https://doi.org/10.17864/1947.000525 (Howard, 2024).

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

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Author Contributions

Charlotte Howard: Conceptualization, Formal analysis, Writing - Original Draft, Visualization. **Michelle T Fountain**: Conceptualization, Writing - Review & Editing, Funding acquisition. **Claire Brittain**: Conceptualization, Writing - Review & Editing, Funding acquisition. **Paul J. Burgess**: Conceptualization, Writing - Review & Editing, Funding acquisition. **Michael P. D. Garratt**: Conceptualization, Writing - Review & Editing, Supervision, Funding acquisition.

3.1 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, I 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, there was no 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.

3.2 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, such as Coccinellidae, Araneae, and parasitoid wasps (Tylianakis et al., 2004;

Taylor and Pfannenstiel, 2008; He and Sigsgaard, 2019). 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 generalist natural enemies, reduction in crop pests, and reduction in crop damage in proximity to 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., 2010b), 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., 2010b), 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, this study 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. I 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.

3.3 Methods

3.3.1 Study sites

Study sites were ten commercial dessert apple orchards (Gala var.) located in Kent, UK and have been previously described by Howard et al. (2024). 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 a year (Figure 1). The average width of the flower margins was 15 m (SD = 9.6 m) (Howard et al. 2024 and Supplemental Table 3.1). 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, 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.

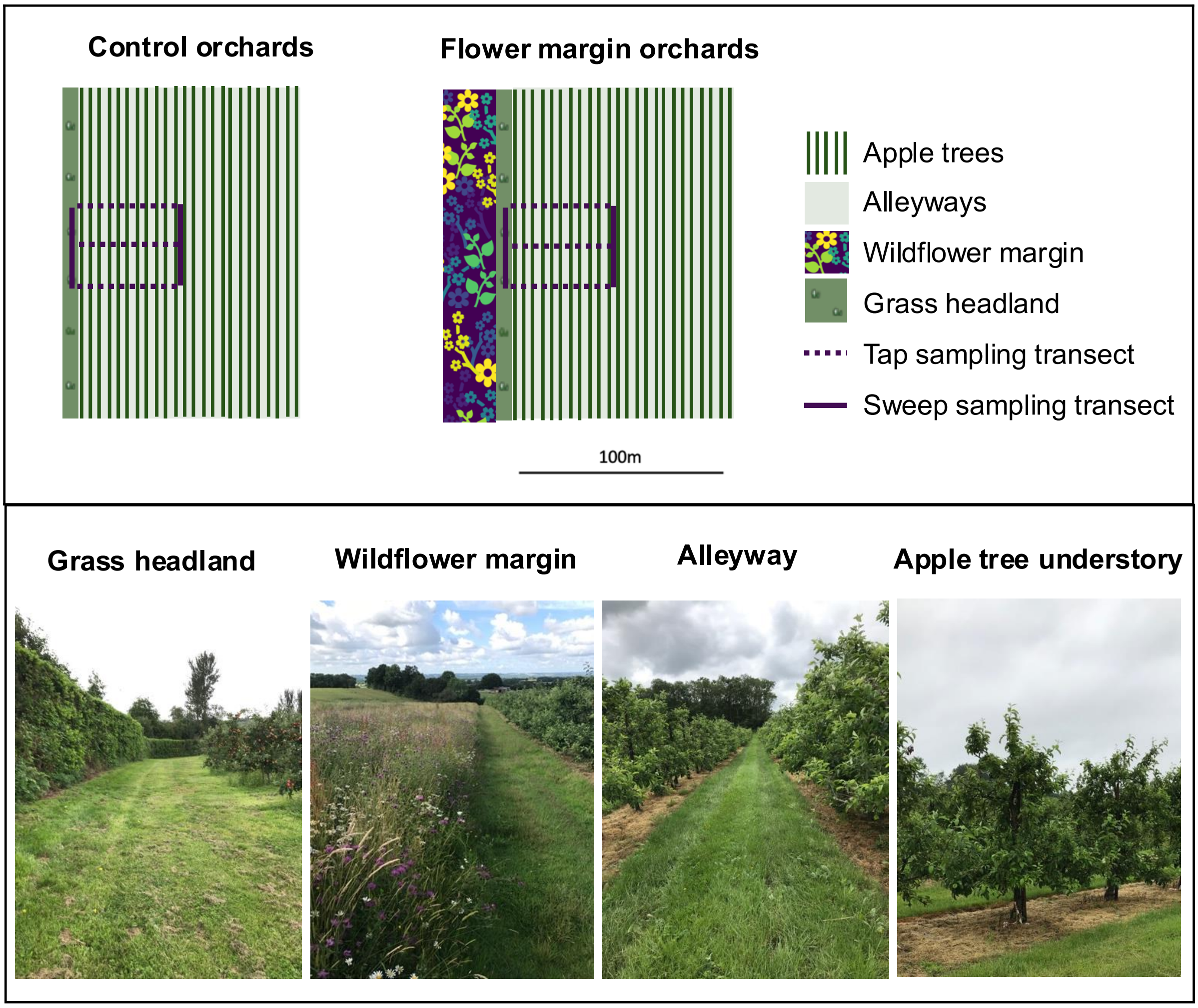

Figure 1: Typical layout of flower margin orchards (n = 5) and control orchards (n = 5) where natural enemies were sampled from apple trees via tap sampling and from ground vegetation via sweep sampling (above), with photographs of each habitat type (below). Vegetation was assessed across the same transects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

3.3.2 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 (Figure 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.

3.3.3 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 (Figure 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.

Table 1. Taxonomic level of identification of sampled natural enemies of *D. plantaginea* (Dib et al., 2010b; 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[1]	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[2]
Harvestmen	Order: Opiliones	Generalist
Spiders	Order: Araneae	Generalist

1 Manual identification to these Families is not possible for nymphs.

2 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., 2010b).

3.3.4 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 x 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) (Figure 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).

3.3.5 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 I 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, I 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 sampling year to aid model convergence where needed (Table 2). The random effect structure was simplified where necessary to avoid over-fitting (Table 2). Generalist and specialist predators were modelled 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).

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. 'Pair' refers to the experimental design whereby each treatment orchard was paired with a control orchard. Random effects were nested in the order in which they appear in the table.

			Fixed Terms							Nested Random Terms		
Response	Sampling Methods	Distribution	Treatment	Distance	Area	Year	Round	Aphid[1] abundance *0.01	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).

3.4 Results

3.4.1 Orchard vegetation

The plant community composition was significantly different between habitat types (F = 10.55, df = 5,49, P = 0.001, Figure 2). The vegetation community in the flower margins was significantly different from the understory areas below the apple trees (Supplemental Table 3.2). By contrast, in both the flower margin and control orchards, the vegetation community of the understory and alleyway areas of the orchard were similar (Figure 2, Supplemental Table 3.2). The vegetation in the alleyway area was similar to that in the headland (Figure 2, Supplemental Table 3.2). 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 3.1. Common flowering species were *Lotus corniculatus* (birds foot trefoil) and *Centaurea nigra* (black knapweed) in the flower margin, *Trifolium repens* (white clover) in the headland and alleyway, and *Epilobium montonum* (broad leaved willow herb) and *Ranunculus repens* (creeping buttercup) in the understory. The mean sward height was 13 cm (SD = 5) in alleyways of flower margin orchards, 12 cm (SD = 5) in alleyways of control orchards, 10 cm (SD = 6) in headlands, and 72 cm (SD = 26) in flower margins.

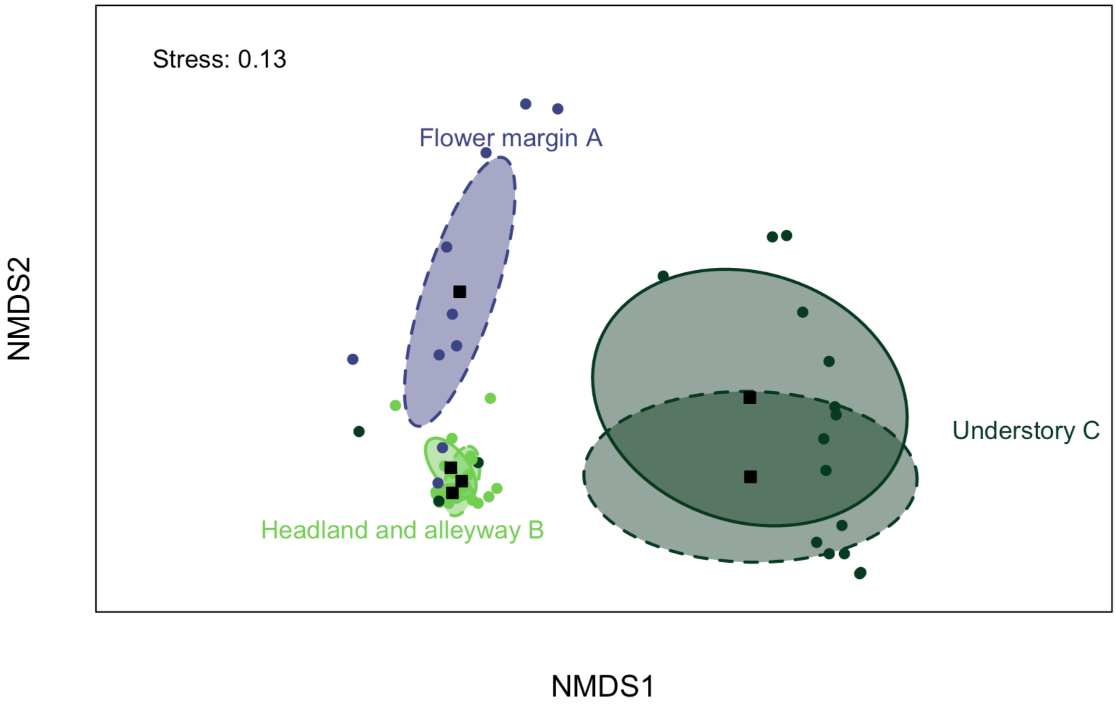

Figure 2: Non-metric multidimensional scaling ordination of relative abundance of vegetation (summer 2021 and 2022) in orchards with and without flower margins (dotted and solid elipses respectively) across different habitat types (based on Bray-Curtis similarity). Ellipses show one standard deviation 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).

3.4.2 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 1,329 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%) (Figure 3).

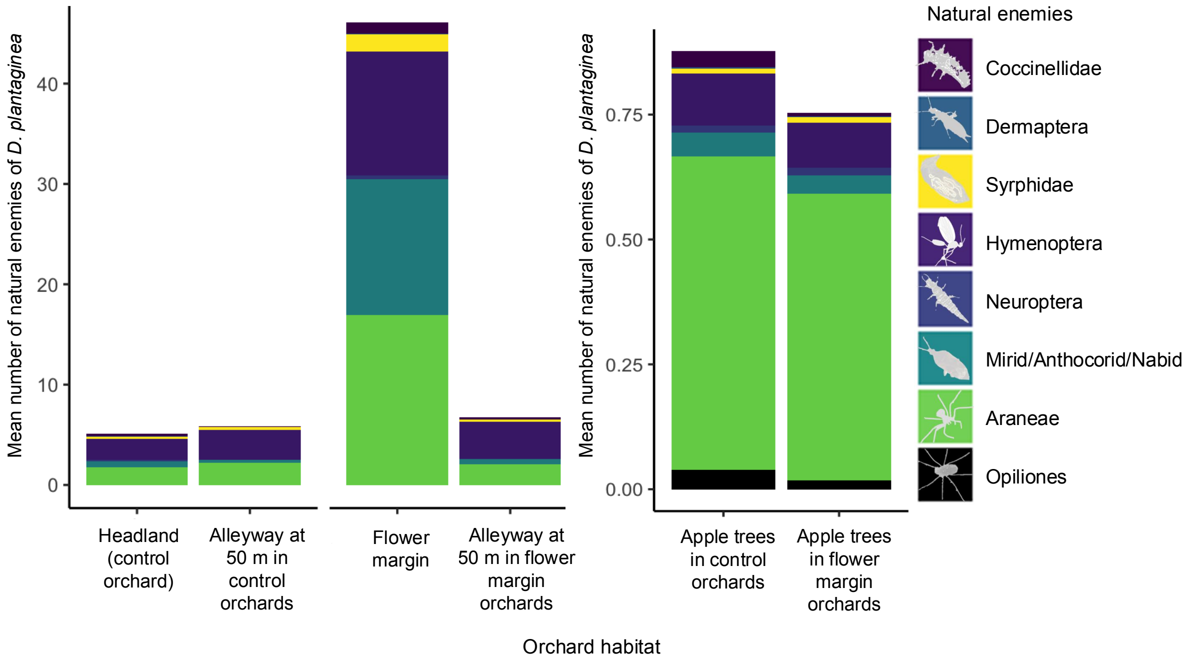

Figure 3: Mean abundance of groups of natural enemies of *D. plantaginea* collected in different orchard habitats across 4 rounds in both 2021 and 2022.

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, $P < 0.05$) (Figure 4). Diversity was also significantly higher in the headland/margin area compared to the central alleyway ($\chi^2 = 13.0$, df = 1, $P < 0.001$) (Figure 4), and was significantly different between months, highest in June and lowest in April ($\chi^2 = 57.213$, df = 3, $P < 0.001$) (Figure 4).

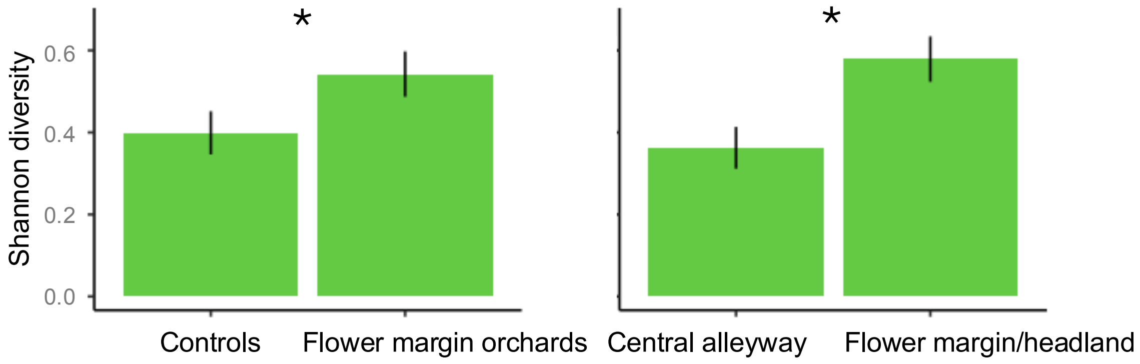

Figure 4*:* Shannon diversity index of natural enemies of *D. plantaginea* in flower margin orchards compared with control orchards (left) and in the orchard alleyway compared to the flower margins and control headland (right). Stars denote significance, P < 0.05.

3.4.3 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 (χ^2 = 12.784, df = 1, P < 0.001) and generalist predators (χ^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 (Figure 5, Supplemental Table 3.3). There was also a significant effect of sampling round where abundance was highest in June and lowest in April (specialists: χ^2 = 196.684, df = 3, P = 0 < 0.001, generalists: χ^2 = 58.824, df = 4, P < 0.001.

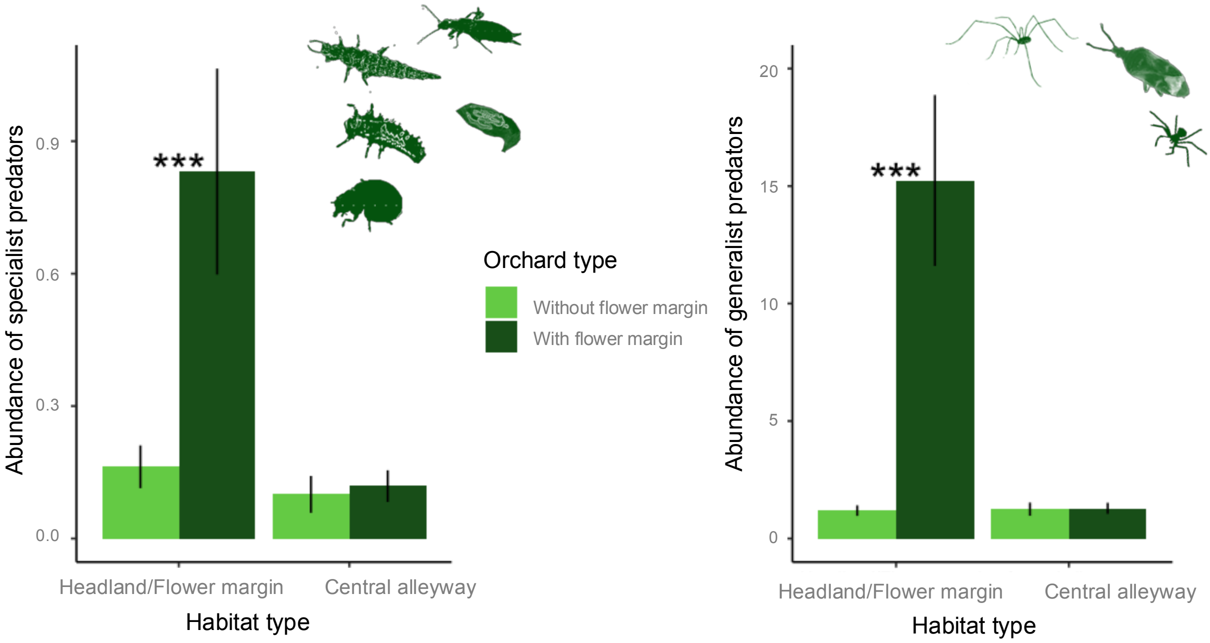

Figure 5: Mean abundance of specialist (left, n = 194) and generalist (right, n = 1,513) predators of *D. plantaginea* in the central alleyways compared to the flower margin or headland in flower margin orchards compared to control orchards across four rounds in 2021 and 2022. Stars denote significance, P < 0.0001.

3.4.4 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 (Figure 6, Supplemental Table 3.4). In 2022, there was no significant difference between the communities of natural enemy taxa across orchard habitats (Figure 6, F=1.578, P=0.051).

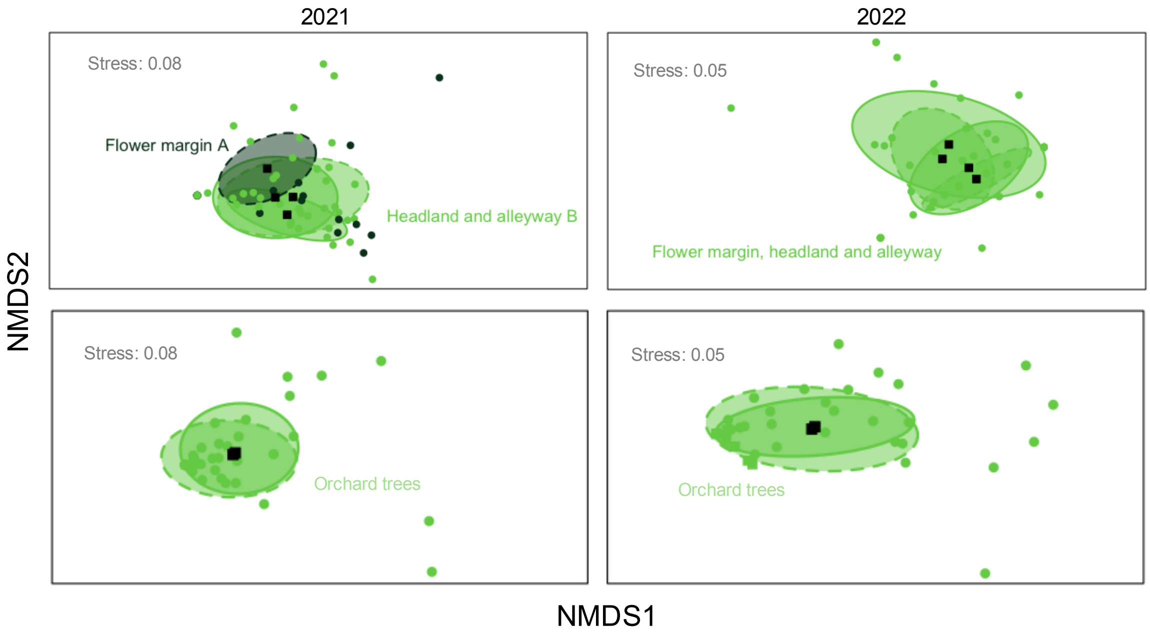

Figure 6: Non-metric multidimensional scaling ordination of relative abundance of natural enemies of *D. plantaginea* (in April, May, June/July, and August) for habitats (headland, flower margin, and 50 m alleyway) in orchards with and without flower margins (dotted and solid elipses respectively) (based on Bray-Curtis similarity), sampled from orchard habitats via sweep-netting (top) and tap sampling (bottom). Ellipses show one standard deviation 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).

3.4.5 Diversity of natural enemies in the orchard trees

In total, 2,296 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 1,326 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 (χ^2 =100.154, df =10 , $P < 0.001$) where diversity was lower in August 2021 in flower margin orchards compared with controls (Supplemental Table 3.3). Shannon diversity significantly decreased with increased distance from the orchard edge (χ^2 = 19.476, df = 4, $P < 0.001$).

3.4.6 Abundance of predators in the orchard trees

There was an interactive effect of presence of a flower margin and distance from the orchard edge (χ^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 3.3). Additionally, there were significantly more specialist predators on apple trees where there was a higher number of aphids (χ^2 = 8.5194, df = 1, $P < 0.01$). There were significantly more specialist predators in 2021 than in 2022 (χ^2 = 31.028, df = 1, $P < 0.001$) and increasingly more in each round (χ^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 (χ^2 = 1.193, df = 1, P = 275; χ^2 = 1.836, df = 1, P = 0.175, respectively). There were significantly more generalists in 2022 (χ^2 = 58.233, df = 1, $P < 0.001$) and fewer with increasing distance from the orchard edge (χ^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 (χ^2 = 30.040, df = 3, $P < 0.001$).

3.4.7 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, $P > 0.05$) (Figure 6).

3.5 Discussion

3.5.1 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 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 margins were sown and were 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. In other crop systems, sown flower margins can increase plant species richness, cover, nectar/pollen supply (Schmidt et al., 2022b), 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; Cahenzli et al., 2019), this study demonstrates that margins continued to have a rich and different plant community five years post sowing.

3.5.2 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. There was 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 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 which can provide arthropods with increased shelter, refuge from pesticides, breeding sites, overwintering sites, moderated microclimate, and also structure for spider webs (Solomon et al., 2000). This can also provide different food sources such as pollen, nectar, and alternative prey (Landis et al., 2000; Favarin et al., 2024). 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). The results of this study 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.

3.5.3 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 the current 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, species diversity or the abundance of particular aphid natural enemies. For example, without species level identification, all predatory Heteroptera were classified as generalists and as such grouped with other generalists including Araneae. However, some heteropteran species, such as *Anthocoris nemorum* and *Atractotomus mali* 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 the current 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., 2010b). 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.

3.5.4 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, there was no evidence of broad differences between natural enemy taxa abundance, diversity, or community structure on the apple trees themselves. However, a previous study has shown 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.

4 Evaluating an emergence experiment method for measuring the effect of flower margins on rosy apple aphid (*Dysaphis plantaginea*) control by parasitoid wasps

4.1 Abstract

Sown or natural flower strips are a commonly used management practice in agroecosystems and have been demonstrated to increase the abundance of predators of orchard pests. In addition to predators, parasites can also play a key role in suppression of orchard pests, but these are comparatively understudied. Of the few previous studies assessing parasitism rates in apple orchards, most have counted parasitoid abundance or a proxy of this, and so direct effects on pest control are hard to ascertain. I collected colonies of a major apple pest, rosy apple aphid (*Dysaphis plantaginea*) and cultured them for enough time that parasitoid wasps could emerge. Unfortunately, the chosen methodology did not yield usable data due to challenges with aphid survival and stowaway predators hiding in the aphid colonies. I discuss the limitations of this method and suggest alternative approaches for future research. Improved knowledge of the effect of flower strips on parasite contribution to suppression of *D. plantaginea* could add valuable insight into the mechanism of how flower margins can reduce pest pressure in orchards to help optimise management for improved pest control.

4.2 Introduction

The suppression of crop pests by their natural predators and parasites (natural enemies) can be a highly environmentally and economically valuable ecosystem service for crop production (Zhang et al., 2016; Begg et al., 2017; Zhang et al., 2018), including for apple production (Cross et al., 2015). To provide pest control services natural enemies require sufficient habitats and plants as they provide resources year-round for shelter, overwintering, nesting, breeding, and food resources in the form of pollen, nectar, and alternative prey (Gurr et al., 2017). However, monoculture cropping and continued habitat loss on agricultural land has reduced these resources and therefore their potential to support beneficial organisms (Emmerson et al., 2016). One method to encourage natural enemies, and their pest control services, is to increase the amount of semi-natural habitat on farmland by establishing 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 providing the necessary resources to support abundant and diverse natural enemy communities (Fountain, 2022).

Parasitoid wasps (Order: Hymenoptera) are a naturally occurring natural enemy of pests in apple orchards (Albert et al., 2017; Santos et al., 2018). The young wasp feeds on the host from the inside, gradually killing it before pupation into an adult wasp (Le Ralec et al., 2010). The killed aphid is referred to as a "mummy" (Figure 1). Some parasitoid wasp species are commercially reared and sold for augmented releases aimed at control of specific target pests (Dassonville et al., 2012), but naturally present parasitoids can also be effective for pest suppression. For example, Quarrel et al. (2017) reported that severe infestations by *Eriosoma lanigerum,* woolly aphid, can be avoided if the parasitoid, *Aphelinus mali,* or European earwig, *Forficula auricularia,* exceeded a threshold density. They found that more than one *A. mali* female per every two trees was required to prevent severe infestation if the *F. auricularia* threshold was not met (>14 per tree) (Quarrell et al., 2017). Most adult parasitoids must feed on sugar, which they mostly obtain from floral resources or 'honeydew' secreting sap-feeders (Tena et al., 2013; Russell, 2015). The provision of floral sugar resources can increase parasitoid longevity (Kishinevsky and Ives, 2024), and in apple orchards, parasitoids benefit from floral resources in terms of fitness (Tylianakis et al., 2004), and abundance (Rodríguez-Gasol et al., 2019).

A major economic pest of commercial apple orchards is rosy apple aphid, *Dysaphis plantaginea* which causes fruit deformation and reduction of fruit size (Blommers et al., 2004). Parasitoid wasps are reported to supress populations of *D. plantaginea* (Bribosia et al., 2005; Dib et al., 2012; Rodriguez-Gasol et al., 2019). However, the role of parasitoids for apple pest control is understudied (Shaw et al., 2021). Most studies on the effect of flower margins focus on predators over parasites, likely due to the comparative ease of identification (Crowther et al., 2023). The effect of flower strips on *D. plantaginea* is uncertain, as is the extent of spill-over from the floral strips, and in other crops it has been shown that abundance of parasitoids can decrease with increasing distance from the flower strips (Lavandero et al., 2005; Tougeron et al., 2023). Although Santos et al. (2018) found no effect of flower strips on proportion of parasitised *D. plantaginea*, Tougeron et al. (2023) showed flower strips in-between rows of apple trees increased persistence and dispersal capacities of released parasitoid wasps (*Aphidius matricariae* and *Ephedrus cerasicola*) and improved biological control of *D. plantaginea* at increased distanced from the release points (Tougeron et al., 2023). Since parasitoid wasps are a key natural enemy preventing severe infestations of aphid species in different cropping systems, improved knowledge of the effect of flower strips on parasitoid contribution to suppression of *D. plantaginea* could add valuable insight into the mechanism of how flower margins can reduce pest pressure in orchards.

Of the few previous studies assessing parasitism rates in apple orchards, most have counted the ratio of aphids to mummies (Albert et al., 2017; Santos et al., 2018). However, Tougeron et al. (2023) observed that aphids tend to leave their colony once parasitised which suggests that counting mummies may not be an ideal method for accurately estimating parasitism rates. Additionally, parasitised aphids which have not yet become a ‘mummy’ are inconspicuous. An alternative method, monitoring parasitoids via trapping (Malaise, sticky, or water/pan), only allows for abundance of parasitoids to be recorded and does not consider the rate of parasitism of pest species (Fraser et al., 2008; Ward et al., 2021; Grupe et al., 2023) and so direct effects on pest control are hard to ascertain. As such, this study tested an emergence experiment whereby *D. plantaginea* colonies were collected from apple orchards and cultured to allow for adult parasitoids to emerge and be counted. This study aimed to establish whether presence of established perennial flower margins increased parasitism of *D. plantaginea* by parasitoid wasps, and if so, at what distance from the flower margin were effects observed.

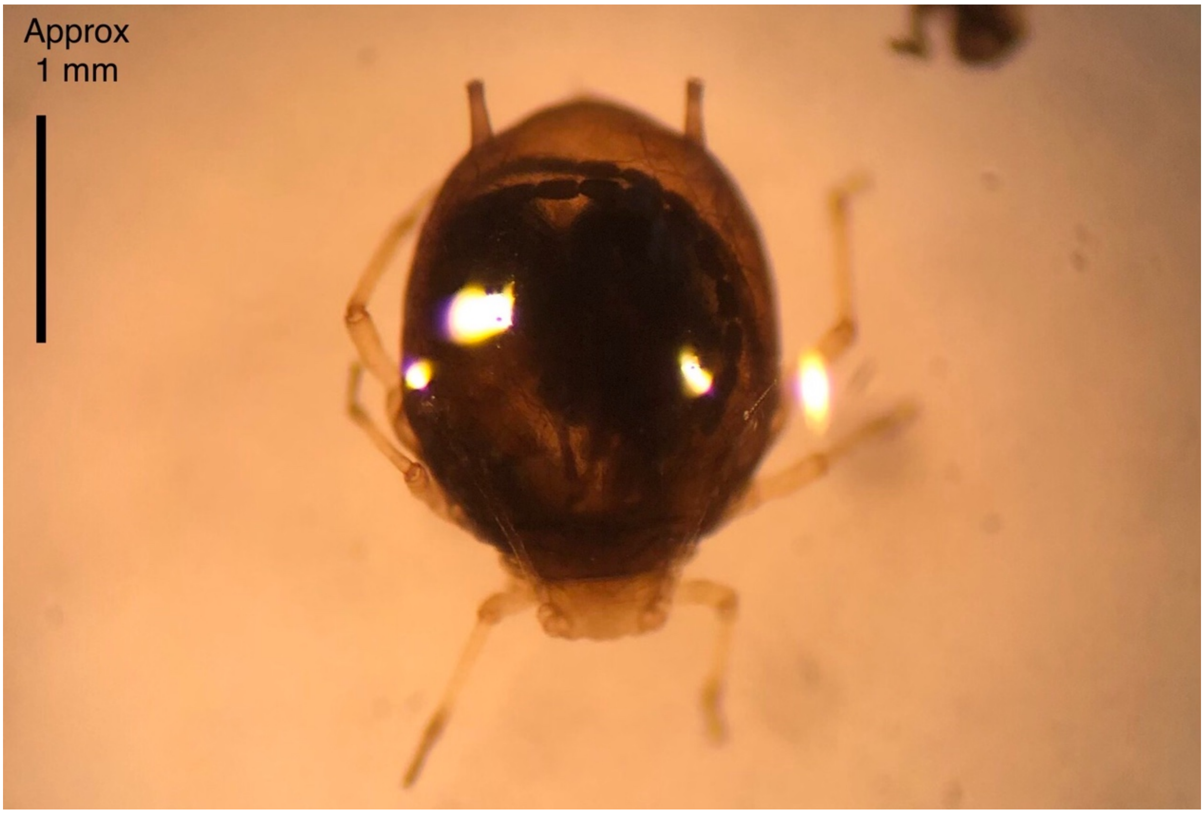

Figure 1: An adult parasitoid wasp (black) with visible antennae, inside *D. plantaginea* (brown) photographed under a light microscope. The parasitoid has pupated (spun a cocoon) inside the host which is now referred to as a “mummy” or “mummified”.

4.3 Methods

4.3.1 Study sites

A full description of the study and sampling methods is described by Howard et al. (2024). Briefly, ten conventional UK commercial dessert apple orchards in South-East England, five of these termed “flower strip orchards” were bordered by an established sown perennial flower strip (2-5 years), and five “control orchards” had only a permanent grass headland 4-5 m wide, typically mown four times a year. The average width of the flower strips was 15 m (SD = 9.6 m) (Howard et al., Supplemental Table 1). All orchards were conventionally managed and used integrated pest management. Flower strip and control orchards were paired on the same farm so that the use of pesticides, nutrients, and mowing was the same between the two orchards, with a distance of 120-410 m between treatments orchards to minimise differences in soil type and aspect and co-use by the same invertebrates. Flower strips were sown with perennial flowering species and grasses designed to offer multiple flowering times, flower shapes, and maximise pollen and nectar resources (Carvell et al., 2022). To encourage earlier flowering, and to keep weeds under control, all flower strips were cut to 8-10 cm annually in autumn, and the cuttings removed (Carvell et al., 2022) and they were not fertilizer or herbicide treated.

4.3.2 Sampling design

We measured effects of the flower strips on parasitism of *D. plantaginea* across the apple growing season. Apple trees were searched for *D. plantaginea* colonies in May, June, and July, 2022. All trees were searched at 0, 5, 10, 20, and 50 m from the orchard edge, with 50 m being close to the centre of the orchards. All searched trees were at least 20 m from the nearest perpendicular orchard edge. Aphids on specific trees (n=45) were being monitored monthly for another study (Howard et al., 2024), so those trees were excluded from searches. Six leaves hosting *D. plantaginea* colonies were cut from six different trees at each distance from the orchard edge (30 per orchard) using pruning scissors. Since *D. plantaginea* causes leaf curling (Blommers et al., 2004), each leaf was uncurled to count the total number of aphids and aphid mummies (host to a pupated parasitoid wasp), any aphid predators or predator eggs were removed (using a fine paintbrush) to avoid predation of aphids or emergence of parasitoids from predator species. The shoot was handled with care to avoid squashing or knocking off any aphids. The colony was left on the leaf to reduce stress to the aphids. Distance from the orchard edge was recorded for each colony.

4.3.3 Mesocosm preparation

A mesocosm design was adapted from protocols for emergence experiments with apple by Universitat Autonoma de Barcelona (unpublished). Each colonised leaf was placed in 25 mL of agar (8.5g agar / L water) in a 30 mL Falcon tube to hydrate the leaf. Tubes of agar were refrigerated with lids on prior to use. The tube was placed in a 330 mL plastic cup which was then covered with mesh ($1.35mm^2$ Enviromesh https://www.enviromesh.co.uk/collections/enviromesh/products/enviromesh-by-the-metre) and secured with two elastic bands (Figure 2).

Figure 2: Emergence mesocosm comprising an apple leaf colonised with *D. plantaginea* inside a 30 mL Falcon tube of agar in a 330 mL plastic cup covered with $1.35\ mm^2$ mesh to contain emerging parasitoid wasps.

4.3.4 Emergence experiment

The samples were transported from the orchards in a cool box with an ice pack to reduce stress to the aphids and the leaves, and stored in a temperature-controlled room at 20 ºC and 12-hours photoperiod for 14 days to accelerate parasitoid emergence. The shortest average lifecycle of parasitoids known to be hosted by *D. plantaginea* (*Aphidius matricariae*, Family: Braconidae, *Ephedrus plagiator* (Generalist parasitoid wasp), Family: Braconidae, *Praon volucre*, Family: Braconidae, *Diaeretiella rapae*, Family: Braconidae) is 14.3 days (Rogers et al., 1972; Sigsgaard, 2000; Stark et al., 2004; Evergreen Growers Supply, 2022). Therefore, mesocosms were incubated for 14 days without the risk of emergence of a second generation. Up to this time, the samples were inspected, and the number of aphid parasitoids were recorded. For any colonies within which a predator was present, the data were disregarded since the original total count of aphids could have been depleted and also any emerged parasitoids could have emerged from the predators rather than the aphids themselves. Natural enemies and non-emerged aphid mummies were collected into 2 mL Eppendorf tubes and submerged in 70% ethanol. A mechanical pooter was used for collection (Watkins and Doncaster, E7081). It was planned that emerged parasitoids and hyperparasitoids would be identified to species level based on morphology of the emerged adults. Samples would be identified under a light microscope (40 X magnification) using ID guides (such as (Broad, 2011)). These were be stored in a -18° C freezer for molecular identification at a later date if required. The ratio of parasitoids to aphids was recorded to calculate percentage parasitism.

4.4 Results

The severity of infestation of the orchards in 2022 was mild since no *D. plantaginea* colonies were present in May or July. In June, colonies of *D. plantaginea* were present in only two of five orchard pairs. The total number of parasitoids which emerged in the mesocosms was three and there was infiltration of these mesocosms, and others, by stowaway Syrphidae, which will have depleted the original aphid colony size by feeding. There were also issues with aphid survival, with a high proportion of aphids not surviving to adulthood, which may not have allowed the opportunity for potential parasitoids to pupate or emerge. No aphid mummies were present upon collection of the colonies.

4.5 Discussion

Whilst some parasitoids did emerge successfully, this method to estimate parasitism rate of *D. plantaginea* was unsuccessful due to stowaway predators and low survival rate of *D. plantaginea* after separation from the host tree. Predator eggs were very small. They are oviposited within the colony (Van Emden and Harrington, 2017), and can be hidden under aphids. For this reason, it is very difficult to remove all predators from the colony. Additionally, aphid predators are hosts to their own parasitoid species. Presence of predators confounds the results because a predator will eat the aphids, sometimes the whole colony, which changes the total number of aphids present, a value necessary to calculate the proportion of emerging parasitoids to aphids (parasitism rate).

The same is also true for the low survival rate of the aphids. Aphid deaths may not have allowed potential parasitoids to pupate or emerge since parasitoid survival will be affected by survival of the host. Some aphids were killed by falling into the agar and becoming stuck. Additionally, counting the number of live aphids remaining in the colony upon emergence of a parasitoid wasp to record the aphid mortality rate was very difficult since the curled leaf was dry and fragile, as were the aphids.

To address these issues, I propose a potential alternative methodology for future studies:

1) Identify single aphids on apple trees (hatched from overwintered eggs ready to start a colony) (fundatrices) or aphid colonies (depending on time of year) and observe this colony in situ for the duration of the experiment.
2) Use two exclusion techniques to stop interference by predators and ants:
    a. Sticky tape around the petiole (leafstalk) to stop crawling predators and ants from interacting with the aphid colony.

    b. A mesh fine enough to exclude oviposition (egg laying) by aerial predators such as adult lacewings and ladybirds, but not so fine as to exclude parasitoid wasps which are smaller.

    Add a parasitoid exclusion net for intervals (e.g. 14-day duration) throughout the season to catch a single life cycle of emerging parasitoids. Record the aphid colony size upon addition of the net (total parasitoids emerged / total colony size = parasitism rate).

3) Repeat across multiple months and years.

By leaving the colonies in situ, this would improve survival rate of *D. plantaginea* and allow for testing in field conditions rather than lab conditions. By excluding predators and ants, this would avoid interference by aphid predators and also potential antagonist effect between ants and parasitoids as evidenced in previous studies (Stewart-Jones et al., 2008). Additionally, since they are enclosed by the mesh, this method would prevent newly-parasitised aphids from leaving the colony as was observed by Tougeron et al. (2023). By repeating across years, this would account for interannual variation as abundance of *D. plantaginea* in apple orchards can vary widely between years (Howard et al., 2024). Identification of parasitoids to species level would be interesting since it could provide insight into parasitoid diversity, but it would be non-essential since it would be clear that *D. plantaginea* was the host which is a benefit since identification of parasitoid wasps to species level is difficult and time consuming (Rodríguez-Gasol et al., 2019; Crowther et al., 2023), and molecular methods can be expensive. The proposed alternative method would allow for comparison of parasitoid activity between flower margin orchards and controls. This could reveal whether parasitoid wasps bolstered by flower margins contribute to the *D. plantaginea* pest control services (Howard et al., 2024). This could be particularly important in warmer climates, for example in the Mediterranean, where parasitoids are a key natural enemy of *D. plantaginea* (Rodríguez-Gasol et al., 2019). It could also be used to measure spill-over distance of parasitoid activity from the margins to clarify the best spatial arrangement of the flowers to maximise control by parasitoids (Lavandero et al., 2005).

In conclusion, the emergence experiment was unsuccessful due to stowaway predators and low survival rate of *D. plantaginea* after separation from the host tree. I suggest an alternative method to investigate the effect of flower margins on parasitism rates where the colony and leaf could remain in situ to improve *D. plantaginea* survival rates and it is suggested how interference by predators and ants could be avoided. The proposed method could add valuable insight into the mechanism of how flower margins can reduce fruit damage by a major economic pest of commercial apple orchards.

5 Perennial flower strips can be a cost-effective tool for suppression of Rosy apple aphid, *Dysaphis plantaginea*

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Author Contributions

Charlotte Howard: Conceptualization, Formal analysis, Writing - Original Draft, Visualization. **Paul J. Burgess**: Conceptualization, Writing - Review & Editing, Funding acquisition. **Michelle T Fountain**: Conceptualization, Writing - Review & Editing, Funding acquisition. **Claire Brittain**: Conceptualization, Writing - Review & Editing, Funding acquisition. **Michael P. D. Garratt**: Conceptualization, Writing - Review & Editing, Supervision, Funding acquisition.

5.1 Abstract

Flower strips can provide many economic benefits in commercial orchards, including reducing crop damage by a problematic pest, rosy apple aphid (*Dysaphis plantaginea*). To explore the economic costs and benefits of this effect, I developed a bio-economic model to compare the establishment and opportunity costs of perennial wildflower strips with benefits derived from increased yields due to reduced *D. plantaginea* fruit damage under high and low pest pressure. This was tested across three scenarios: 1) a flower strip on land which would otherwise be an extension of the standard grass headland, 2) a flower strip on land which could otherwise be used to produce apples, and 3) a flower strip in the centre of an orchard.

Through reduction of *D. plantaginea* fruit damage alone, the results of the model showed that flower strips on the headland can be a positive economic investment. If non-crop land was not available, establishment of a flower strip in the centre of an orchard, instead of the edge, could recoup opportunity costs by providing benefits to crops on both sides of the flower strip. This study can help guide the optimal placement of flower strips and inform subsidy value for these schemes.

5.2 Introduction

It has been estimated that between 8% and 15% of the global yield of six major annual crops is lost due to pest damage (Oerke, 2006). Pest populations can multiply rapidly without suppression from their natural predators and parasites (natural enemies) (Karp et al., 2013) and the loss of natural habitat and landscape features in agricultural landscapes can have negative impacts on the organisms essential for pest-control services (Dainese et al., 2019; Emmerson et al., 2016). Habitat management on or around farms, for example flower strips (Crowther et al., 2023), can mitigate these effects by providing resources for natural enemies, thereby reducing reliance on chemical pest-control (Cahenzli et al., 2017; Judt et al., 2023).

Flower strips can provide breeding and food resources for natural enemies year-round, and from year-to-year. They can be sown or naturally generated, and can border the crop, often on unproductive land, or as strips between the crop rows (Fountain 2022). The optimal size needed for biological control is uncertain but larger areas are expected to increase biological control services (Blaauw and Isaacs, 2012). Sown perennial flower borders can increase abundance and diversity of natural enemies, both in the border and adjacent crop, and can reduce pest abundance in comparison to fields with only grass borders (Crowther et al., 2023). Spill-over of biocontrol benefits, from a flower strip into an orchard is uncertain, and likely context specific, but effects up to 50 m into the crop area have been recorded (Howard et al., 2024; Wyss, 1995; Woodcock et al., 2016) with evidence of reduced crop pest damage (Crowther et al., 2023; Howard et al., 2024). Importantly, flower strips have a host of additional benefits, for example: suppression of other insect pests (Fountain, 2022), improving pollination (Ortega-Marcos et al., 2022), soil protection, and increasing biodiversity (Haddaway et al., 2018).

Although sown flower strips provide benefits, they also incur costs. These include the capital costs of establishment including the seed mix and ground preparation. There are also ongoing maintenance costs, although less than establishment costs, which can comprise one to two cuts per year, preferably with the cuttings removed (Carvell et al., 2022). A second potential cost is the opportunity cost of the land used for the flower strips, which in some instances could be used for additional crop (Kleijn et al., 2019). As such, the creation of flower-rich plots on farmland has been subsidised in the UK, EU and USA. Governmental agri-environmental schemes can offer economic incentives for flower-rich plots as part of Integrated Pest Management to support biodiversity (for example, the Countryside Stewardship grants in the UK) (Rural Payments Agency and Natural England, 2024). In addition to governmental schemes, charity and industry-driven incentives might offer economic support or expertise to farmers for habitat creation and environmental improvements, for example by WWF and Air Wick (2021) (e.g. hand collect and drill diverse seed-mix for flower strip establishment), Royal Countryside Fund (2023) (e.g. offer grants, free programmes, and local support), and National Lottery Heritage Fund (2023) (e.g. offer grants). Although agri-environmental schemes are designed for environmental benefits, some may pay-for-themselves in terms of yield and crop quality benefits, or reduced production costs (Kleijn et al., 2019; Blaauw and Isaacs, 2014). However, the cost: benefits of 'ecological intensification' are less often studied than the ecological effects (Kleijn et al., 2019). For ecological intensification, such as flower strips, a lack of scientific investigation and knowledge into economic benefits, and direct or opportunity costs, under a range of context-specific scenarios may be limiting uptake of these methods by growers (Kleijn et al., 2019). As such, improved knowledge is needed on how flower strips should be implemented to achieve yield benefits.

Apple is a major crop that has been used to study the effects of flower strips both spatially and temporally (Senior et al., 2020; Howard et al., 2024). It is a high value crop and one of the most widely grown fruits in the world, with 93 million tonnes harvested globally in 2021 (Food and Agricultural Organization, 2023). In 2020, 200,000 tonnes of dessert apples were produced in the UK (Defra, 2020b). In most temperate regions, such as the UK, apple orchards are highly manipulated and they receive repeated applications of insecticides (Simon et al., 2011a).

A significant economic pest of apple is rosy apple aphid, *Dysaphis plantaginea* (Passerini), which causes fruit deformation and reduction of fruit size (Blommers et al., 2004). Aphid infestations in commercial orchards are typically treated using insecticides (Dib et al., 2010b; Penvern et al., 2010), and untreated orchards can incur losses of up to 80% (C. Schulz, 2003, pers. comm. in Qubbaj et al., 2005). Flower strips can be used as a tool to sustainably aid *D. plantaginea* suppression up to 50 m into the crop area (Howard et al., 2024), although the economic costs and benefits of this method are unknown. The development of a bio-economic model, based on experimental results, is one method to determine the benefits and costs of flower strips for different years and spatial arrangements (Castro et al., 2018). To inform management decisions by land managers it is critically important to understand the economic costs and benefits of different approaches, particularly over time.

The objective of this study was to develop and use a bio-economic model to compare the establishment and opportunity costs of perennial wildflower strips at the border and centre of orchards with benefits derived from increased yields due to reduced *D. plantaginea* fruit damage. To account for inter-annual variation, I used experimental results from a year with lower levels of *D. plantaginea* infestation (25% of trees damaged), termed 'low infestation', and a year with higher levels (65% of trees had fruit damage), termed 'high infestation' (Howard et al., 2024). I then evaluated the economic costs and benefits of flower strips under three scenarios: 1) a flower strip on land which would otherwise be an extension of the standard grass headland, 2) a flower strip on cropland which could otherwise be used to produce apples, and 3) a flower strip in the centre of an orchard.

5.3 Methods

5.3.1 Modelling approach

We developed a spreadsheet model in Microsoft Excel describing the benefits and costs of a flower strip in an apple orchard. Biophysical data for the benefits and costs associated with perennial flower strips, and on the level of damage caused by *D. plantaginea* in apple orchards, were used to develop the bio-economic model (Howard et al., 2024). Data were generated from a two-year study in ten conventional UK commercial dessert apple orchards of the variety Gala in South-East England in 2021 and 2022. A full description of the study and sampling methods is described by Howard et al. (2024). Briefly, five orchards, termed “flower strip orchards” were bordered by an established sown perennial flower strip (2-5 years), and five “control orchards” had only a permanent grass headland 4-5 m wide, typically mown four times a year (Figure 1). The average width of the flower strips was 15.3 m (SD = 9.6 m) (Howard et al., 2024, Supplemental Table 1). All orchards were conventionally managed. Flower strip and control orchards were paired on the same farm so local landscape context and the use of pesticides, nutrients, and mowing were similar. A distance of 120-410 m was maintained between the orchards with flower strips and those without, minimising co-use by the same invertebrates and differences in soil type and aspect. Flower strips were sown with perennial flowering species and grasses designed to offer multiple flowering times, flower shapes, and to maximise pollen and nectar resources (details in Carvell et al., 2022). To encourage earlier flowering, and to keep weeds under control, all flower strips received no fertilizer or herbicide, and they were cut to 8-10 cm annually in autumn, and the cuttings removed (Carvell et al., 2022). To measure effects of the flower strips on pest control and crop production in 2021 and 2022, apples per tree were recorded at 0, 5, 10, 20, and 50 m from the orchard edge along three transects in each orchard (45 trees per orchard). Then the proportion of fruit damaged by *D. plantaginea* was recorded on the same trees. At final fruit set, fruit damaged by *D. plantaginea* was identified by extremely reduced size and malformed shape, often with puckering around the calix, to the degree that the fruit was unmarketable. Class 2 fruit were considered undamaged.

5.3.2 Data inputs

5.3.2.1 Biophysical parameters of the study area data

Within the bio-economic model a sample plot size of about 1 ha (21.1 m + 55.0 m x 124 m = 9440 m^2) was set which was based on the mean dimensions of the study areas in flower strip orchards described by Howard et al. (2024). The width of the flower strip and the grass headlands were set at 15.3 m and 5.8 m respectively, and it was assumed that they run alongside an orchard that was 124 m long. To model the effect of distance from the edge of the orchard, the yields within the orchard were subdivided into five sub-plots comprising trees at distances of 0-2.5, 2.5-7.5, 7.5-15, 15-35, and 35-55 m from the flower strip (Table 1). In the field study the data were collected up to 50 m into the orchard, so it was assumed that there was no additional pest control benefit of a flower strip beyond 55 m into the orchard. As such the flower strip and control orchards were assumed to be the same past 55 m. Within each sub-plot distance, I assumed the same number of apples per tree between the wildflower and the control treatments (Table 1) and a uniform yield response to *D. plantaginea* within each subplot. Although the area covered in Scenario 3 (21.1 m + 110 m x 124 m = 16260 m^2) was greater than Scenario 1 and 2, all of the results were standardised to the net margin per hectare. For the economic model, the area of the sample was determined by Equation 1.

$A_s = L * W$ Equation 1

Let:
L: Length of the field (m)
W: Width of the sample (m)
A_s: Area of the sample (m^2)

5.3.2.2 Yield and fruit damage data

An economic analysis was completed for each year, 2021, which had a high incidence of *D. plantaginea* (65% of trees had fruit damage), and 2022, which had a low incidence (25% of trees damaged) (Howard et al., 2024). The inclusion of a flower strip reduced the proportion of fruit loss in both years, but whereas the level of damage was reduced from 11.94% to 3.97% in 2021 when incidence was high, the reduction was only from 1.33% to 1.00% in 2022 when incidence was lower (Table 1). The severity of *D. plantaginea* infestation, and the level of fruit damage, can vary widely with apple variety (Razmjou et al., 2014), management (Porcel et al., 2018), weather, foliar nitrogen and tree age (Brown and Myers, 2010), so infestation levels are all relative. The fresh mass of a Gala apple in the UK can vary between 0.12 and 0.16 kg so a mean mass of 0.14 kg was set for the analysis (The Basin Pantry: https://thebasinpantry.com.au/royal-gala/ Ukrainian food platform: https://ukrainian-food.com.ua/products/product/gala-apple).

Table 1. Number of apples per tree and proportion of fruit lost recorded at different distances from the edge of the orchard in a year with low levels of infestation by *D. plantaginea* (2022), and high levels (2021).

	Low levels of infestation (2022)				High levels of infestation (2021)			
Distance from edge of orchard (m)	Number of apples per tree		Proportion of fruit lost (%)		Number of apples per tree		Proportion of fruit lost (%)	
	Without	With flower strip	Without	With flower strip	Without	With flower strip	Without	With flower strip
0-2.5	68	68	1.31	4.06	66	66	8.12	4.93
2.5-7.5	74	74	1.08	0.22	62	62	12.83	3.09
7.5-15	80	80	2.77	0.75	73	73	9.60	5.01
15-35	89	89	0.87	1.35	68	68	10.58	3.03
35-55	76	76	1.32	0.55	61	61	14.43	4.60
Mean[a]			1.33	1.00			11.94	3.97

a: Weighted mean (proportional to sample area).

5.3.2.3 Economic data

Within the economic analysis I calculated an establishment cost for creating the flower strips of £1145/ha which included the average costs of ploughing, shallow power harrowing, ring rolling, broadcasting, and the cost of the wildflower seed (Table 2).

Table 2. Assumptions regarding the establishment cost of a flower strip, the value of apples and grants for flower strips.

		Cost	Gain
Flower strip			
Establishment cost	Labour cost of creating flower strip (£/ha)	119.71	
	Labour cost of creating (per flower strip) (£)	21.85	
	Wildflower seed cost (£/ha)	1,024.92	
	Wildflower seed cost (per flower strip) (£)	187.95	
Annual cost	Cost of mowing grass once (£/ha/yr)	28.20	
	Cost of mowing grass once (per flower strip) (£)	5.17	
Annual subsidy	Countryside stewardship (£/ha/yr)		673.00
Crop area			
Annual cost	All production costs (£/ha/yr)	24,465.00	
Revenue	Wholesale price Gala apple 2021 (DEFRA) (£/kg)		1.01
	Wholesale price Gala apple 2022 (DEFRA) (£/kg)		1.06

The annual maintenance costs were based on one mowing of the flower strips and four mowing events for a grass headland. An annual cost per mowing event of £28.20 /ha was assumed based on the farmers' own labour, tractor/machinery fuel use, repairs and depreciation (Redman, 2020). The average annual costs associated with apple production included crop sundries (such as tree and stake replacement), harvesting (labour cost), grading and packaging, annual value of initial establishment costs, pruning, and husbandry (Redman, 2020). The default subsidy received for the flower strip was set as £673/ha/yr (Rural Payments Agency and Natural England, 2024) (Table 2). One of five flower strips was sown with a different perennial seed mix which had a lower cost. However, for simplicity, the model assumes that the same seed mix was used for all five strips (Table 3). The assumed mean wholesale price of Gala apples in the UK was £1.01 per kg in 2021 and £1.06 per kg in 2022 (Defra,

2022) (Table 2). Average wholesale price accounting for aphid damage (£/m^2) was determined by Equation 2. For each scenario (e.g., with and without flower strips), the total benefits (B_t), total costs (C_t) and differences in net benefits (ΔN_b) (£/m^2) were calculated to determine the economic impact of flower strips using Equations 3-6. This was extrapolated to the total sample area to compare economic outcomes at scale (£) and converted to comparable values (£/ha).

$$P_a = (1 - L_p) * F_m * P_w \quad \textit{Equation 2}$$

Let:

P_a: Average wholesale price accounting for aphid damage (£/m^2)
L_p: Proportion of apples lost due to aphids
F_m:Fresh mass of fruits (kg/m^2)
P_w: Average wholesale price (£/kg)

$$B_t = P_a + S_c \quad \textit{Equation 3}$$
$$C_t = C_e + C_m \quad \textit{Equation 4}$$
$$N_b = B_t - C_t \quad \textit{Equation 5}$$

$$\Delta N_b = N_b^{Flower\ Strip} - N_b^{Control} \quad \textit{Equation 6}$$

B_t: Total benefits (£/m^2)
S_c :Countryside Stewardship (£/m^2)
C_t: Total costs (£/m^2)
C_e: Equivalent annual value of establishment costs (£/m^2)
C_m: Annual maintenance costs (£/m^2)
N_b: Net benefits (£/m^2)

5.3.3 Temporal aspects

To account for the opportunity cost to immobilizing capital in long-term projects, future benefits and costs were reduced or "discounted" using an approach developed by Faustmann (1849). To account for the upfront costs of establishment and the public preference for money now rather than later, the net present value (NPV; £/ha) of establishing the flower strip was calculated, where *C* is the cost in year *t* (£/ha), *i* is the discount rate, and *t* is the year from flower strip establishment to *T* which is the assumed duration of the flower strip (Faustmann, 1849; Equation 7).

$$NPV = \sum_{t=0}^{t=T} \frac{C^t}{(1+i)^t} \quad \text{Equation 7}$$

Let :
C: Cost in year *t* (£/ha)
i : Discount rate
t: Year from flower strip establishment to *T*
T: Assumed duration of the flower strip

Secondly, an equivalent annual value (EAV; £/ha/yr) of establishing the flower strip was calculated using Equation 8 by multiplying the NPV from Equation 4 with a function of the discount rate *i* and the longevity of the flower strip, *n* (Table 2).

$$EAV = i\ .NPV\frac{(1+i)^n}{(1+i)^n-1}$$ Equation 8

Let:
i: Discount rate
n: Longevity of the flower strip

For the analysis a discount rate of 4% was assumed. Although this is lower than the time-value of money indicated by most farmers, it is similar to the discount rate of 3.5% used by the UK Government in cost-benefit analysis (HM Treasury, 2023) and was varied between 0.7% and 4% to reflect changes between 2021 and 2024 (Department of Health, 2024) as part of the sensitivity analysis (Section 5.3.6).

The longevity of perennial flower strips are uncertain (Brittain et al., 2022; Schmidt et al., 2022b; Fountain, 2022) and will likely vary, for example with different seed mixes (Schmidt et al., 2020), or by location (Pfiffner et al., 2019) (e.g. due to natural weed pressures, and soil fertility (Schmidt et al., 2020), and management (Mateos-Fierro et al., 2021; Herz et al., 2019)). Within the second year of the field study, four of the flower strips had been established for five years, and the fifth strip for two years, so assumed benefits of the flower strips for up to ten years was speculative. Apple orchards themselves can remain in place for up to 25 years.

5.3.4 Accounting for variation in apple tree density

The yield of apples from an apple orchard can vary with season, apple variety, the density of apple trees, apple tree age and branch formation. Howard et al. (2024) reported that there were fewer apples per m^2 in the five study orchards on sites bounded by a flower strip than by a grass border, but this result was not statistically significant ($\chi 2 = 0.557$, df = 1, $p > 0.05$). Hence, in the economic analysis it was assumed that the number of apples per m^2 was the same in both the flower strip and the control orchards (Table 1). Within the area of apple trees a consistent tree density of 0.24 trees per m^2 was assumed for both flower strip and control orchards (but see supplemental Table 1 and 2 for details and results for actual apple density data from the sites). The assumed number of apples was greater in 2022 than 2021 to reflect inter annual variation recorded in the orchards (Table 1).

5.3.5 Modelled Scenarios

5.3.5.1 Examining the effect of flower strip location

There are management implications and variable costs associated with where flower plots are placed within orchards, and this may also result in different levels of pest control due to spillover extent of beneficial arthropods. Therefore, to examine the impact of the flower strip relative to a control, three spatial arrangement scenarios were considered (Figure 1). As stated, the flower border was 15.3 m wide, and the headland was 5.8 m wide.

Scenario 1 comprised a flower strip established on unproductive land which could not be planted with apple trees (**Headland border**).

Scenario 2 comprised a flower strip on an area which could be planted with apple trees (**Cropland border**).

Scenario 3 comprised a flower strip in the centre of the orchard which could have been planted with apples (**Central strip**) (Figure 1).

Although the area covered in Scenario 3 was greater than Scenario 1 and 2, all of the results were standardised to the net margin per hectare.

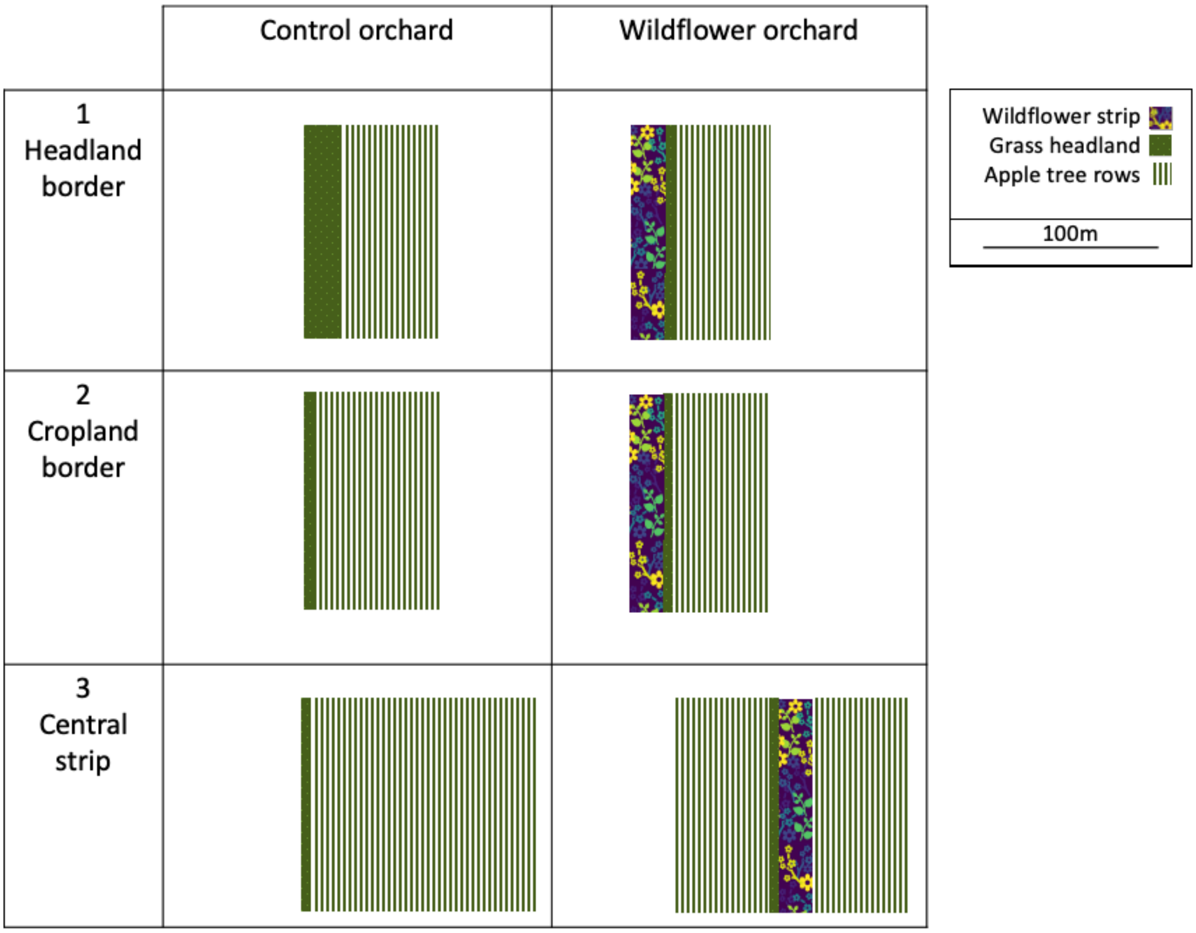

Figure 1. Representation of the orchard area represented by the economic model under three scenarios: 1) Headland border where the flower strip was established on a grass headland, 2) Cropland border where the flower strip was established on cropland, and 3) Central strip where the flower strip was established on cropland in the centre of an orchard

5.3.6 Sensitivity analysis

Across the scenarios I also tested the sensitivity of the equivalent annual value of a flower strip to both longevity of the flower strip (1 – 10 years), changes in the subsidy amount from 0 to 200% of the default value of £673/ha/yr, and pest pressure levels (low to high). Production costs of dessert apples can vary, for example with yield size, so the sensitivity of the equivalent annual value of a flower strip to production costs was tested (Redman, 2020). A range of discount rates were tested between 0.7% and 4% to reflect changes between 2021 and 2024 (Department of Health, 2024).

5.4 Results

The equivalent annual value over five years of the cost of establishing the wildflower strips was £315/ha/yr, and over ten years was £154/ha/yr.

5.4.1 Wildflower strip on headland (Scenario 1)

The yield benefits from the presence of the wildflower strip meant that in a year of low pest incidence the return from the wildflower treatment was similar to the control (only increasing by +£15/ha/yr) whereas in the year of high pest incidence, the predicted net margin of the wildflower treatment would increase by +£1152/ha/yr. The mean benefit over the two years was +£583/ha/yr) (Table 4). The equivalent annual value differed by £271/ha/yr between a subsidy of 0 and 200% (Figure 2 and 4). The equivalent annual value differed by £200/ha/yr between a flower strip which lasts for one year and a strip which lasts for 10 years (Figure 2 and 4). The equivalent annual value differed by £5 between a discount rate of 0.7% and 4% (Figure 4).

5.4.2 Wildflower strip bordering cropland (Scenario 2)

By contrast, planting wildflowers on land which could have been used for apple trees resulted in a reduction in net margin of -£210/ha/yr in a year of low incidence (2022) and an increase in net margins equivalent to +£2670/ha/yr in a year of high pest incidence (2021). The mean change in net margin was an increase of +£1230/ha/yr) (Table 4). The equivalent annual value differed by £271/ha/yr between a subsidy of 0 and 200% (Figure 2). The equivalent annual value differed by £3219/ha/yr between high and low apple production costs (Figure 3 and 4). The equivalent annual value differed by £200/ha/yr between a flower strip which lasts for one year and a strip which lasts for 10 years (Figure 2 and 4). The equivalent annual value differed by £5 between a discount rate of 0.7% and 4% (Figure 4).

5.4.3 Wildflower strip in the centre of an orchard (Scenario 3)

The economic benefits of planting a wildflower strip in the centre of an orchard were calculated to be better than in Scenario 2, because the benefits of the wildflower strip were assumed to be effective in two directions, (i.e. on both sides of the strip). In a year of low pest incidence, the flower strip resulted in an increase in the net margin of +£552/ha/yr. In a year of high pest incidence, the margin from the wildflower treatment was +£2997/ha/yr more than in the control. The mean increase in net margin was +£1775/ha/yr (Table 4). The equivalent annual value differed by £157/ha/yr between a subsidy of 0 – 200% (Figure 2). The equivalent annual value differed by £1869/ha/yr between high and low apple production costs (Figure 3 and 4). The equivalent annual value differed by £116/ha/yr between a flower strip which lasts for one year and a strip which lasts for 10 years (Figure 2 and 4). The equivalent annual value differed by £3 between a discount rate of 0.7% and 4% (Figure 4).

Table 4. Calculated annual margins (based on revenue minus changes in marginal costs) of three scenarios for locating a flower strip; 1) Headland border, 2) Cropland border, 3) Central strip (for flower strips which last 5 years), including the added value when subsidy is considered.

Pest infestation levels	Scenario	Flower strip orchard			Control orchard			Difference			Subsidy
		Yield (t/ha/yr)	Revenue (£/ha/yr)	Margin accounting for costs (£/ha/yr)	Yield (t/ha/yr)	Revenue (£/ha/yr)	Margin accounting for costs (£/ha/yr)	Yield (t/ha/yr)	Revenue (£/ha/yr)	Margin accounting for costs (£/ha/yr)	
Low	1) Headland border	18	19562	1809	29	31210	1794	-11	-11648	15	136
Low	2) Cropland border	18	19562	1809	23	24629	2019	-5	-5067	-210	136
Low	3) Central strip	21	22714	2146	30	31780	1594	-9	-9066	552	79
High	1) Headland border	14	14637	-3115	13	13439	-4267	1	1198	1152	136
High	2) Cropland border	14	14637	-3115	17	16825	-5785	-3	-2188	2670	136
High	3) Central strip	17	16996	-3572	17	16819	-6569	0	177	2997	79

Note: high pest infestation: 2021; low pest infestation: 2022

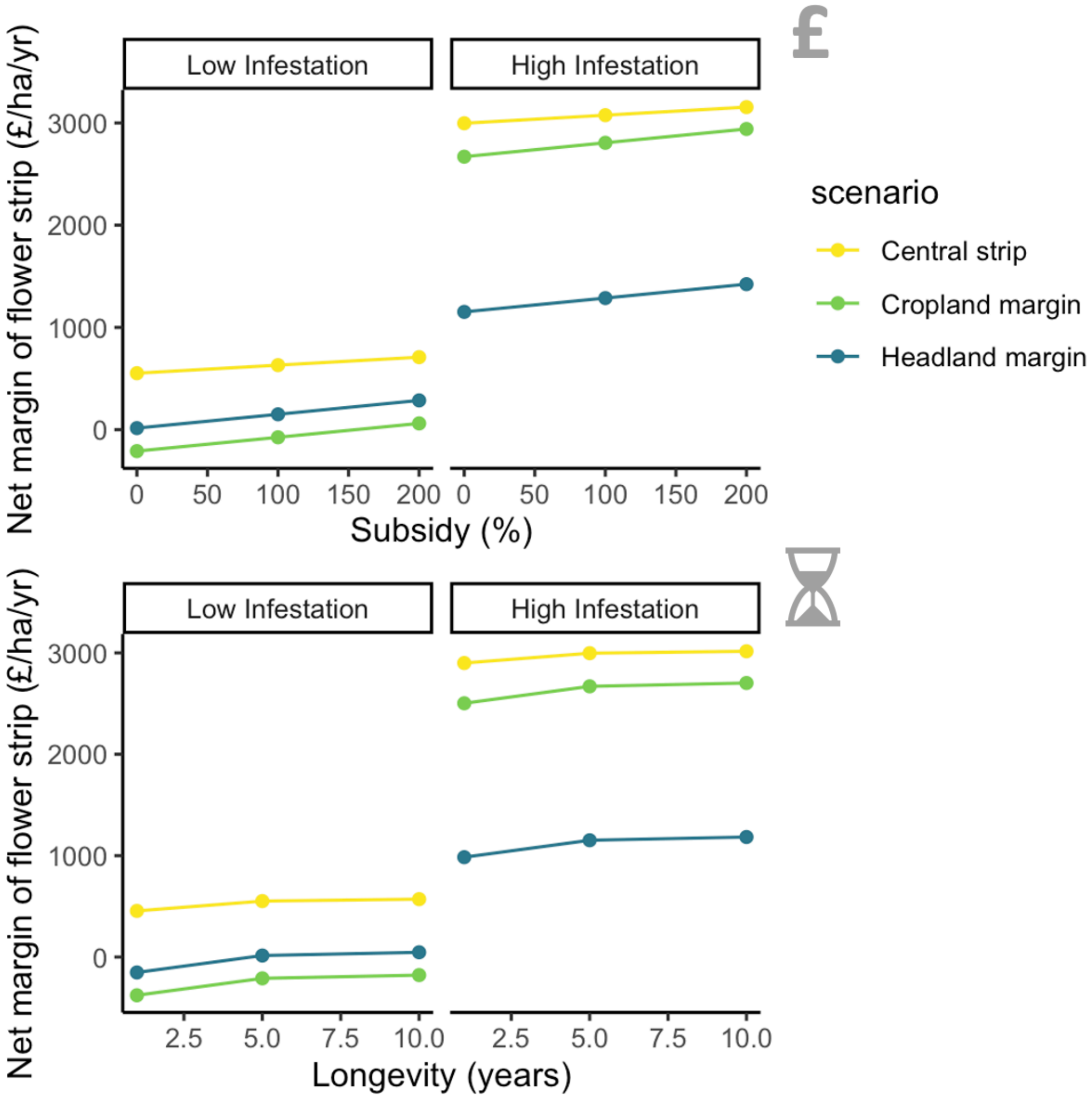

Figure 2. Sensitivity of equivalent annual value of the net benefit of the presence of a flower strip according to subsidy amount (top) and longevity of the strip before resowing is required (bottom) (without subsidy), in a year with a low aphid infestation (2022, left), and high (2021, right), under three scenarios; 1) Headland border, 2) Cropland border, 3) Central strip. The default subsidy was £673/ha/yr (Countryside Stewardship grant in the UK, 2021 and 2022 (Rural Payments Agency and Natural England, 2024)).

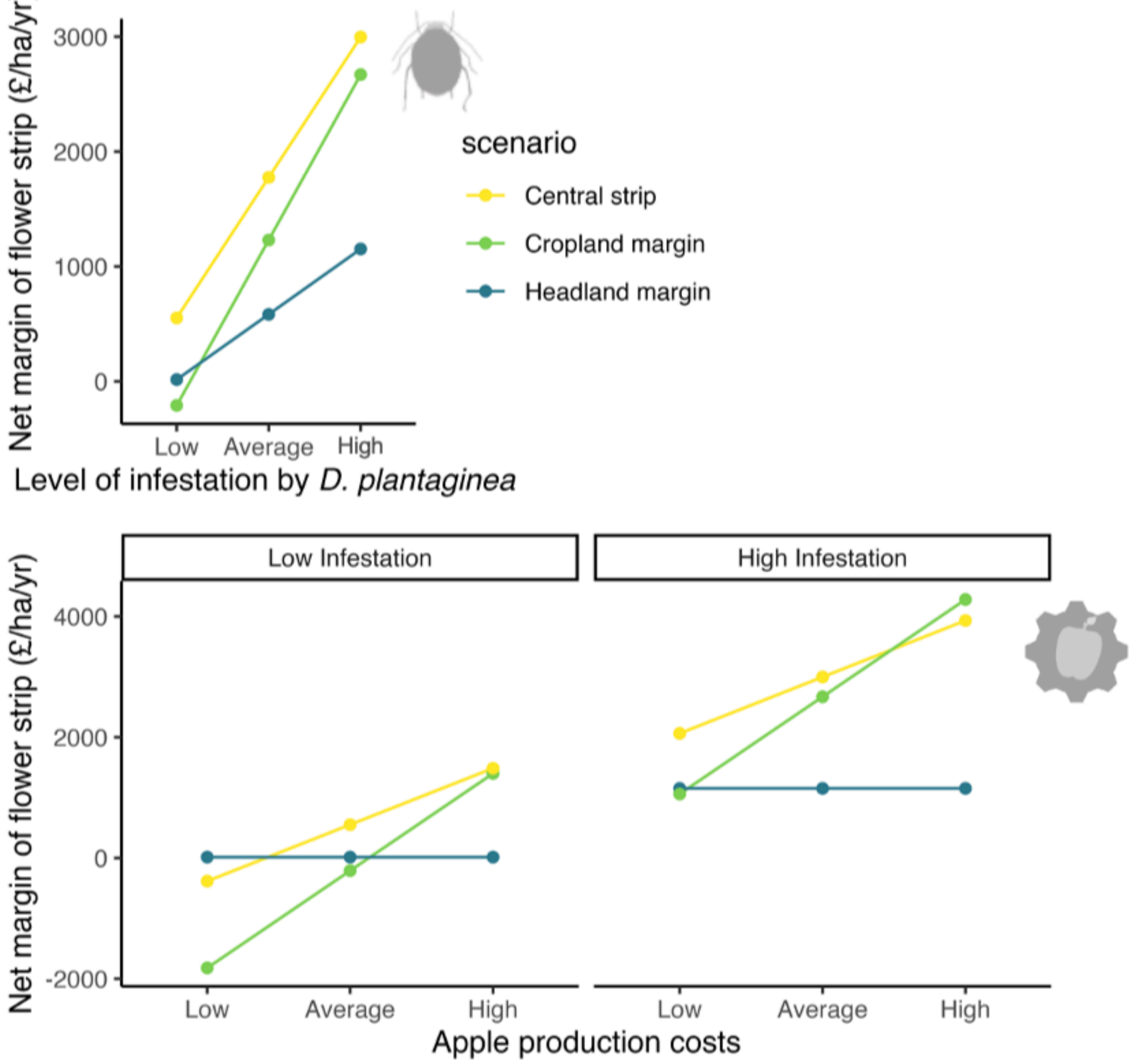

Figure 3. Sensitivity of equivalent annual value of the net benefit of the presence of a flower strip according to level of pest infestation (top) and apple production costs (bottom) (default production costs = £24465/ha/yr); in a year with a low aphid infestation (2022, left), and high (2021, right), under three scenarios; 1) Headland border, 2) Cropland border, 3) Central strip (without subsidy and with flower strips which last five years before re-sowing).

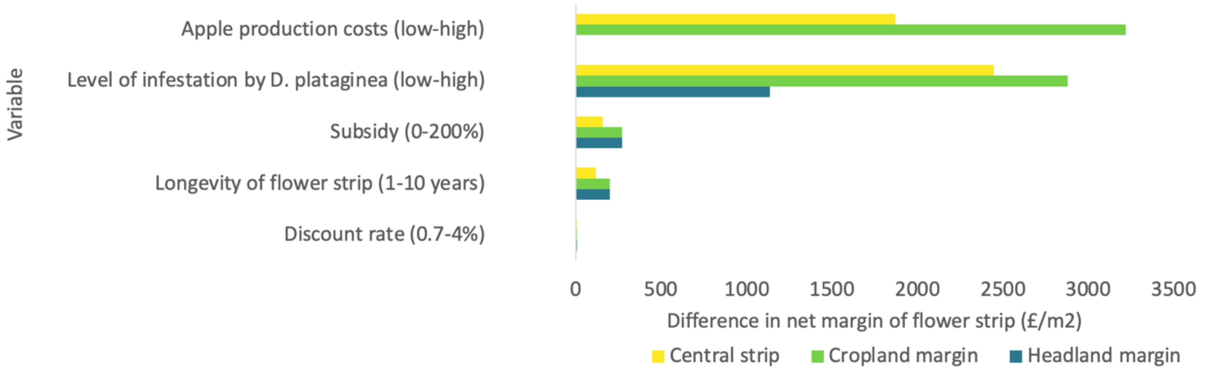

Figure 4. Equivalent annual value of the net benefit of the presence of a flower strip according to each tested variable in the sensitivity analysis under three scenarios; 1) Headland border, 2) Cropland border, 3) Central strip.

5.5 Discussion

5.5.1 Flower strip on headland

The severity of the aphid infestation had a large effect on the change in net margin due to presence of a flower strip. In 2022, all the orchards had a low level of *D. plantaginea* infestation, but even then the flower borders 'paid for themselves' compared to standard primarily grass headlands. In 2021, there was a higher level of infestation by *D. plantaginea* in the orchards and flower borders provided significant economic benefits to growers by reducing *D. plantaginea* fruit damage compared to standard, primarily grass, headlands. When a subsidy (£673/ha/yr) was taken into account, flower borders provided significant economic benefits to growers in both years (Rural Payments Agency and Natural England, 2024). Such information surrounding the economic costs and benefits could encourage adoption of this pest control method by allowing farmers to evaluate the monetary value (Blaauw and Isaacs, 2014; Ortega-Marcos et al., 2022). To my knowledge, ours is the first study to conduct an economic analysis of flower borders for pest control. Few studies have investigated the effect of flower borders on yield or monetary benefits of pest-control services in apple orchards (Herz et al., 2019; Kleijn et al., 2019; Fountain, 2022), a trend observed across many crops (Crowther et al., 2023). A recent study by Jacobsen et al. (2022) found no impact of flower borders on the number of damaged apples compared to controls. Since Jacobsen et al. (2022) examined only ten randomly selected apples per tree, perhaps this was not enough to identify statistical differences in fruit damage. By contrast, Howard et al. (2024) assessed all fruits on each of 450 trees (mean total apples per tree = 93, SD = 73) and found that in years of high infestation, only a low percentage of the total fruits were damaged in flower strip and control orchards (4% and 12% respectively), and similar rates of damage in a year of low infestation (1% and 1% respectively).

5.5.2 Flower strip on cropland

The extent of economic benefits or costs of flower strips were context specific. Flower borders on cropland led to economic costs when the *D. plantaginea* infestation level was low, because the pest control benefits did not outweigh the opportunity costs. Since the subsidy was not enough to compensate for those opportunity costs, and made little difference to the equivalent annual value of the establishment cost, the subsidy would have needed to be at least £210 to offset the losses in the year when the aphid pest was less of a problem, although it should be noted that the scope for increasing such subsidies is constrained by international trade rules, for example World Trade Organization’s Green Box rules. However, during a year of high infestation levels by *D. plantaginea*, flower borders led to economic benefits to the growers even though the land could have otherwise been cropland.

5.5.3 Central flower strips

Flower strips in the centre of the orchard provided benefits in a year with low infestation due to the assumption that *D. plantaginea* pest control benefits would be experienced on both sides of the flower strip instead of only one side. During a year of high infestation, they led to similar economic benefits to the growers as did flower borders. The change in location of the strip, from the border to the centre, was enough to compensate for the opportunity costs. For crops generally, yield effects have been little studied and there are only few examples of evidence that flower strips can lead to a sufficient increase in crop yield through ecosystem control services to cover both establishment and opportunity costs (pest control: (Tschumi et al., 2016) pollination:(Pywell et al., 2015)).

5.5.4 Sensitivity of the net margins

The net margins for flower strips on the headland showed lower levels of sensitivity to the change in the level of infestation by *D. plantaginea* compared to if flower strips replaced tree rows. This is because the opportunity costs were compensated for only when the pest control benefits were higher. Net margins of flower strips at different locations showed similar sensitivity to the longevity of the flower strips and the subsidy amount and showed much less sensitivity to these than to infestation levels and apple production costs. Apple production costs were estimated to range between £16471/ha/yr and £32458/ha/yr for 2021 (Redman, 2020). This is not necessarily linked with differences in yield, although several post-harvest costs are relative to the number of apples marketed (Redman, 2020). Net margin of presence of both a flower strip on cropland, and a strip in the centre of the orchard, showed similar sensitivity to apple production costs, particularly during a year with high levels of *D. plantaginea* infestation, since the increased pest control benefits of a central strip somewhat compensated for the opportunity costs of a flower strip which replaces apple trees. Under low apple production costs, when *D. plantaginea* infestation was low and flower strips only lasted for five years, growers lost money for both cropland borders and central strips, whereas under average production costs, growers lost money only for cropland borders. The fruit damage benefits did not compensate for the opportunity costs and apple production was less expensive. A benefit of a flower strip on headland is that apple production costs have no effect on the net margin.

5.5.5 Benefits of flower strips

In this study, only the benefits of reduced *D. plantaginea* damage and subsidies were considered. However, there are many other potential benefits of flower strips which could be included in future models. For example, control of other pests such as, woolly aphid, tortricids or codling moth (Bostanian et al., 2004; Fountain, 2022) which are increasingly problematic due to the withdrawal and increasing restrictions on pesticide use (Frelih-Larsen et al., 2023). Additionally, there are ecosystem service benefits such as carbon sequestration (Harbo et al., 2022), pollination (Blaauw and Isaacs, 2014; Morandin et al., 2016; Ortega-Marcos et al., 2022), and soil protection from flooding and erosion (Haddaway et al., 2018). Flower borders on headlands can be added to areas which would otherwise be unsuitable for apple trees, for example areas which temporarily flood, or are infertile, rocky, or impractical in shape. Flower borders could also potentially reduce the number of crop protection sprays required by reducing pest populations, and consequently reduce pesticide costs (e.g. Li et al., 2021). This could be investigated in future studies by working closely with agronomists to create custom integrated pest management programmes for each orchard where the application of aphicides would be a last resort. Currently, the threshold for an insecticide application to control *D. plantaginea* is one aphid per orchard (AHDB, 2024).

There may also be non-monetary benefits of flower strips such as improvements to biodiversity (Haddaway et al., 2018), conservation of wild and managed pollinator species (Ortega-Marcos et al., 2022), support for farmland birds (Schmidt et al., 2022a), and landscape aesthetics and public perception (Uyttenbroeck et al., 2016). If a full cost-benefit analysis were to consider these wider societal benefits, these might outweigh the opportunity costs associated with a cropland flower strip when pest control benefits are less evident. The price of seed mix for establishing sown flower strips can vary (Schmidt et al., 2020), but since the establishment costs made little difference to the equivalent annual value of the flower strips when longevity varied (number of years they last before resowing), this was less important than location of the flower strips and level of infestation by *D. plantaginea*. Due to the interannual variation in infestation levels by *D. plantaginea*, the equivalent annual value of flower strips can also vary inter-annually, meaning the pest control benefits cannot be expected to be consistent across the life of the orchard. However, the benefits of flower strips might become more consistent if wider benefits were also considered. Pesticide withdrawals are leaving fruit growers with fewer effective products (Cressey, 2017), hence the growing importance of sustainable tools for pest suppression.

Apple prices and the volatility observed in orchard profitability are also influenced by market dynamics, which can significantly impact farm businesses in the long term. Apple profitability can be affected by trade policies, availability of apples, and changes in market demand such as consumer demand for organic or sustainable produce (Yamoah and Acquaye, 2019; Hou et al., 2022; Staton et al., 2022). This further stresses the importance of strategies to mitigate pest-related financial swings. By investing in practices that enhance pest management, such as the use of flower strips, farms can reduce vulnerability to fluctuating pest outbreaks, which may improve long-term profit stability. Beyond short-term economic benefits, a resilient farming system helps mitigate risks, protect yields, and provide consistent product supply, thereby enhancing a farm's capacity to cope with the unpredictable nature of both pest dynamics and market conditions (Huss et al., 2022).

5.5.6 Alleyway plantings

Alleyway plantings between rows of orchard trees are an alternative spatial arrangement for flower strips in orchards which does not result in opportunity costs (Staton et al., 2021). On average, these would each be approximately 23% the size of the flower strips used in the current study since the alleyway in the UK is typically 3-4 m wide, although they would cover a greater overall area as there would be multiple strips. As such it may not be accurate to assume that the spatial effect of these flower strips on *D. plantaginea* fruit damage to be the same as that of 15.3 m wide flower strip, and for this reason alleyway strips were not included in the economic model. However, they should be the focus of future studies with data on the effects of alleyway strips on pest control. Few studies have considered effects of alleyway plantings on fruit damage, and those few which did have often found no effect on fruit damage by *D. plantaginea,* which could be due to pesticide use (McKerchar et al., 2020) or use of newly established, rather than mature, strips (Campbell et al., 2017; Cahenzli et al., 2019; Howard et al., 2024; Herz et al., 2019). However, economic modelling by Staton et al. (2021) indicated that flowering perennial alleyway plantings increased farm income by £231 per ha of agroforestry compared with mown understories based on *D. plantaginea* damage to apples, mowing costs, and income from subsidy (Staton et al., 2021). The spill-over distance required would be smaller than for borders since the flowers are spread throughout the orchard which could improve efficiency in providing natural enemies for the crop. However, it must be noted that alleyway plantings can have logistical drawbacks such as domination by grasses in nutrient-rich soils (Pfiffner et al., 2019), competition for nutrients with very young orchard trees (Herz et al., 2019), and interference with farm machinery and activities (Rodríguez-Gasol et al., 2019; Mateos-Fierro et al., 2021; Ortega-Marcos et al., 2022).

5.5.7 Effect of orchard variation

Although the result was not statistically significant, the number of apples per meter squared was greater in the control orchards than the flower strip orchards ($P > 0.05$). In the economic analysis it was assumed that the number of apples per meter squared was the same in both the flower strip and the control orchards. The number of apples produced by an orchard can vary greatly with factors such as tree density, tree height, branch formation, and pollination deficits, and it is expected that flower strips would have only affected the latter, probably in a positive way (Garratt et al., 2023). As such, I assumed a fixed apple density in the model to simplify and standardise the analysis of the potential economic benefits. Additionally, since the flower strips were 2-5 years old and studies suggest that older borders may be more effective (Herz et al., 2019), it must also be considered that the borders could have been less profitable in the first year after re-sowing. These results could differ across countries since UK orchards may not be representative of orchards globally. For example, the composition of apple varieties grown in UK orchards may not be representative of global orchards (Garratt et al., 2023). Similarly, agricultural landscapes in the UK consist of smaller, patchier apple orchards, which are well mixed with semi natural habitat and other crop-types compared with countries that grow apples more intensively, such as Italy (Damos et al., 2015; Sander et al., 2019; Hassan et al., 2020).

5.5.8 Conclusion

Flower strips provided significant economic benefits to growers by reducing fruit damage by *D. plantaginea* compared to standard headlands, particularly in a year with high levels of *D. plantaginea* infestation. The net benefit of the flower strips was more affected by the location of the flower strips within the orchard and the apple production costs than the annual subsidy received for flower strips or the establishment costs and longevity of the flower strip. In a year with low infestation by *D. plantaginea,* the model suggests that flower strips on the headland could be a positive economic investment. If non-crop land were not available, establishment of a flower strip in the centre of an orchard could recoup most of the associated opportunity costs and also provide additional yield benefits during years with high levels of *D. plantaginea* infestation. In a year with high infestation by *D. plantaginea*, the model indicated that apple production was unprofitable due to the lower yield and high percentage of unmarketable fruits. Although this study shows flower plots can deliver economic benefits to growers by reducing pest damage, information on the additional benefits provided by flower strips such as pollination, conservation, and mitigation or adaptation to climate change are needed to establish the full societal benefits and costs. This could help to guide policy for future flower-rich plots and subsidy amounts.

6 Synthesis

This thesis aimed to evaluate the ecological and economic effects of perennial flower margins for *D. plantaginea* control in UK apple orchards considering effects on natural enemy populations, predation rate, and fruit damage and how this is influenced by location and from year to year. This chapter synthesises the key findings of the thesis, how they addressed the aim, and the contexts on which they may be dependent. Possible future research directions are identified.

6.1 Key findings

The results of the thesis can be synthesised into 4 key findings as follows:

1. Presence of a flower margin reduced the spread of *D. plantaginea* on infested trees*,* and subsequently reduced the number of trees with fruit damage, with effects seen up to 50 m from the flower margin (Chapter 2).
2. A flower margin provided a distinct plant community, and its presence increased natural enemy diversity in orchard ground vegetation compared to orchards without flower margins (Chapter 3).
3. The reduction in the spread of *D. plantaginea* and percentage of trees with apple damage varied between years and at different distances from the orchard edge, and hence, so did the economic net costs/benefits of a flower margin (Chapter 2 and 5).
4. A modelled flower margin on the headland area more often provided an economic net benefit in terms of reduced *D. plantaginea* fruit damage, although in some instances, so did a flower margin on crop land depending on its location within the orchard (Chapter 5).

6.2 *Dysaphis plantaginea* control

6.2.1 Neutral effects of flower margins for *D. plantaginea* control

In this study, in flower margin orchards compared to controls, there was a reduction in the spread of *D. plantaginea* in the apple trees. There was also a reduction in the number of trees with fruit damage. However, some data suggested low efficacy of flower margins for *D. plantaginea* control. There were no effects of flower margins on abundance or likelihood of presence of the most abundant specialist predators in the *D. plantaginea* colonies, Syrphidae and Coccinellidae (Chapter 2). Additionally, predation of aphids from bait cards was lower in flower margin orchards compared with controls at mixed distances from the orchard edge (Chapter 2) and there was no effect of flower margins on the community structure or abundance of natural enemies on the apple trees (Chapter 3). The following sections discuss these findings.

6.2.1.1 Interference through ant mutualism

Whilst the effects of flower margins on ant attendance was not a main focus of this work, ants were attending *D. plantaginea* colonies and the aphid-ant mutualism may have been affected by the flower margins. There were fewer trees with ants present in flower margin orchards compared with controls in April and July, but not in May or June (Chapter 2). Aphid colonies were smaller in April and July since each colony grows from a single fundatrix (egg laying female) in the spring, and following peak abundance in June, migration to the secondary host, plantain, occurs in July (Blommers et al., 2004). Ants prefer to obtain sugar resources from plants, for example as nectar, when aphid colonies are small (Katayama et al., 2013). Perhaps in April and July, whilst the colonies were small, ants preferred to obtain sugar from the diverse floral resources provided by the flower margins, whereas in control orchards the ants tended aphids for longer. Therefore, the mutualistic relationship between *D. plantaginea* and ants could be affected by flower margins. If so, since attending ants defend aphids from predators, which accelerates colony growth (Stewart-Jones et al., 2008), and can disperse aphids to create additional colonies (Collins and Leather, 2002), this could mean that ants interfered with predator presence in the colonies or on the trees, obscuring the effects of flower margins on the predator abundance. This has been studied for other aphid crop pests, *Aphis cracivora* and *Megoura crassicauda* (Cowpea aphid and Vetch aphid) where extrafloral nectaries were able to attract ants, but lost their efficacy when aphid colony size increased (Sakata and Hashimoto, 2000; Katayama and Suzuki, 2003). However, the potential of ant mutualism disruption for *D. plantaginea* control has been demonstrated, using artificial provisioning of sucrose solution, which can significantly reduce *D. plantaginea* populations in apple orchards by reducing ant attendance and increasing enemy pressure (Nagy et al., 2015). Similarly, Pålsson et al. (2020) used intercropping of apple with a companion plant, *Vicia faba* (black bean) infested with *Aphis fabae* (black bean aphid) to investigate the effect on ant attendance of *D. plantaginea*. A higher number of *D. plantaginea* colonies remained active in the apple control, whilst they were almost eradicated from apple trees by the intercropping since ants were diverted onto the companion plants (Pålsson et al., 2020). Future studies should investigate the effects of flower margins on *D. plantaginea* ant attendance. The results of this thesis suggest that crop damage should be measured for studies investigating the efficacy of flower margins on pest control since effects on natural enemies or aphid pests alone may not reflect the level of control being delivered due to their ecological interactions with other organisms.

6.2.1.2 Other effects on natural enemies

Whilst there was no effect of the flower margins on abundance of Coccinellidae or Syrphidae inside the aphid colonies, or effects on natural enemy communities in the trees, there could have been other effects on natural enemies outside of what was measured in this study. For example, some natural enemy groups may have had improved longevity, fitness or predation activity from the pollen and nectar resources provided by the flower margins (Tylianakis et al., 2004; van Rijn et al., 2013; Gonzalez et al., 2016; Rodríguez-Gasol et al., 2019; He et al., 2021; Kishinevsky and Ives, 2024). Perhaps recording specialist natural enemies as adults in the flower margin whilst they use the floral resources for pollen would help determine whether these species are utilising the floral resources and whether this promotes their contribution to pest control in adjacent orchards. Other methods which have been used to assess the contribution of natural enemy taxa to pest control services include analysing the gut contents of predators and laboratory feeding studies to determine their prey, exclusion cages to compare pest control with and without presence of natural enemy taxa, and environmental DNA metabarcoding of plants to detect which species are visiting (Macfadyen et al., 2015; Lefebvre et al., 2017; Hodgkiss et al., 2022; Marshall and Beers, 2022). Camera trapping can also be used to determine the importance of predator species on herbivore abundance (Seimandi-Corda et al., 2024), but this may not be suited to *D. plantaginea* since the colonies are inside curled leaves.

Flower margin orchards had greater natural enemy diversity in the ground vegetation, despite the ground vegetation plant community in the orchard being the same as control orchards (Chapter 3). Aphidophagous hoverfly species can be highly mobile as adults, travelling 50–250 m from a pollen source (Harwood et al., 1994; Wratten et al., 2003) and may travel these distances to locate aphid colonies. The shortest distance between a flower margin orchard and its corresponding control orchard was 119 m, so co-use by the same invertebrates was possible for the highly mobile natural enemies, although too great a distance could have led to a different farm or landscape composition making it more difficult to isolate the effect of the flower margin from that of management or landscape contexts (see Section 6.5.3).

6.2.2 Positive effects of flower margins for *D. plantaginea* control

The *D. plantaginea* and fruit damage results showed a positive effect of the flower margins for *D. plantaginea* control, particularly in 2021 when *D. plantaginea* infestation levels were higher. Presence of a flower margin reduced the spread of *D. plantaginea* on infested trees, and subsequently reduced the number of trees with fruit damage. In a year with high levels of infestation, the percentage of trees with fruit damage was reduced from 80% to 48% and this effect reached 50 m from the flower margin into the orchard (Chapter 2). To my knowledge, this is the first study to find a significant reduction in the incidence of fruit damage at harvest in orchards provisioned with flower margins compared with control orchards, and the first to demonstrate reduced *D. plantaginea* damage in conventionally managed fruit orchards with flower margins. As discussed in Chapters one and two, only a few studies have investigated the effects of flower strips on fruit damage by *D. plantaginea*. For example, Campbell et al., (2017) measured the effect of flower margins in apple orchards and found no impact on yield, despite finding positive effects on natural enemy communities, as did Jacobsen et al., (2022). Similarly, a large-scale pan-European study, Cahenzli et al., (2019) found reductions in fruit damage by *D. plantaginea* after the second fruit drop, but not at harvest, perhaps due to commercial quality fruit thinning practices (the removal of damaged fruits prior to harvest in a commercial orchard). Section 6.5 discusses the potential context dependencies of the effects of flower margins and suggests reasons why there was a yield benefit in this study whilst others have found no effect.

6.3 Economic effects

6.3.1 Net costs of flower margins for *D. plantaginea* control

The extent of economic benefits or costs of flower strips were context specific. Under some modelled scenarios, the flower strips led to a net economic cost in terms of *D. plantaginea* control, for example when the level of *D. plantaginea* infestation was low and a flower border replaced crop land which could have otherwise been used to grow apple trees. In this context, pest control benefits did not outweigh the opportunity costs, including with the subsidy. Under these circumstances, only when apple production costs were high did a cropland margin pay for itself by reducing *D. plantaginea* damage, due to apple production sometimes being unprofitable. However, the economic benefits in a year of high infestation could be enough to compensate for the losses in a year of low infestation to achieve long-term economic balance overall. Apple prices and the volatility observed in orchard profitability are also influenced by market dynamics, which can significantly impact farm businesses in the long term. Apple profitability can be affected by trade policies, availability of apples, and changes in market demand such as consumer demand for organic or sustainable produce (Yamoah and Acquaye, 2019; Hou et al., 2022; Staton et al., 2022). This further stresses the importance of strategies to mitigate pest-related financial swings. Future work should focus on the long-term economic benefits of perennial flower margins. Flower strips may still be cost effective under these scenarios when also considering the many other wider economic benefits. By investing in practices that enhance pest management, such as the use of flower strips, farms can reduce vulnerability to fluctuating pest outbreaks, which may improve long-term profit stability. Beyond short-term economic benefits, a resilient farming system helps mitigate risks, protect yields, and provide consistent product supply, thereby enhancing a farm's capacity to cope with the unpredictable nature of both pest dynamics and market conditions (Huss et al., 2022).

Whilst the focus of this study was *D. plantaginea* fruit damage, flower strips have been found to encourage control of other apple pests. For example, in an orchard which had used no insecticides for five years, plots with wildflower alleyways had 9% damaged fruits compared to 33% damaged fruits in control orchards, primarily due to reduced damage by several pests in the presence of beneficial arthropods supported by flower strips (Bostanian et al., 2004). A pan-European study reported that flower strips reduced apple damage by *C. pomonella* (codling moth) (Cahenzli et al., 2019), which is one of the most economically damaging apple pests, capable of causing complete crop loss (Beers et al., 2003). Flower strips also have the potential to improve crop quality since they can improve pollination services after three or more years (Blaauw and Isaacs, 2014; Albrecht et al., 2020). Garratt et al. (2023) identified that by improving fruit number and quality, pollinators contributed more than £16 k per hectare in 24 UK apple orchards, and found that initial fruit set and seed set deficits were reduced by abundant bumblebees, and orchards with a greater abundance of solitary bees saw lower deficits in fruit size (Garratt et al., 2023). These additional wider economic benefits of flower margins could improve the economic viability of flower margins and should be considered in a full economic assessment.

6.3.2 Economic benefits of flower margins for *D. plantaginea* control

Flower strips on the grass headland led to economic benefits to the grower. In 2022, all the orchards had a low level of *D. plantaginea* infestation, but even then, the flower borders 'paid for themselves' compared to standard primarily grass headlands and led to net benefits when the subsidy was accounted for. Similarly, flower strips in the centre of the orchard provided economic benefits, even in a year with low *D. plantaginea* infestation, despite replacing land which could have otherwise been used for growing apple trees. This was due to the assumption that *D. plantaginea* pest control benefits would be experienced on both sides of the flower strip instead of only one side (Chapter 5). The change in location of the strip, from the border to the centre, was enough to compensate for the opportunity costs. This is an important finding since growers and practitioners ultimately make the decision whether to invest in establishing flower strips, plus the maintenance costs time and effort. A 2-year experiment comparing sunflower fields with and without flower strips in central Spain surveyed local farmer opinions on flower strips as a method of pest control (Ortega-Marcos et al., 2022). Whilst these farmers acknowledged the biodiversity benefits, most did not notice yield benefits, and all were concerned about the spread of invasive weeds from flower strips (Ortega-Marcos et al., 2022). Zhang et al. (2018) reported that, based on interviews with 85 participants, EU farmers expressed a relatively low confidence in the efficacy of natural pest control compared with insecticides, especially under high pest damage levels (Zhang et al., 2018).

The work in this thesis is the first economic analysis of flower borders for pest control. A recent study by Jacobsen et al. (2022) found no impact of flower borders on the number of damaged apples compared to controls, however, since they examined only ten randomly selected apples per tree, perhaps this was not enough to identify statistical differences in fruit damage. In other crops, Li et al. (2021) reported that monofloral strips adjacent to aubergine greenhouses led to a reduction in aphid pest pressure and subsequently, led to a reduction in the amount of required insecticide. A cost analysis revealed that this reduction in insecticide use, in combination with the increase in crop value based on environmentally friendly practices, suggested this strategy could be economically viable

(~+14,700 RMB per greenhouse) (Li et al., 2021, Supplementary Materials). In a 4-year study in rice fields, growing nectar-producing plants reduced major lepidopteran pest abundance, increased grain yields by 5%, and overall resulted in economic benefits of 7.5% (Gurr et al., 2016). Similarly, Blaauw and Isaacs (2014) reported that perennial flower margins improved blueberry pollination and subsequently increased crop yields enough to exceed the costs of wildflower establishment and maintenance. These studies show promise for the economic value of flower margins, although few studies have investigated the effect of flower borders on yield or monetary benefits of pest-control services in apple orchards (Herz et al., 2019; Kleijn et al., 2019; Fountain, 2022; Crowther et al., 2023). Further studies, across crop types, are required to determine the economic value of flower strips for agricultural pest control (Kleijn et al., 2019), and to determine the context dependencies (Section 1.5). Overall, perennial flower margins provided an economic benefit for *D. plantaginea* control, despite the focus on only a single pest species. When considering the wider potential economic benefits of flower margins, it is likely that they would be economically sustainable. This information gives apple growers informed decision-making abilities to invest land area, time, and money in creation of floral habitat adjacent to apple orchards, although further studies in this area are required.

6.4 Wider effects

6.4.1 Neutral wider effects of flower margins

Even the use of modern, more selective pesticides may detrimentally affect non-target organisms such as natural enemies via sub-lethal effects such as hindering reproduction, predation, development time, and longevity (Schmidt-Jeffris, 2023). Pollinators and pollination services may also be negatively affected (Reshi et al., 2025). In these studies, the growers were asked to continue normal management and orchards of the same apple variety of similar age were treated with aphicide applications in the same way. However, flower margins may have the potential to reduce the number of aphicide applications. Studies in other crops have suggested that flower strips could potentially reduce the amount of insecticide required for aphid and lepidopteran pest control. In six organic commercial greenhouses in northern China, Li et al. (2021) tested monofloral strips adjacent to greenhouses and measured pest and predator abundance in the crop and the flowers along with yield and insecticide use over two years. Heavily infested plants were sprayed with a higher volume of insecticide than plants with low pest numbers and total volume was recorded. Pest abundance, including two aphid species (*Myzus persicae* and *Aphis gossypii*), was reduced by 43% in greenhouses adjacent to flower strips compared with controls, predator numbers were twenty times higher, and insecticide use was reduced by 34% (Li et al., 2021). Similarly, in a 4-year study in rice fields, growing nectar-producing plants reduced major lepidopteran pest abundance enough to reduced insecticide applications by 70% (Gurr et al., 2016). Whilst flower margins may have the potential to reduce insecticide spays, this remains to be directly tested in apple orchards.

6.4.2 Positive wider effects of flower margins

The presence of flower margins reduced the reliance on chemical pest control by diversifying the *D. plantaginea* control methods. Relying mainly on pesticides is less sustainable due to potential future restrictions, or loss in efficacy, for example due to insecticide resistance or non-target effects, so additional methods could improve long-term ecological sustainability of apple orchards (Shaw et al., 2021; Ryalls et al., 2024). Presence of flower margins increased the diversity of plant species and provided a unique plant community structure. Spillover of natural enemy diversity from the flower margins into the orchard ground herbage demonstrates long-reaching effects on the surrounding communities. Biodiversity, particularly species richness, is important for ecosystem services (Dainese et al., 2019). Diversity may be a driver of yield resilience in crop (the ability of yield to recover from adverse disturbances) (Dardonville et al., 2020). Considering emerging invasive apple pests, such as *Aphis spiraecola* (spirea aphid) and *Halyomorpha halys* (brown marmorated stink bug) (Dardonville et al., 2020; Pajač Živković et al., 2023), alongside recent losses of some conventional insecticides (Shaw et al., 2021), and more unpredictable climates (Dalhaus et al., 2020), yield resilience is an important trait for commercial apple orchards. For a system that relies heavily on biodiversity-mediated ecosystem services, such as pollinator abundance and diversity for pollination (Weekers et al., 2022; Garratt et al., 2023) and natural enemies to keep pest populations from rapidly growing out of control (Karp et al., 2013), increased species richness to promote ecosystem function could be highly valuable for the long-term sustainability of commercial orchards (Ryalls et al., 2024). Additionally, since *D. plantaginea* abundance and fruit damage varied greatly between years, the potential for flower margins to bolster populations of alternative prey could be of high importance to sustain natural enemy populations at times when *D. plantaginea* is less abundant. For example, Gardarin (2023) tested eight different perennial seeds mixes using flower strips within blocks of different annual arable crops and found that increases in the percentage of Fabaceae cover increased predator–prey ratio (in the pea–barley intercrop, oilseed rape) and aphid parasitism rate (in maize, spring pea). It was suggested that legumes in a flower strip may have acted as a reservoir for non-pest aphids to sustain populations of natural enemies of pest aphids (Gardarin, 2023). However, alternative prey may instead deter natural enemies from pest species by offering a distraction or a higher-quality diet, for example in a six-year study in an experimental organic apple orchard, Mezőfi et al. (2020) investigated the biocontrol potential of spiders in apple canopies by assessing their natural prey in field conditions, day and night. They found that arboreal hunting spiders showed a preference for alternative prey and a negative selectivity for pest species (Mezőfi et al., 2020). Other potential ecological benefits of flower margins include support for farmland birds (Schmidt et al., 2022a), support for pollinators and pollination (Blaauw and Isaacs, 2014; Morandin et al., 2016; Ortega-Marcos et al., 2022), and reduced requirements for chemical inputs (e.g. (Li et al., 2021)) leading to wider soil, water and air pollution reductions, although the extent of the ecological benefits is likely context dependent (Section 1.5). The findings of this thesis suggests that presence of flower margins, by increasing natural enemy richness in the flowers themselves, and the adjacent orchard, improved the overall ecological value and sustainability of apple orchards. Diversification of *D. plantaginea* control methods is more sustainable in the long-term than relying solely on chemical control methods.

6.5 Context dependencies

6.5.1 Flower strip age

The efficacy of the flower margins could be dependent on flower strip age. The flower margins under investigation in this study were 2-6 years since establishment. Similarly, in a recent agroforestry study, using 6-year-old sown flower strips, there was a reduced percentage of apples lost to *D. plantaginea* for trees with spontaneous flowering understories compared with both mown herbage and arable crop (Staton et al., 2021). In the current study, and that of Staton et al. (2021), perhaps the maturity of the flower strips led to more effective reduction of fruit damage by *D. plantaginea*. In apple orchards, only a minority of previous studies have investigated well-established strips (Albert et al., 2017; Cahenzli et al., 2017; Cahenzli et al., 2019; Jacobsen et al., 2022) (although Jacobsen et al. (2022) replaced 5-year-old, less-diverse strips). A review by Herz et al. (2019) indicated that older flower strips may be more effective at reducing insect pests and promoting their natural enemies, as in other crops (Blaauw and Isaacs, 2015). Campbell et al. (2017) tested the efficacy of flower strips that targeted beneficial arthropods using 1-2 year-old strips in apple orchards (Campbell et al., 2017). They reported that total natural enemy richness was 90% higher in flower strips which included open-nectar plants compared to concealed-nectar plants, but found no effect on apple yield (Campbell et al., 2017). It may require several years to build up a natural enemy population for effective pest control. For example, Bostanian et al. (2004) reported that it took several seasons for flowering plants to provide effective biocontrol before obtaining 90% clean apples in the fifth year of the study, from 5% in year one (Bostanian et al., 2004). Similarly, predatory arthropod taxa are differently affected over time by changes in apple pest management. For example, Simon et al. (2024) studied arthropod communities in three orchards that differed in pest management (organic, IPM, and conventional), each of which drastically decreased pesticide use during the course of the study. Dermaptera quickly displayed a strong direct increase in numbers in the conventional system to the same level as the low-input and organic orchards, whereas epigeal and arboreal Araneae showed no recovery four years after the change in pest management practices (Simon et al., 2024). In other crops, research by Ganser et al. (2019) reported that the effects of wildflower strips compared to wheat fields as an overwintering resource over four years of study differed between arthropod taxa in each year (Ganser et al., 2019). Perhaps there is a settling period over the first few years post-establishment whilst the arthropod community is changing. Future work should monitor the effects of flower margins beyond the first two years after establishment and should investigate the longevity of the margins compared to the current average productive lifespan of commercial dessert apple orchards of 25 years, or 13 years for more intensive orchards (Alaphilippe et al., 2016a).

6.5.2 Flower strip size

The economic viability of the flower margins for *D. plantaginea* control may depend on the size of the flower margin. The flower margins were on average 15 m wide, and the effects of the flower margins occurred at least 50 m into the orchard (reduced spread of aphids, reduced incidence of fruit damage, and increased natural enemy diversity in the orchard ground vegetation). Narrower flower margins would incur reduced establishment and opportunity costs, for example they would require a smaller volume of seeds and a smaller area of land. However, it is not guaranteed that a smaller flower strip would provide the same effect. The optimal size of flower strips for apple pest control services is unknown. Blaauw and Isaacs (2012) investigated whether plot size affected the magnitude of biological control provided by natural enemies of *Aphis glycines* (soybean aphid) using replicated plots ranging in size from 1 to 100 m^2, one year after planting them with year-old perennial seedlings. As flower patch size increased, natural enemy abundance, richness, and diversity also increased, which subsequently increased biological control of *A. glycines* (Blaauw and Isaacs, 2012). Similarly, Tscharntke et al. (2002) reported that percentage of parasitism of *Meligethes aeneus* (rape pollen beetle) increased for larger sizes of flower-rich grassland habitats. Along with the total area covered, the patch size of the flower margins may also be important to consider, since several small fragments of flower-rich grassland habitats were found to support more parasitoid species than the same area composed of only one or two fragments (Tscharntke et al., 2002). Future studies could investigate the importance of flower margin size for *D. plantaginea* control. Future work could also investigate whether the effects a flower margin of this size could reach further than 50 m, to reveal whether this size is likely to be sufficient for *D. plantaginea* control in larger orchards, longer than 100 m in total.

6.5.3 Landscape context

The ecological effects of flower strips may be dependent on landscape context. According to the "intermediate landscape complexity hypothesis", the presence of flower strips may not have strong effects in a highly complex landscape since a variety of habitats are already present, and highly simplified landscapes may not have sufficient source populations of natural enemies to benefit strongly (Tscharntke et al., 2012). Instead, an intermediate landscape may feel the strongest effects (Kleijn et al., 2011). Martin et al. (2019) synthesised data from 49 studies (1515 landscapes) across Europe, to test the effect of edge density (landscape configuration) on arthropods in crop fields and field margins and their pest control services. Overall, in landscapes with high edge density, pest control improved 1.4-fold, but effects on specific taxa varied with dietary, dispersal, or overwintering ecology (Martin et al., 2019). The response of natural enemies to non-crop habitat in surrounding landscapes is highly variable across different cropping systems and geographies (Karp et al., 2018). In perennial systems compared to arable crops, less is known about the combined effects of landscape context and local agricultural management for pest control (Daelemans et al., 2023), although in apple orchards, Hambäck et al. (2020) reported that the effect of landscape diversity can have opposite effects on different natural enemy taxa, and Happe et al. (2019) found that the effect of landscape diversity was inconsistent across countries (Happe et al., 2019). Apple production landscapes vary considerably across countries, with some regions adopting more intensive practices compared to the UK. Though recent years have seen a shift toward more intensive systems, apple production has become highly concentrated and intensively managed in some countries (Damos et al., 2015; Sander et al., 2019), particularly in Italy where trees are planted at much closer spacing to increase yield per hectare which improves production efficiency (Hassan et al., 2020). In contrast, the UK's apple production is typically less concentrated with orchards being more spread out and smaller in scale. This raises important questions about the transferability of the study's findings to regions with more intensive apple production systems. To better understand the influence of landscape context, future research should assess the effectiveness and spillover distance of flower strips across different countries, landscapes and orchard management practices.

6.5.4 Flower strips in conjunction with other *D. plantaginea* control methods

The efficacy of flower margins may be improved when used in conjunction with other *D. plantaginea* control methods. In this study the flower margins were established alongside conventionally managed orchards deploying conventional aphicides such as flonicamid, spirotetramat and acetamiprid. Many of the more recent studies investigating the effect of flower strips on apple pest control (2017 onwards) have been in organic or insecticide-free orchards (for example: Cahenzli et al., 2019; Jacobsen et al., 2022; Favarin et al., 2024), with fewer studies in orchards using Integrated Pest Management (Campbell et al., 2017; McKerchar et al., 2020). Whilst it is uncertain whether the efficacy of flower margins for *D. plantaginea* control is affected by the use of modern conventional insecticides, McKerchar et al. (2020) suggested that the use of conventional plant protection products could detrimentally affect natural enemies in orchards, masking any effects of interrow flower strips on pest control services. They found interactive effects with cumulative insecticide and acaricide toxicity values for natural enemy groups (Anthocoridae, Chrysopidae, Miridae, parasitoids and predatory mites), for example, Family richness and diversity of natural enemies were greater in year three in orchards associated with lower toxicity values. Organic management often enhances the abundance of many taxa, including arthropods (Wyss and Pfiffner, 2006) and a comparative study reported reduced *D. plantaginea* abundance and higher natural enemy abundance in organic orchards than in orchards using conventional and integrated pest management (Dib et al., 2016c). The natural pest control of *D. plantaginea* was suggested to be disrupted by the chemical insecticides used in IPM and conventional orchards (Dib et al., 2016c). Since organic apple orchards are the minority, covering approximately only 2.5% of the land used for global apple production (Ryalls et al., 2024), future work should investigate the effects of flower margins for *D. plantaginea* control in conventional orchards, and compare this with organic orchards, to understand the impact of current pesticide use on the pest control effects of flower strips.

Flower strips have also been investigated in conjunction with parasitoid release (*Aphidius matricariae* and *Ephedrus cerasicola*) for biocontrol of *D. plantaginea*. Apple trees located at various distances from parasitoid release points were monitored for two years across the aphid season in plots with and without flower strips in an organic apple orchard (Tougeron et al., 2023). At the peak infestation date, alleyway flower strips reduced the presence of *D. plantaginea* by 33.4%, compared to plots without flower strips (Tougeron et al., 2023). Whilst this effect was weaker with increasing distance from the parasitoid release points, the results suggested that presence of flower strips could marginally compensate for this effect (Tougeron et al., 2023). The authors suggest that flower margins may improve the persistence and dispersal capacities of parasitoid wasps (Tougeron et al., 2023). Perennial flower strips have also been investigated over a three-year period in conjunction with mating disruption by semiochemicals and herbivory-induced volatiles for attracting natural enemies (Pålsson et al., 2022). Although suction samples were consistently richer in generalist predators when multiple tools were used in combination, there was no reduction in populations of artificially established *D. plantaginea* colonies, potentially due to the lack of ant exclusion (Pålsson et al., 2022). Liu et al. (2024) used a combination of attractive plants for predators (*Cnidium monnieri* or *Brassica napus*) with plants that repel pests (*Ocimum basilicum* or *Mentha haplocalyx*) in between rows of apple trees. They reported that these combinations improved biological control of *Aphis spiraecola* on apple compared to control plots without flowers (Liu et al., 2024). Similarly, mono-floral plots infested with non-apple aphids between rows of apple trees have been found to reduce, and almost eradicate, *D. plantaginea* colonies in apple tree plots compared with control plots (Pålsson et al., 2020). Further studies are required to understand the full potential of flower strips as a supporting tool alongside other *D. plantaginea* control methods. An interesting area for further exploration is the potential for combining flower strips with netting to control *Cydia pomonella*. Specifically, it would be worth investigating whether netting could be applied at key times, such as after flowering to protect fruit from egg-laying adults, and subsequently removed to allow for the spillover of natural enemies from the flower strips into the orchard trees. This approach could offer a dynamic method for pest management while maintaining biodiversity and natural predator populations. Future studies should assess the feasibility of such an integrated pest management strategy, considering factors like timing, netting durability, practicality for the farmer and the ecological interactions between flower strips and pest control agents.

6.6 Conclusion

Flower margins were effective, economically viable, and likely to be ecologically and agronomically sustainable. The results of this thesis suggest that perennial flower margins were an effective method for *D. plantaginea* control, although further studies are needed to elucidate the mechanism behind this, and the complex ecological interactions. Efficacy of flower strips for *D. plantaginea* control may depend on flower margin age, the natural enemy taxa involved, and the co-use of other aphid suppression methods. Overall, perennial flower margins provided an economic benefit despite the focus on only a single pest species. When considering the wider potential economic benefits of flower margins, such as improved pollination and reduced pesticide requirements, it is likely that they would be economically sustainable. This information gives apple growers informed decision-making abilities to invest land area, time, and money in creation of floral habitat adjacent to apple orchards, although further studies in this area are required. The findings of this thesis suggests that presence of flower margins, by increasing natural enemy richness in the flowers themselves, and the adjacent orchard, improved the overall ecological value and sustainability of apple orchards. Diversification of *D. plantaginea* control methods will be more sustainable in the long-term than relying solely on chemical control methods. This is one of few studies to investigate crop damage, one of few to use well-established margins (>3 years), and the first study to conduct an economic analysis of flower margins for pest control. Building a complete picture of the value of flower margins may improve uptake. Since apple is one of the most widely produced fruits, and global production is increasing, the use of flower margins has the potential to provide widespread environmental, economic, and sustainability benefits. Important gaps and challenges remain. The mechanisms behind enhanced pest suppression, such as interactions between natural enemies and pests, require further investigation. Factors such as flower margin age, size, and landscape context also remain under-explored, influencing the ecological and economic viability of this strategy. This limits our understanding of how flower strips perform across varying conditions and locations, hindering the ability to provide broadly applicable, evidence-based recommendations for their implementation. Future research should prioritize long-term studies to monitor flower margin effectiveness over their productive lifespan, particularly in apple orchards with differing management practices, for example, conventional vs. organic or intensive vs non-intensive. Exploring the integration of flower margins with modern pest control methods, such as biocontrol or selective pesticide use, could improve their ease of use for farmers and integration with farm operations. Comparative studies across diverse geographies and landscape complexities are necessary to determine optimal design and implementation conditions. Building a holistic understanding of flower margins, including their co-benefits, such as impact on pollinators and ecosystem resilience, will guide their adoption and enhance sustainability in apple production systems.

7 References

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8 Supplementary

Supplementary numbering relates to the associated chapters.

Supplemental Table 2.1: Site information for study orchards.
See https://besjournals.onlinelibrary.wiley.com/action/downloadSupplement?doi=10.1111%2F1365-2664.14598&file=jpe14598-sup-0001-TableS1.xlsx

Supplemental Table 2.2: Amount of perennial and grass seed mix used to establish flower margins in orchards 1-4 and 5 (kg/ha), and percentage species composition.

	Orchard Pair			
	1-4		5	
Perennial species	% of mix	kg/ha	% of mix	kg/ha
Achillea millefolium (Yarrow)	1.24	0.21	0.46	0.11
Anthyllis vulneraria (Kidney Vetch)	1.24	0.21	0.00	0.00
Barbarea vulgaris (Winter-cress)	4.98	0.83	0.00	0.00
Centaurea nigra (Common Knapweed)	7.48	1.25	1.10	0.28
Daucus carota (Wild Carrot)	2.50	0.42	0.92	0.23
Galium verum (Ladys Bedstraw)	0.00	0.00	0.92	0.23
Knautia arvensis (Field Scabious)	0.00	0.00	0.92	0.23
Leontodon hispidus (Rough Hawkbit)	4.98	0.83	0.00	0.00
Leucanthemum vulgare (Oxeye Daisy)	2.50	0.42	0.92	0.23
Lotus corniculatus (Birdsfoot Trefoil)	4.98	0.83	6.43	0.95
Malva moschata (Musk Mallow)	0.00	0.00	0.73	0.18
Onobrychis viicifolia (Native Sainfoin wildflower)	0.00	0.00	1.38	0.34
Plantago media (Hoary Plantain)	1.24	0.21	0.73	0.18
Plantago lanceolata (Ribwort Plantain)	0.00	0.00	0.92	0.23
Prunella vulgaris (Self Heal)	0.00	0.00	0.92	0.23
Primula veris (Cowslip)	2.50	0.42	0.09	0.02
Ranunculus acris (Meadow Buttercup)	7.48	1.25	0.46	0.11
Reseda lutea (Wild Mignonette)	1.24	0.21	0.00	0.00
Sanguisorba minor (Salad Burnet)	0.00	0.00	1.84	0.46
Silene dioica (Red Campion)	1.24	0.21	0.92	0.23
Silene latifolia (White Campion)	0.00	0.00	0.46	0.11
Stachys officinalis (Betony)	0.00	0.00	0.46	0.11
Taraxacum officinale(Dandelion)	4.98	0.83	0.00	0.00
Trifolium pratense (Red Clover)	1.24	0.21	0.00	0.00
Trifolium resupinatum (Persian Clover)	0.00	0.00	5.97	0.88
Sown perennial flowers % of TOTAL	49.86	8.33	26.54	5.37
Grass species				
Cynosurus cristatus (Crested Dogstail)	12.54	2.09	12.40	3.10
Festuca rubra (Slender-creeping Red-fescue)	12.54	2.09	0.00	0.00
Festuca rubra ssp. commutata (Chewing's Fescue)	12.54	2.09	18.37	4.59
Poa pratensis (Smooth-stalked Meadow-grass)	12.54	2.09	13.77	3.44
Phleum bertolonii (Smaller Catstail)	0.00	0.00	10.10	2.53
Agrostis capillaris (Common Bentgrass)	0.00	0.00	4.59	1.15
Trisetum flavescens (commercial Yellow Oatgrass)	0.00	0.00	0.46	0.11
Festuca ovina (sheeps fescue)	0.00	0.00	13.77	3.44
Sown grasses % of TOTAL	50.14	8.38	73.46	18.37

Supplemental Figure 2.1: Strip of grass in between rows of apple orchard trees (i.e interrow area) (left), strip of grass surrounding the apple orchard (i.e. headland area) bordered by a windbreak hedge (centre), and apple orchard with a flower margin (right).

Supplemental Table 2.3: Tukey adjusted multiple comparison of significant interactive terms of 2-part hurdle model showing the significance of differences between flower margin and control orchards: A) Percentage of trees with fruit damage by rosy apple aphids (spread), and B) Percentage of damaged apples on affected trees (severity). Stars denote significance; * = P < 0.05, ** = P < 0.01, *** = P = 0.

Year	Distance (metres)	Odds Ratio	SE	Z Ratio	P Value	Significance
2021	0	4.730	2.687	2.736	0.006	**
2022	0	1.303	0.702	0.492	0.623	NS
2021	5	14.857	9.362	4.282	0.000	***
2022	5	4.689	3.204	2.262	0.024	*
2021	10	5.301	2.980	2.968	0.003	**
2022	10	3.992	2.556	2.162	0.031	*
2021	20	3.853	2.110	2.463	0.014	*
2022	20	0.478	0.271	-1.302	0.193	NS
2021	50	8.012	5.238	3.183	0.001	**
2022	50	3.505	2.415	1.821	0.069	NS

Year	Distance (metres)	Odds Ratio	SE	Z Ratio	P Value	Significance
2021	0	0.811	0.410	-0.414	0.679	NS
2022	0	0.350	0.199	-1.848	0.065	NS
2021	5	1.126	0.588	0.227	0.821	NS
2022	5	0.845	0.546	-0.260	0.795	NS
2021	10	1.075	0.547	0.142	0.887	NS
2022	10	0.590	0.382	-0.815	0.415	NS
2021	20	2.599	1.352	1.837	0.066	NS
2022	20	0.360	0.209	-1.763	0.078	NS
2021	50	2.574	1.319	1.845	0.065	NS
2022	50	0.140	0.084	-3.295	0.001	**

Supplemental Table 2.4: Tukey adjusted multiple comparison of significant interactive terms of presence/absence binomial model showing the significance of differences between flower margin and control orchards: Percentage of orchard trees with Formicidae (ants) present. Stars denote significance; * = P < 0.05, ** = P < 0.01.

Round	Odds Ratio	SE	Z Ratio	P Value	Significance
April	16.041	16.884	2.637	0.008	**
May	0.762	0.292	-0.708	0.479	NS
June	0.822	0.291	-0.553	0.580	NS
July	3.706	2.047	2.371	0.018	*

Supplemental Table 2.5: Tukey adjusted multiple comparison of significant interactive terms in binomial models showing the significance of differences between flower margin and control orchards: Percentage of bait aphids eaten from cards 5 to 8 days after deployment. Stars denote significance; * = P < 0.05, ** = P < 0.01, *** = P = 0.

Distance (metres)	Round	Odds ratio	SE	Z ratio	P value	Significance
0	1	1.36	0.71	0.60	0.55	NS
5	1	1.03	0.54	0.07	0.95	NS
10	1	2.86	1.49	2.02	0.04	*
20	1	5.06	2.64	3.11	0.00	***
50	1	3.55	1.85	2.42	0.02	*
0	2	0.37	0.19	-1.92	0.05	.
5	2	2.00	1.04	1.33	0.18	NS
10	2	5.65	2.95	3.32	0.00	***
20	2	5.81	3.04	3.37	0.00	***
50	2	1.20	0.62	0.34	0.73	NS
0	3	0.27	0.14	-2.49	0.01	*
5	3	1.91	1.00	1.24	0.21	NS
10	3	1.49	0.78	0.76	0.45	NS
20	3	2.10	1.10	1.42	0.16	NS
50	3	3.90	2.04	2.61	0.01	*

Supplemental Table 2.6: Calculation of approximate equivalent kg/ha difference according to differences in number of trees with apple damage and severity per tree.

	Average Percentage of Apples Per Damaged Tree	Average Percentage of Trees With Damaged Fruit	Average Yield of a Gala Orchard in 2021 (kg/ha)	Yield Accounting for Damage (kg/ha)
Control Orchards	0.111	0.8	35000	3108
Flower Margin Orchards	0.041	0.48	35000	688.8
Difference (kg/ha)				2419

Supplemental Table 3.1: Mean percentage cover of plant groups found in orchard habitats in orchards with and without a flower margin. Interrow = alleyway, C = control orchard, T = flower margin orchard.

Species	Flower margin	Interrow C	Headland	Interrow T	Undersotry C	Understory T
Agricultural White Clover, *Trifolium repens*	8.59	0.00	0.00	7.29	0.00	0.00
Annual Daisy, *Bellis annua*	0.00	0.35	0.00	0.00	0.00	0.15
Bare Ground	1.59	2.63	10.62	1.19	31.27	19.06
Birds Foot Trefoil, *Lotus corniculatus*	10.23	0.00	0.00	0.00	0.00	0.00
Black Knapweed, *Centaurea nigra*	26.78	0.00	0.00	0.00	0.00	0.00
Bristly Oxtongue, Helminthotheca echioides	0.00	0.00	0.00	0.00	1.18	0.00
Broad Leaved Willow Herb, *Epilobium montonum*	0.00	0.00	0.00	0.00	2.11	1.85
Broadleaf Dock, Rumex obtusifolius	0.15	0.02	0.01	0.38	0.00	0.06
Butter Daisy, Melampodium divaricatum	0.12	0.00	0.00	0.00	0.00	0.00
Common Centaury, Centaurium erythraea	0.00	0.02	0.00	0.00	0.00	0.00
Common Fleabane, Pulicaria dysenterica	0.00	0.03	0.18	0.00	0.02	0.03
Common Grandsel, *Senecio vulgaris*	0.00	0.00	0.00	0.00	1.21	0.33
Common Ragwort, Jacobaea vulgaris	0.00	0.00	0.01	0.00	0.00	0.00
Common Vetch, *Vicia sativa*	0.00	0.00	0.08	0.00	0.00	0.00
Creeping Buttercup, *Ranunculus repens*	2.21	3.74	0.07	1.54	3.26	0.18
Curly Dock, Rumex crispus	0.52	0.20	0.00	0.00	0.94	0.00
Dandelion, Taraxacum officinale	1.06	2.27	0.68	0.65	0.18	0.15
Dead Vegetation	0.00	8.80	0.00	1.75	44.02	52.41
Dwarf Thistle, *Cirsium acaule*	0.28	0.00	0.00	0.00	0.00	0.00

Field Speidwell, *Veronica persica*	0.00	0.00	0.02	0.00	0.44	0.20
Field Thistle, *Cirsium arvense*	2.86	0.00	0.00	0.00	0.20	0.39
Goosegrey, Argentina anserina	0.05	0.29	0.00	0.06	0.00	0.00
Grass	30.13	79.73	78.76	81.36	9.36	22.15
Greater Knapweed, *Centaurea scabiosa*	1.67	0.00	0.00	0.00	0.00	0.00
Hairy Bittercress, *Cardamine hirsuta*	0.00	0.00	0.00	0.00	0.26	0.00
Hedge Bedstraw, *Galium mollugo*	0.13	0.00	0.00	0.00	0.00	0.00
Hoary Groundsel, Packera werneriifolia	0.00	0.00	0.00	0.09	0.00	0.00
Hoary Willowherb, Epilobium parviflor	0.00	0.00	0.00	0.00	0.49	0.24
Hungarian Chamomile, matricaria chamomilla	0.00	0.00	1.99	0.00	0.00	0.00
Lesser Trefoil, *Trifolium dubium*	0.00	0.00	0.07	0.00	0.00	0.00
Many Seeded Goosefoot, *Lipandra polysperma*	0.00	0.00	0.00	0.00	0.00	1.52
Moss	0.00	0.00	0.00	0.00	0.00	0.12
Oxeye Daisy, Leucanthemum vulgare	6.98	0.10	0.06	0.00	1.11	0.14
Plantain, Plantago spp	0.07	0.49	2.60	0.07	0.34	0.33
Prinose Bramble, *Rubus pruinosus*	0.00	0.00	0.00	0.00	0.77	0.03
Purple Deadnettle, *Lamium purpureum*	0.00	0.00	0.00	0.00	0.11	0.00
Red Clover, Trifolium pratense	0.85	0.00	0.00	0.00	0.00	0.00
Redshank, Persicaria maculosa	0.00	0.00	0.00	0.00	0.00	0.00
Salad Burnet, Sanguisorba minor	0.07	0.08	0.00	0.00	0.00	0.15
Scarlet Pimpernickle, *Anagallis arvensis*	0.00	0.00	0.00	0.00	0.00	0.00
Selfheal, Prunella vulgaris	0.00	0.05	0.01	0.00	0.13	0.00
Small Fleabane, Pulicaria vulgaris	0.00	0.00	0.00	0.00	2.11	0.00

Spiney Snowthistle, *Sonchus asper*	0.00	0.00	0.00	0.00	0.00	0.03
Square Stalked Willow Herb, *Epilobium tetragonium*	0.00	0.00	0.01	0.00	0.42	0.32
Stinging Nettle, *Urtico dioica*	0.03	0.00	0.00	0.00	0.00	0.00
Thyme Leaved Speedwell, *Veronica serpyllifolia*	0.00	0.17	0.04	0.00	0.00	0.00
Twiggy Spurge, Euphorbia waldsteinii	0.78	0.00	0.00	0.00	0.00	0.00
Unknown	0.00	0.00	0.33	5.34	0.00	0.00
White Clover, Trifolium repens	1.34	1.04	4.33	0.00	0.00	0.15
Wild Carrot, *Daucus carota*	0.66	0.00	0.00	0.00	0.00	0.00
Yarrow, Achillea millefolium	2.84	0.00	0.13	2.69	0.04	0.00

Supplemental Table 3.2: Pairwise PERMANOVA Results (Holm adjusted *P*-values) showing significant differences between plant community composition in habitats in orchards with and without a flower margin. WFM = flower margin, interrow = alleyway, C = control orchard, T = treatment orchard, df= degrees of freedom. Stars denote significance; * = P < 0.05.

Pairs	DF	F model	R^2	P-value	P-adjusted	Significance
WFM vs interrowT	1	10.66	0.37	0.00	0.02	*
WFM vs headland	1	9.03	0.36	0.00	0.02	*
WFM vs interrowC	1	12.23	0.42	0.00	0.02	*
WFM vs understoryC	1	8.85	0.34	0.00	0.02	*
WFM vs understoryT	1	10.12	0.37	0.00	0.02	*
interrowT vs headland	1	1.13	0.07	0.31	0.94	
interrowT vs interrowC	1	0.73	0.04	0.57	1.00	
interrowT vs understoryC	1	15.04	0.47	0.00	0.02	*
interrowT vs understoryT	1	15.47	0.48	0.00	0.02	*
headland vs interrowC	1	3.71	0.20	0.02	0.06	
headland vs understoryC	1	12.53	0.46	0.00	0.02	*
headland vs understoryT	1	13.64	0.48	0.00	0.02	*
interrowC vs understoryC	1	16.96	0.51	0.00	0.02	*
interrowC vs understoryT	1	17.37	0.52	0.00	0.02	*
understoryC vs understoryT	1	0.67	0.04	0.55	1.00	

Supplemental Table 3.3: Tukey adjusted multiple comparison of significant interactive terms to compare response variables of mixed models between flower margin and control orchards for the following factor levels; type of orchard area (edge= flower margin or headland, centre = central alleyways), distance from the orchard edge, and sampling round and year. Stars denote significance; * = P < 0.05, ** = P < 0.01, *** = *P* = 0.

Respone variable	Factor levels	Ratio	SE	DF	Null	Z-ratio	P-value	Significance
	Area types							
Sweep specialist abundance	centre	0.84	0.28	Inf	1.00	-0.51	0.61	NS
	edge	0.20	0.04	Inf	1.00	-7.66	0.00	***
Sweep generalist abundance	centre	0.82	0.24	Inf	1.00	-0.69	0.49	NA
	edge	0.14	0.04	Inf	1.00	-7.40	0.00	***
	Distance							
Tap abundance specialists	0	1.82	0.64	Inf	1.00	1.72	0.08	NS
	5	0.67	0.28	Inf	1.00	-0.95	0.34	NS
	10	3.04	1.32	Inf	1.00	2.55	0.01	*
	20	2.59	1.30	Inf	1.00	1.90	0.06	NS
	50	1.07	0.50	Inf	1.00	0.15	0.88	NS
	Round	Year	Estimate	SE	DF	T-ratio	P-value	Significance
Tap diversity	1	2021	0.02	0.05	113	0.36	0.72	NS
	2	2021	0.16	0.09	556	1.87	0.06	NS
	3	2021	0.08	0.05	113	1.63	0.11	NS
	4	2021	0.17	0.05	113	3.30	0.00	***
	1	2022	0.09	0.05	113	1.82	0.07	NS
	2	2022	0.01	0.05	113	0.13	0.90	NS
	3	2022	0.09	0.05	113	1.77	0.08	NS
	4	2022	-0.10	0.05	113	-1.94	0.05	NS

Supplemental Table 3.4: Pairwise PERMANOVA Results (Holm adjusted p-values) showing significant differences between natural enemy community composition in orchard habitats in orchards with and without a flower margin (edgeT= flower margin, edgeC= headland, centreT = central alleyway in flower margin orchards, centreC = central alleyway in control orchards). Stars denote significance; * = P < 0.05, ** = P < 0.01.

Pairs	DF	F model	R^2	P-value	P-adjusted	Significance
centreC vs centreT	1	0.404	0.013	0.856	0.856	
centreC vs edgeT	1	4.888	0.133	0.001	0.006	**
centreC vs edgeC	1	1.543	0.049	0.178	0.534	
centreT vs edgeT	1	3.689	0.098	0.006	0.024	*
centreT vs edgeC	1	1.080	0.033	0.372	0.744	
edgeT vs edgeC	1	5.501	0.139	0.003	0.015	*

Supplemental Table 5.1. Number of apples per tree and proportion of fruit lost at different distances from the edge of the orchard in a year with high levels of infestation by *D. plantaginea* (2021), and low levels (2022), from actual yield data.

	Low levels of infestation (2022)				High levels of infestation (2021)			
Distance from edge of orchard (m)	Number of apples per tree		Proportion of fruit lost		Number of apples per tree		Proportion of fruit lost	
	Without	With flower strip	Without	With flower strip	Without	With flower strip	Without	With flower strip
0-2.5	116	68	1.31	4.06	108	66	8.12	4.93
2.5-7.5	100	74	1.08	0.22	119	62	12.83	3.09
7.5-15	103	80	2.77	0.75	146	73	9.6	5.01
15-35	118	89	0.87	1.35	111	68	10.58	3.03
35-55	110	76	1.32	0.55	116	61	14.43	4.6

Supplemental Table 5.2. Calculated annual margins (based on revenue minus changes in marginal costs) of three scenarios for locating a flower strip; 1) Headland border, 2) Cropland border, 3) Central strip (for flower strips which last 5 years), including the added value when subsidy is considered.

Infestation level	Scenario	Calculated annual margin (revenue minus change in marginal costs) without subsidy (£/ha/yr)			Subsidy
		Flower strip orchard	Control orchard	Difference	
Low	1) Headland border	1809	5337	-3528	136
Low	2) Cropland border	1809	6774	-4965	136
Low	3) Central strip	2146	6877	-4731	79
High	1) Headland border	-3115	3149	-6264	136
High	2) Cropland border	-3115	3786	-6901	136
High	3) Central strip	-3572	3478	-7050	79

Note: 2021: high pest incidence; 2022: low pest incidence