

# Using non-bee and bee pollinator-plant species interactions to design diverse plantings benefiting crop pollination services

B.G. Howlett<sup>a,\*</sup>, J.H. Todd<sup>b</sup>, B.K. Willcox<sup>c</sup>, R. Rader<sup>d</sup>,  
W.R. Nelson<sup>a</sup>, M. Gee<sup>a</sup>, F.G. Schmidlin<sup>a</sup>, S.F.J. Read<sup>a</sup>, M.K. Walker<sup>a</sup>,  
D. Gibson<sup>a</sup>, and M.M. Davidson<sup>a</sup>

<sup>a</sup>The New Zealand Institute for Plant and Food Research Limited, Christchurch, New Zealand

<sup>b</sup>The New Zealand Institute for Plant and Food Research Limited, Auckland, New Zealand

<sup>c</sup>University of Reading, School of Agriculture Policy and Development, Reading, United Kingdom

<sup>d</sup>University of New England, School of Environmental and Rural Science, Armidale, NSW, Australia

\*Corresponding author: e-mail address: Brad.Howlett@plantandfood.co.nz

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## Abstract

Protecting, establishing and managing biodiverse semi-natural habitats is one strategy within the concept of ecological intensification of agriculture that supports insect pollinator abundance and diversity in agroecosystems. However, without accounting for species-level relationships between insects, crops and non-crop vegetation, diverse semi-natural habitats may not lead to improved crop pollination, and could create pest reservoirs. Possibly thousands of non-bee insect species contribute to global crop pollination, but research has largely focussed on bees. Thus, key information to best manage habitats that target wider crop pollinator diversity and abundance is lacking. We demonstrate the concept of designing mixed species native plantings (a type of semi-natural habitat) based on plant-insect interactions to increase abundance and diversity of non-bee and bee crop pollinators in an intensively managed agricultural landscape. We used existing refereed and grey literature to identify and anticipate interactions between pollinators, natural enemies and pests with native plants and crop species to design and establish plantings on three farms. We anticipated the designed plantings would support 21 pollinating species, 20 of which were verified in observational surveys 5 years post-establishment. While anticipated bee-plant species interactions were largely confirmed, actual networks of the non-bee pollinators, were larger and more complex than expected, indicating the plantings were particularly effective in supporting these interactions. Most immature life-stages of non-bee pollinators were not directly supported by plantings and separate strategies should consider larval requirements. Presenting the plant-pollinator networks to relevant industries has been a powerful tool for incentivising their support for designed habitats on farms.



## 1. Introduction

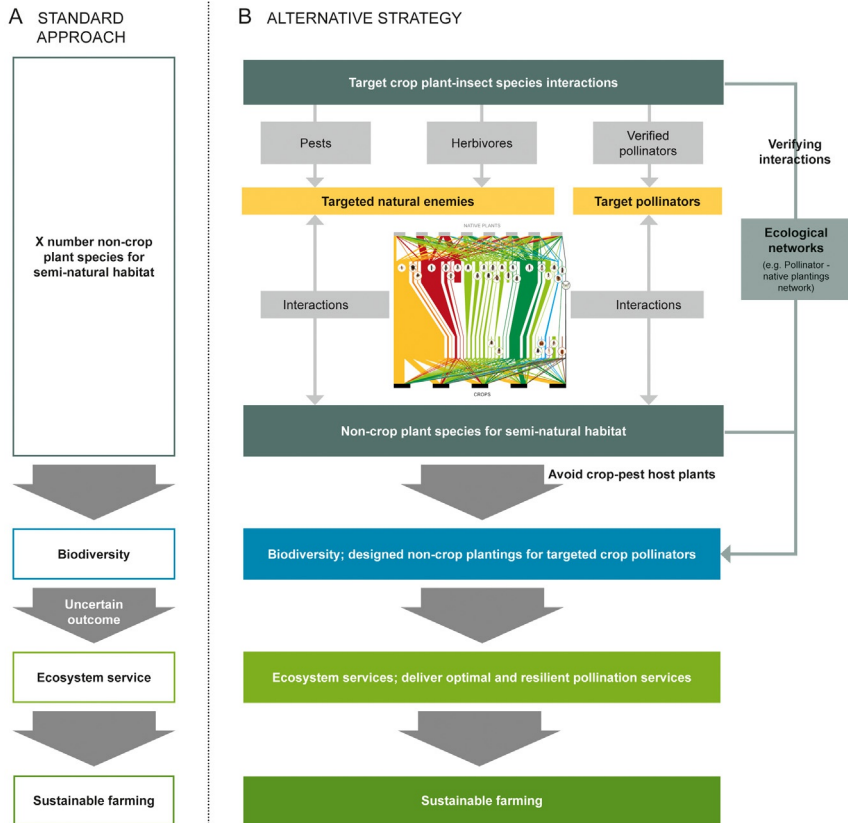
The intensification of arable landscapes through increased mechanisation, broad scale crop rotations, increased field sizes and intensive use of pesticides and fertilisers has led to increased farm productivity/area (Beckmann et al., 2019; chapter “Ecosystem services and the resilience of agricultural landscapes” by Bennett et al.; Helfenstein et al., 2020). However, it has also lead to loss of non-cropped habitat and landscape features with a corresponding reduction in landscape heterogeneity and biodiversity (Kremen and Miles, 2012; Stoate et al., 2001). This has contributed to a reduction in ecosystem services, such as pollination and pest control (UNEP, 2005), resulting in a desire to utilise strategies aimed at restoring such services (Bartual et al., 2019; Deguines et al., 2014).

Supporting insect biodiversity within agroecosystems can facilitate the provision of multifunctional services (Isaacs et al., 2009; Landis, 2017) that can reduce crop yield deficits and reliance on insecticides and other agrichemical inputs (Bianchi et al., 2006; Cahenzli et al., 2019; Garibaldi et al., 2016; Morandin et al., 2016; O'Rourke and Jones, 2011; Roubos et al., 2014;

Veres et al., 2013). For pollination, increasing species diversity helps ensure the presence of efficient pollinating species (Lowenstein et al., 2015). Moreover, increasing beneficial insect functional diversity (insect species contributing to different ecological functions, such as pollination services and pest control) also improves ecosystem service resilience against abiotic and biotic drivers (e.g., changing climate or invasive species; Burkle et al., 2017; Aizen et al., 2020). For example, in agroecosystems exposed to environmental disturbances, greater insect diversity may increase the probability of tolerant species surviving and performing functions that were previously performed by species eliminated by the disturbance (Elmqvist et al., 2003). Furthermore, some species such as syrphid flies (hover flies) contribute both pollination and biocontrol functions (Dunn et al., 2020).

To increase beneficial insect services, a number of aligned strategies have been proposed including reduced and selective use of pesticides, protection of habitats that support life-cycle requirements, intercropping and crop rotations, all of which are components of ‘ecological intensification’ (Bommarco et al., 2013; Kovacs-Hostyanszki et al., 2017). However, there is still a need for underpinning research to achieve optimal outcomes from such strategies. For example, knowledge on the identity of the potentially vast number of wild crop pollinating species, their interactions with plants, and their effectiveness as crop pollinators, is limited (Rader et al., 2020) (see Section 2). Consequently, strategies around establishing flowering plants aimed at promoting crop pollinator diversity within agroecosystems may not currently support all wild crop pollinators. Additionally, little consideration appears to have been given to potentially detrimental species (e.g., crop pests) that could interact with flowering plants established for pollinators and other beneficial insects (Pywell et al., 2005; Sutter et al., 2018; Tschumi et al., 2018).

While protecting existing natural habitat on and around farms can support beneficial insects that enhance crop yields (Garibaldi et al., 2016), establishing or re-introducing semi-natural habitats (see Section 3) does not guarantee improved crop yields, even when they improve bee species diversity (Nicholson et al., 2020). This may be partly because we lack a full understanding of how the plant species contained within such habitats are used by the insects that pollinate crops (Nichols et al., 2019). To incentivise growers to invest in measures that support pollinators and other beneficial insect diversity, the benefits need to be clearer, and more certain, in terms of farm productivity and/or biodiversity conservation. Unless growers see a broader value, there is a risk that simple ecological benefits will not result in uptake of these interventions (Cullen et al., 2013).



**Fig. 1** Schematic diagram of the steps to undertake the design of non-crop plantings to suit local crop requirements for ecosystem services derived from insect presence. With the standard approach (A), often the outcome has been seen as increased biodiversity as a result of interventions, while in the alternative designed non-crop plantings approach (B) we aim for specific insects with functions that support food production. Pests are insect herbivores that can cause economic loss.

For growers of crops dependent on insect pollination, the verification of those beneficial bee and non-bee species that contribute to crop pollination, and how they interact with non-crop vegetation, provides a platform for designing and establishing habitat that targets particular pollinators (Fig. 1). Previous studies focused on identifying non-crop plant species primarily aimed at enhancing bee diversity through establishing semi-natural habitats on farms for improved conservation and crop pollination outcomes

(Nichols et al., 2019; Williams and Lonsdorf, 2018). Although the benefits of providing habitats that support non-bee pollinators has been acknowledged (Burkle et al., 2017), there is currently a lack of studies that have explored the design of semi-natural habitat for non-bee crop pollinating species. This likely reflects the limited knowledge on the contributions these species make to crop pollination and the resources needed by these species, which may differ with landscape context (Cook et al., 2020; Rader et al., 2016, 2020).

With an understanding of known crop pollinators and their interactions with identified non-crop plants, along with an understanding of the use of those plants by crop pests, there is opportunity to design habitats that assure delivery of pollination (and potentially other insect-mediated) ecosystem services (Fig. 1). Constructing pollinator and pest networks that assess the interplay of insects and plants can support and direct the selection of plant species to ensure the resulting planted communities promote beneficial, crop-pollinating species and minimise pest problems (Section 4). Thus, a move to a predictive agroecology that incorporates the ecological concepts of resilience, stability and capacity for self-organisation, and targets specific desired functions and complementary functional traits, can link these semi-natural habitats with proven agricultural crop yield benefits (Bohan et al., 2013; Menz et al., 2011).

In this chapter we:

- (1) Provide an overview of knowledge pertinent to establishing non-crop plantings (a type of semi-natural habitat) within agricultural systems to boost insect crop-pollinator diversity.
- (2) Review current knowledge of insect pollinators, plant-pollinator interactions, the role and adoption of semi-natural habitat within agroecosystems, and the potential to explore opportunities to better understand and facilitate improved design of semi-natural habitat.
- (3) Assess the concept of using species interactions as the basis for designing and establishing habitats (hereafter referred to as ‘designed plantings’) that boost verified crop pollinating insects (but not pests) for five associated crops. We tested the concept using a highly modified, intensively-managed arable landscape in New Zealand as a model system.
- (4) Discuss how our concept for designing non-crop plantings is an advance on other strategies for supporting insect pollinators, and elucidate its feasibility for application as part of a farm management system.



## 2. The diversity of wild insect crop pollinators

While it is known that more diverse pollinator communities at the field scale can provide better pollination services to crops (Garibaldi et al., 2016; Mallinger and Gratton, 2015; Winfree et al., 2018), the current lack of knowledge on the contribution made by different insect species to crop pollination is a major limitation when designing on-farm plant habitats targeted at optimising pollination services. Research has been heavily skewed towards understanding the role of bee species as crop pollinators (Rader et al., 2020). But even for this taxon, little is known about the efficacy of most species as crop pollinators, or the landscape requirements (e.g., plant species, land use, soil type) that drive flower-visitation and site selection for nesting and the development of progeny (Gill et al., 2016).

### 2.1 Verified crop pollinating insects—A need to know more

The opportunity to better harness a wide array of pollinators for improved crop pollination is significant. Currently, the number of insect species recorded visiting and pollinating crops is a fraction of the estimated  $\geq 500$  million insect species able to pollinate plants (Ollerton, 2017). In a recent review of the top 105 most widely grown crops (fruit or seed for human consumption) reliant on animal pollination, Hymenoptera (mostly bees) visited 93%, Diptera 72%, Lepidoptera 54% and Coleoptera 51%, of flowering crop species (Rader et al., 2020). Moreover, the authors reported 194 animal families visiting crop flowers with 40.9% ( $n = 43$ ) of these being visited by  $\geq 10$  and mango recording the most with 59 families (Rader et al., 2020—supplementary data). From just seven bee families, Kleijn et al. (2015) reported 785 crop flower visiting species. However, from an agroecosystem perspective, the actual numbers of insect species that effectively pollinate crop plants is currently difficult to ascertain as we lack widespread verification of which species are actually delivering this service. Flower visitors are not always pollinators, for example, nectar robbers avoid contact with stigmas and anthers despite being flower visitors (Kevan and Baker, 1983).

For most crops requiring insect pollination, bees are regarded as the most important (Winfree, 2010). As pollinators, they tend to have a higher per flower visit effectiveness than non-bees (Rader et al., 2016). Typically they have more body hair and carry more loose body pollen than non-bees; variables that have been linked to greater stigmatic pollen deposition (Howlett et al., 2011; Stavert et al., 2018). Moreover, certain bee species have behavioural characteristics that make them very effective pollinators

of particular crops. For example, buzz pollination (bee vibrating to loosen pollen from anthers) of solanaceous crops (Garibaldi et al., 2017), or flower tripping (a common requirement in Fabaceae where the bee triggers a structural change in a flower allowing for pollination (Palmer-Jones and Forster, 1965). Despite their efficiency as crop pollinators, only a small number of the >20,000 species (Ascher and Pickering, 2020) are commonly managed for pollination (33 species/genera are listed by Garibaldi et al., 2017). Of these, the managed western honey bee (*Apis mellifera* Linnaeus, 1758), is most widely utilised to provide this service due to its widespread availability and ability to pollinate many crops (Garibaldi et al., 2017), ability to be transported and placed within target fields (Goodwin, 2012), and available information about recommended stocking rates (Rollin and Garibaldi, 2019).

Less research has been conducted on non-bee insects as crop pollinators and their potential for management. A review of literature published 1950–2018 by Rader et al. (2020) found that assessments of non-bee pollination efficiency, measured as single visit stigmatic pollen deposition (SVD), had been conducted in only 19 crops, and measures of fruit/seed set following non-bee visits had been conducted in only 15 different crops. This compared with studies on bee pollinator efficiency, where SVD had been measured in 36 crops and fruit/seed set assessed for 39 crops. Assessments of non-bee pollinators have been comparatively overlooked in pollination studies (Földesi et al., 2020), possibly because of a limited ability to identify specimens to a meaningful taxonomic level when active in crops and an assumption that they are not efficient pollinators (Rader et al., 2016). Without knowing the identity of wild pollinating species proven to be efficient crop pollinators, it is difficult to devise targeted on-farm management strategies that can deliver quantifiable crop pollination services. Moreover, unlike bees, that are typically central-place foragers (focussed on the hive or nest site), non-bee crop pollinators tend not to be constrained by a nest location and so are capable of utilising a much wider landscape. Various species of crop pollinating flies, for example, will move from flowering crops into the surrounding environment (Mesa et al., 2013; Rader et al., 2011) and may not return. However, a small number of species are now produced commercially for crop pollination (Rader et al., 2020).

## 2.2 Understanding crop pollinator life histories and population dynamics

Beyond wild pollinator identity there is also a lack of knowledge or consideration of their life-histories and the key factors that drive their population

dynamics in agricultural landscapes (Cook et al., 2020; Pisanty and Mandelik, 2015). Without this knowledge, growers cannot reliably depend on their services as crop pollinators and are unable to use targeted management strategies to increase abundances of known pollinating species. Life-histories of the immature stages of non-bee crop pollinators are particularly variable, and commonly their requirements differ greatly from those of adult life stages (Rader et al., 2020). Therefore, the establishment or maintenance of floral-rich habitat that is utilised by a diversity of adult-stage pollinators likely needs coupling with separate strategies to support their various immature life-stage requirements. Implementing both strategies is likely to pay-off, however, because unlike adult bees that are required to return to their nests to provision their larvae with pollen (Greenleaf et al., 2007), adult flies, butterflies and beetles are capable of long-range dispersal to colonise new areas within a season (Rader et al., 2016; Williams, 1957; Wotton et al., 2019) and provisioning for both adult and larval stages may support local and migrating individuals. Many non-bee pollinators are also highly fecund with multiple generations per year, so are able to respond rapidly to changes in resource availability (Rader et al., 2020). Consequently, providing resources for the different life-stages of certain non-bee pollinators may result in a rapid increase in these species' populations. These pollinators can then supplement honey bees (both abundance and species richness) to improve seed or fruit set (Garibaldi et al., 2013).



### **3. Semi-natural habitats and their potential to better support crop pollinators**

One way to achieve increased beneficial insect diversity is through the management, enhancement or establishment of semi-natural habitats (Gill et al., 2016). Holland et al. (2017) defined a semi-natural habitat as a community of non-crop plant species outside or within a crop. It covers a broad array of plant communities commonly included within agri-environment schemes across Europe (e.g., grassland areas, ground-covers in permanent crops, buffer strips, habitat managed for wildlife, and land taken out of production), as well as woodland, hedgerows, floral strips, and beetle banks (grass mound habitats for predatory beetles and other ground dwelling beneficial insects). Such on-farm habitats have been demonstrated to increase bee diversity within localised areas (Nicholson et al., 2020; Ricketts et al., 2008). However, designing the 'optimal' habitat for insect pollinators



and other beneficial insects, or identifying plant species to enhance existing semi-natural habitats, is not simple (Gill et al., 2016).

A problem in designing these habitats is that while woodland, grassland and field boundaries such as hedgerows, are common non-crop habitats found on farmland in Europe, the plant species composing these are rarely reported (Holland et al., 2017). Given that plant species composition has a profound effect on invertebrate community assemblages (Schaffers et al., 2008), evaluating the efficacy of such semi-natural habitats in supporting beneficial insects is difficult without this knowledge. Likewise, understanding how different insect species interact with crop and non-crop plant species within the agricultural landscape is required to quantify their beneficial services to crops. For example, a number of studies of floral strips in agricultural landscapes have focused on designing improved seed/plant mixes that support a broader range of bee-plant species interactions to improve crop pollination and species conservation (Menz et al., 2011; Nichols et al., 2019; Williams and Lonsdorf, 2018). In highly modified agroecosystems where large areas of native flora have been extirpated from the landscape, designed semi-natural habitats (i.e., ‘designed plantings’) provide an opportunity for farmers to increase plant biodiversity on their farms. Using knowledge of plant-insect species interactions could ensure these designed plantings also support insect species that provide ecosystem services.



## **4. Evaluating plants that support crop pollinators**

### **4.1 On-farm pollinator-p-plant species interactions**

Identifying and planting near crops a mix of plant species that attract and support a high diversity and abundance of pollinators has been widely considered a way to increase the quality and stability of pollination services (Garibaldi et al., 2013; Hoehn et al., 2008; Kleijn et al., 2015; Menz et al., 2011; Orford et al., 2016; Winfree and Kremen, 2009). Pollinators and plants exist within communities that can be portrayed as a network of interacting species. In these communities, a core subset of well-connected generalist plant and insect species that many specialist species can also interact with provides robustness and resilience to the network (Bascompte et al., 2003) and also potentially to the pollination services. Such generalist plant species that are visited by a high proportion of pollinator species occupy a central position in a network (Martín González et al., 2010). Identifying and deploying such central plant species has a high probability of improving

pollination services in agroecosystems. This is because plant species that are visited by a wide diversity of insect species increase the likelihood that some of those insects will fill pollination niches that overlap among plants, connecting potentially isolated parts of the network (Emer et al., 2016; Martín González et al., 2010). The potential for central plant species to facilitate or compete for pollination services with targeted crops or plants may be highly context-dependent and influenced by complex spatio-temporal dynamics. In the context of deploying central plant species within habitat restoration projects, they can increase flower visitor diversity without affecting the network structure of flower visitors to resident plant species (Maia et al., 2019). However, these outcomes may not be consistent. For example, a study from the United Kingdom found that presence of the invasive central plant species *Impatiens glandulifera* Royle reduced insect visitation and seed set in the native *Stachys palustris* L. (Chittka and Schürkens, 2001). Moreover, competition for pollinators between simultaneously flowering crops, is an example of where designing agricultural systems based on careful consideration of spatial and temporal flowering may result in better yield outcomes through the improved facilitation of on-farm pollination services (Grab et al., 2017).

Where crops have specialised flowers, central plant species that tend to possess generalised traits may sometimes be inadequate to support the insects that are able to pollinate these crops. For example, fabaceous plants such as red clover have specialised flowers that are reliant on insect pollinators that are capable of ‘flower tripping’. These insect species, such as long-tongued bumble bees (*Bombus ruderatus* (Fabricius, 1775), *Bombus hortorum* (Linnaeus, 1761)), are the most efficient pollinators of red clover. However, despite being considered generalist flower visitors with a preference for flowers with deep corollas in Europe (Rasmont et al., 2015), these bee species do not always visit plants with generalist flowering traits. Therefore, they may not be present when pollination services are needed. For instance, in New Zealand where bumble bees were introduced to pollinate exotic crops, the long tongued species visit very few native plant species (Donovan, 2007). Consequently, to benefit from their pollination service, growers deploy colonies of long-tongued bumble bees (Donovan, 2007; Howlett and Donovan, 2010). Therefore, along with central plant species, a knowledge of peripheral plant species that can support insects capable of pollinating crops with specialised flowers is also useful.

## 4.2 Networks to assess pollinator-plant interactions

Identification of central and targeted specialised plant species can be done through literature searches and databases, through analysis of published networks (Maia et al., 2019) or empirically by evaluating candidate plants species through observational field surveys or experiments (e.g., Lundin et al., 2019; Robson, 2014). Identification of the insect species visiting different plant species, including crops, enables plant species to be selected that are most likely to increase the diversity of pollinators known to pollinate crops. Knowledge of the insect species that contribute (or could contribute) to crop pollination is crucial in order to identify non-crop plant species for designed semi-natural habitats.

Ecological networks are one approach that provides insight into how central and specialised non-crop plant species can be used within designed plantings to support pollinators and other beneficial insects (e.g., insect natural enemies), while minimising the disservice coming from pest insects. Network approaches are a frequently used tool to describe the structure and function of ecological communities and recent reviews highlight their scope for exploring ecosystem complexity, stability and associated feedback loops affecting these (Delmas et al., 2019; Landi et al., 2018; Newman, 2010). Network models have been increasingly employed to explore and evaluate pollinator-plant communities within agricultural landscapes. These include guiding plant selection and assessing the effectiveness of plantings for ecological restoration (Forup et al., 2008; Maia et al., 2019). In the productive landscape, networks have been used to evaluate the effects of land use on pollinator assemblage interactions with crop plant production, and benefits of nearby plant diversity for crop pollination through pollinator spillover (Saunders and Rader, 2019; Sritongchuay et al., 2019). They have also been used to identify plant species that support native bee communities and to identify shared pollinator taxa between crops (Russo et al., 2013; Willcox et al., 2019). Thus, networks can be used to select plants or identify areas of plant diversity that benefit crop pollination (Russo et al., 2013).

However, the selection and establishment of plants that diversify known crop pollinators, that improve pollination networks within agroecosystems, need to consider both the beneficial and harmful insects that may be attracted to particular plants and the consequences for crop yields. Currently, available tools for selecting plant species have focussed on improving pollination only (e.g., M'Gonigle et al., 2017; Robson, 2014). We propose that ecological

networks that extend known species interactions between plants and all insect groups (i.e., not just pollinators) can be used to guide the selection of plants to ensure crops benefit, but are not harmed, by planting schemes in agricultural areas. These selections should be verified with interactions (functions) quantified through planting experiments (e.g., [Lundin et al., 2019](#)).



## 5. Case study: Designed plantings to support non-bee and bee crop pollinators

Our study was conducted in an intensified agricultural region of New Zealand where arable farmers commonly grow a broad range of mass flowering vegetable and herbage seed crops requiring insect pollination. Growers in the region rely heavily on managed honey bees to pollinate these crops, but there is opportunity to improve the contribution made by verified wild bee and non-bee pollinators. The aim was to design and establish non-crop plantings (in this case native New Zealand plant species) on farms to support the pollinating species, but not pest species, of five seed crops: pak choi (*Brassica rapa* subsp. *chinensis* (L.) Hanelt), carrot (*Daucus carota* subsp. *sativus* (Hoffm.) Schübl. and G. Martens), radish (*Raphanus sativus* L.), white clover (*Trifolium repens* L.) and onion (*Allium cepa* L.). The designs were based on existing information on plant–insect species interactions. To assess the success of our designs, we then compared the anticipated plant–insect interactions with actual interactions 5 years following the establishment of designed plantings on three farms. More specifically, we assessed whether:

- (i) the anticipated insect species that are known to provide pollination services to the crops were observed within the plantings;
- (ii) the designed plantings provided central plant species capable of supporting diverse generalised pollinators and whether specific plants that supported more specialised crop–pollinating species were needed;
- (iii) a variety of plant species was needed to support all targeted insect species, or whether a single native plant species would suffice;
- (iv) immature life–stages requirements of the verified pollinators, as described in the literature, were likely to be supported by the plantings.

### 5.1 The study system

As with a number of regions in the world settled by Europeans, the landscape of the Canterbury Plains (43.64S; 172.09E) has undergone significant change. The introduction of a myriad of exotic species began in the 19th century and, along with exotic livestock and crops, the Canterbury Acclimatisation



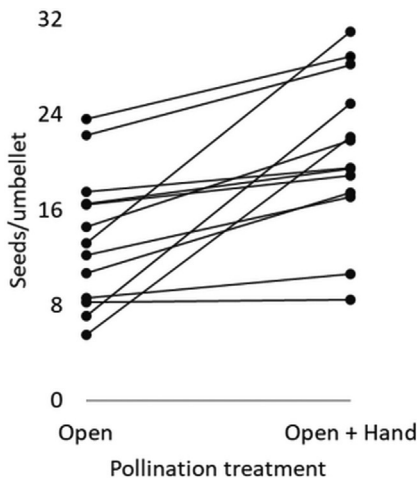
**Fig. 2** Intensive agriculture dominates land use on the Canterbury Plains, New Zealand.

Society (founded 1864) became heavily active in introducing a broad range of birds, fish, insects and plants from around the globe (Skewes, 2018). The ubiquity of many of these introduced species and the loss of native plants and animals has resulted in the landscape becoming more evocative of locations in Europe, Australia or North America (Fig. 2). Today the region is dominated by a mosaic of livestock and arable farms. Over the last 35 years, the region has undergone significant agricultural intensification as widespread irrigation has seen large scale conversion of extensively farmed livestock (sheep) areas into high-yielding dairy production (Harrison and Gomez, 2013; Smith and Montgomery, 2004). Agricultural intensification has corresponded with a reduction in landscape complexity, particularly through the loss of remnant native forest vegetation, where <0.5% remains (Thompson et al., 2003), and the removal of exotic shelterbelts (tall, dense plantings of woody species to protect livestock and crops from weather) or hedgerows (short, woody species creating barriers between fields and other land uses). Shelterbelts are predominantly exotic tree species (e.g., pine, *Pinus radiata* D. Don, and macrocarpa, *Hesperocyparis macrocarpa* Hartw.) and hedgerows are mainly gorse (*Ulex europaeus* L.) (Price, 1993). An estimated 556 km of shelterbelts have been removed from the Plains within a 10 year period (1995–2004) largely to support expansion of centre-pivot and linear-spray irrigation systems capable of efficiently irrigating larger fields (Tait and Cullen, 2010).

This occurred despite the known negative impacts resulting from the removal of shelterbelts, including loss of shade, increased evapotranspiration and loss of animal biodiversity (Millner and Roskrige, 2013; Tait and Cullen, 2010).

As with other agriculturally-intensified systems around the globe (FAO, 2011; Robinson and Sutherland, 2002), there is evidence of yield deficits in insect pollinated crops grown within the region. This is evident for hybrid vegetable carrot seed crops, a crop commonly grown by arable farmers (Fig. 3), and also for open pollinated white clover where seed yields were half their potential (Goodwin et al., 2011).

Growers of insect pollinated crops in Canterbury rely on managed honey bee (*A. mellifera*) hives for crop pollination, hired at a cost of \$200–250 NZD (€ 114–143) per hive (Ministry for Primary Industries, 2018). Recommended stocking rates throughout these crops are approximately six hives/ha for carrot, radish, onion, white clover, apple, stonefruit and berry crops (Goodwin, 2012). In Canterbury, the approximate production area for insect pollinated crops includes: 7849 ha vegetable seed, 1103 ha berries, 312 ha apples and 81 ha stonefruits (Aitken and Warrington, 2018; Hampton et al., 2012).



**Fig. 3** Yield deficits within 13 hybrid carrot vegetable seed fields in Canterbury 2018. Data compares mean seed set (per umbellet) on umbels exposed to insects (open pollinated) versus hand pollinated umbels also exposed to insects (open + hand pollinated). Mean seed yield from open + hand pollination treatments were higher in all fields varying from 2.5% to 75.2%. Replicates of each treatment  $n = 12/\text{field}$ . In each field, treatments were conducted at opposing corners (5 m inside boundary) and in the centre with four treatment sets/point. Standard errors for open pollinated umbellet seed counts for each field  $\leq \pm 2.3$ ; open + hand  $\leq \pm 3.4$ .

Therefore, for these crops alone we estimate regional expenditure on honey bee pollination services is likely to be \$M 11.2–14.1 NZD (€M 6.4–8.0)/pa (2019).

Despite agricultural intensification and grower reliance on managed honey bees, a number of verified crop pollinating endemic and exotic wild bee and non-bee species occur throughout the region (Table 1). This knowledge has been disseminated by industry bodies to some extent (Foundation for Arable Research, 2012, 2018), however, strategies targeting their management remain limited. A number of these pollinators contribute to the pollination of multiple crop species and their efficiency for each crop varies. For example, for white clover, the short-tongued species, *Bombus terrestris* (Linnaeus, 1758), is considered to be a more efficient pollinator than either of the long tongued bumble bees (Plowright and Plowright, 1997) or western honey bees (*A. mellifera*; Howlett et al., 2019). Some hover flies (e.g., *Eristalis tenax* (L.)) and/or blow flies (Calliphoridae) are efficient pollinators of pak choi (*Brassica rapa* L., Rader et al., 2009), carrot (*Daucus carota* L.; Howlett, 2012) and onion (*Allium cepa* L.; Howlett et al., 2017), but these flies are unlikely to effectively pollinate white clover (*Trifolium repens* L.; Howlett et al., 2019). Arable farmers may grow all of these crops on their farms. Consequently, on-farm strategies are needed to support diverse and functionally complementary mixes of wild insect species, able to pollinate all crops and mitigate the risk of yield deficits.

The ability to identify key wild bee and non-bee insects that contribute to the pollination of multiple mass flowering crop species grown within the Canterbury region also provides an essential platform to design habitat that can support these insects. Elsewhere, studies have focussed on identifying combinations of plant species that may support crop pollinating bees only (Menz et al., 2011; Nichols et al., 2019; Williams and Lonsdorf, 2018), overlooking the potential to support non-bee pollinators that can add complementarity and redundancy to crop pollination services (Rader et al., 2016; Stavert et al., 2018). Native New Zealand plant species established on farms where no other natural vegetation existed were found to increase the abundance of particular fly and bee species visiting sentinel flowering plants within Canterbury's intensified agricultural landscape (MacDonald et al., 2018). As a novel approach, to optimise the abundance and diversity of bee and non-bee pollinators on farms, semi-natural habitats could be improved further by designing a specific mix of native plant species that support the targeted verified crop pollinating species. This could be achieved by selecting a combination of plant species that together supply nectar and pollen resources

**Table 1** Perennial native plant species established on arable farms and the number of flower visiting insect and crop pollinating species associated based on existing data collated 2011/12.

Priority or secondary	Plant species	No. of insect flower visitors	No. of crop pollinators
Priority	<i>Carmichaelia australis</i> R.Br. <sup>a</sup>	3	2
	<i>Carpodetus serratus</i> J.R. Forst & G. Forst.	5	4
	<i>Cordyline australis</i> (G. Forst.) Hook. f. <sup>a</sup>	18	13
	<i>Corokia cotoneaster</i> Raoul	7	3
	<i>Discaria toumatou</i> Raoul <sup>a</sup>	4	2
	<i>Fuchsia excorticata</i> (Forst. & Forst. f.) L. f.	2	2
	<i>Veronica salicifolia</i> (G. Forst.) Pennell <sup>a</sup>	18	9
	<i>Hoheria angustifolia</i> Raoul	8	5
	<i>Kunzea serotina</i> (de Lange) Tolken <sup>a</sup>	21	7
	<i>Leptospermum scoparium</i> J.R. Forst. & G. Forst. <sup>a</sup>	27	10
	<i>Lophomyrtus obcordata</i> Burret	8	5
	<i>Myoporum laetum</i> G. Forst	3	3
	<i>Ozothamnus leptophyllus</i> (G. Forst.) Breitw. & J.M. Ward <sup>a</sup>	8	3
	<i>Phormium tenax</i> J.R. Forst. & G. Forst. <sup>a</sup>	14	6
	<i>Pittosporum tenuifolium</i> Banks & Solander. ex Gaertn.	4	2
	<i>Pittosporum eugenoides</i> A. Cunn.	4	2
	<i>Sophora microphylla</i> Aiton	7	5



Secondary	<i>Coprosma crassifolia</i> Colenso	0	0
	<i>Coprosma intertexta</i> G. Simpson	0	0
	<i>Coprosma lucida</i> J.R. Forst., G. Forst.	1	1
	<i>Coprosma propinqua</i> A. Cunn.	—	—
	<i>Coprosma robusta</i> Raoul	1	1
	<i>Coprosma rotundifolia</i> A. Cunn.	0	0
	<i>Coprosma rubra</i> Petrie	0	0
	<i>Coprosma virescens</i> Petrie	0	0
	<i>Griselinia littoralis</i> Raoul	—	—
	<i>Muehlenbeckia astonii</i> Petrie	—	—
	<i>Olearia fragrantissima</i> Petrie	0	0
	<i>Olearia paniculata</i> (J.R. Forst. & G. Forst.) Druce	0	0
	<i>Plagianthus regius</i> (Poit.) Hochr.	1	1
	<i>Podocarpus totara</i> G. Benn. ex D. Don	1	1
	<i>Prumnopitys taxifolia</i> (Banks & Sol. ex D. Don) de Laub.	1	1
	<i>Pseudopanax arboreus</i> (L.f.) Philipson	1	1
	<i>Pseudopanax crassifolium</i> (Sol. ex A. Cunn.) C. Koch	1	1

<sup>a</sup>Indicates plants included in flower-visiting insect surveys.

— Indicates no data available.

Priority plant species were chosen to support crop pollinators but not pest species on three farms. The secondary plant species were included to fill gaps in canopy and/or help suppress weeds, or provide an upper canopy layer.

to these pollinators over an extended period. Designs could also include plant species that support other beneficial insects but avoid those that may support crop pests (Howlett et al., 2013b).

## 5.2 Methods

### 5.2.1 Design and establishment of native semi-natural habitats

To identify plants deemed suitable for inclusion in designed plantings we gathered data from published research, grey literature (reports and unpublished data), and databases. These were reviewed in 2011–12 to synthesise knowledge on interactions between plant species (native and exotic plant species) and known arable insect pollinators, natural enemies and pest species within the study region. Our review assessed insects associated with native and exotic plant species (predominantly crop plant species, plus common shelterbelt (pine, macrocarpa) and hedgerow (gorse) plants). An insect herbivore was characterised by having at least one life stage that was known to feed on a plant species and could pass on to the next life stage or lay fertile eggs. Pests were defined as herbivorous insects capable of causing economic damage, requiring active intervention to maintain populations below damaging levels. For our verified pollinators and flower visiting insect natural enemies, an association with a plant species was established where at least one life stage of the insect was known to visit flowers on that plant species. In addition to investigating insect associations with native plants, we also included associations with a broad range of vegetable and arable crops grown in Canterbury, including our five focus crops; pak choi (*B. rapa* subsp. *chinensis* (L.) Hanelt), carrot (*D. carota* subsp. *sativus* (Hoffm.) Schübl. & G. Martens), radish (*Raphanus sativus* L.), white clover (*T. repens*) and onion (*A. cepa*). Additional crop species commonly grown on arable farms and included in the review of existing information were: turnip (*B. rapa* subsp. *rapa* L.); oilseed rape (*B. napus* L.); cabbage, broccoli, cauliflower (*B. oleracea* L.); potato (*Solanum tuberosum* L.); peas (*Pisum sativum* L.); beans (*Phaseolus vulgaris* L.); field pumpkin (*Cucurbita pepo* L.); squash (*C. moschata* Duchesne); lettuce (*Lactuca sativa* L.); cereals (including common wheat (*Triticum aestivum*); oats (*Avena sativa*); barley (*Hordeum vulgare* L.)); alfalfa seed (*Medicago sativa* L.); red clover seed (*Trifolium pratense* L.); grass seed (including *Lolium perenne* L. and *L. multiflorum* Lam.).

For native plant species, we limited the list to non-crop species known to grow in the study region, assuming that these species would have the best chance to establish. We also assessed literature, and included expert advice from landscape architects and ecologists, regarding the potential invasiveness

of each plant species and the need to incorporate additional plant species to ensure successful establishment of plantings, long term, in exposed farm environments (e.g., incorporation of plants that provide shade and shelter; Howlett et al., 2013b, Foundation for Arable Research, 2018).

Using the collated information, we selected perennial native plant species that were linked to the crops via pollinators and flower-visiting natural enemies for inclusion into the designed plantings on three farms (Fig. 4). We excluded plants that support pest species known to cause economic losses to the crops grown on these farms. Plants chosen had an estimated maturity height of 1–15 m, except *Podocarpus totara* G. Benn. ex D. Don which can grow to 30 m. We also chose native plants reported to peak in flowering prior to or following the peak flowering of crop species to minimise potential competition between crops and native plantings (Davidson and Howlett, 2010). The composition of the native plantings was designed to also ensure a closed canopy within 4–5 years after establishment to minimise/inhibit weed growth. The plants were grown from seed sourced from remnant native species in the region and to help the native seedlings (25–35 cm tall) establish, a slow release fertiliser (20 g) was added at the base of the plant at time of planting. The seedlings were protected by CombiGuards (4 × 35 cm tall bamboo stakes, 1 × 0.4 m<sup>2</sup> mulch mat, 1 × 30 cm high plastic sleeve). Weeds were controlled using herbicide (Granstar<sup>®</sup>: mixture of glyphosate and tribenuron-methyl) for the first 3 years following planting.

### 5.2.2 Surveys of targeted insect species

We limited our assessment to 21 previously verified pollinating species (or species groups where particular species were not easily distinguishable from each other during surveys) as listed in Table 2. Our assessments also included eight known flower visiting insect natural enemies (three were also



**Fig. 4** Designed planting on three arable farms, consisting of native species that were surveyed for flower-visitors in 2018.

**Table 2** Pollinating insects of five crops frequently grown by farmers on the Canterbury Plains, New Zealand. Larval-life stages are briefly described from the literature.

Insect		Crops verified pollinating						Adult peak activity period (months) <sup>a</sup>	Generations pa.	Larval Requirements	Global distribution (outside NZ)
Family; Genus	Species	Pak choi	Onion	Radish	Carrot	White clover					
Apidae; <i>Apis</i>											
1	<i>mellifera</i>	√ <sup>1</sup>	√ <sup>3,4</sup>	√ <sup>4</sup>	√ <sup>4</sup>	√ <sup>5</sup>	10	>2	Man-made hives (moveable) <sup>9</sup>	Cosmopolitan <sup>9</sup>	
<i>Bombus</i>											
2	<i>terrestris</i>	√ <sup>1</sup>	√ <sup>3,4</sup>	√ <sup>4</sup>	√ <sup>4</sup>	√ <sup>5</sup>	9 <sup>9</sup>	1 <sup>9</sup>	Cavities, undisturbed earth <sup>9</sup>	Eur, Afr, Asia, Aus, S. Am, Mex. <sup>28,32</sup>	
3	<i>hortorum/ ruderatus</i>					√ <sup>Φ5</sup>	4 <sup>9</sup>	1–3 <sup>9</sup>	Cavities, undisturbed earth <sup>9</sup>	<i>B. hort.</i> : Eur, Asia, <i>B. rud.</i> : Eur, Afr, S. Am <sup>29</sup> ,	
Halictidae; <i>Lasioglossum</i>											
4	<i>sordidum</i>	√ <sup>1</sup>	√ <sup>3,4</sup>		√ <sup>4</sup>		7 <sup>9</sup>	2 <sup>9</sup>	Undisturbed earth <sup>9</sup>	Endemic <sup>9</sup>	
Colletidae; <i>Leioproctus</i>											
5	<i>huakiwi/ imitatus/ monticola*</i>	√ <sup>1</sup>	√ <sup>3,4</sup>				4 <sup>9</sup>	1 <sup>9</sup>	Undisturbed earth <sup>9</sup>	Endemic <sup>9</sup>	
6	<i>fulvescens</i>	√ <sup>7</sup>	√ <sup>8</sup>				4 <sup>9</sup>	1 <sup>9</sup>	Undisturbed earth <sup>9</sup>	Endemic <sup>9</sup>	

7	<i>vestitus/pango</i>			$\sqrt[4]{\Phi^8}$	$4^9$	$1^9$	Undisturbed earth <sup>9</sup>	Endemic <sup>9</sup>	
Calliphoridae; <i>Calliphora</i>									
8	<i>vicina</i>		$\sqrt[4]{\phantom{x}}$		$\sqrt[4]{4,6}$	$9^{10}$	$\geq 1^{15}$	Meat/meat products <sup>18</sup>	Cosmopolitan <sup>18</sup>
9	<i>stygia</i>	$\sqrt[4]{\phantom{x}}$	$\sqrt[4]{3,4}$		$\sqrt[4]{\phantom{x}}$	$9^{10}$	$\geq 1^{15}$	Meat/meat products <sup>18</sup>	Aus <sup>18</sup>
<i>Lucilia</i>									
10	<i>sericata</i>		$\sqrt[4]{3,4}$			$9^{10}$	$\geq 1^{15}$	Meat/meat products <sup>18</sup>	Cosmopolitan <sup>30</sup>
Polleniidae; <i>Pollenia</i>									
11	<i>pseudorudis</i> *	$\sqrt[4]{\phantom{x}}$				$6^{10}$	?	Earthworm parasite <sup>18</sup>	Eur, N. Am. <sup>31</sup>
Sarcophagidae; <i>Oxysarcodexia</i>									
12	<i>varia</i>	$\sqrt[4]{\phantom{x}}$				$9^{10}$	$\geq 1^{15}$	Rotting vegetation, Dung <sup>19,20</sup>	S. Am., Aus, Pac <sup>33,34</sup>
Tachinidae; <i>Protohystricia</i>									
13	<i>alcis</i> *	$\sqrt[4]{\phantom{x}}$				$3^{11,12}$	?	Insect parasitoid <sup>21</sup>	Endemic <sup>23</sup>

Continued

**Table 2** Pollinating insects of five crops frequently grown by farmers on the Canterbury Plains, New Zealand. Larval-life stages are briefly described from the literature.—cont'd

Insect		Crops verified pollinating						Generations pa.	Larval Requirements	Global distribution (outside NZ)
Family; Genus	Species	Pak choi	Onion	Radish	Carrot	White clover	Adult peak activity period (months) <sup>a</sup>			
<i>Proscissio</i>										
14	sp.						3 <sup>11,12</sup>	?	Insect parasitoid <sup>22,23</sup>	Endemic <sup>23</sup>
Stratiomyidae; <i>Odontomyia</i>										
15	<i>cloris</i> *	√ <sup>2,4</sup>				√ <sup>4</sup>	3 <sup>11,12</sup>	?	Wetlands <sup>24</sup>	Endemic <sup>35</sup>
Syrphidae; <i>Eristalis</i>										
16	<i>tenax</i>	√ <sup>1</sup>	√ <sup>3,4</sup>	√ <sup>8</sup>	√ <sup>4</sup>		10 <sup>13</sup>	>2 <sup>16</sup>	Aquatic Decomposing organics <sup>25</sup>	Cosmopolitan <sup>36</sup>
<i>Helophilus</i>										
17	<i>hochstetteri</i>		√ <sup>4</sup>				6 <sup>13</sup>	?	Aquatic Decomposing organics?	Endemic <sup>37</sup>
18	<i>seelandicus</i>		√ <sup>4</sup>				11 <sup>13</sup>	?	Aquatic Decomposing organics?	Endemic <sup>37</sup>

<i>Melangyna</i>								
19	<i>novaezelandiae</i>	√ <sup>1</sup>	√ <sup>4</sup>	√ <sup>4</sup>	7 <sup>13</sup>	~2 <sup>17</sup>	Predator – soft bodied insects <sup>26</sup>	Endemic <sup>37</sup>
<i>Melanostoma</i>								
20	<i>fasciatum</i>	√ <sup>1</sup>	√ <sup>4</sup>	√ <sup>4</sup>	8 <sup>13</sup>	~2 <sup>17</sup>	Predator – soft bodied insects <sup>26</sup>	Endemic <sup>37</sup>
Bibionidae; <i>Dilophus</i>								
21	<i>nigrostigma</i>	√ <sup>1</sup>			3 <sup>14</sup>	?	Terrestrial, decaying vegetation <sup>27</sup>	Endemic <sup>38</sup>

<sup>a</sup>Number of months per year.

Superscript numbered references: 1. Rader et al. (2009); 2. Howlett et al. (2011); 3. Howlett et al. (2017); 4. Rader et al. (2016); 5. Howlett et al. (2019); 6. Howlett (2012); 7. Unpublished data set 1; 8. Unpublished data set 2; 9. Donovan (2007); 10. Howlett et al. (2016); 11. Howlett et al. (2009b); 12. Howlett et al. (2018); 13. Manaaki Whenua Landcare Research (n.d.); 14. Harrison (1990); 15. Cottam et al. (1998); 16. Dziock (2006); 17. Wratten et al. (1995); 18. Dear (1986); 19. Miller and Walker (1984); 20. Bishop (1998); 21. Eyles (1965); 22. Merton (1982); 23. Schnitzler (2016); 24. Winterbourn and Gregson (1981); 25. Rotheray (1993); 26. Early (1984); 27. Harrison (1990); 28. Rasmont et al. (2008); 29. Rasmont and Iserbyt (2014); 30. Williams et al. (2014); 31. Heath et al. (2004); 32. Acosta et al. (2016); 33. Meiklejohn et al. (2012); 34. Pape (1996); 35. Schmidlin et al. (2018); 36. Howlett and Gee (2019); 37. Thompson (2008); 38. Harrison (1990).

Ticks indicate verified pollinators of each crop; \* = verified species from flower-visiting collected specimens ( $n \geq 12$ ); superscript  $\phi$  categorises pollinators based on loose body pollen distribution. Regional abbreviations: Eur: Europe, Afr: Africa, Aus: Australia, S. Am: South America, N. Am: North America, Mex: Mexico, Pac: Pacific Islands. Insect numbers are used as references within insect-plant species networks (Figs. 7 and 9). Superscript numbers are references

**Table 3** Insect natural enemies and their insect prey/hosts found within arable crops on the Canterbury Plains, New Zealand that were observed visiting flowers during the survey described in [Section 5.2.2](#).

Insect		Predator/Parasitoid of:
Family; <i>Genus species</i>		
Syrphidae; <i>Melangyna</i>		
19	<i>novaezelandiae</i>	Larvae generalist predators of aphids and caterpillars <sup>1</sup>
<i>Melanostoma</i>		
20	<i>fasciatum</i>	Larvae generalist predators of aphids and caterpillars <sup>1</sup>
Tachinidae; <i>Protohystricia</i>		
13	<i>alcis</i> *	Parasitoid of Porina moth <i>Wiseana cervinata</i> (Walker, 1865) and others in genus <sup>2</sup>
<i>Pales</i>		
22	<i>usitata</i> *	Parasitoid of Porina moth <i>Wiseana cervinata</i> (Walker, 1865) and others in genus <sup>2</sup>
23	<i>marginata</i> *	Parasitoid of tortricid and psychid moths <sup>3</sup>
Coccinellidae; <i>Adalia</i>		
24	<i>bipunctata</i>	Adults, larvae predators of several aphid spp. <sup>1</sup>
<i>Coccinella</i>		
25	<i>undecimpunctata</i>	Adults, larvae predators of several aphid spp. <sup>1</sup>
Hemerobiidae; <i>Micromus</i>		
26	<i>tasmaniae</i>	Adults, larvae predators of several aphid spp. and mealy bugs (Pseudococcidae) <sup>1</sup>

Superscript numbered references: 1. [Early \(1984\)](#); 2. [Eyles \(1965\)](#); 3. [Frost et al. \(2016\)](#).

Insect numbers are used as references within insect–plant species networks ([Figs. 7 and 9](#)). Superscript numbers are references. \* = verified species from flower-visiting collected specimens ( $n \geq 12$ ).

pollinators) ([Table 3](#)) and four known flower visiting pest species ([Table 4](#)). In all but three plant–pollinator interactions, single visit stigmatic pollen deposition was used as the measure of pollination efficiency. The exceptions were for the interactions of three species with white clover. Here, *B. terrestris* has been verified a pollinator based on seed yields ([Cecen et al., 2007](#)). *Bombus hortorum/ruderatus* and *Leioproctus vestitus/pango* were also deemed pollinators based on the amount and distribution of loose white clover



**Table 4** Insect crop pest species and their impact within arable crops on the Canterbury Plains, New Zealand, that were observed visiting flowers during the survey described in [Section 5.2.2](#).

Insect	Plant pest of:
Family; <i>Genus species</i>	
Anthomyiidae; <i>Delia</i>	
27 <i>platura</i>	Larvae: seeds of many plants <sup>1</sup>
Syrphidae; <i>Eumerus</i>	
28 <i>funeralis</i> / <i>strigatus</i>	Larvae: a variety of bulbs and roots, minor pest <sup>2</sup>
Pentatomidae; <i>Glaucias</i>	
29 <i>amyoti</i>	Adults/nymphs feed on many native and exotic (e.g., crop) plants <sup>3</sup>
Pieridae; <i>Pieris</i>	
30 <i>rapae</i>	Larvae: phytophagous, particularly damaging Brassicaceae spp. <sup>1</sup>

Superscript numbered references: 1. [Butcher \(1984\)](#); 2. [Somerfield \(1984\)](#); 3. [Charles \(1998\)](#).

Insect numbers are used as references within insect-plant species networks ([Figs. 7 and 9](#)). Superscript numbers are references.

pollen on the bodies of collected individuals. These were found to be similar to honey bees and *B. terrestris* that had also been collected visiting white clover florets ([Howlett et al., 2019](#); authors unpublished data).

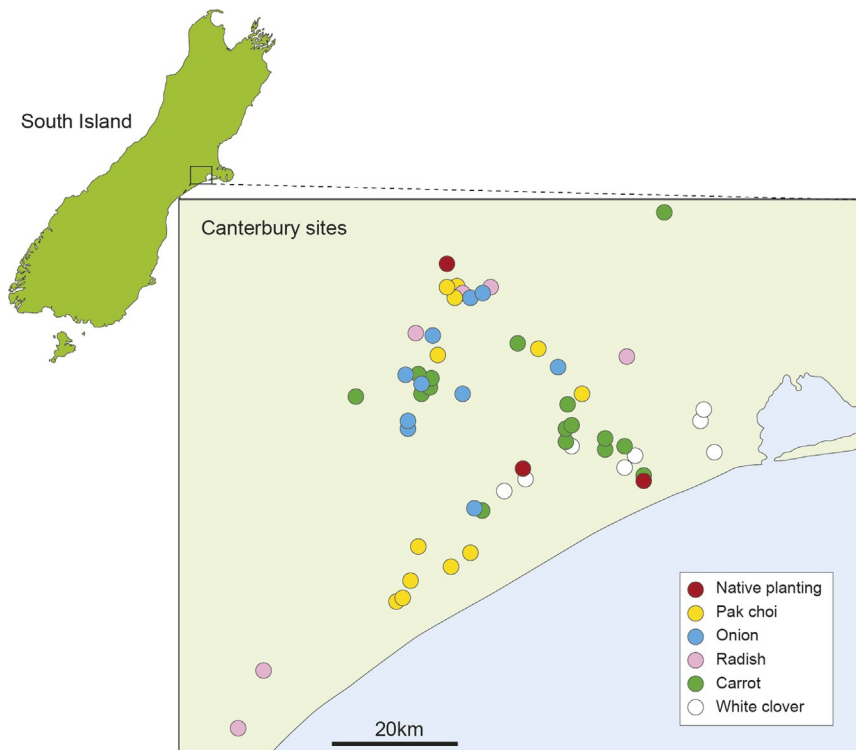
#### 5.2.2.1 Surveys of designed plantings

Five years following planting, pollinators and flower-visiting insect natural enemies and pests were surveyed on a subset of eight native plant species within the designed plantings across three farms ([Fig. 4](#)) ([Schmidlin, 2018](#); [Schmidlin et al., 2018](#)). This subset of plant species was chosen because they represented potential central and modular plant species (i.e., supported more specialist pollinators) and were in flower during the survey period. The plantings had been established in 2013 ([Fig. 4](#)). Full details of the survey method and the planting design are described in [Schmidlin et al. \(2018\)](#). Plant species observed were *Carmichaelia australis* R. Br., *Cordylina australis* (Forst. f.) Endl., *Discaria toumatou* Raoul, *Veronica salicifolia* G. Forst., *Kunzea serotina* de Lange et Toelken, *Leptospermum scoparium* J.R. Forst. et G. Forst. var. *scoparium*, *Ozothamnus leptophyllus* (G. Forst.) Breitw. et J.M. Ward, *Phormium tenax* J.R. Forst. et G. Forst. Where possible, six fully flowering plants of each

species were surveyed per farm/site from September 2017–February 2018 (Schmidlin, 2018). Surveyed plants were evenly spaced throughout the sites. Each site was surveyed weekly at a time between 9:00 and 15:00.

#### 5.2.2.2 Surveys of crops

So that we could construct unweighted and weighted binary networks to verify whether the native plants were supporting the desired diversity of beneficial crop pollinating and natural enemy insect species, we used observational survey data collected from 55 arable crop fields consisting of five different crop species (pak choi  $n = 13$  fields; onion  $n = 10$ ; carrot  $n = 18$ ; radish  $n = 6$  and white clover  $n = 18$ ) in Canterbury (Fig. 5). Survey data from these crops were collected over multiple years between 2004 and 2019 using standardised methods that were specific to each crop species. Details of methods used for onion and pak choi are described in Howlett



**Fig. 5** Locations of designed plantings and five mass-flowering vegetable seed crop species surveyed for insect flower visitors on the Canterbury Plains New Zealand 43.64° S; 172.10° E.

et al. (2009b), and for white clover, radish and carrot in Howlett et al. (2013a). In summary, pak choi, radish and white clover flower-visiting insects were observed across a single day at multiple points (radish, white clover = 3 points, B. pak choi = 5 points) within each fully flowering field using quadrats of known area. For onion and carrot, 150 fully flowering umbels (75 cytoplasmically male sterile and 75 male fertile) were observed across multiple points (carrot = 3, onion = 5) within each field. Observations per field were conducted within a single day at survey times 10:00, 12:00, 14:00 and 16:00. As these surveys were originally intended to focus on diurnal insect pollinators, we restricted observations to insects with body length > 3 mm. This was because smaller insects had not been found to be influential crop pollinators, despite having been previously recorded in high abundances within crop fields (Howlett et al., 2009a; Walker et al., 2009, 2011).

### **5.2.3 Analyses to verify support of key pollinators by designed plantings**

To explore whether the designed plantings supported insect species beneficial to crops (pollinators, natural enemies) but not pest species, we used bipartite networks as a tool to visualise flower visitors and assess their use of crop and native plants. The network figures presented utilise either presence/absence data (unweighted binary networks for both anticipated and actual interactions) or flower-visitor count data (weighted networks of actual interactions). In addition to network figures, we calculated relevant network metrics, including network connectivity ( $L$ , total number of interactions), connectance ( $C$ , number of observed interactions/no. of possible interactions) and node specialisation ( $d'$ ), to assess the use of native plants and crops by insect species in these systems. Using the 'species level' function in the bipartite package v. 3.5.2 (Dormann, 2011; Dormann et al., 2008), we calculated node specialisation ( $d'$ ) for lower nodes (plant species), with node specialisation ( $d'$ ) values ranging from 0 (highly generalised) to 1 (highly specialised) (Blüthgen et al., 2006). Thus, for our analysis, a plant species with low  $d'$  would mostly interact with insect taxa that are common across plant types, while plant species with high  $d'$  would mostly interact with insect taxa not found interacting with other plant types. The bipartite package in R was used to create all network figures and to calculate their corresponding metrics (Dormann et al., 2008).

To investigate patterns of insect community composition across crops and native plantings we also used distance-based redundancy analysis

(db-RDA) (Legendre and Anderson, 1999). The analysis included planting-type (crop or native), plant species, and flowering month as explanatory variables. Analyses were based on Bray-Curtis dissimilarity distances, which accounts for both species composition and total abundance and excludes joint absences (Anderson et al., 2011). We tested the significance of the model, each of the constrained axes and all terms by permutation. 95% confidence ellipses for planting-type were projected onto the resulting plot to illustrate the differences in insect community composition. The R packages ‘vegan’ v. 2.5-6 (Oksanen et al., 2018) and ‘ggplot2’ v. 3.3.0 (Wickham, 2016) were utilised in these analyses.

#### 5.2.4 Review of life-cycle requirements of surveyed insects

We conducted a systematic literature search to assess whether the native plantings might support the target insect life cycles, with particular focus on the immature life stages. We searched three databases, in the order of WoS (Web of Science), CAB (Commonwealth Agricultural Bureaux) and ProQuest. Our search strategy included the terms season\* or climat\* or larva\* or life cycle or life-cycle or habitat or habitats or distribution or climat\* or Food or feeds or Zealand or nz or ‘n.z.’) AND ((*Lasioglossum* and (*sordidum* or *cognatum*))) OR (*Leioproctus* and (*huakiwi* or *fulvescens* or *vestitus* or *monticola* or *pango*)) OR *Bombus* and (*terrestris* or *ruderatus* or *hortorum*)) OR (‘*Lucilia sericata*’ or (*Calliphora* and (*vicina* or *stygia*))) OR (‘*Pollenia pseudonidis*’ or ‘*Oxysarcodexia varia*’ or ‘*Delia platura*’ or *Proscissio* or *Pales* or *Protohystricia*) OR (‘*Dilophus nigro stigma*’ or ‘*Eristalis tenax*’ or ‘*Helophilus hochstetteri*’ or ‘*Helophilus seelandicus*’ or *Odontomyia* or ‘*Melangyna novaezelandiae*’ or ‘*Melanostoma fasciatum*’ or ‘*Pieris rapae*’ or ‘*Glaucias amyoti*’ or *Eumerus* or ‘*Adalia bipunctata*’ or ‘*Coccinella undecimpunctata*’ or ‘*Micromus tasmaniae*’). Reference lists were scanned and additional published and grey literature texts were selected, reviewed and relevant data tabulated.

## 5.3 Results

### 5.3.1 Insect-plant associations: Plants for inclusion in designed plantings

Our literature and database review of 103 native, 41 non-shelterbelt exotic and 3 exotic species (*P. radiata*, *C. macrocarpa*, *U. europaeus* used commonly by farmers as shelterbelts) found a total of 839 herbivorous insects associated with at least one of these plants of which 375 were associated with natives. Of the native plant species reviewed, just seven crop pest species were associated with them. Based on these findings, we avoided native plants

associated with major (economically damaging) pest insects. We selected a list of priority plant species (support multiple verified crop pollinating species) and secondary species (suppress weeds or fill canopy gaps) to be included in the designed plantings on three farms. Not all species were established on all farms as sites varied with respect to local climatic conditions, soil type and restrictions imposed by farming practices (e.g., exposure to irrigation). A total of 750 plants of 34 species (17 priority) were established on farm 1; 2009 plants, 33 species (16 priority) on farm 2 and 1500 plants, 30 species (14 priority) on farm 3. A minimum of 80% of the total number of plants established were priority species.

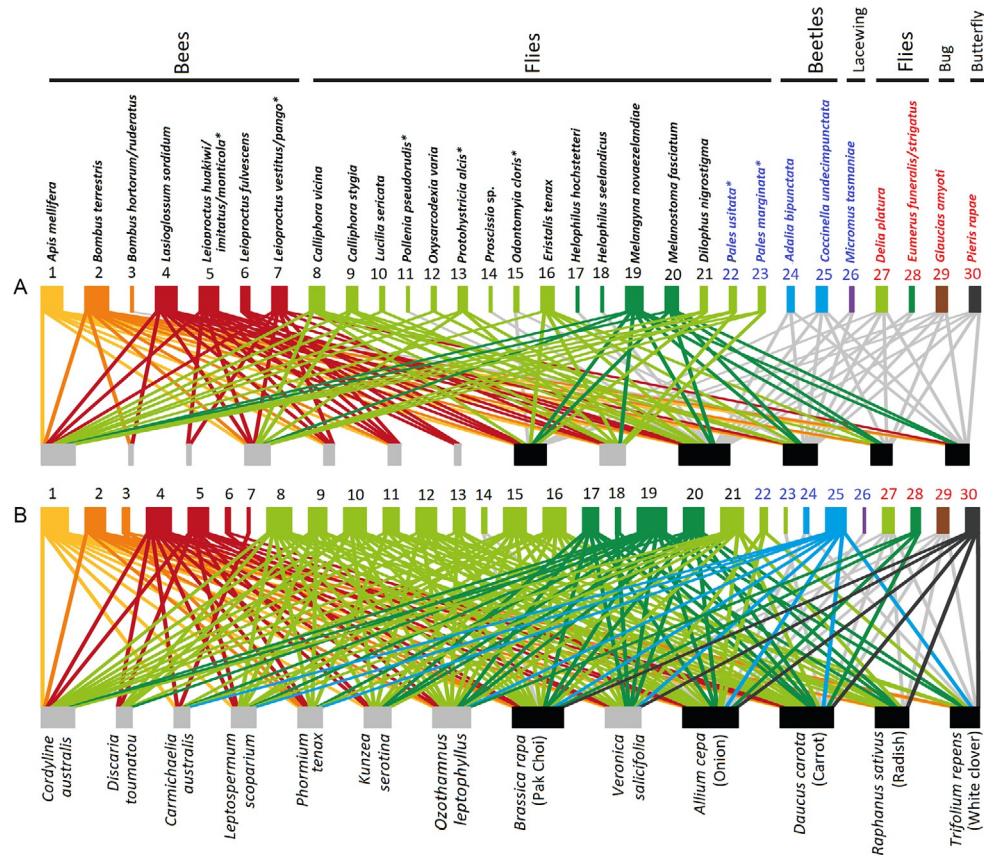
### 5.3.2 Insect flower visitors: Anticipated versus observed

#### 5.3.2.1 Anticipated flower visitor network

An unweighted binary network of anticipated interactions between the 30 flower-visiting insect species/species groupings (Tables 2–4), the eight native plant species (*Ca. australis*, *Co. australis*, *D. toumatou*, *V. salicifolia*, *K. serotina*, *L. scoparium*, *O. leptophyllus*, *P. tenax*) and five crop species (pak choi, onion, carrot, radish, white clover) was constructed based on the review of existing data (Fig. 6A).

The total number of predicted interactions (network connectivity,  $L$ ) was 147, and connectance ( $C$ ) (proportion of realised interactions) was 0.38. Overall, the anticipated network predicted that bees (all species combined) would interact with all plant species in the network whereas flies (all species combined) would link with just 61.5% of the 13 crop and 37.5% of the native plant species (Fig. 6A). When considered individually, all but six insect pollinator species in the network were expected to interact with at least one crop and one native plant species. The six species that were not anticipated to interact across both plant types were the bumble bees *B. hortorum/ruderatus* and the fly pollinators *Pollenia pseudorudis* Rognes, 1985\*, *Odontomyia doris* (Walker, 1854)\*, *Proscissio* sp., *Helophilus hochstetteri* Nowicki, 1875 and *H. seelandicus* Gmelin, 1790 (Fig. 6A). The three natural enemies (two coccinelid beetles and a lacewing) and five pest species were only anticipated to interact with crop plants.

The number of plant species visited (node size) per flower-visiting insect species varied greatly, with the most generalist flower-visitor bee species anticipated to be *Lasioglossum sordidum* (Smith, 1853) ( $n = 12$  plant species), *B. terrestris* ( $n = 11$  plant species) and *A. mellifera* ( $n = 10$  plant species) (Fig. 6A).



**Fig. 6** Unweighted binary networks showing flower–visitor interactions with eight native plants (grey) and five crops (black) based on (A) anticipated interactions determined from a review of existing data prior to establishment of native plantings, and (B) observation data recording flower–visitor interactions with eight native plants within the native plantings (5 years after establishment on three farms) and five crops (surveyed 2004–2019). Plant species are ordered in sequence of peak flowering from September (*Co. australis*) through to February (*T. repens*). Insect species (top) labelled with black font are crop pollinators, blue are insect natural enemies, and red are crop-pest species. Pale grey linkages show insects were found interacting with only crop plants or native plants, coloured linkages are for insects interacting with both. \*Species based on the identification of collected specimens ( $n \geq 12$  individuals collected across fields).

### 5.3.2.2 Observed flower visitors: Unweighted network

An unweighted binary network of the interactions observed from our survey data within the designed plantings and crops (i.e., 22,515 interactions between flower-visitors and crops, and 2871 interactions between flower-visitors and native plants) is shown in Fig. 6B. This verified all but 17 of the anticipated insect-plant interactions in the network predicted by the review of existing literature data (Fig. 6A).

These observational surveys revealed higher network connectivity than the anticipated network, ( $L = 194$ ;  $C = 0.50$ ). This was predominantly through an increase in observed non-bee linkages (anticipated network  $C = 0.26$ , observed network  $C = 0.47$ ), particularly to native plant species (anticipated  $C = 0.12$ , observed  $C = 0.36$ ) (Fig. 6).

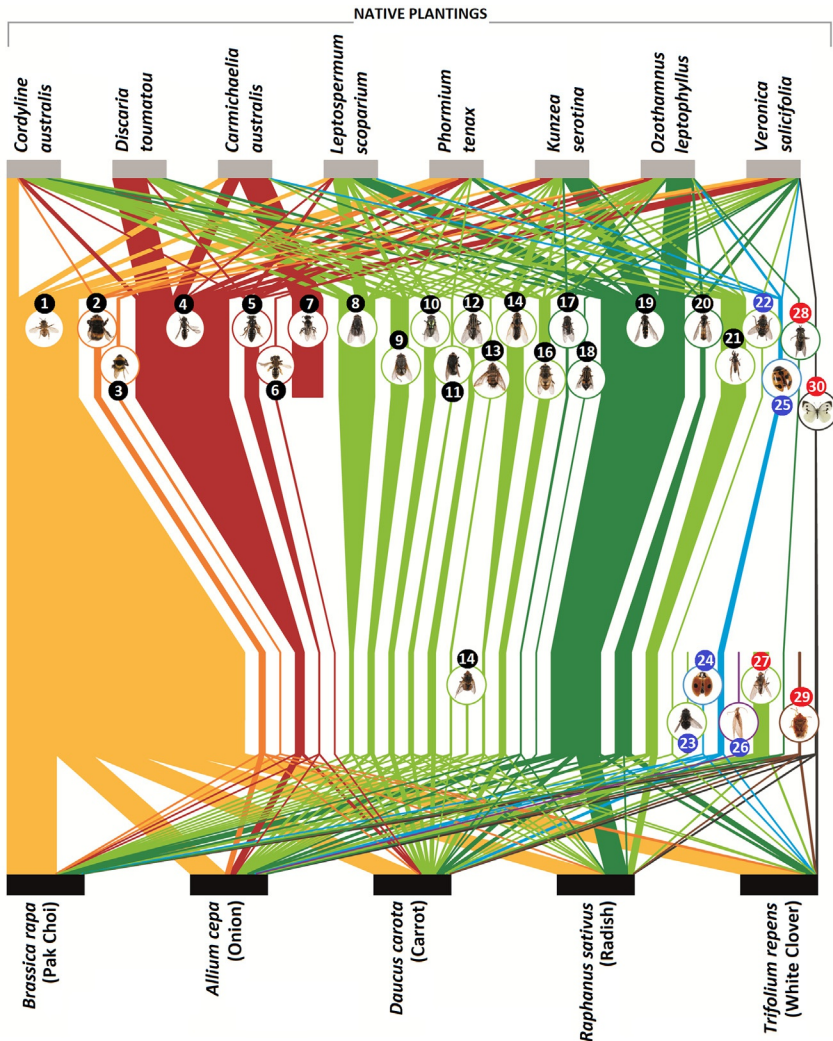
The increase in network connectance with the observed networks was also reflected in the increased node sizes of many of the flower visitors, indicating a higher number of plant species were visited than anticipated, particularly by fly pollinators (insects 8–21, Table 1, Fig. 6).

### 5.3.2.3 Observed flower-visitors: Weighted network

The weighted binary network constructed from the observational (abundance) data (Fig. 7) showed that the native ground-nesting bee, *La. sordidum*, was the most important wild pollinator with respect to flower visits, visiting all native plant species (dominating visits to *D. toumatou*) and visiting three crop plant species (pak choi, onion and carrot). Overall, native solitary ground-nesting bees (genera *Lasioglossum* and *Leioproctus*) represented a greater proportion of the wild pollinator assemblage (insect species 2–21 in Fig. 7) within the designed plantings compared to crops. *B. terrestris* was observed visiting a range of native species flowers, and this was the only wild bee species visiting all crop flowers (Fig. 7). Honey bees were the most abundant pollinator of crop species, but this is not surprising because in all surveys, managed hives had been placed within or adjacent to crop fields for pollination. Fly species that visited flowers of native plants represented a high proportion of flower-visiting insects to crops, dominating observed wild pollinator visits (Fig. 7). Along with the bee, *La. sordidum*, the highest number of interactions with plant species (i.e., widest flower-visitor nodes) within the weighted native plant network belonged to the native syrphid fly, *Melangyna novaezelandiae* (Macquart, 1855).

One anticipated interaction was between *Le. vestitus* Donovan (2007)/*pango* Donovan (2007) and white clover. This native bee grouping contains the only native bee species implicated in the pollination of this crop (Donovan, 2007; unpublished data) (Fig. 8). Although present on all three





**Fig. 7** Weighted and quantitative flower-visitor networks based on the number of observed flower–visitor interactions with eight native plants along the top (grey) and five crop species along the bottom. Insects 1–21 are crop pollinators; 19, 20, 22–26 are insect natural enemies; and 27–30 insect crop pests. The yellow node represents honey bees, orange nodes are bumble bees, red are native ground nesting bees, green are non-syrphid flies, dark green are syrphid flies, blue are coccinellid beetles, purple are lacewings, brown are homoptera (bug) and black are butterflies. Refer Fig. 5 for species identification.

farms with designed plantings, it was only observed to interact with a single native plant species, *Ca. australis* (Fig. 6B and 7).

Four of the seven insect natural enemies were observed on flowers of native plants, however the strength of the linkages were relatively weak (Fig. 7), providing little evidence that the plantings were effective in





**Fig. 8** The native species group, *Leiopactus vestitus/pango*, are the only native bees documented to forage on, and likely to pollinate, white clover. While it readily visited the native plant *Carmichaelia australis* (left), it was not observed visiting white clover fields in this case study.

promoting increased abundances of these insects on farms. An exception was the syrphid fly, *M. novaezelandiae* that strongly interacted with all native plants as an adult flower visitor, but whether this was reflected in greater abundance of their insectivorous larvae was not examined.

### 5.3.3 Central and specialised plant species

#### 5.3.3.1 Anticipated versus observed plant-insect flower-visitor networks

The unweighted binary network of anticipated interactions (Fig. 6A) showed some variability in node sizes for each native plant species (i.e., richness of insect species visiting their flowers), but most supported a majority of the verified crop-pollinators, thereby showing promise as central plant species. *Co. australis* (pollinator species = 16), *L. scoparium* (pollinator species = 12) and *V. salicifolia* (pollinator species = 12) supported the highest species richness of crop pollinators and can be considered particularly good matches to support crop pollinator communities (Fig. 6A).

The unweighted binary network constructed from the observational survey data (Fig. 6B) elucidated larger node sizes for all plant species (i.e., more insect species visited) than was anticipated (Fig. 6A). Of the native plants, *O. leptophyllus*, was visited by the most pollinator species ( $n = 17$ ), whereas it was anticipated that it would be visited by just three species. Seven pollinating species interacted with *Ca. australis*, the lowest connectivity of the native species assessed, however, the anticipated network predicted that just two species would interact with this plant. Although *Ca. australis* was included in the plantings as a peripheral species that could support the native bee white clover pollinator *Le. vestitus/pango*, the observed network found it linked to more species. Non-bee pollinators represented the majority of all observed insect flower-visiting species across all plants (Fig. 6B).

The weighted binary network constructed from the observational survey data further demonstrated that most of the native plant species supported a diversity of crop pollinators, less so flower-visiting natural enemies, and least

of all the flower-visiting pest insects (Fig. 7). For the pests, just two weak linkages were recorded, each a single visit between the syrphid fly *Eumerus funeralis*/*strigatus* and the plant *O. leptophyllus*, and between the lepidopteran *Pieris rapae* (L.) and *V. salicifolia*. This weighted network further highlighted the strength of the interaction between the peripheral plant, *Ca. australis*, and the bee group, *Le. vestitus*/*pango*, with the bee group representing 24.0%–65.6% of all insect visits to this plant across the three farms (Fig. 7).

### 5.3.3.2 Flower-visitor assemblages: Comparisons between native plantings and crops

Across the native plantings and crops, planting type (12%,  $F_{(1,127)} = 23.277$ ,  $P = 0.001$ ), flowering species (18%,  $F_{(11,127)} = 3.147$ ,  $P = 0.001$ ) and the month of flowering (2%,  $F_{(2,127)} = 1.867$ ,  $P = 0.002$ ) explained 32% of the variation in flower-visitor assemblage composition (db-RDA). In the resulting plot, we have focused on the relationship between planting types (Fig. 9A). The CAP1 axis accounts for 13% of the variation due to constrained variables ( $F_{(1,127)} = 24.281$ ,  $P = 0.001$ ) and polarises crop plants against native plants, with two species *A. mellifera* and the hover fly, *M. novaezelandiae*, being more associated with crop plants. With the removal of honey bees (a managed pollinator) from the ordination, the CAP1 axis still retains polarisation between planting types, though it is somewhat reduced (Fig. 9B). The results from this reduced db-RDA found that the constrained variables planting type (5%,  $F_{(1,126)} = 9.355$ ,  $P = 0.001$ ), flowering species (19%,  $F_{(11,126)} = 3.03$ ,  $P = 0.001$ ) and time of flowering (2%,  $F_{(2,126)} = 9.355$ ,  $P = 0.035$ ) explained 26% of the variation in flower-visitor assemblage composition (Fig. 9B).

### 5.3.4 Insects supported by each native plant species

When taken altogether, the eight native plant species were visited by all but one crop-pollinating species. However, for each individual plant species, interactions between pollinator (and other flower-visitor) nodes and the strength of these interactions varied greatly (Fig. 10). Plant species that supported the most crop-pollinating species, out of the total of 21 species, were *O. leptophyllus* with 15, *Co. australis* with 14 and *V. salicifolia* with 13 pollinating species. In contrast, *Ca. australis* had linkages to just six pollinating species. Of the 21 pollinating species, just two were observed visiting all plants; the ground-nesting bee *La. sordidum*, and the syrphid fly *M. novaezelandiae*. However, all but two pollinating species visited multiple plant species; *B. hortorum*/*ruderratus* was only observed visiting *P. tenax* and *Le. vestitus*/*pango* only visited *Ca. australis*.

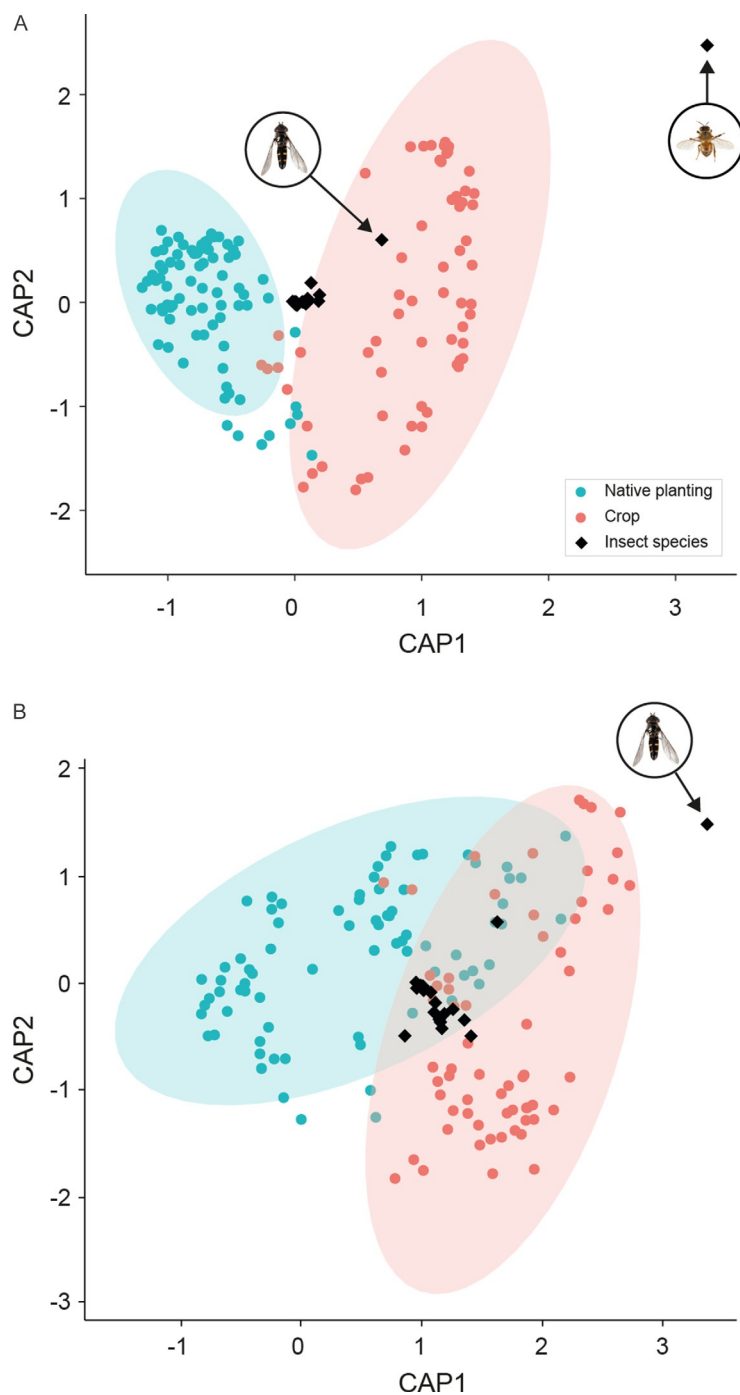


Fig. 9 See figure legend on next page.

In general, native plant species tended to be more uneven in their linkage strengths compared to crop species (i.e., flower visitation tended to be dominated by a smaller proportion of common species). Specialisation was highest for *Ca. australis* ( $d' = 0.59$ ), followed by *D. toumatou*, ( $d' = 0.38$ ). The remaining native plant species had  $d'$  values of 0.22–0.29, with *P. tenax* having a low value ( $d' = 0.12$ ) similar to crop species ( $d'$  values of 0.10–0.14). Hence,  $d'$  values for most of the native species still reflect generalised pollinator assemblages. Pollinators were widely shared whereas pest species were rarely shared between native plants and crops.

### 5.3.5 Food requirements of immature crop pollinating insects

Our systematic literature search on the life-histories of New Zealand bee and non-bee crop flower visitors found 2607, 4439 and 3083 references from Web of Science Core Collection (WoS); CAB Direct; and ProQuest respectively. We selected 204 CAB records and, after duplicates were removed, 39 WoS and 37 ProQuest records. From these, a further 69 published and grey literature records were identified following a scan of cited references. From a selection of these references we found, the food requirements of immatures of each flower-visiting species varied widely across the verified crop pollinators, flower visiting insect natural enemies and pest species (Tables 2–4).

For the crop pollinating species, it is unlikely that the native plants themselves could be directly attributed to supporting their immature life-stages. The larvae of all the bee species depend on adults providing sustenance (Donovan, 2007). Of the bees, *A. mellifera* requires human management with the potential for short-lived colonies establishing within plant cavities (not as yet observed in plantings). The *Bombus* species nest in varied habitats with preferences for pre-existing cavities (Donovan, 2007) and the native

**Fig. 9—Cont'd** Biplots of the db-RDA showing individual target insect species (each black diamond represents a species) and their relationship with crops (blue dots) or native plantings (pink dots). (A) Includes honey bees and wild insect species and (B) wild insect species only. Blue dots represent community composition of flower-visiting insects across native planting sites (eight native plant species assessed), each dot representing one survey day. Pink dots represent community composition of flower-visiting insect species to crops (five species) with each dot representing one survey day. Ellipses represent the 95% confidence interval around group centroids. The axes explain variation while being constrained to account for planting type differences. Variance explained by both axes were significant ( $P = 0.001$  in both cases). The most outlying black diamonds in A and B represent honey bees (pictured in A) and the hover fly *Melangyna novaezelandiae* (pictured in A and B).

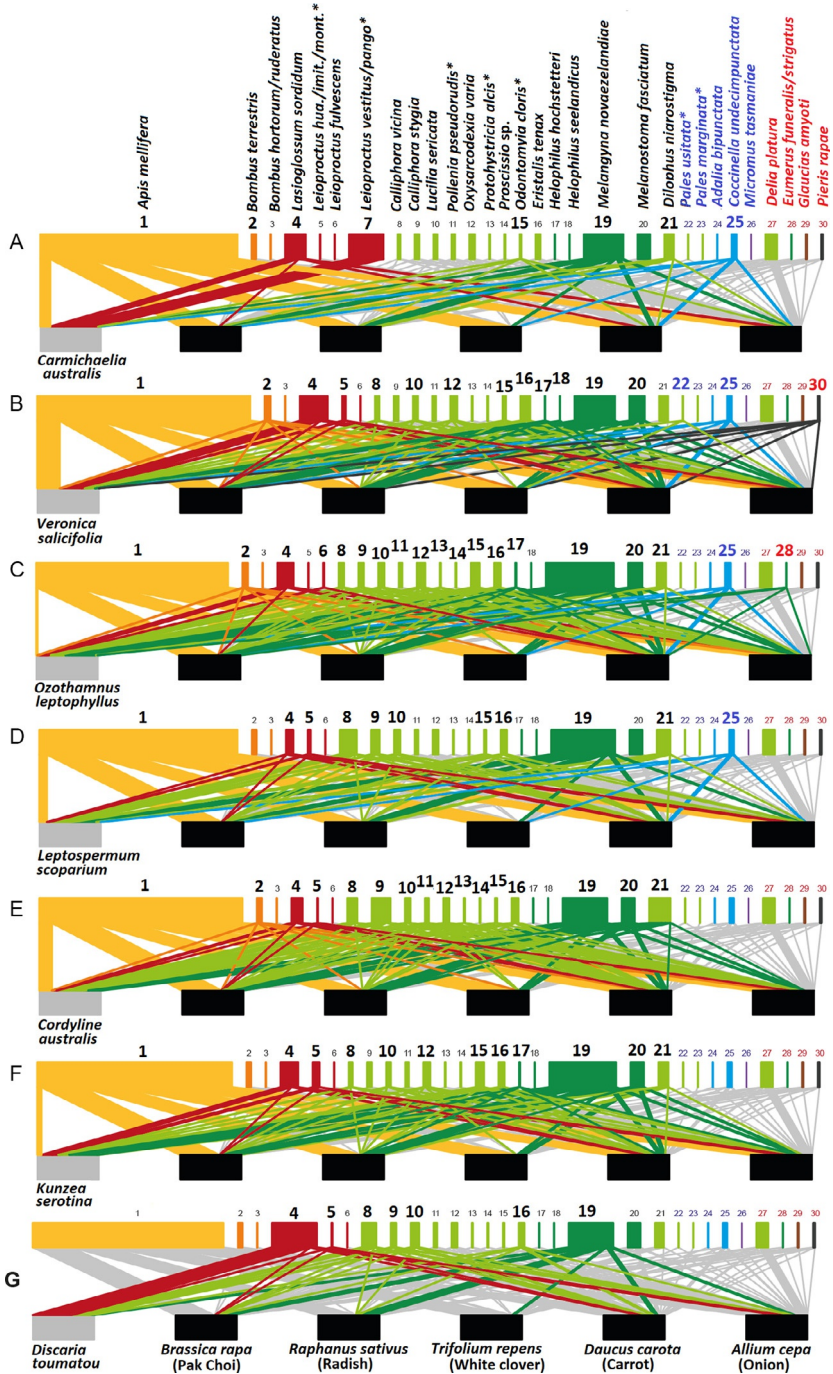


Fig. 10 See figure legend on next page.

solitary bees, *Leioproctus* and *Lasioglossum* species, require undisturbed earth for nest establishment (Table 1). Of the fly pollinators, the larvae of three calliphorid species typically consume vertebrate carcasses, two syrphids and two tachinids feed on other insects, a calliphorid on earthworms and a bibionid on decomposing vegetation (e.g., leaf litter) (Table 1). Of the insect natural enemies, all larvae were predators of other insects (Table 2). However, for the pests, nymphs of the native *Glaucias amyoti* feed on a wide range of plant species including native species such as *Cordyline australis* and *Veronica* spp. (Martin, 2010). It is considered a minor pest species of our study crops in Canterbury and to date has not required large scale applications of pesticides to control populations.

## 5.4 Discussion

We demonstrated that by understanding plant–insect interactions at the species level, it is possible to design and establish combinations of non-crop plant species focused specifically on desirable plant–insect interactions within an intensified agricultural system. With only a sub-set of our native plant species assessed, and observations restricted to flower–visiting insect interactions, we found anticipated plant–insect species interactions can reflect actual (observed) interactions. However, the designed plantings supported non-bee crop pollinators more than expected. We also found it is possible to support specialised pollinators through the inclusion of peripheral plant species in the network, but found no evidence that a single plant species acting as a central ‘hub’ could support all of the desired pollinators.

In the study system, farmers typically grow and rotate several broad acreage, annually mass-flowering insect pollinated crops (Millner and Roskrug, 2013). These can benefit from different suites of pollinators and beneficial insects for optimal yields (Donovan, 2007; Howlett, 2012; Howlett et al., 2009a,b, 2017; Rader et al., 2009). Here we have taken advantage of the knowledge generated over numerous studies that have quantified or

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**Fig. 10—Cont’d** Weighted (quantitative) flower-visitor networks based on the number of observed flower–visitor interactions with each of the eight native plant species and five crop plants. Insects 1–21 are crop pollinators; 19, 20, 22–26 are insect natural enemies and 27–30 insect crop pests. The yellow node represents honey bees, orange nodes are bumble bees, red are native ground nesting bees, green are non-syrphid flies, dark green are syrphid flies, blue are coccinellid beetles, purple are lacewings, brown are homoptera (bug) and black are butterflies. Coloured bars (not grey) indicate the insect visits the flowers of both the native plant species and crops. Refer to Fig. 5 for insect species identification.



described the functional role provided by wild pollinators of arable seed crops in the Canterbury region (Table 2) (Howlett, 2012; Howlett et al., 2017, 2019; Rader et al., 2009). Our study offers a path forward to a more targeted and efficient use of the limited semi-natural habitat on arable farms to support beneficial insect diversity capable of delivering yield benefits. Moreover, our use of eco-sourced plants sourced from remnant indigenous species that are also used in regional ecological restoration programmes, offers an opportunity to further enhance regional biodiversity.

#### 5.4.1 Current semi-natural vegetation

Existing shelterbelts on the Canterbury Plains are predominantly composed of wind-pollinated conifer species, particularly pine and macrocarpa (Price, 1993). Remnant gorse hedges are being removed due to the weed status of this species (Isern, 2007). Our review of existing data suggests pine trees have an association with one species of vegetable or arable crop pests (*Costelytra giveni* (formerly *zealandica*) (White)), while the only pollinators reported to be associated with any of the three plant species were *A. mellifera* and *B. terrestris*. In contrast, we demonstrated that our sub-set of eight native plant species supported all but one (an uncommon tachinid fly species) of our targeted bee and non-bee pollinators. The native plants species chosen for the plantings were associated with three minor aphid pest species (*Aphis gossypii* Glover, *Aulacorthum solani* (Kaltenbach), *Macrosiphum euphorbiae* (Thomas)), but otherwise had no reported associations with recognised, economically important vegetable and arable crop-pest species based on existing information. Our surveys did not find evidence that the native plantings supported an abundance flower visiting pest species 5 years following establishment on farms. Although, we acknowledge that these insects (i.e., flower visitors) are only a subset of potential pest species with foliar and sapsucking herbivores not surveyed. Consequently, potential pest-plant interactions need to be further validated by broadening functional group coverage in surveys and determining whether the non-crop plants are primary hosts for all life stages of pest species. We must also consider whether any of the approximately 375 herbivorous insects associated with the non-crop plants could become pests in the future through land use or climate change, or whether these semi-natural habitats could promote the establishment and spread of incursions of invasive species.

There is likely to be significant scope to select a mix of indigenous and introduced plant species that will both support on-farm beneficial insect biodiversity but also fulfil the traditional shelterbelt/hedgerow roles.

These include livestock and crop protection, reduced soil erosion and the provision of timber resources (Hawke et al., 1999; Horvath et al., 1997; Zhang et al., 2004).

### 5.4.2 Immature stages

The species composition of the plantings in this study (Table 2) was not based specifically on the requirements of the immature life stages of beneficial insects that vary widely between species (Table 1, and references therein). In most cases, larval life stage requirements are not directly met by the designed plantings themselves. In New Zealand, *Apis mellifera* are largely associated with managed beekeeping (Donovan, 2007). The young age of the plants in the designed plantings at the time of the surveys were unlikely to provide suitable cavities for feral honey bees to establish nests. Also, the presence of the parasitic mite, *Varroa destructor*, has greatly reduced the prevalence of feral colonies in New Zealand (Donovan, 2007; Iwasaki et al., 2015). *Bombus* species in New Zealand nest in a variety of uncultivated habitats (e.g., gardens, embankments) often within unoccupied cavities (Donovan, 2007). For solitary ground nesting bees, non-cropped habitat is considered to be favourable for nest sites (Cole et al., 2020). All three designed planting sites have likewise been found to provide suitable nesting habitat for native solitary ground nesting bees with mean  $\pm$  S. E nest densities of *La. sordidum* of  $14.0 \pm 1.1 \text{ m}^2$  and *Leioproctus* spp. of  $1.48 \pm 0.2 \text{ m}^2$  (Howlett, unpublished data).

For non-bee pollinators, the habitat of the designed plantings may potentially support *D. nigro stigma* larvae that feed within leaf litter (Harrison, 1990). All other non-bee pollinators had larvae that fed on vertebrate carcasses, invertebrates, decomposing material within aquatic environments, effluent, dung or rotting vegetation (refer to Table 1 for references). Therefore, to protect or enhance these crop pollinators requires an understanding of immature development sites, in addition to designed plantings that support the adult life stages.

### 5.4.3 Assessing pollinator diversity through network analyses

Observational surveys of flower–visitor interactions with non-crop plants 5 years following the establishment of designed plantings on the three arable farms revealed a much more diverse and generalised flower visitor network (reflected by the higher connectance value) than anticipated from the review of existing data (Fig. 6A and B). The surveys supported most of the anticipated bee–plant species interactions based on the review of existing data.



However, they also revealed a much larger, more complex web of connectance between non-bees (particularly flies) and non-crop plants. This added capacity to support a more diverse assemblage of pollinators provides an opportunity to extend pollinator complementarity and redundancy within these systems that could provide on-farm resilience of pollination services (Bohan et al., 2013; Menz et al., 2011). That is, a number of non-bee species that are efficient crop pollinators (Rader et al., 2009, 2016) vary widely in their activity depending on weather (Howlett et al., 2013a), and will readily visit crops when honey bee visitation could be limited by adverse weather or competition for pollination from other nearby flowering plants. Therefore, assuming the same insects provide the same functions across non-crop plants and crops together, we would anticipate that these combinations of plant species would support resilience of pollination services, thus alleviating the potential impact of limited pollinator/plant species loss.

#### **5.4.4 Node linkages—Assessing the plant–insect species interactions**

Our assessment of eight non-crop plant species (about a quarter of the plant species established within the designed plantings, Table 1) demonstrated these plants together supported all but one verified crop–pollinator species, four of eight natural enemy insect species, while just two flower visits observed were by pest species. However, the composition of flower visitors within the designed plantings was different to that observed within the crops, even when honey bees (managed within crop fields) were removed from the analysis.

The higher proportional representation of native solitary ground-nesting bees visiting non-crop plants compared to crops, as highlighted in the weighted network (Fig. 7), may reflect the presence of nests within the non-tilled earth at planting sites, a requirement for these bees to successfully rear offspring (Donovan, 2007). This is in contrast to the heavy tillage that occurs on cropland. We anticipate that with more designed plantings established around arable crops, an increase in native bees visiting crop flowers will occur as populations respond to more reliable floral resource availability and undisturbed earth for nesting. Stavert et al. (2018) found the visitation of several *Leioproctus* species to flowering pak choi was strongly negatively correlated with increasing agricultural land use versus semi-natural habitat. Therefore the creation of designed plantings should be expected to positively impact such species. However, given bees are central-place foragers, the spacing of such habitat is likely to impact their delivery of crop

pollination services, particularly for small ground nesting species that may rarely travel beyond 150m from their nest sites (Hofmann et al., 2020).

A number of the native plant species supported pollinator assemblages that can benefit the pollination of crops (e.g., *L. scoparium*, *O. leptophyllus*, *Co. australis*). These plant species provided high centrality, thus improving niche overlap with other species that can enhance pollination across plants (Emer et al., 2016; Martín González et al., 2010). In contrast, the flower-visitor assemblage of *Ca. australis* was most closely associated with white clover (both Fabaceae). This was despite not observing our targeted module of linkages between the solitary ground-nesting bee grouping *Le. vestitus/pango* with white clover and *Ca. australis* due to the absence of this insect in our crop surveys. Seed production of white clover underpins the sheep, beef and dairy industries in New Zealand as it is a key component of grazing pasture (Moot et al., 2009). If we see more *Ca. australis* (and other plants species that support this native bee group) established on farms that grow white clover for seed, we anticipate an increase in this group's abundance and contribution to white clover pollination.

Given that flower-visitor assemblages differed between the non-crop plant species themselves, it is not surprising that flower assemblages differed over time. Each native plant species typically experienced peak flowering for a discrete period of 2–3 weeks (Schmidlin, 2018). However, the selected priority plant species throughout the designed plantings (Table 1) were chosen together to provide floral resources to support flower visitors over an extended period (Davidson and Howlett, 2010; Howlett et al., 2013b). Consequently, only the plant species flowering at the time of the survey were observed for flower-visiting insects. The population dynamics of particular insect species can also vary substantially over time, both for wild bees (Donovan, 2007) and non-bees (Howlett et al., 2016) and will therefore contribute to an alteration in flower visitor assemblage compositions over time.



## 6. Conclusions and future directions

### 6.1 Verifying non-bee and bee crop pollinators to design on-farm plantings

For farmers of insect-pollinated crops wanting to diversify their crop pollinators, and thereby increase yield, we believe our approach towards designing and establishing non-crop plantings based on verified non-bee and bee crop pollinators is an important advancement because it uses the desired

insect-plant interactions to guide planting in support of ecosystem services. Protecting or establishing semi-natural habitats is recommended as part of ecological intensification, a concept, which for pollinators, consists of a set of strategies aimed at enhancing their on-farm diversity and provision of services (Bommarco et al., 2013; Garibaldi et al., 2019; Kovacs-Hostyanszki et al., 2017). However, there is opportunity for refinement by better utilising semi-natural habitat to target verified crop pollinating species and natural enemies (Bartual et al., 2019). Current guidelines for growers who desire to establish non-crop plantings are limited by the lack of understanding regarding the breadth of crop pollinating species, the reliability of their services to crop pollination, and practices that can unintentionally impact their abundances. This is particularly relevant to non-bee pollinators where knowledge of life stage requirements has been poorly described or communicated (Cook et al., 2020). In addition to bee species, we examined the requirements (adult non-crop plant interactions and immature requirements) of non-bee crop pollinating insect species. This has not been evident in similar studies that have largely focussed on bee species (Menz et al., 2011; Nichols et al., 2019; Russo et al., 2013; Williams and Lonsdorf, 2018). Non-bees can be efficient and important pollinators of a number of crops with some also being useful natural enemies of pest insects (Rader et al., 2016).

To guide the selection of non-crop plant species for on-farm establishments we focussed on insect species that are verified pollinators of multiple crops typically grown in rotation. This contrasts with studies that choose plant species primarily for ecological restoration from which associated increases in pollinator diversity may secondarily lead to crop pollination benefits (Menz et al., 2011; Nichols et al., 2019). An exception is the study by Williams and Lonsdorf (2018) who modelled known watermelon pollinating bee species to assess non-crop plant combinations that could provide pollination services to farmers of this crop, although these were not verified in on-farm tests.

Five years following establishment on farms, we found that the designed plantings supported the anticipated bee species. However, our underestimation of the diversity and dominance of fly pollinator-crop interactions was likely due to data records being focussed on bee-plant interactions. Rader et al. (2016) have highlighted that many studies globally have focussed on bee-plant interactions more so than non-bee-plant interactions. Such biases are also apparent regarding the design of on-farm habitat to support pollinators. Although studies have explored opportunities to design habitat to

support bee diversity, including species that pollinate crops (Menz et al., 2011; Nichols et al., 2019; Williams and Lonsdorf, 2018), we strongly recommend the inclusion of non-bees given their role as crop pollinators. Ignoring non-bee pollinators creates the risk that designed plantings may deliver sub-optimal crop pollination services and miss opportunities to optimise the value of often limited semi-natural areas on farms in support of ecosystem service delivery.

## 6.2 Support of targeted crop pollinating species

The plant species included in our designed plantings were largely considered central plant species that aimed to support the breadth of verified crop pollinating insects across crops. As suggested by other studies (Menz et al., 2011; Williams and Lonsdorf, 2018), we also selected plant species that would provide an extended and continuous source of floral resources to support the adult insects when they were most active. We chose plant species that were reported to not flower at the same time as the crops to minimise possible competition for insect pollinators. However, flowering can be influenced by unpredictable variables, such as ambient temperature, water and mineral availability, light quality and even neighbouring vegetation (Bernier and Périlleux, 2005). Thus, there is a possibility that some of our non-crop plants could flower at the same time as the flowering crops, but this was not examined.

Although most of the chosen non-crop plants supported diverse pollinating species, no single plant species supported all target insects highlighting the need for multiple plant species within such plantings. Our results show that peripheral plant species can support crop species that require more specialised insect pollination (i.e., *Ca. australis* (Fabaceae) supporting the white clover pollinator *Leioproctus vestitus/pango*) (Table 1).

The number of plant species required to support a targeted community of pollinators that provide adequate benefits including functional complementarity and redundancy (Bohan et al., 2013; Kaiser-Bunbury et al., 2017; Menz et al., 2011), is likely to vary substantially depending on crop type and pollinators available within a landscape. The flexibility to select combinations of plant species that will dovetail with other land use restrictions/requirements is likely to affect the scale and effectiveness of a planting and willingness of growers to adopt the approach. For example, farmers may require plantings that will not interfere with overhead irrigation systems (e.g., pivot irrigation) or movement of farm equipment, but that will provide

shelter for crops and livestock, or deliver other ecosystem benefits such as carbon sequestration, nutrient cycling, erosion control and protection of riparian environments.

Although the evidence suggest designed plantings can support adult stages of non-bee crop pollinators, our literature review found in many cases they are unlikely to directly support immature life stages. Awareness of all insect life stages, understanding how farming practices will affect their presence and survival, and tailoring land management to support the immature stages of beneficial species is necessary to ensure viability of populations providing ecosystem services. It is likely that a number of insect species that could be valuable generalist crop pollinators may have disappeared because landscape intensification has removed habitat required by immature life stages (as suggested for particular wild bee species; [Donovan et al., 2010](#)). Research is required to determine anthropogenic impacts across life-stages and the potential benefits of re-establishment through the provision of suitable habitat or other conditions.

### 6.3 Pests and insect natural enemies

The provision of habitat that supports natural enemies of crop pests is a common international goal, for reducing pesticide usage ([Petit et al., 2020](#)). As part of designing plantings to support crop pollinating insects, we need to understand the potential for such plantings to support problematic invertebrate and vertebrate crop pest species ([Pywell et al., 2005](#); [Sutter et al., 2018](#); [Tschumi et al., 2018](#)), the insect natural enemies of these pests ([Bartual et al., 2019](#); [Holland et al., 2020](#)), as well as avoiding the selection of invasive plant species. For instance, [Pywell et al. \(2005\)](#) found the brassica beetle pest, *Meligethes aeneus* Fab., was more abundant in mature hedges than mature field margins, although the impact of this pest reservoir on susceptible crops was not determined. In contrast, numbers of the winter-sown oilseed rape pests *Meligethes* spp. were found to be positively associated with bare ground, and negatively with increasing litter cover ([Sutter et al., 2018](#)). Consequently, numbers of overwintering individuals were found to be highest in oil-seed rape crops, followed by forest edge habitats, with the lowest numbers in forest interiors or flower strips ([Sutter et al., 2018](#)). The complexity of interactions between insects in semi-natural habitat and crops was also illustrated by [Tschumi et al. \(2018\)](#). They found that while semi-natural grassland adjacent to cereal crops increased wheat (*Triticum aestivum* L.) seed predation (a negative interaction), it decreased predation of beneficial earthworm prey,

*Dendrobaena* sp., (a positive interaction), but had no effect on predation of a weed seed (*Galeopsis tetrahit* L.) or pest larvae of the mealworm, *Tenebrio molitor* L. This result suggests that such semi-natural grassland habitat may not be optimal for improving pest control in that system.

It may also be challenging to reconcile the habitat requirements of different functional groups. For instance, [Bartual et al. \(2019\)](#) found predatory flies and parasitic wasps were found in highest abundance along woody habitat edges, whereas bee and honey bee numbers were greater in areal herbaceous semi-natural habitats compared to the interior of areal woody habitats. As seen in the presented case study, consideration of the known interactions between insects and plants and their trait preferences is an important first step in selecting plants for designed plantings. Selection of plants associated with beneficial insects, while excluding plants associated with pest species, increases the likelihood these plantings will provide benefits to the adjacent crops. We anticipate that future monitoring of our designed plantings over time will demonstrate we have minimised the risk of negative impacts, and maximised positive associations such as with insect natural enemies.

## 6.4 Future opportunities

We view our approach of designed non-crop plantings will have broad application across agroecosystems containing crops reliant on insect pollination. A number of the verified pollinators we included in our study are either widespread globally ([Table 1](#)) or have life history traits that are supported by, or less impacted by, agriculturally intensified landscapes ([Jauker et al., 2013](#); [Rader et al., 2020](#); [Stavert et al., 2018](#)). For example, species with adult life stages that are generalist in their utilisation of available floral resources and/or whose immatures feed on readily available substrates found on farms are likely to be supported by these plantings independent of crop or location ([Forrest et al., 2015](#); [Kremen et al., 2018](#); [Rader et al., 2020](#)). A possible limitation for broader scale application of designed plantings at this point is the lack of data verifying which insects are pollinators and the breadth of their contribution to the pollination of a broad range of crops, particularly non-bee species ([Cook et al., 2020](#); [Rader et al., 2020](#)). It is also probable that information on the suitability of a range of candidate non-crop plant species to support beneficial insects is lacking, requiring further field studies. Collection of these data is important to develop matrices of plant–pollinator interactions that can be used to guide planting designs of anticipated interactions.

It is also important to consider the potential role of other insects that may be visiting crop flowers that were not assessed here or in other studies. These include nocturnal pollinators (Hahn and Bruhl, 2016; Macgregor and Scott-Brown, 2020) and small, difficult to observe, insect flower visitors (Walker et al., 2011); although some crops are pollinated by these groups, little is known of their potential contribution to the pollination of most crops (Rader et al., 2020). Previous studies of two crop species, onion and pak choi, did not find small (<3 mm body length) flower visiting insects to be important contributors to crop pollination, despite being abundant within crops (Howlett et al., 2009a,b; Walker et al., 2009, 2011), but this may differ for other crops.

Although we have demonstrated that designed plantings can support targeted crop pollinators, we have not yet assessed whether this translates to crop yield benefits. Other studies assessing whether floral strips enhanced crop yields have found inconsistent results with some showing positive yield benefits (e.g., Blaauw and Isaacs, 2014; Ganser et al., 2018) that were not reported by others (e.g., Campbell et al., 2017; Nicholson et al., 2020). A large number of factors may also influence how effective designed plantings are for yield gains, including pollinator movements into surrounding landscapes, the distance that insects are willing, or able, to move (Greenleaf et al., 2007; Rader et al., 2011), and the amount of land available for such establishments. A study by Morandin and Winston (2006) estimated that, for canola, maximum yield and profit would be obtained if 30% of land was left uncultivated within 750 m of field edges. However, such measure may not be palatable to growers who aim to maximise profits per hectare. We believe there is significant scope to deliver improved pollination services (and other ecosystem services) using existing semi natural habitat that is designed specifically with the right non-crop plants to support the desired services.

The plants established in our designed plantings were all native species, capable of surviving for many years (most being woody, perennial species). The cost of establishing plantings is relatively expensive, at €6400/1000 plants, with further maintenance costs over two further seasons costing €1300 (Foundation for Arable Research, 2018). However beyond that time, no extra costs are anticipated. In contrast, floral strips can require frequent maintenance (i.e., re-sowing), although they have the benefit of more flexibility in the location, size and configuration within the landscape. Our expectation is that the targeted pollinating insect species will persist in the landscape in association with plantings, but monitoring over time is required to verify this. At native plant restoration sites, plant–pollinator interactions have been found to be dynamic with persistent pollinators re-organising their plant interactions over time (Ponisio et al., 2017). Whether this also

occurs in designed plantings and has flow on effects regarding non-crop and crop–pollinator interactions will be important to study as it may impact the reliability of these insects as crop pollinators.

We also believe our approach can help to develop a more nuanced understanding of the pollinator services that can be delivered to crops through on-farm native plant rehabilitation and restoration projects. In doing so it may limit potential conflicts between different community groups driven by opposing wellbeing values on land use decisions regarding agricultural production or biodiversity conservation (([Henle et al., 2008](#); [Young et al., 2005](#); [Skrimizea et al., 2020](#)). By knowing the benefits that specific native plant species (alone and in combination) can provide to crop production, farmers may be more willing to establish native habitat (either as designed plantings or ecological restoration). This could allow opportunity to bring together multiple actors (e.g., farmers, councils, indigenous people, scientists, local communities) to cohesively deliver broad scale regional land use change that better balances community wellbeing ([chapter “Scales matter: Maximising the effectiveness of interventions for pollinators and pollination”](#) by Faichnie et al.), land-sharing—sparing opportunities ([chapter “Combining land-sparing and land-sharing in European landscapes”](#) by Grass et al.) that also enhances regional biodiversity ([Kleijn et al., 2020](#)).

We have found that when non-scientists (farmers, industry representatives, and community trust volunteers) have been shown the ecological networks, as presented in our case study, they have immediately understood the value of our designed native plantings. In New Zealand, key industry bodies that oversee crops that require insect pollination (Zespri (kiwifruit), New Zealand Avocados, Foundation for Arable Research (seed crops)) have been pro-active in supporting further research and promoting our approach to their growers. We have found the presentation of network figures provide a tangible measure of the plant-animal interactions that can make a difference to a farmer’s choice to set aside land for non-crop plantings. It may be an approach that could assist in incentivising more crop growers who may not be motivated by the current strategies presented within the ecological intensification framework ([Kleijn et al., 2019](#)).

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