RESEARCH ARTICLE

Different landscape features within a simplified agroecosystem support diverse pollinators and their service to crop plants

Thijs P. M. Fijen · **Samantha F. J. Read** ·
Melanie K. Walker · **Megan Gee** ·
Warrick R. Nelson · **Brad G. Howlett**

Abstract

Context Landscape simplification is a main driver of insect decline, threatening crop pollination services. Changes in functional features in simplified agroecosystems may impact the abundance of wild pollinators.

Objectives Here, we studied whether different pollinator groups based on life-history are differentially associated to landscape features, and how this affects crop pollination service delivery.

Methods Using window traps in a highly simplified agroecosystem, we surveyed pollinator abundances and diversity associated with: (1) bare fence-lines separating pastures (control), (2) conifer hedgerows (3) farm gardens of diverse exotic plant species (4) effluent-ponds, (5) newly established native-plantings, (6) gorse (*Ulex europaeus*) hedgerows and (7) open water channels across six to twelve dairy farms. We also measured pollination service delivery to potted pak choi (*Brassica rapa*) plots near features 1–5 on six farms.

Results Pollinators at gardens, native-plantings, and effluent-ponds delivered significantly more pollination service than at bare fence-lines, with flies being more effective pollinators than bees at all features assessed. Taxa delivering the service also differed across features. The native bee *Lasioglossum sordidum* delivered more pollination at garden and native-planting features than at other features, drone flies (*Eristalis tenax*) contributed the majority of pollination service at effluent-ponds and bare fence-lines, while calliphorid flies contributed most pollination at conifer hedgerows.

Conclusions Conversion of functional features to bare fence-lines negatively affects on-farm pollinator diversity and its service to crop plants. However, farmers can benefit from enhancing features containing diverse plant species that support non-bee and bee species proven to deliver measurable crop pollination services.

Thijs P. M. Fijen and Brad G. Howlett contribute to joint lead authorship.

T. P. M. Fijen (✉)
Plant Ecology and Nature Conservation Group,
Wageningen University, Droevendaalsesteeg 3a,
6708 PB Wageningen, The Netherlands
e-mail: thijs.fijen@wur.nl

S. F. J. Read · M. K. Walker · M. Gee · W. R. Nelson ·
B. G. Howlett (✉)
Christchurch Mail Centre, New Zealand Institute
for Plant and Food Research Limited, Private Bag 4704,
Christchurch 8140, New Zealand
e-mail: brad.howlett@plantandfood.co.nz

Introduction

Landscape simplification is a main driver of pollinator species declines (Potts et al. 2010). Three-quarters of globally important crops are at least partly dependent on pollinators for yield (Klein et al. 2007), yet agricultural specialization (e.g. large scale monocultural fields) and intensification (e.g. high artificial input levels) have resulted in simplified landscapes with low pollinator diversity (Garibaldi et al. 2016) and reduced pollination services (Dainese et al. 2019). At the same time, the market for insect-dependent crops is growing (Aizen et al. 2008), particularly because insect-dependent crops contribute to a healthy diet (Eilers et al. 2011). Therefore, to ensure agroecosystem pollination service resilience, growers are encouraged to protect or boost the abundance and diversity of wild pollinating species (Garibaldi et al. 2011; Minarro and Garcia 2018) such as through restoring natural landscape features (Dainese et al. 2019).

Non-productive landscape features (hereafter landscape features) in intensive, simplified agricultural landscapes are usually highly functional for farmers, but prone to change if their functionality is no longer deemed important. For example, shelterbelts protect crops and livestock from inclement weather (Gregory 1995; Marshall and Moonen 2002), effluent storage ponds contain livestock waste, irrigation channels supply water, and homestead gardens provide aesthetic value (Aguilar-Støen et al. 2008). The presence of these features can change markedly over time because of economic and environmental pressures. For example, in the agriculturally intensified Canterbury Plains region of New Zealand, the adoption of large pivot irrigation systems has resulted in removal of exotic shelterbelts because they otherwise block the pivot system (Tait and Cullen 2006). Furthermore, exotic gorse used as a hedgerow is an invasive weed and its removal is actively encouraged (Broadfield and McHenry 2019). Lastly, open water channels (particularly for border dyke irrigation) have been closed to reduce the negative effects of nutrient run-off, and to improve water use efficiency (ECan 2017). If these features influence wild pollinator abundances, then their removal by farmers may have unforeseen impacts on pollination services.

We have limited knowledge on how different pollinators associate with different features in agricultural landscapes, and such associations may differ between species based on their life-stage requirements (Table 1; Rader et al. 2020). Bee abundance and diversity generally benefit from semi-natural habitat containing an abundance and diversity of flowers, but some species may depend more on early-flowering hedgerows (Wood et al. 2018). For non-bee insect pollinators, the larval requirements are very diverse. In most cases these can be categorized into distinct ecological groups (eco-groups) depending on their larval stage, for example, detritus feeders (e.g. cattle feces or dead organic material) or carnivores (e.g. aphid predators). In contrast, adults commonly visit crop flowers to consume pollen or nectar (Rader et al. 2016). Landscape features beneficial to bees may not be for flies or other pollinators (Schirmel et al. 2018; Cole et al. 2020). To improve pollinator diversity and abundances in agricultural landscapes, it is therefore necessary to establish how they differ in their association with these landscape features.

Even less clear is whether wild pollinators associated with such features provide crop pollination services (but see Castle et al. 2019). Pollinator species are not equally effective in pollinating different crops (Rader et al. 2009; Howlett 2012). While some hover flies can deposit equal amounts of pollen as managed honey bees (i.e. equal efficiency), the sheer abundance of honey bees can make them more effective (Rader et al. 2009). However, relying only on honey bees for crop pollination is risky, as they are not always effective (Garibaldi et al. 2013; Fijen et al. 2018), predictable (Gaffney et al. 2019), or active (Howlett et al. 2013; Rader et al. 2013). In contrast, supporting a diversity of wild pollinators can ensure the presence of more efficient crop pollinators (Fijen et al. 2018). Particular landscape features may be preferred by the most effective pollinator species, thereby supporting the highest crop pollination service contribution. However, note that the sum of less efficient pollinator species associated with a different landscape feature could approach or exceed the service of a single efficient species (Stavert et al. 2018). Knowing the potential pollination service associated with different landscape features can therefore aid in assessing the multi-functionality of these features for farmers.

In this study, we assessed how different commonly occurring on-farm landscape features in an intensified agricultural landscape influenced wild pollinator

Table 1 Flower visitors including pak choi (*Brassica rapa* subsp. *chinensis*) pollinators in the Canterbury Plains region of New Zealand and their known landscape associations

Family	Insect species	Verified crop pollinator	Association with landscape	Eco-group
Apidae	*Apis mellifera*	Yes	Managed hives, feral populations succumb to *Varroa destructor* mite	Social bee
	Bombus terrestris	Yes	Mainly in urban areas, less so in native vegetation, ground cavity nesting	Social bee
	Bombus hortorum	No	Common in improved pasture, road verges, shingle river margins and non-native scrub	Social bee
	Bombus ruderatus	No	Common near road verges, shingle river margins, in improved pasture and non-native scrub. Ground, cavity nesting	Social bee
Halictidae	*Lasioglossum sordidum*	Yes	Nests in undisturbed soil in native, urban, agricultural habitats	Ground-nesting bee
Colletidae	*Leioproctus huakiwi/imitatus*	Yes	Generalist flower visitors of native and exotic plants, nests in undisturbed soil in native, urban, agricultural habitats	Ground-nesting bee
Calliphoridae	*Calliphora vicina*	Yes	Common in urban habitats, around woody vegetation, larvae in meat/meat products, also in dung	Carrion-feeding
	Calliphora stygia	Yes	Common in woody vegetation, across many habitats e.g. coastal sand dunes, native habitat and open fields, larvae in meat/meat products	Carrion-feeding
	Calliphora quadrimaculata	No	Larvae in meat/meat products, also in dog faeces, decaying snow tussock	Carrion-feeding
	Lucilia sericata	No	Common in urban habitats and around hedgerows, larvae in meat/meat products, also in dung	Carrion-feeding
Muscidae	*Hydrotaea rostrata*	No	Larvae in meat/meat products, also in biosolids	Carrion-feeding
Polleniidae	*Pollenia pseudorudis*	Yes	Larvae in earthworms, adults cluster around buildings for hibernation	Earthworm-feeding
Sarcophagidae	*Oxysarcodexia varia*	No	Adults common in open pasture. Maggots also in rotting vegetation, dog faeces	Manure-feeding
Anthomyiidae	*Anthomyia punctipennis*	No	Larvae in decaying vegetables, fungi, dung, sometimes carrion	Plant-feeding
	Delia platura	No	Larvae in stems and seeds of various crops	Plant-feeding
Stratiomyidae	*Odontomyia* spp.	Yes	Common near and in shallow water of ponds or swamps	Wetland predator
Tachinidae	*Protohystricia alcis*	Yes	Moth (Porina) parasitoid	Moth predator
Syrphidae	*Eristalis tenax*	Yes	Larvae in stagnant water. Common in agroecosystems, particularly dairy farms	Wet-detritus feeding
	Helophilus hochstetteri	Yes	Larvae are 'rat-tailed maggots', like *E. tenax*	Wet-detritus feeding
	Melangyna novaezelandiae	Yes	Larvae feed on aphids and Lepidopteran larvae	Aphid-feeding
	Melanostoma fasciatum	Yes	Consume aphids and Lepidopteran larvae, common in grassland, vegetable, cereal and field crops, gardens, low growing vegetation	Aphid-feeding
	Eumerus funeralis	No	Larvae in bulbs/roots	Plant-feeding
Bibionidae	*Dilophus nigrostigma*[1,C]	Yes	Larvae found to be highly aggregated in grassland and under leaf litter	Dry-detritus feeding

Based on these we have categorised insects into twelve eco-groups. Further details on the association with the landscape, including references, are provided in Table S1

Adapted from (Howlett et al. 2021)

abundance and their service delivery to *Brassica rapa* subsp. *chinensis* (pak choi) plants, commonly grown for vegetable-seed production in the study region (Canterbury Plains, New Zealand). We conducted studies across twelve farms to examine whether different features support similar or different pollinators or groups of pollinators (eco-groups based on life-history), and to evaluate estimated pollen delivery by insects associated with these features. We discuss whether landscape features are sites supporting wild pollinator diversity and the implications for on-farm management strategies that maintain or enhance pollinator services to crop plants.

Methods

Study area

The Canterbury Plains, New Zealand (43.636°S, 172.100°E), is an intensive agricultural area covering 750,000 ha, characterized by a mosaic of livestock (mainly dairy, sheep) and cropping farms. Land devoted to dairy farming has expanded by 238% since 2002, to reach approximately 250,000 ha in 2019 (New Zealand Dairy Statistics 2002–03 & 2019–20), in conjunction with irrigated land (507,000 ha in 2015, a 177% increase since 2002; Brown 2016). Large-scale fixed-pivot and spray systems now irrigate 50% of all irrigated land while border-dyke irrigation coverage has reduced by 48% between 2010 and 2015 to 28,000 ha (Brown 2016). We used intensive dairy farms as our experimental sites because they are rather uniform in landscape composition (i.e. all highly simplified with < 5% semi-natural habitat cover) and do not contain mass-flowering crops that may temporarily change insect abundance (Stanley and Stout 2014), especially honey bees brought in for pollination.

We selected six dairy farms representative for the Canterbury plains, based on farm design and annually collected dairy farm statistics (DairyNZ 2018), in the austral summers of 2007–2008 and, to increase sample size, 2018–2019 (totaling n = 12 farms). These ranged from 319.5 to 540.5 ha in area, and were separated by at least four kilometers to make sure pollinator communities were independent between farms (Fig. S1). The farms follow a daily rotational grazing system, with our chosen sites consisting of pasture

swards dominated by rye grass (*Lolium perenne* L.) and white clover (*Trifolium repens* L.) with separate fields bordered with different features. For this study, we focused in both years on bare fence-lines (as a control), effluent-ponds, gardens (containing mostly non-native plant species such as rose, fuchsia, oak, rhododendron, magnolia, camellia) and tall, exotic conifer hedgerows of either Monterey pine (*Pinus radiata* D. Don) or Monterey cypress (*Hesperocyparis macrocarpa* (Hartw.) Bartel). In 2007, we additionally included 1–1.5 m tall, exotic gorse (*Ulex europaeus* L.) hedgerows and water channels (1–2 m deep with flowing water), while in 2018 we included six month old multispecies native hedgerows. All farms contained all the landscape features, and each unique feature per farm was represented by a single sample location.

Insect abundance—window trapping

To test how different agricultural landscape features were related to insect abundances, we used window trapping (Howlett et al. 2009). Traps were placed in yellow trays, to increase their general attractiveness for many species of insect pollinators within the families Apoidea (Leong and Thorp 1999) and Diptera (Proctor et al. 1996). Window traps have been shown to correlate well with observed abundances of bee and non-bee crop flower visitors (Howlett et al. 2009). Traps were located within five meters of each landscape feature on each farm (to sample association to that landscape feature), and at least 500 m apart from other features (to avoid attraction from different landscape features). Traps were left out for 18 days in November–December 2007, 20 days in November 2018 and seven days in January 2019. These sampling periods match the flowering period of pak choi seed production crops, and other insect-dependent crops in New Zealand (Howlett et al. 2021), and insect communities in this agricultural system vary little over the season (Howlett et al. 2021), limiting a potential temporal bias. Traps were emptied and refilled weekly and insects collected, stored and identified to the lowest taxonomic level possible.

Pollination service delivery

To see how the different features affect pollinator service delivery, we used potted pak choi, *Brassica*

rapa subsp. *chinensis* (L.) Hanelt) (Brassicaceae) as our focal plants in 2018–2019 only. Pak choi is grown in this region for commercial seed production and attracts a diversity of insect pollinators (Howlett et al. 2009). For the cultivar used, the efficiency (rate of stigmatic pollen delivery) of a variety of bee and non-bee pollinators has been quantified (Rader et al. 2009; Howlett et al. 2011) and used in other studies (Stavert et al. 2016). Insect pollinators increase seed set of *Brassica rapa*, and is usually pollination limited (Rader et al. 2013). Moreover, the pollinators of this crop often pollinate other mass flowering seed crops (*Brassica* spp., onion, carrot, white clover, radish) grown in the region (Howlett et al. 2021).

We raised pak choi plants on the experimental fields of the New Zealand Institute for Plant and Food Research Limited (PFR), Lincoln, Canterbury (decimal degrees: − 43.640, 172.4862). Within one week of flowering onset, plants were excavated and individually potted into 2L pots prior to observational surveys on six farms in 2018. To ensure the selection of evenly vigorous plants for experiments (i.e. development of inflorescences and foliage) newly potted plants were placed in a fully sunlit, wind protected location at PFR and watered daily for 3–7 days.

On each observation day, we placed fifteen flowering pak choi plants at the same locations as window traps when these were not activated. We counted the number of pollinators visiting the flowers of all fifteen pak choi plants for five minutes per landscape feature per farm, and repeated observations six times per day on set hours (9:30, 10:30, 11:30, 13:00, 14:00 and 15:00 h) to cover peak diurnal activity patterns (Rader et al. 2013; Fijen and Kleijn 2017). The order of observations per feature was randomized between farms, but fixed within farm for logistic reasons. Observations took place in the period between 29 November 2018 and 30 January 2019. Four farms were visited three times, one farm four times, and one farm two times because of high wind speeds (> 20 km h^{-1}) that negatively impacts flower visitation (Howlett et al. 2013). Plants were observed for pollinators on average 90 ± 19.0 SD minutes per landscape feature per farm. We counted the number of open pak choi flowers, and we used new plants with similar number of flowers on each observation day. Pollinators were identified to the species level, and occasionally only to genus level if species could not be caught (< 1%).

To translate pollinator abundances to pollen delivery per visit, we used estimates of single-visit pollen depositions and legitimate stigmatic visitation rates of the most frequent pollinators of pak choi. We used earlier (own) published single-visit pollen depositions of twelve common pak choi pollinators (Rader et al. 2009). To improve these estimates, we collected new data on more individuals of the same, and three additional pak choi pollinator species, using the same cultivar and methods (Rader et al. 2009; Howlett et al. 2017). In short, we determined the average pollen deposited on a virgin stigma from single visits of a pollinator species, and corrected for the passive self-pollination of a flower (i.e. number of pollen deposited without a pollinator visit). Furthermore, we used direct observations to estimate the rate of stigmatic contact for the common pak choi pollinator species to translate efficiency (pollen/visit) into effectiveness (total pollen deposited/species; Rader et al. 2009). For pollinators that could be named only to genus level in the plant observations (e.g. *Leioproctus* sp.), we assumed that the pollen deposition and rate of stigmatic visits were similar to a congeneric species [e.g. *Leioproctus fulvescens*, (Smith 1876)], which is true in most cases (Grab et al. 2019).

Analyses

To test whether different features showed different insect abundances, and to account for sampling effort between catching periods, we first calculated the average number of insects caught per day for each landscape feature per site. We did this separately for each species and eco-group. Eco-groups were based on life-history requirements or preferences that may explain relationships with certain landscape features, for example wet-detritus feeders could particularly be associated with effluent ponds (Tables 1 and S2).

We used mixed effect modelling (function *lmer* in the lme4 package; Bates et al. 2015) to test whether the number of caught individuals (response) per species or eco-groups responded differently across features (i.e. interaction between species or eco-group and feature). We used farm as our random structure to account for farm differences. Insect numbers might be affected by year effects and to take that into account we also included sampling year as a covariable. As we sampled only two years, and on different farms, we refrain from drawing

trend conclusions. Because poisson and negative binomial models showed overdispersion, we $\log_{10}(+$ minimum count)-transformed the counts per species per day, and $\ln(+$ minimum count)-transformed the counts per eco-groups per day and used gaussian error distributions. The significance of main effects and interactions was tested using log-likelihood ratio tests, and only non-significant interactions were removed from the models (Zuur et al. 2009). For visualization purposes, we used contrast plots in the visreg-package (Breheny and Burchett 2017), and back-transformed the data.

In a separate analysis, we calculated the number of unique species observed on the pak choi plants per observation day (only in 2018–2019), and tested for differences between features using mixed effect modelling with observation day, nested within farm, as our random structure. We tested for differences between features using a Tukey HSD test at the 5% level.

To estimate pollen delivery to pak choi associated with different landscape features (only in 2018–2019), we averaged the visitation rates of each species per feature per site, standardized to 100 open flowers (visitors/100 flowers/5 minutes; Garibaldi et al. 2020). We then calculated the number of stigmas visited in that period and subsequently the estimated number of pollen grains deposited per second. Using this method we had pollen delivery estimates for 86% of our pak choi visitors (12 species). Of the 14% missing visitors, most were rare species with low abundances, but of these, two flies were common [*Delia platura* (Meigen, 1826) (38%) and *Oxysarcodexia varia* (Walker, 1836) (29%)], which are known to have low body pollen loads (Levesque and Burger 1982). Body pollen has been shown to be positively correlated with single-visit pollen deposition for pak choi (Howlett et al. 2011). We are therefore confident that we have reliable estimates of the majority of pollen delivery. Lastly, we summed the total pollen delivery per second per landscape feature per site and tested for differences between features using mixed effect modelling, and using farm as our random structure. We tested for differences between features using Tukey HSD tests at the 5% level.

All analyses were performed in R version 4.0.2 (R Core Team 2020).

Results

In total, we trapped 22,380 insects of 33 species in 540 trapping days, with flies being the most abundant (52.9%), followed by beetles (17.9%) and bees (17.5%; Table S2). We also observed 4,433 insects of 32 species visiting the potted pak choi plants, of which 68.5% were flies and 30.2% were bees (Table S3).
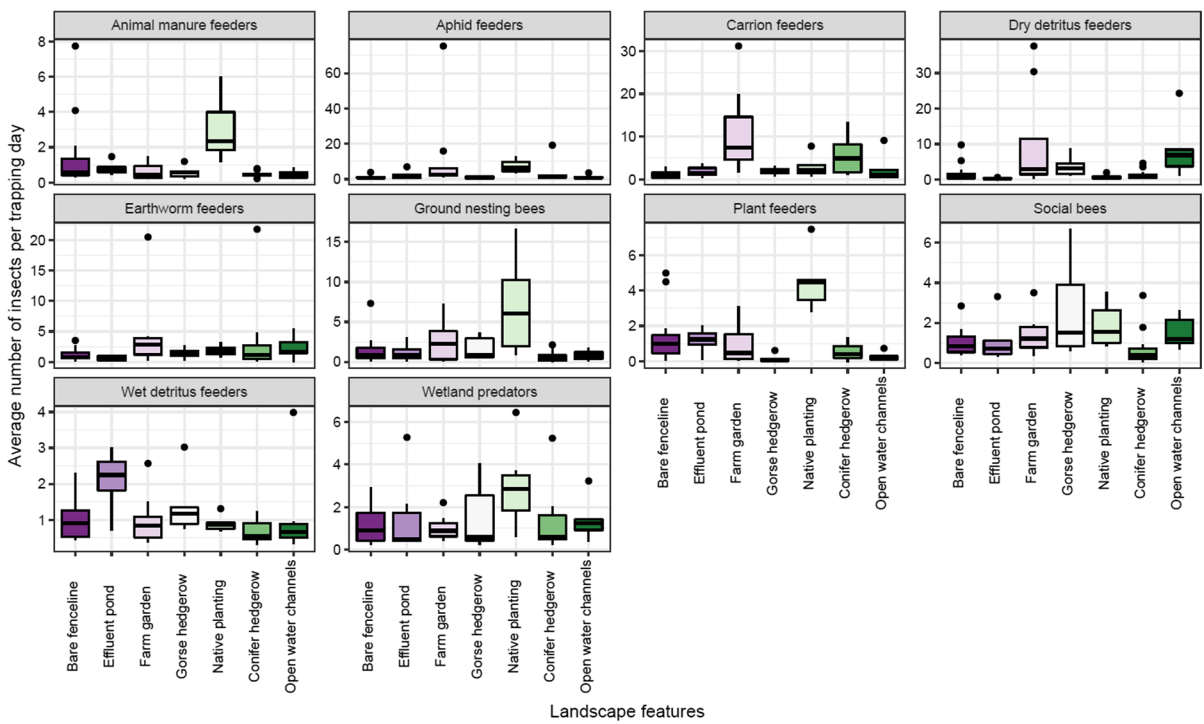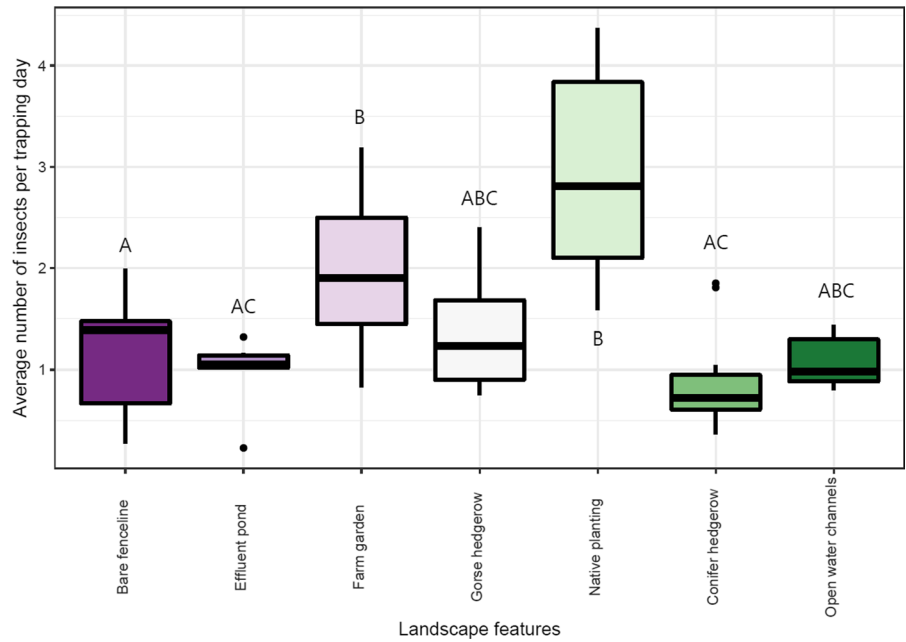
Window traps

Insect species differed in their responses across features [interaction species × landscape feature: χ^2 (192) = 724.42, p < 0.001; Fig. S1], and numbers were slightly lower in 2018–2019 than in 2007 [χ^2 (1) = 22.71, P < 0.001]. Significantly more insects were caught next to native-plantings and gardens compared with bare fence-lines, effluent-ponds and conifers (p < 0.001), but not from the other features (Fig. 1). Patterns were different between the eco-groups, with ground nesting bees being more frequently caught next to native-plantings, and carrion-feeders next to gardens or conifers [interaction eco-group × landscape feature: χ^2 (54) = 190.40, p < 0.001; Fig. 2]. Also across eco-groups, we caught fewer insects in 2018–2019 than in 2007 [χ^2 (1) = 6.63, p = 0.01].

Estimated pollen delivery

Estimated pollen deposition was highest near gardens (mean = 0.54 ± 0.14 SD pollen/second), followed by native-plantings (mean = 0.46 ± 0.18 SD pollen/second), effluent-ponds (mean = 0.43 ± 0.16 SD pollen/second), conifers (mean = 0.36 ± 0.16 SD pollen/second) and lastly fence-lines (mean = 0.30 ± 0.14 SD pollen/second). Compared with fence-lines, the estimated pollen delivery to the pak choi plants was significantly higher next to effluent-ponds (mean difference: 0.13 ± 0.04 se, z = 3.20, p = 0.012), gardens (mean difference: 0.23 ± 0.04 se, z = 5.54, p < 0.001) and native-plantings (mean difference: 0.16 ± 0.04 se, z = 3.81, p = 0.001), but not different next to conifers (mean difference: 0.07 ± 0.04 se, z = 1.70, p = 0.43). Estimated pollen delivery was furthermore significantly higher next to gardens than conifers (mean difference: 0.16 ± 0.04 se, z = 3.84, p = 0.001). The other features did not differ significantly from each other

Fig. 1 Average number of insects trapped per day next to the different landscape features. Based on window trapping on twelve farms in austral summers of 2007–2008 and 2018–2019. Results are averaged for all species, but individual species responded differently to landscape features (Fig. S1). Letters indicate significance between groups. Thick lines within boxplots indicate median, box indicates first/third quartiles, whiskers show the 1.5* interquartile range, and black dots are outliers

Fig. 2 Average number of insects trapped per day next to the different landscape features, divided per eco-group. Based on window trapping on twelve farms in austral summers of 2007– 2008 and 2018–2019. Thick lines within boxplots indicate median, box indicates first/third quartiles, whiskers show the 1.5* interquartile range, and black dots are outliers

in terms of estimated pollen delivery across sites (Fig. 4).

Contribution to pollination service made by different pollinating species

There were marked differences in the numbers of different pollinator species that deliver services to pak choi across features (Fig. 3). On average, pak choi next to gardens were visited by the highest number of species (mean 10.3 ± 3.1 SD), followed by native-plantings (mean 9.7 ± 3.4 SD), conifers (mean 9.2 ± 2.8 SD), effluent-ponds (mean 7.9 ± 2.5 SD) and fence-lines (mean 7.4 ± 2.6 SD). Pak choi at gardens were visited by significantly more species than at fence-lines (mean difference: 2.89 ± 0.77 se, $z = 3.75$, $p = 0.002$) and ponds (mean difference: 2.44 ± 0.77 se, $z = 3.17$, $p = 0.01$). Pak choi at native plantings were visited by significantly more species than at fence-lines (mean difference: 2.22 ± 0.77 se, $z = 2.89$, $p = 0.03$) but not significantly different from other features ($p > 0.05$).

In total, twelve species contributed to the provision of pollination services to pak choi across all features (Fig. 4), with flies being the dominant pollinators (70% of total estimated pollen delivery). Of these, drone flies [*Eristalis tenax* (Linnaeus 1758)] alone contributed an estimated 37% of the entire pollen deposition across all farms. Of the bees, the ground-nesting *Lasioglossum sordidum* (Smith 1853) contributes the majority of pollination

service across all features (21% of estimated total pollen delivery). Pollen deposition per visit differed markedly between pollinator species (Table S4).

E. tenax was estimated to contribute most of the pollination service to pak choi near effluent-ponds (56%) and fence-lines (53%), whereas its contribution was proportionally lower near gardens (23%) and conifers (26%; Fig. 4). Together, the two carrion-feeding flies *Calliphora stygia* (Fabricius 1781) and *C. vicina* Robineau-Desvoidy, 1830 were the most important pollinators of pak choi near conifers (16% and 27% of estimated total pollen deposited, respectively) but in contrast, did not contribute substantially to pollination next to fence-lines (6% and 3% of estimated total pollen deposited, respectively; Fig. 4). The aphid predating hover flies, *Melangyna novaezelandiae* (Macquart 1855) and *Melanostoma fasciatum* (Macquart 1850), the dry detritus feeding fly *Dilophus nigrostigma* (Walker 1848) and the moist-ground invertebrate predators *Odontomyia* sp. were estimated to contribute more pollination services next to gardens (6%, 3%, 6% and 4%, respectively) and native-plantings (3%, 5%, 4% and 4%, respectively) compared with fence-lines (2%, 3%, 2% and 4%, respectively) and effluent-ponds (2%, 1%, 1% and 2%, respectively; Fig. 4). Of the bees, *L. sordidum* was an important pollinator at four features (31% near natives, 24% near gardens, 16% near effluent-ponds, and 17% near fence-lines) but contributed relatively little to pollination near conifers (10%; Fig. 4).

Fig. 3 Average number of species visiting flowers of potted pak choi plants per landscape feature. Results based on plant observations on six farms in austral summer of 2018–2019. Letters indicate significance between groups. Thick lines within boxplots indicate median, box indicates first/third quartiles, whiskers show the 1.5* interquartile range, and black dots are outliers
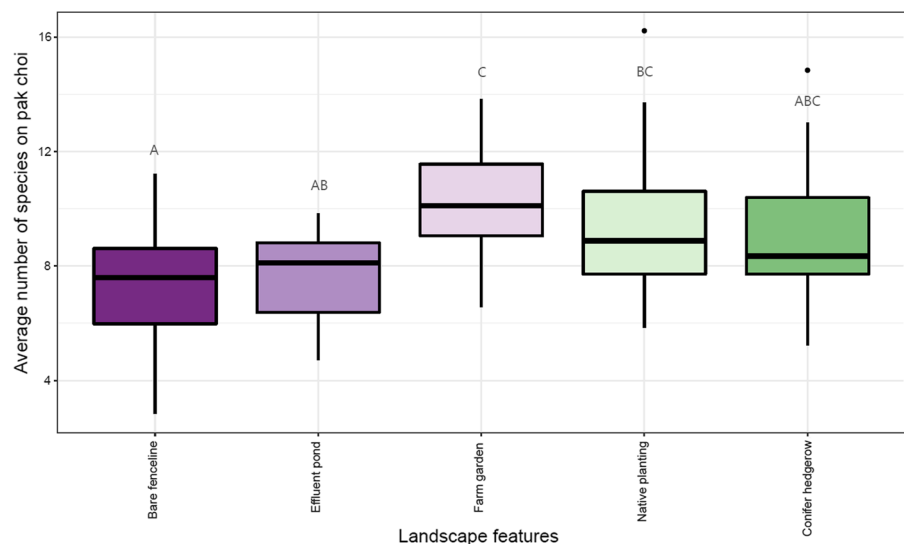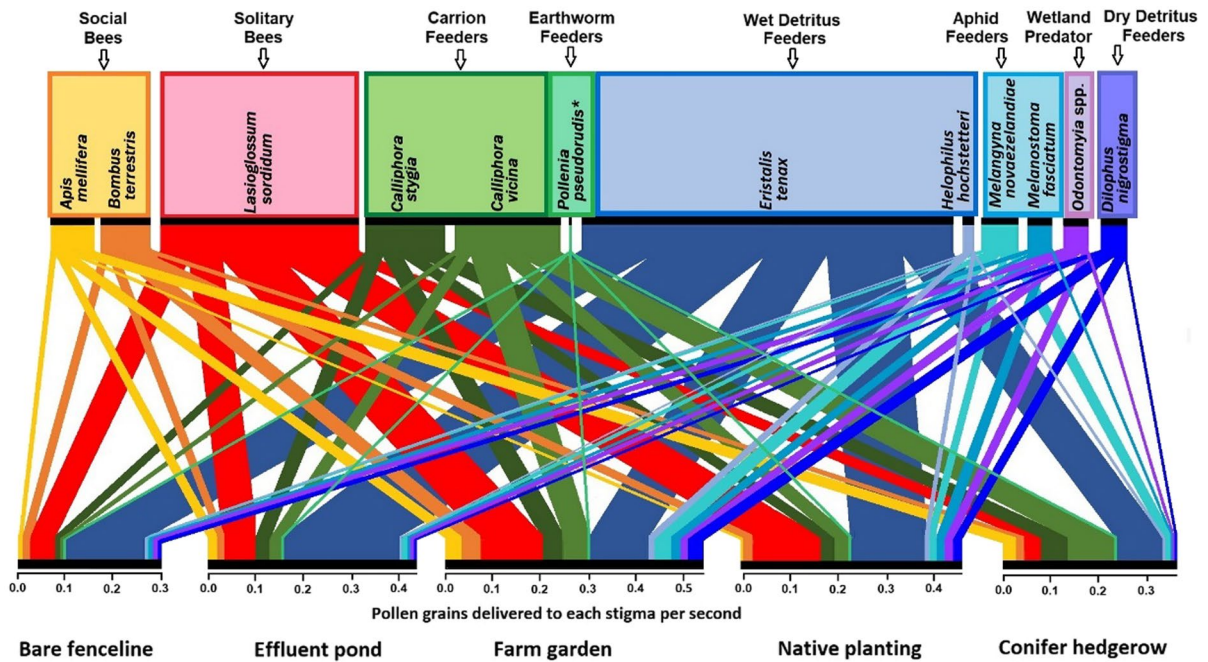
Fig. 4 Rate of stigmatic pollen deposition (grains per second) by twelve wild pollinating species to pak choi plants at five landscape features. All features were assessed per farm across six farms in the austral summer of 2018–2019. Yellow, orange, and red nodes are bee species. Green, blue and purple nodes are fly species

Discussion

We show that common functional landscape features in an intensively farmed agroecosystem are sites supporting on-farm wild pollinator species that contribute to crop plant pollination. Different insect species and their assigned eco-groups were associated more frequently with some features than others, which reflected their life-histories. Based on our measure of pollinator effectiveness, estimated pollination service delivery to pak choi plants was highest near features where farmers had purposely established multiple plant species (gardens and native-plantings), and lowest at bare fence-lines. Pak choi near dairy effluent-ponds and single species conifer hedgerows also received more pollination service compared with fence-lines. While two species (*E. tenax* and *L. sordidum*) delivered the majority of pollination services near all landscape features, those features where plant diversity had been established provided a higher diversity of crop pollinators. We therefore show that maintenance of landscape features can provide crop pollination services, despite not being established for this intention.

Pak choi plants received the highest pollination service near features containing mixed plant species (multi-species native-plantings and gardens; Fig. 4) probably reflecting the greater support of niches for different insects at these features (Marshall and Moonen 2002). This was also reflected in higher numbers of species observed visiting pak choi flowers next to these features (Fig. 3), and the higher number of insects caught next to multi-plant species features compared with single-species gorse and conifer hedgerows (Fig. 1). However, pollen delivery next to conifer hedgerows, although lower on average than mixed plant species features, did not differ significantly from natives, suggesting that even single species, non-flowering exotic hedgerows support pollination services to crops.

The introduced drone fly (*E. tenax*) and the endemic *L. sordidum* together contributed almost 60% of all pollen delivery, but in some cases delivery by the other species was equally large or even larger (e.g. next to conifer hedgerows). Overall, crop pollination is generally delivered by a few common pollinators (Kleijn et al. 2015), but a recent study has shown that the identity of dominant pollinators can

differ regionally (Winfree et al. 2018). Here, we found that even at the spatial scale of a farm, the identity of dominant pollinators can differ depending on the type of adjacent landscape feature. For example, despite calliphorid flies having relatively low pollen deposition rates (Table S4), they were the dominant pollen depositors next to conifer hedgerows. This supports the idea that both abundant and less-abundant species can be important to crop pollination (Fijen et al. 2018, 2019; Winfree et al. 2018), and that the sum of multiple less efficient pollinator species can be as effective as one highly efficient pollinator species, even at the farm scale. Conversely, landscape features could be implicated in the uneven distributions of pollinators within and between crop fields (Howlett et al. 2005) potentially affecting crop yields.

That some pollinator species were more associated with particular landscape features (Table 1), highlights a risk of losing their services to crops should these features disappear. For example, the drone fly (*E. tenax*) with open water features, and the calliphorid flies with conifer hedgerows (Supporting information Fig. S1). The ubiquity of these pollinator species in intensively farmed agroecosystems is likely due to life-history traits less affected by current management practices (Redhead et al. 2018). This can be because they can use a wide range of floral species, have high fecundity, produce multiple generations in a year and are highly mobile (Redhead et al. 2018; Rader et al. 2020). However, removing these last patches of non-productive habitat from an agroecosystem will not only likely decrease the total abundances of these highly efficient pollinators (Rader et al. 2009; Redhead et al. 2018), but also those already severely affected by agricultural simplification (Stavert et al. 2018).

Flies were the dominant group of crop pollinators in our study, and their contribution to global crop pollination is frequently underestimated (Rader et al. 2016, 2020). Management aimed at enhancing crop pollination is generally targeted at bees, through provision of flower rich semi-natural habitat as sites that provide nectar and pollen resources and nest sites for wild bee pollinators (Wood et al. 2016; Albrecht et al. 2020), but this might not be effective for enhancing non-bee pollinators (Schirmel et al. 2018; Rader et al. 2020). While bees generally collect pollen for their larvae, most flies depend on other resources for larval development (Table 1). Such pollinators may require

features that are not necessarily beneficial for bees, for example, effluent-ponds for the common drone fly (*E. tenax*; Fig. S1). It is therefore important that management aimed at enhancing crop pollination focusses on providing resources for important non-bee pollinators too.

Although we focused only on pollinators and their pollination service to crop plants, certain species also provide additional functional services that may affect farmers and local communities. For example, they may control pests or provide nutrient cycling (Doyle et al. 2020). Alternatively, they can have undesirable impacts such as sheep blow-fly strike caused by species including *Lucilia sericata* and *C. stygia* (Morris 2005). Understanding and accounting for the multiple functional services and risks provided by insects associated with landscape features is necessary to ensure management strategies garner broad community support (Faichnie et al. 2021).

Our study used a combination of window traps and observational surveys to assess pollinator abundances and pollen delivery. In agroecosystems, window traps have previously been shown to be correlated with observational surveys, highlighting their usefulness at collecting data on a range of different crop pollinators (Howlett et al. 2009). The window traps identified a larger species community, likely because the sample effort was larger. However, window traps have the same disadvantages as pan traps, as they are relatively less-attractive in flower-rich patches than in flower-poor patches, and should therefore not be used for monitoring population trends (Portman et al. 2020). Additionally, they do not sample which pollinators contribute to crop pollination, and how much. Because of these biases, we used plant observations and single-visit pollen deposition estimates. In this study we found broadly similar patterns between trap catches and insects observed on pak choi plants for the most common wild pollinators across different features. Because we combine these methods, we could reliably link the associations of insects to different features with pollen deposition.

Our results indicate that relatively simple functional landscape features (e.g. shelterbelts or aesthetic features) support insect populations, and subsequently crop pollination delivery, and plant species-rich features perform better in supporting pollinators than simple features. Nevertheless, recent developments on the Canterbury Plains have

shown that these landscape features can be removed quickly when their intended function is not required anymore, or if they are a nuisance for farm management practices. By removing these features, there is a danger that the provision of crop pollination is overlooked and unwittingly lost. Restoration of native habitat, such as the native-plantings in our study, can provide promising ways to enhance the aesthetic, conservational, and crop pollination value of otherwise simplified and intensive agricultural landscapes (Norton and Miller 2000). However, further studies are needed to test how the crop pollination delivery next to these landscape features translates to crop yield gain at commercial field scales (Kleijn et al. 2019). To aid pollinator conservation in agricultural landscapes, policy instruments and financial incentives, such as the Conservation Reserve Program in the United States (Begosh et al. 2020) and agri-environmental schemes in the European Union (Scheper et al. 2013), may convince farmers to protect or restore landscape features that support insect pollinators, although their success depends on the local circumstances (Scheper et al. 2013). Further understanding of the relationship between landscape features and ecosystem services will provide farmers with the knowledge to better assess the positive or negative consequences of retaining or removing various landscape features from their farm that may be driven by changing farming practices or needs.

Data availability Data supporting the results of this study will be made publicly available in Dryad upon publication.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

References

Aguilar-Støen M, Moe SR, Camargo-Ricalde SL (2008) Home gardens sustain crop diversity and improve farm resilience in Candelaria Loxicha, Oaxaca. Mexico Hum Ecol 37(1):55–77

Aizen MA, Garibaldi LA, Cunningham SA, Klein AM (2008) Long-term global trends in crop yield and production reveal no current pollination shortage but increasing pollinator dependency. Curr Biol 18(20):1572–1575

Albrecht M, Kleijn D, Williams NM, Tschumi M, Blaauw BR, Bommarco R, Campbell AJ, Dainese M, Drummond FA, Entling MH, Ganser D, de Groot AG, Goulson D, Grab H, Hamilton H, Herzog F, Isaacs R, Jacot K, Jeanneret P, Jonsson M, Knop E, Kremen C, Landis DA, Loeb GM, Marini L, McKerchar M, Morandin L, Pfister SC, Potts SG, Rundlof M, Sardinas H, Sciligo A, Thies C, Tscharntke T, Venturini E, Veromann E, Vollhardt IMG, Wackers F, Ward K, Wilby A, Woltz M, Wratten S, Sutter L. (2020) The effectiveness of flower strips and hedgerows on pest control, pollination services and crop yield: a quantitative synthesis. Ecol Lett 23(10):1488–1498

Bates D, Maechler M, Bolker B, Christensen RHB, Singmann H, Dai B, Eigen C+, Rcpp, LinkingTo (2015) Package 'lme4'

Begosh A, Smith LM, McMurry ST, Harris JP (2020) Influence of the Conservation Reserve Program (CRP) and playa wetlands on pollinator communities in the Southern High Plains, USA. J Environ Manage 256:109910

Breheny P, Burchett W (2017) Visualization of regression models using visreg. R J 9(2):56

Broadfield N, McHenry MT (2019) A world of gorse: persistence of *Ulex europaeus* in managed landscapes. Plants 8(11):523

Brown P (2016) Canterbury detailed irrigated area mapping. C16010/1. Aqualinc, pp 38

Castle D, Grass I, Westphal C (2019) Fruit quantity and quality of strawberries benefit from enhanced pollinator abundance at hedgerows in agricultural landscapes. Agric Ecosyst Environ 275:14–22

Cole LJ, Kleijn D, Dicks LV, Stout JC, Potts SG, Albrecht M, Balzan MV, Bartomeus I, Bebeli PJ, Bevk D, Biesmeijer JC (2020) A critical analysis of the potential for EU Common Agricultural Policy measures to support wild pollinators on farmland. J Appl Ecol 57(4):681–694

Dainese M, Martin EA, Aizen MA, Albrecht M, Bartomeus I, Bommarco R, Carvalheiro LG, Chaplin-Kramer R, Gagic V, Garibaldi LA, Ghazoul J (2019) A global synthesis reveals biodiversity-mediated benefits for crop production. Sci Adv 5(10):13

Dairy NZ (2018) New Zealand dairy statistics 2017–18. DairyNZ, Hamilton. https://www.dairynz.co.nz/media/5790451/nz-dairy-statistics-2017-18.pdf. Accessed 22 Mar 2022

Doyle T, Hawkes WLS, Massy R, Powney GD, Menz MHM, Wotton KR (2020) Pollination by hoverflies in the anthropocene. Proc Biol Sci 287(1927):20200508

ECan (2017) Canterbury water management strategy targets progress report 2017. Christchurch

Eilers EJ, Kremen C, Smith Greenleaf S, Garber AK, Klein AM (2011) Contribution of pollinator-mediated crops to nutrients in the human food supply. PLoS ONE 6(6):e21363

Faichnie R, Breeze TD, Senapathi D, Garratt MPD, Potts SG (2021) Scales matter: maximising the effectiveness of interventions for pollinators and pollination. In: Bohan DA, Vanbergen AJ (eds) The future of agricultural landscapes, Part II, advances in ecological research. Academic Press, Cambridge, pp 105–147

Fijen TPM, Kleijn D (2017) How to efficiently obtain accurate estimates of flower visitation rates by pollinators. Basic Appl Ecol 19:11–18

Fijen TPM, Scheper JA, Boekelo B, Raemakers I, Kleijn D (2019) Effects of landscape complexity on pollinators are moderated by pollinators' association with mass-flowering crops. Proc Biol Sci 286(1900):20190387

Fijen TPM, Scheper JA, Boom TM, Janssen N, Raemakers I, Kleijn D (2018) Insect pollination is at least as important for marketable crop yield as plant quality in a seed crop. Ecol Lett 21(11):1704–1713

Gaffney A, Bohman B, Quarrell SR, Brown PH, Allen GR (2019) Limited cross plant movement and non-crop preferences reduce the efficiency of honey bees as pollinators of hybrid carrot seed crops. Insects 10(2):34

Garibaldi LA, Carvalheiro LG, Vaissière BE, Gemmill-Herren B, Hipólito J, Freitas BM, Ngo HT, Azzu N, Sáez A, Åström J, An J (2016) Mutually beneficial pollinator diversity and crop yield outcomes in small and large farms. Science 351(6271):388–391

Garibaldi LA, Sáez A, Aizen MA, Fijen T, Bartomeus I (2020) Crop pollination management needs flower-visitor monitoring and target values. J Appl Ecol 57(4):664–670

Garibaldi LA, Steffan-Dewenter I, Kremen C, Morales JM, Bommarco R, Cunningham SA, Carvalheiro LG, Chacoff NP, Dudenhöffer JH, Greenleaf SS, Holzschuh A (2011) Stability of pollination services decreases with isolation from natural areas despite honey bee visits. Ecol Lett 14(10):1062–1072

Garibaldi LA, Steffan-Dewenter I, Winfree R, Aizen MA, Bommarco R, Cunningham SA, Kremen C, Carvalheiro LG, Harder LD, Afik O, Bartomeus I (2013) Wild pollinators enhance fruit set of crops regardless of honey bee abundance. Science 339(6127):1608–1611

Grab H, Branstetter MG, Amon N, Urban-Mead KR, Park MG, Gibbs J, Blitzer EJ, Poveda K, Loeb G, Danforth BN (2019) Agriculturally dominated landscapes reduce bee phylogenetic diversity and pollination services. Science 363(6424):282–284

Gregory N (1995) The role of shelterbelts in protecting livestock: a review. N Z J Agric Res 38(4):423–450

Howlett B, Butler R, Nelson W, Donovan B (2013) Impact of climate change on crop pollinator activity in New Zealand. MPI Technical Paper No: 2013/30, Ministry for Primary Industries. pp 45. www.mpi.govt.nz/document-vault/4101.

Howlett B (2012) Hybrid carrot seed crop pollination by the fly *Calliphora vicina* (Diptera: Calliphoridae). J Appl Entomol 136(6):421–430

Howlett BG, Donovan BJ, McCallum JA, Newstrom LE, Teulon DAJ (2005) Between and within field variability of New Zealand indigenous flower visitors to onions. New Zealand Plant Protection 58:213–218

Howlett BG, Evans LJ, Pattemore DE, Nelson WR (2017) Stigmatic pollen delivery by flies and bees: methods comparing multiple species within a pollinator community. Basic Appl Ecol 19:19–25

Howlett BG, Todd JH, Willcox BK, Rader R, Nelson WR, Gee M, Schmidlin FG, Read SF, Walker MK, Gibson D, Davidson MM (2021) Using non-bee and bee pollinator-plant species interactions to design diverse plantings benefiting crop pollination services. In: Bohan DA, Vanbergen AJ (eds) The future of agricultural landscapes, Part II, advances in ecological research. Academic Press, Cambridge, pp 45–103

Howlett BG, Walker MK, Newstrom-Lloyd LE, Donovan BJ, Teulon DAJ (2009) Window traps and direct observations record similar arthropod flower visitor assemblages in two mass flowering crops. J Appl Entomol 133(7):553–564

Howlett B, Walker M, Rader R, Butler R, Newstrom-Lloyd L, Teulon D (2011) Can insect body pollen counts be used to estimate pollen deposition on pak choi stigmas. New Zealand Plant Protection 64:25–31

Kleijn D, Bommarco R, Fijen TPM, Garibaldi LA, Potts SG, van der Putten WH (2019) Ecological intensification: bridging the gap between science and practice. Trends Ecol Evol 34(2):154–166

Kleijn D, Winfree R, Bartomeus I, Carvalheiro LG, Henry M, Isaacs R, Klein AM, Kremen C, M'gonigle LK, Rader R, Ricketts TH (2015) Delivery of crop pollination services is an insufficient argument for wild pollinator conservation. Nat Commun 6:7414

Klein AM, Vaissiere BE, Cane JH, Steffan-Dewenter I, Cunningham SA, Kremen C, Tscharntke T (2007) Importance of pollinators in changing landscapes for world crops. Proc Biol Sci 274(1608):303–313

Leong JM, Thorp RW (1999) Colour-coded sampling: the pan trap colour preferences of oligolectic and nonoligolectic bees associated with a vernal pool plant. Ecol Entomol 24(3):329–335

Levesque CM, Burger JF (1982) Insects (Diptera, Hymenoptera) associated with *Minuartia groenlandica* (Caryophyllaceae) on Mount Washington, New Hampshire, USA, and their possible role as pollinators. Arct Alp Res 14(2):117–124

Marshall E, Moonen A (2002) Field margins in northern Europe: integrating agricultural, environmental and biodiversity functions. Agric Ecosyst Environ 89:5–21

Minarro M, Garcia D (2018) Complementarity and redundancy in the functional niche of cider apple pollinators. Apidologie 49(6):789–802

Morris MC (2005) Tests on a new bait for flies (Diptera: Calliphoridae) causing cutaneous myiasis (flystrike) in sheep. N Z J Agric Res 48(1):151–156

Norton DA, Miller CJ (2000) Some issues and options for the conservation of native biodiversity in rural New Zealand. Ecol Manag Restor 1(1):26–34

Portman ZM, Bruninga-Socolar B, Cariveau DP, Morrison W (2020) The state of bee monitoring in the United States: a call to refocus away from bowl traps and towards more effective methods. Ann Entomol Soc Am 113(5):337–342

Potts SG, Biesmeijer JC, Kremen C, Neumann P, Schweiger O, Kunin WE (2010) Global pollinator declines: trends, impacts and drivers. Trends Ecol Evol 25(6):345–353

Proctor M, Yeo P, Lack A (1996) The natural history of pollination. HarperCollins Publishers, New York

R Core Team (2020) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Rader R, Bartomeus I, Garibaldi LA, Garratt MP, Howlett BG, Winfree R, Cunningham SA, Mayfield MM, Arthur AD, Andersson GK, Bommarco R (2016) Non-bee insects are important contributors to global crop pollination. Proc Natl Acad Sci U S A 113(1):146–151

Rader R, Cunningham SA, Howlett BG, Inouye DW (2020) Non-bee insects as visitors and pollinators of crops: biology, ecology, and management. Annu Rev Entomol 65:391–407

Rader R, Edwards W, Westcott DA, Cunningham SA, Howlett BG (2013) Diurnal effectiveness of pollination by bees and flies in agricultural *Brassica rapa*: Implications for ecosystem resilience. Basic Appl Ecol 14(1):20–27

Rader R, Howlett BG, Cunningham SA, Westcott DA, Newstrom-Lloyd LE, Walker MK, Teulon DA, Edwards W (2009) Alternative pollinator taxa are equally efficient but not as effective as the honeybee in a mass flowering crop. J Appl Ecol 46(5):1080–1087

Redhead JW, Woodcock BA, Pocock MJO, Pywell RF, Vanbergen AJ, Oliver TH (2018) Potential landscape-scale pollinator networks across Great Britain: structure, stability and influence of agricultural land cover. Ecol Lett 21(12):1821–1832

Scheper J, Holzschuh A, Kuussaari M, Potts SG, Rundlöf M, Smith HG, Kleijn D (2013) Environmental factors driving the effectiveness of European agri-environmental measures in mitigating pollinator loss–a meta-analysis. Ecol Lett 16(7):912–920

Schirmel J, Albrecht M, Bauer PM, Sutter L, Pfister SC, Entling MH (2018) Landscape complexity promotes hoverflies across different types of semi-natural habitats in farmland. J Appl Ecol 55(4):1747–1758

Stanley DA, Stout JC (2014) Pollinator sharing between mass-flowering oilseed rape and co-flowering wild plants: implications for wild plant pollination. Plant Ecol 215(3):315–325

Stavert JR, Linan-Cembrano G, Beggs JR, Howlett BG, Pattemore DE, Bartomeus I (2016) Hairiness: the missing link between pollinators and pollination. PeerJ 4:e2779

Stavert JR, Pattemore DE, Bartomeus I, Gaskett AC, Beggs JR (2018) Exotic flies maintain pollination services as native pollinators decline with agricultural expansion. J Appl Ecol 55(4):1737–1746

Tait PR, Cullen R (2006) Some external costs of dairy farming in Canterbury. In: Australian Agricultural and Resource Economics Society Annual Conference, p 8–10

Winfree R, Reilly JR, Bartomeus I, Cariveau DP, Williams NM, Gibbs J (2018) Species turnover promotes the importance of bee diversity for crop pollination at regional scales. Science 359(6377):791–793

Wood TJ, Gibbs J, Rothwell N, Wilson JK, Gut L, Brokaw J, Isaacs R (2018) Limited phenological and dietary overlap between bee communities in spring flowering crops and herbaceous enhancements. Ecol Appl 28(7):1924–1934

Wood TJ, Holland JM, Goulson D (2016) Providing foraging resources for solitary bees on farmland: current schemes for pollinators benefit a limited suite of species. J Appl Ecol. https://doi.org/10.1111/1365-2664.12718

Zuur A, Ieno EN, Walker N, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer Science & Business Media, New York