



RESEARCH PAPER

Co-flowering plants support diverse pollinator populations and facilitate pollinator visitation to sweet cherry crops

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Abstract

Many food crops depend on animal pollination to set fruit. In light of pollinator declines there is growing recognition of the need for agro-ecosystems that can sustain wild pollinator populations, ensuring fruit production and pollinator conservation into the future. One method of supporting resident wild pollinator populations within agricultural landscapes is to encourage and maintain floral diversity. However, pollinator visitation to crop plants can be affected either positively (facilitation) or negatively (competition) by the presence of co-flowering plants. The strength and direction of the facilitative/competitive relationship is driven by multiple factors, including floral abundance and the degree of overlap in pollinator visitation networks. We sought to determine how plant-pollinator networks, within and surrounding sweet cherry (*Prunus avium*) orchards, change across key time points during the cherry flowering season, in three growing regions in Australia. We found significant overlap in the suite of flower visitors, with seven taxa (including native bees, flies, hoverflies and introduced honey bees, *Apis mellifera*) observed visiting cherry and other co-flowering species within the orchard and/or the wider surrounding matrix. We found evidence of pollinator facilitation with significantly more total cherry flower visits with increasing percent cover of co-flowering plants within the wider landscape matrix and increased visitation to cherry by honey bees with increasing co-flowering plant richness within the orchard. During the cherry flowering period there was a significant positive relationship between pollinator richness on cherry and pollinator richness on co-flowering plants within the orchard and the area of native vegetation surrounding orchards. Outside of the crop flowering season, co-flowering plants within the orchard and wider landscape matrix supported the same pollinator taxa that were recorded visiting cherry when the crop was flowering. This shows wild plants help support the pollinators important to crop pollination, outside of the crop flowering season, highlighting the role of co-flowering plants within pollinator-dependent cropping systems.

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Introduction

Pollinators are integral to plant reproductive function and provide important pollination services for many crop species

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(Aizen et al., 2008; Garibaldi et al., 2013; Klein et al., 2007). Currently, many pollinator-dependent crops rely heavily upon the temporary deployment of managed honey bee (*Apis mellifera*) hives during crop bloom to provide these pollination services (Cunningham et al., 2002; Jay, 1986; McGregor, 1976). However, several studies report that a wide range of native wild pollinators, besides playing an important role in pollinating plants more widely, also contribute to pollination of crops (Garibaldi et al., 2013; Kremen, 2008; Rader et al., 2016), including sweet cherry (*Prunus avium*) (Holzschuh et al., 2012).

Mass-flowering crops, such as cherry, apple and almond, typically offer a bountiful floral resource for insects, but one that only lasts for a short part of the year. Within these systems, growers often augment the natural pollination service from wild insects and feral (in the case of Australia) honey bees with managed honey bee hives, generally brought in at the beginning of the crop flowering period and then removed afterwards and transported to other foraging sites. In contrast, resident wild pollinator populations must persist in these landscapes beyond just the crop flowering period, and for this to happen they need access to floral resources throughout the year (Blaauw & Isaacs 2014; Timberlake et al., 2019), as well as other key resources such as nesting habitat and sites (Harmon-Threatt, 2020).

Typically, agricultural landscapes are characterised by the dominance of one or relatively few crop species, with loss of native vegetation in the surrounding area leading to landscape simplification (Landis, 2017). However, in many such systems, weedy flowering plant species that persist as groundcover within and between crop rows are common and may increase insect abundance and diversity (Carvalho et al., 2011; Saunders et al., 2013), as may the presence of co-flowering species adjacent to the crop (Carvalho et al., 2012). Studies have found that co-flowering plants can increase the diversity and abundance of pollinators visiting crops which, in turn, can enhance crop productivity, as demonstrated for pumpkin (Hoehn et al., 2008), sunflower (Carvalho et al., 2011), apples (Földesi et al., 2016), almonds (Alomar et al., 2018) and sweet cherry (Eeraerts et al., 2019; Holzschuh et al., 2012). This can be considered as facilitation when spill-over of pollinators into the crop from co-flowering species results in increased crop pollination.

On the other hand, previous studies have also highlighted that co-flowering plants may compete with fruit trees for pollination services (Free, 1968; Osterman et al., 2021). In the Australian context, the total removal of co-flowering weeds such as clover (*Trifolium repens*), cape weed (*Arctotheca calendula*) and Paterson's curse (*Echium plantagineum*) has been recommended prior to introducing managed honey bee hives, to avoid the possibility of competition with the crop for honey bee visits (Somerville, 1999). Whilst, clearly, there is potential for co-flowering plant species to compete with the crop for pollinator visits, interactions are dynamic and can grade from competition to facilitation and

vice versa (Samnegård et al., 2011). These interactions can change with flower abundance (Carvalho et al., 2014; Ghazoul, 2006) and the species richness of the plant community (Ghazoul, 2006), with both floral traits and plant species relatedness playing a part in indirectly influencing pollination networks (Carvalho et al., 2014).

Mass-flowering crops like cherries offer an opportunity to investigate the dynamic nature of co-flowering plant-pollinator interactions, as they bloom for a short period of time with distinct early, peak and late parts to their flowering season and they overlap with the main flowering season of many non-crop species. Given honey bees are introduced and the dominant managed pollinator of many crops in Australia (Cunningham et al., 2002) there is a risk that perturbations such as drought and fire may affect the crop pollination industry (Cunningham et al., 2002). As such, wild pollinators are an increasingly important part of maintaining healthy and sustainable agro-ecosystems and crop production. Therefore, understanding the trade-offs between competition and facilitation for crops is important for evaluating the benefits of floral enhancements and co-flowering species in support of wild pollinator populations. Previous research has focussed on determining the degree to which mass flowering crops such as oranges (González-Varo & Vilà 2017.), mangoes (Simba et al., 2018) and strawberries (Trillo et al., 2020) share pollinators with co-flowering plants within adjacent natural habitats. Research on cherries has focussed on the availability of semi-natural habitat and flowering ground vegetation and their effects on cherry yield (Holzschuh et al., 2012), pollinator diversity (Eeraerts et al., 2019) and pollinator reproduction (Eeraerts, Piot et al., 2021). However, with a few notable exceptions, (e.g. Grab et al., 2017; Kovács-Hostyánszki et al., 2013), relatively few studies have sought to evaluate the extent to which pollinator networks overlap across the crop flowering season (although see Simba et al., 2018) and the similarity of networks of co-flowering species outside of this period (see Martins et al., 2018; Simba et al., 2018). Furthermore, to our knowledge, very few have focussed on evaluating networks within sweet cherry and co-flowering plants within both the orchard and the broader landscape matrix, however, see Eeraerts et al. (2021b).

We conducted an experiment across three Australian cherry growing regions and two flowering seasons, to determine the degree of flower visitor overlap between sweet cherry and co-flowering species both within the cherry orchards themselves and in the wider vegetation matrix surrounding the orchards. Specifically, we asked: (1) What co-flowering plant species and associated flower visitors are present before, during (early, peak and late) and after the cherry flowering season and how do they change over time? (2) What is the degree of overlap between the flower visitor assemblage of cherry and co-flowering plant species and how does this change across the crop flowering period? (3) How does the local plant species richness and percent cover of co-flowering plants within the orchard and wider matrix

affect pollinator richness and pollinator visitation to cherry flowers?

Materials and methods

Experimental design

The study was conducted across two sweet cherry (*Prunus avium* L.) flowering seasons in three growing regions - Bilpin, (33.5000° S, 150.5333° E), Orange, (33.2833° S, 149.1000° E) and Young, (34.18014° S 148.18020° E), in NSW, Australia (for specific orchard details see [Table 1](#) and [Appendix A: Fig. 1](#)). The study took place in the 2017 and 2018 crop flowering seasons in Bilpin (two orchards) and Orange (four orchards) and in the 2018 and 2019 seasons in Young (four and three orchards, respectively). Orchards ranged in size from 1 to 15 ha. The two orchards in Bilpin were separated by 6.09 km. Orchards in Orange were separated by a minimum of 1.96 km, a maximum of 5.64 km, and a mean of 3.46 km, and those in Young by a minimum of 1.8 km, a maximum of 7.0 km and a mean of 3.95 km. Each region differed in the amount of native vegetation and intensity of agricultural production. Bilpin is surrounded by two National Parks with all orchards surrounded by native vegetation. Orange is characterised by more intensely altered landscapes and larger commercial orchards and Young, although retaining some native vegetation, has this largely restricted to linear roadside verges. Pollination services were augmented by imported honey bee hives at one of the two orchards in Bilpin, one of the four in Young and all four in Orange ([Table 1](#)) throughout the entirety of the study, although feral populations of honey bees exist across all sites.

Cherry flower visitor observations and sampling

Insect visitation was surveyed in September through to October 2017 (Bilpin and Orange), 2018 (Bilpin, Orange and Young) and 2019 (Young), on one day during the early, peak and late cherry bloom periods. Nine flowering cherry trees were randomly chosen on each of the three observation days. On each study tree we haphazardly selected a sub-branch that had at least one open flower and, for five minutes, recorded all insects that came into contact with the reproductive parts of the cherry flowers. Observations were only paused to catch insects that could not be identified immediately for later identification and to catch representatives of the observed taxa to determine whether they carried cherry pollen. Insects were captured in specimen jars and immediately placed in an ice box (to limit grooming of pollen) in the field and then transferred to a -20° freezer for storage until microscopic analysis. Highly abundant and readily identified insects were identified to species level e.g. *Apis mellifera* and *Tetragonula carbonaria*, however others were identified to genus, family or order due to the difficulty in

identifying insects to species level whilst on the wing (See [appendix A](#) for the taxonomic level of pollinator groups). Observations on cherry were undertaken twice per day, once between 08:00 and 11:59 and again between 12:00 and 16:00 to ensure that we obtained representative samples of the entire pollinator assemblage. In addition, before and after each 5-min flower visitor survey, the temperature and wind speed were recorded using a Kestrel (2000) anemometer. All observations were restricted to fine weather days, which were characterised by predominantly clear sky, no rain and with temperatures >13 °C, and wind speeds <8 km/h.

All orchards contained multiple cultivars of cherry. However, observations were restricted to one cultivar per orchard, which was the dominant flowering cultivar at the time of the surveys (see [Table 1](#)). To determine the flowering stage of the cherry bloom (early, peak and late), the number of immature buds, open and dehisced flowers on each of three sub-branches were counted for each of the nine selected trees. Early bloom was defined as having <50% flowering; peak bloom as greater than 50% flowering and less than 20% dehisced flowers; and late bloom as greater than 30% dehisced flowers and less than 10% of buds remaining.

Determining whether cherry flower visitors carry cherry pollen on their body

Insects captured foraging on cherry were removed from freezer storage and examined under a dissecting microscope to determine if they were carrying cherry pollen on their body. Sticky tape was used to remove any pollen and then mounted on a microscope slide. In the case of bees that store pollen in tibial corbiculae, the legs with corbiculae were removed prior to a whole-body examination to ensure that only pollen available for pollination (i.e. on the body) ([Thomson et al., 2000](#); [Thorp, 2000](#)) was recorded. Each slide was compared to a reference slide of cherry pollen collected from the study site. Sweet cherry pollen cannot be visually differentiated microscopically from other *Prunus* species or *Rosaceae* pollen. All *Prunus* and *Rosaceae* pollen found on insects was inferred as cherry pollen, given the abundance of cherry trees in bloom and, to our knowledge, based on visual surveys, no other *Rosaceae* species were flowering in the study areas. Each slide was thoroughly scanned at 400x magnification and the number of cherry pollen grains recorded; values are presented as means ± standard error for each taxon determined.

Co-flowering plant flower-visitor observations and sampling

To determine the diversity and abundance of co-flowering plants and their flower visitors within cherry orchards, we

Table 1. Location and site details for each cherry orchard study site.

Orchard	Sweet cherry variety studied	Other cherry cultivars grown	Area occupied by cherry trees (ha)	Area of co-flowering plants within orchard (ha)	Area of native vegetation within 500m radius of orchard (ha)	Cherry trees (approx. n)	Managed honey bee hives (n)
Bilpin (2017 & 2018)							
1	Empress	Lapin, Ron's Seedling, Stella	0.7	3.4	27.8	400	10
2	Lapin	Ron's seedling, Van	0.6	2.1	47.9	300	0
Orange (2107 & 2018)							
1	Kordia	Lapin, Chelan, Van, Sweetheart, Sylvia	5	12.3	0.7	12,000	24
2	Kordia	Samba, Black star, Simone.	2	4.8	0.3	2,500	2
3	Sylvia	Lapin, Kordia, and Sunburst	1	6.4	15.2	3,000	12
4	Kordia	Lapin, Black star	5.6	4.1	2.1	4,500	8
Young (2018 & 2019)							
1	Ron's seedling	Lapin, Emperors, Supreme, Black Douglas, Ulster	4.9	4.9	10	1,050	0
2	Ron's seedling	Lapin, Sweetheart	6.1	5.1	17.3	6,000	0
3	Ron's seedling	Lapin, Supreme, Vista, Vega	3.7	3	6.2	2,500	15
4	Lapin	Ron's Seedling, Empress	6	4.5	10.7	1,700	0

Region	Year	Season	Number of interactions (degree) between flower visitors observed on cherry and co-flowering species										
			<i>Apis mellifera</i>	<i>Lassioglossum</i> spp.	Syrphidae spp.	Diptera spp.	<i>Tetragonula carbonaria</i>	<i>Homalictus</i> spp.	Coccinellidae spp.	Formicidae spp.	Coleoptera spp.	Lauxaniidae spp.	<i>Exoneura</i> spp.
Bilpin	2017	early	Red		Orange	Orange			Orange		Yellow		
		peak	Red		Orange	Orange			Orange		Yellow		
		late	Red		Orange	Orange			Orange		Yellow		
	2018	early	Red		Orange	Orange			Orange		Yellow		
		peak	Red		Orange	Orange			Orange		Yellow		
		late	Red		Orange	Orange			Orange		Yellow		
Orange	2017	early	Red	Orange	Orange	Orange							
		peak	Red	Orange	Orange	Orange		Red					
		late	Red	Orange	Orange	Orange		Red					
	2018	early	Red	Orange	Orange	Orange				Yellow			
		peak	Red	Orange	Orange	Orange				Yellow			Yellow
		late	Red	Orange	Orange	Orange				Yellow			Yellow
Young	2018	early	Orange	Orange	Orange	Orange				Yellow			
		peak	Orange	Orange	Orange	Orange				Yellow			
		late	Orange	Orange	Orange	Orange				Yellow			
	2019	early	Orange	Orange	Orange	Orange				Yellow			
		peak	Orange	Orange	Orange	Orange				Yellow			
		late	Orange	Orange	Orange	Orange				Yellow			

Fig. 1. The number of interactions (degree) between flower visitors observed on cherry and co-flowering species within the orchard and/or wider matrix across three sites (Bilpin, Orange and Young) and two years throughout the cherry flowering period. Red indicates that the flower visitor taxa was observed visiting all three vegetation types - cherry, wider matrix and within-orchard. Orange indicates the flower visitor was observed visiting the cherry and one other vegetation type, yellow indicates that the flower visitor was only observed visiting cherry, while white indicates that the species was not observed visiting cherry at that time point.

used a combination of quadrats and transects. Nine 5×5 m permanent quadrats were established within each orchard, between rows of cherry trees. Quadrats were randomly located to capture the variation in ground vegetation cover between rows. In addition, nine 10×10 m permanent quadrats (Bilpin orchards) or three 5×60 m transects (Orange and Young orchards) were randomly positioned within the wider, native vegetation matrix (i.e. off-farm). In Bilpin, quadrats were placed at least 10 meters from the forest edge, however in Orange and Young native vegetation was often restricted to linear road-side strips and therefore transects were undertaken within these areas. The difference in observation plot types between Bilpin and Orange/Young reflects differences in the nature and density of the surrounding vegetation. In Bilpin this was predominantly native (forest) vegetation, while in Orange and Young native vegetation was restricted to linear stands of remnant vegetation along adjacent roadsides. The percentage flowering of each species, and insect visitation to each flowering species, were measured in each quadrat/transect. Identification of each flowering species was undertaken in the field with voucher specimens collected to confirm identity, using taxonomic keys (Pellow et al., 2009) and identification guides (Richardson et al., 2011). Percentage flowering was calculated as the mean sum of the proportion of open flowers (all species combined) present within each quadrat / transect survey. Within each quadrat or transect observations of insect visitation to all flowering plants were conducted through five-minute observation periods for quadrats and 15 min for transects (Orange and Young only), twice per sampling day, between 08:00 and 11:59 and again between 12:00 and 16:00. A total of 1.5 h of observations within each habitat type (cherry, within orchard (non-crop) and surrounding vegetation matrix) were undertaken on each sampling day. Observations were conducted by moving slowly throughout the areas where flowers were present for the duration of the

survey period whilst being careful not to disturb the foraging behaviour of flower visitors. Observations in all three habitat types were carried out on the same day, for each of the three cherry bloom time points. In addition, co-flowering orchard and matrix flowers were surveyed on two further occasions – approximately six weeks prior to flowering and six weeks after cherry flowering had finished.

In addition to crop species, orchards contained and were surrounded by a wide range of flowering plants, including native and non-native species, forming varied co-flowering plant communities. The area of co-flowering species within the orchard and the native vegetation within the surrounding vegetation matrix was calculated using Google Earth Pro© by zooming to the highest resolution and using the polygon measure function and ground-truthed in the field to ensure accuracy. The area of co-flowering species within each orchard was summed and, for the wider matrix surrounding each orchard, we calculated the total area of native vegetation within a 500 m radius (78.5 ha) from the middle of the orchard. Whilst the area of each orchard, and thus the extent to which the 500 m radius extended beyond the crop, differed between orchards, we wanted to gain a true description of the natural vegetation available to pollinators foraging throughout the orchard. We deemed a 500 m radius to be appropriate given the typical foraging range of many native Australian pollinators particularly native bees, is presumed to be 500 m (Smith et al., 2017).

Data analysis

Habitat-pollinator networks and indices

Quantitative bipartite habitat-pollinator networks were constructed in R version 3.6.2 (R Core Team, 2021) using the *igraph* package (Csardi & Nepusz, 2006). Networks were produced for each combination of region (Bilpin,

Orange, Young), year (2017, 2018, 2019), and cherry flowering phase (before, early, peak, late, after) by habitat/vegetation type (cherry, within orchard and wider matrix). The pollinator species were specified as nodes, and the sum of interactions across orchards within each habitat type were specified as edges. Node size was determined by the degree (number of different interactions) and edge thickness determined as $\ln(a_{ij} + 1)$ where a is the number of interactions observed for pollinator i and habitat j . The degree metric was also calculated for each of the flower visitors observed visiting the crop to determine the overlap between those visiting cherry and other co-flowering species within the orchard and/or wider matrix during the periods of early, peak and late cherry bloom.

Several network indices were then calculated using the *bipartite* package (Dormann et al., 2009). These included connectance, which is the proportion of realised links of all possible links between pollinators and habitats within a single network. The connectance metric was used to determine if the cherry crop attracted pollinators from the surrounding area. Interaction diversity, which was described by Blüthgen et al. (2006) and is based on the calculation for Shannon diversity, was used to calculate the effective number of links (Blitzer et al., 2012), which is the number of interactions that, if occurring equally, would result in the same interaction diversity, and interaction evenness (Blüthgen et al., 2008) and which were used to determine the variation in interaction frequency. Although network indices such as nestedness and modularity are commonly used to describe bipartite networks, they were excluded from this study due to their insensitivity to spatial and temporal change (Redhead et al., 2018).

Taxonomic richness and visitation and the determination of competition or facilitation for pollinator visitation to cherry

Generalized linear mixed effect models were used to determine how co-flowering species richness and abundance influence cherry visitation by pollinators. Response variables were (1) the total visitation by all flower visitors to cherry trees, (2) the abundance of honey bees visiting cherry trees, (3) the abundance of native bees visiting cherry trees and (4) the taxonomic richness of flower visitors to cherry trees. Visitation, abundance and richness data were summed across the nine cherry trees within an orchard for both the am and pm observation periods and were calculated for each cherry flowering period (early, peak, late). Exploratory statistical analyses showed that (1)–(3) were best modelled using generalized linear mixed effect models using a negative binomial distribution and (4) was best modelled using a Poisson distribution. Diagnostic plots were assessed to identify extreme outliers. In total there were two such observations relating to days with extreme visitation and which could best be described as a swarming event, the impact of which we did not want to influence the analysis. In both

cases (one for honey bee abundance and one for native bee abundance) the value was larger than the third quartile plus five times the inter quartile range ($Q_3 + 5 \times IQR$) and around twice as large as the second largest observation. Consequently, one observation was removed from the analysis of (2) the abundance of honey bees visiting cherry trees and from (3) the abundance of native bees visiting cherry trees and two observations were removed from the analysis of (1) the total visitation by all flower visitors to cherry trees.

For each of the four response variables the set of potential fixed effects included region, year, season (early, peak and late), number of managed honey bee hives, area occupied by cherry trees, area within orchard, area of native vegetation within 500 m radius of orchard, the percentage flowering in the orchard and wider matrix (calculated as the mean sum of the percentage of open flowers (all species combined), across all nine quadrats within the orchard or wider matrix), flowering species richness within the orchard and wider matrix, and floral area within the orchard and wider matrix (area \times mean sum of the percentage of open flowers for all plant species across all nine quadrats). For models (1)–(3) the set of potential fixed effects included also flower visitor abundance of the same species in the orchard and in the wider matrix and for (2) – (3) flower visitor abundance of the opposite species to cherry trees i.e. native bees in (2) and honey bees in (3), and for (4) flower visitor richness in the orchard and in the wider matrix. All models include orchard as a random effect. Due to collinearity the following pairs of variables were always entered in separate models: (1) percentage flowering within the orchard and floral area within the orchard, (2) percentage flowering within the wider matrix and floral area within the wider matrix, (3) flowering plant richness within the orchard and wider matrix and (4) area of native vegetation (within 500 m radius) and the area occupied by cherry trees.

Using Akaike's Information Criterion for small sample sizes (AICc) all candidate models with all possible combinations of fixed effects were compared. The top (maximum of three) best fitting models (with $\Delta AICc < 2$) were further examined (due to correlated predictor variables no model averaging was done) and for the best fitting model the significance of fixed effects was tested and multicollinearity was checked using variance inflation factors (VIFs). All VIFs were below 2.

All analyses were carried out using the packages 'lme4', 'lmerTest' and 'MuMIn' in R version 4.0.4 (Bates et al., 2015; Kuznetsova et al., 2017; Bartholomée et al., 2020; R Core Team, 2021).

To assess how pollinator visitation changes through the cherry flowering season, interactions of pollinator taxa with flowering phase were explored. We restricted analysis of crop visitation to two taxa - honey bees and native bees - that made up 92% of all visits, because other groups (e.g. Diptera) were observed too infrequently for meaningful analysis. Wilcoxon-Mann-Whitney tests were used to test whether the observed differences between honey bee visits

and native bee visits to cherries at early, peak and late season were statistically significant.

Results

Pollinator networks within the orchard, wider vegetation matrix and on cherry

We found a wide variety of co-flowering plant species within orchards across the survey period at Bilpin in 2017 (twelve) and 2018 (eight), Orange in 2017 (thirteen) and 2018 (nine) and Young 2018 (four) and 2019 (three). Most of these were weeds (introduced exotic plant species), of which the most visited plant species was *Arctotheca calendula* (cape weed) which received 29% of all flower visits, *Hypochaeris* / *Taraxacum* spp (these two genera were grouped together given the difficulty in accurate identification in the field) which received 21%, and *Fumaria muralis* which received 19% of all flower visits. These exotic weed species were found growing between the cherry trees throughout the orchards and occasionally within the surrounding wider matrix. The surrounding vegetation quadrats in Bilpin were predominantly national park, comprising native Australian wet sclerophyll forest with several species observed to be in flower throughout the cherry flowering season. We observed six co-flowering species in the surrounding vegetation matrix in Bilpin in 2017 and one in 2018. In Orange there were six co-flowering species recorded in off-farm transects in 2017 and five in 2018, while in Young there was one species recorded in 2018 and none in 2019. The most frequently visited plant species within the surrounding matrix was *A. calendula* the introduced cape weed, which received 26% of all flower visits (Appendix A: Table 4), however all of these visits were only observed at one orchard. The next most visited plant species were both native - *Pultenaea flexilis* which received 21% and *Pittosporum undulatum* which received 16% of visits (Appendix A: Table 5).

Visual inspection of the networks (see Appendix A: Tables 1–3) and calculation of the degree of interactions between taxa observed visiting the cherry and the other habitats (within the orchard and/or wider matrix) (Fig. 1) identified overlap in the flower visitor assemblages for cherry and other co-flowering species, both within the orchard and the wider vegetation matrix, at all three locations. Taxonomic groups that overlapped between vegetation types within a given location included *Apis mellifera*, Diptera spp, Syrphidae spp, Coccinellidae spp (Bilpin only), *Homalictus* spp (Orange only), *Lasioglossum* spp (Orange and Young) and *Tetragonula carbonaria* (Bilpin only). Each of these main flower visitor taxa was found to carry *Prunus* pollen on their body and, given the absence of *Prunus* species other than cherry, we refer to them as cherry pollinators. Eighteen of the 20 sampled *A. mellifera* were carrying *Prunus* pollen,

with an average of 51 ± 12 (SE) pollen grains each. 17 of the 20 *Lasioglossum* samples (70 ± 21 grains) and 16 of the 20 *T. carbonaria* (102 ± 32 grains) samples had crop pollen on their torsos, while only 2 of the 15 Diptera samples were carrying *Prunus* pollen (11 ± 1).

In general, our pollinator networks show that there are similar interactions between plants and pollinators throughout the cherry flowering season, with very few plants or pollinators observed before the crop flowering period, although surveys were not undertaken before cherry flowering in 2017 in Bilpin and Orange (see Appendix A: Tables 1). Within each region, annual network connectance at early, peak and late cherry bloom was relatively consistent (Table 2). Interaction evenness differed between years with slightly higher evenness across the flowering stages in 2017 in both Bilpin and Orange compared to 2018. In Young, interaction evenness was higher across all flowering stages in 2019 compared with 2018 (Table 2).

Plant species richness and pollinator taxonomic richness within and surrounding cherry orchards

During the period of cherry bloom there were co-flowering species present, either within the orchard or the surrounding vegetation matrix, with mean species richness ranging from 1 - 6 (Appendix A: Fig. 2). Prior to cherry flowering, typically, mean plant and pollinator richness was low ranging from 0 - 1 and 0 - 0.5, respectively. After crop flowering, we observed modest numbers of co-flowering plants consistently across years and locations, within the orchards (Appendix A: Fig. 2), despite relatively low numbers in the wider vegetation matrix. In both Bilpin and Orange in 2017 (Appendix A: Fig. 2A and C) and 2018 (Appendix A: Fig. 2B and D) co-flowering plant species richness was typically highest within the orchard compared to in the wider matrix, with pollinator richness being highest on co-flowering plants within the orchard and on the cherry crop. Within the wider landscape in both Bilpin and Orange, flowering plants were only observed during the cherry flowering season, whilst at Young in 2018 (Appendix A: Fig. 2E) other flowering plants were only observed before the cherry flowering season and not at all during or after crop flowering in 2019 (Appendix A: Fig. 2F). Co-flowering species richness was lowest in Young (Appendix A: Fig. 2E and F) and highest in Bilpin (Appendix A: Fig. 2A and B).

Determining competition or facilitation for total, honey bee and native bee visits to cherry

Total number of visits to cherry flowers was positively related with the area of native vegetation ($\beta = 0.024 \pm 0.001$, $z = 3.21$, $p = 0.001$), significantly decreased during the late season (compared to peak) ($\beta = -0.45 \pm 0.15$, $z = -$

Table 2. Bipartite network indices for three cherry growing regions, during early, peak and late cherry bloom, in Bilpin ($n = 2$) and Orange ($n = 4$, 2017, 2018) and Young ($n = 4$, 2018, $n = 3$, 2019). Network indices include the connectance, interaction diversity, interaction evenness, number of flower visitors and the effective number of links.

Region	Year	Season	Connectance	Interaction Diversity	Interaction Evenness	Flower visitors (n)*	Links
Bilpin	2017	early	0.58	1.97	0.56	11	7.16
		peak	0.46	1.66	0.52	8	5.22
		late	0.63	2.07	0.63	9	7.99
	2018	early	0.56	1.38	0.48	6	3.99
		peak	0.53	1.24	0.46	5	3.46
		late	0.50	1.21	0.49	4	3.34
Orange	2017	early	0.75	1.76	0.63	8	5.80
		peak	0.67	2.29	0.75	7	9.79
		late	0.61	1.74	0.60	6	5.68
	2018	early	0.57	1.25	0.41	7	3.50
		peak	0.61	1.14	0.40	6	3.14
		late	0.47	0.76	0.29	5	2.14
Young	2018	early	0.76	1.08	0.43	6	2.94
		peak	0.69	1.48	0.53	8	4.38
		late	0.64	1.46	0.56	7	4.33
	2019	early	0.88	1.61	0.77	4	4.99
		peak	0.9	1.76	0.76	5	5.81
		late	0.71	1.60	0.60	7	4.94

* Species or higher taxa.

3.05, $p = 0.002$) and significantly increased with the percentage cover of co-flowering plants within the surrounding matrix ($\beta = 0.02 \pm 0.01$, $z = 1.98$, $p = 0.048$). The early season was not significantly different (compared to peak) ($\beta = 0.02 \pm 0.15$, $z = 0.16$, $p = 0.876$) (Table 3).

There was a significant positive relationship between honey bee visits to cherry flowers and the richness of co-flowering plant species within the orchard ($\beta = 0.15 \pm 0.05$, $z = 2.79$, $p = 0.005$). The year of the observation was not significant (compared to 2017); 2018 ($\beta = 0.28 \pm 0.19$, $z = 1.4$, $p = 0.136$) and 2019 ($\beta = -0.26 \pm 0.29$, $z = -0.848$, $p = 0.380$) (Table 3).

The best fitting model for native bee visitation to cherry flowers showed that visits significantly increased with native bee visits to co-flowering plants within the orchard ($\beta = 0.04 \pm 0.01$, $z = 2.61$, $p = 0.009$), that there was a significant positive effect of the number of honey bee visits to the cherry and native bee visitation ($\beta = 0.02 \pm 0.01$, $z = 2.80$, $p = 0.005$) and the percent cover of flowering plants within the native vegetation significantly increased visitation ($\beta = 0.14 \pm 0.02$, $z = 7.22$, $p < 0.001$), providing evidence of facilitation. The year of the observation was significant (compared to 2017); 2018 ($\beta = -1.35 \pm 0.34$, $z = -4.02$, $p < 0.001$) and 2019 ($\beta = -1.04 \pm 0.50$, $z = -2.08$, $p = 0.037$) (Table 3).

We also found a significant positive relationship between taxonomic richness of pollinators visiting co-flowering plants within the orchard and those observed visiting cherry flowers ($\beta = 0.10 \pm 0.05$, $z = 2.07$, $p = 0.039$) and a significant positive relationship between pollinator richness to cherry and the area of native vegetation ($\beta = 0.01 \pm 0.01$, $z = 2.15$, $p = 0.032$). The

floral area within the orchard was not significant ($\beta = 0.26 \pm 0.13$, $z = 1.96$, $p = 0.051$) (Table 3).

Significantly more honey bees, compared to native bees, were observed visiting cherry during the early ($n = 539$ honey bees/199 native bees, $W = 326.5$, $p < 0.001$), compared with the peak ($n = 667/97$, $W = 345$, $p < 0.001$) and late ($n = 380/49$, $W = 342.5$, $p < 0.001$) flowering periods. Pollinator visitation to cherry was greatest during peak flowering ($n = 849$); this was not significantly different to early flowering ($n = 802$, $\beta = -0.007 \pm 0.160$, $z = -0.046$, $p = 0.963$) but did differ significantly from late flowering ($n = 446$, $\beta = -0.462 \pm 0.160$, $z = -2.886$, $p = 0.004$) (Table 3). However, the taxonomic richness of pollinators visiting cherry did not change significantly throughout the cherry flowering season ($F = 2.165$, $df = 2$, $p = 0.1267$).

Discussion

Our study highlights the complex nature of relationships between pollinator-dependent crops, such as cherry, and co-flowering plants. Contrary to predictions by Somerville (1999) that co-flowering “weeds” within orchards will compete with cherry trees for visitations, our results show that co-flowering plant richness within the orchard significantly increases honey bee and native bee visitation to cherry flowers, although this was not observed for total insect visitation. Interestingly, the total number of pollinators visiting cherry flowers was found to significantly increase with increasing percentage cover of flowering species within the wider matrix; this finding was also reported

Table 3. Top (maximum of three) best fitting models (with $\Delta\text{AICc} < 2$) describing the effect of percentage flowering, co-flowering plant richness within the orchard and wider matrix and visitation by native bees within the orchard for (1) total visitation by flower visitors to cherry (2) honey bee visitation to cherry flowers (3) native bee visitation cherry flowers and (4) flower visitor richness to cherry flowers. Only variables occurring in the best fitting models are presented in the table. The models for (1) – (3) were analysed using Generalised Linear Mixed Models with negative binomial distribution and (4) with a Poisson distribution. The overall model fit (R^2) is divided into marginal R^2 (R^2_m) and conditional R^2 (R^2_c) (Nakagawa & Schielzeth, 2013; Nakagawa et al., 2017).

	Intercept	OS abundance cherry	SS abundance orchard	Pollinator richness orchard	Plant richness orchard	Area NV	Area orchard	Percentage flowering orchard	Percentage flowering wider matrix	FA orchard	FA wider matrix	Season/ year/ region	df	AICc	ΔAICc	R^2_m	R^2_c
1 Total visits	3.12					0.02			0.02			season	7	459.7	0.00	0.44	0.59
	3.14					0.02					0.08	season	7	459.9	0.20	0.44	0.59
	2.77					0.03	0.05		0.02			season	8	460.6	0.95	0.48	0.59
2 Honey bees	2.67				0.15							year	6	455.2	0.00	0.23	0.50
	2.56				0.13	0.01						year	7	456.0	0.75	0.32	0.51
	2.64		0.01		0.13							year	7	456.1	0.84	0.30	0.50
3 Native bees	0.22	0.02	0.04						0.14			year	8	217.2	0.00	0.67	0.67
	1.31		0.04				-0.18			0.99	0.28	region	9	217.3	0.12	0.73	0.73
	1.31		0.04				-0.17		0.07	1.00		region	9	217.5	0.36	0.72	0.72
4 Richness	0.36			0.10		0.01				0.26			5	196.2	0.00	0.23	0.23
	0.51			0.11		0.01							4	197.4	1.21	0.17	0.17
	0.42			0.09		0.01		0.01					5	197.8	1.61	0.21	0.21

OS = opposite species; SS = same species; NV = native vegetation, FA = Floral area; df = degrees of freedom; AICc = Akaike information criterion for small sample sizes; ΔAICc = AICc score difference between best model and the model being compared; R^2_m = marginal R^2 ; R^2_c = conditional R^2 .

by Lundin et al. (2017) when comparing visitation to wild-flower plantings in almond orchards. Our study also found a significant positive relationship between the taxonomic richness of pollinators visiting cherry flowers and that of those visiting co-flowering species within the orchard. Network analysis showed an overlap in the taxa that visit cherry flowers and co-flowering plants both within the orchard and the wider landscape matrix throughout the cherry flowering season. Furthermore, the same suite of cherry flower visitors was also observed visiting co-flowering species within the orchard and wider matrix, outside of the cherry flowering period.

Our findings highlight that co-flowering species are supporting native pollinators, feral (given that not all orchards stocked honey bee hives) and managed honey bees, both during and outside the cherry flowering season. Co-flowering communities with diverse flowering phenologies have been shown to help maintain pollinator populations within farms by providing floral resources outside of the crop flowering season (Mallinger et al., 2016; Mandelik et al., 2012; Nicholls & Altieri 2013). It is likely, therefore, that there is a facilitative effect of having flowering species within and surrounding our cherry orchards year-round. Indeed, Carvalheiro et al. (2011) found that the presence of weeds allowed pollinators to persist within sunflower cropping systems and that weed diversity increased flower visitor diversity and ameliorated the negative effects of isolation from natural habitat. Therefore, retaining flowering weedy species, especially within areas with very little natural vegetation, may help native pollinators persist in agro-ecosystems and may provide vital resources in times of drought or following fires. Conserving and promoting native pollinator populations may be especially important if the *Varroa* mite arrives in Australia and threatens the pollination services provided by managed and unmanaged honey bees, as seen elsewhere in the world (Iwasaki et al., 2015).

Our network analysis reveals the degree to which the flower visitor assemblage is shared between cherry and co-flowering plant species, an interaction that was found to facilitate cherry visitation. Previous studies that have sought to determine whether there is a spillover of pollinators from co-flowering plants, including within orchard rows (Mayer & Lunden 1991), floral enhancement strips and from native vegetation to adjacent crops, have reported highly variable results in terms of crop pollination and yield (Albrecht et al., 2020; Blauw & Isaacs 2014; Garibaldi et al., 2011; Lundin et al., 2017; Morandin & Kremen 2013). A study by Pywell et al. (2015) found that the creation of wildlife habitat within farmland resulted in increased crop yield, while Eeraerts et al. (2021) also noted that orchards and semi-natural habitat provide complementary nesting and food resources for pollinating insects. Enhancing or conserving native vegetation or other flowering species within farms is likely important for the long-term facilitative benefits for cherry pollination, as positive effects of floral enhancements may take several years to develop (Albrecht et al., 2020).

Although the taxonomic level to which we were able to identify pollinators differed from species such as *A. mellifera* and *T. carbonaria*, to genus, family or order we are confident in the accuracy with which we were able to identify these taxonomic groups. This approach in taxonomic level identification is common in many field studies (Carvalheiro et al., 2011; Stanley & Stout, 2014) and we recognise that the resolution of species level interactions was not possible in this study.

The role of co-flowering species in supporting or enhancing crop pollination is complex and may depend not only on landscape context and the degree of landscape simplification/complexity (Dainese et al., 2019), but also on the timing of crop and non-crop plant flowering, and the diversity of co-flowering species. Facilitative effects were found with increases to both percent flower cover (within the orchard and wider matrix) and within-orchard pollinator richness which led to increased visitation and taxonomic richness of insect visits to cherry. However, these results may be context-dependent. For example, relationships may depend on factors such as inherent differences in plant attractiveness, abundance and diversity which could influence the relationship between co-flowering plants and the crop.

The facilitative effects of co-flowering species - both within the orchard and wider matrix - for cherry flower visitation rates found in our study is in line with the findings of Holzschuh Holzschuh et al. (2012) for sweet cherry in Germany. Their study revealed that wild bee visitation increased with the proportion of high-diversity habitat in the surrounding (1 km) landscape and that this resulted in an increase in fruit set and yield in cherry trees (Holzschuh et al., 2012). They found that two thirds of flower visitors were honey bees, but that fruit set was correlated only with wild bee visitation, a result that they attributed to the greater pollination efficiency of wild bees. A similar conclusion has also been made by Eeraerts et al., and Meeus (2020). Likewise, Eeraerts et al. (2019) found that semi-natural habitat and flowering plants in the herb layer within cherry orchards can help support pollinator species richness and diversity. In addition, Schüepp et al. (2014) found that pollinators visited cherry flowers more often in areas with more woody semi-natural habitat compared to those with less but that fruit set was reduced when there was a high density of co-flowering species.

The nature of the surrounding landscape context has also been shown to influence wild pollinator diversity. For example, Eeraerts et al. (2017) found that wild pollinator diversity decreased with intensive fruit production. It has also been noted that increasing honey bee abundance does not compensate for the lost pollination services provided by wild pollinators to sweet cherry (Eeraerts et al., 2017). Although we did not measure fruit set following native bee or honey bee visitation, future studies should consider incorporating this, as well as resultant fruit quality measurements, to gain a more complete understanding of the interactions between co-flowering plants and pollinator-dependent crops.

Substantial differences in the number of co-flowering plants found before and after the cherry flowering season reflect the time of year in which sampling took place. Observations prior to the start of cherry flowering were undertaken during winter (July 2017, July–August 2018) when very few pollinators were active and relatively few co-occurring plants were in flower. The greater pollinator richness observed during the cherry flowering period, compared to the earlier survey, is likely associated with the warmer temperatures at this time and the spring flowering season for many co-occurring species. This may also help to explain why we found significantly more honey bees than native bees during the early cherry flowering period, as honey bees are active at lower temperatures than most native bee species in Australia (Burrill & Dietz 1981; Heard & Hendrikz 1993). The decline in plant and pollinator richness seen once cherries had finished flowering (November–December 2017, and December 2018), coincided with much higher temperatures and associated dieback of weedy plants (most of which are annuals) within the orchards.

Our results highlight the role of diverse non-crop floral resources in supporting native pollinator communities and pollination services within agro-ecosystems, both during and outside of crop flowering. Conservation of native pollinators is important not only for current crop production but may also help to provide more stable pollination services into the future.

Authors' contributions

A-MG, SAP and JMC conceived the ideas and designed the methodology, A-MG and LEB collected the data, A-MG, COB and CK analysed the data; A-MG, COB, CK, LEB, JMC and SAP wrote the manuscript.

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Declaration of Competing Interest

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

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Supplementary materials

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