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Co-Flowering Species Richness Increases Pollinator Visitation to Apple Flowers

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Abstract: Co-flowering plants can experience an array of interactions, ranging from facilitation to competition, the direction and strength of which are often dependent on the relative abundance and diversity of the plant species involved and the foraging behavior of their pollinators. Understanding interactions between plant–pollinator networks and how they change over time is particularly important within agricultural systems, such as apples, that flower en masse and that also contain non-crop co-flowering species both within the farm and the surrounding landscape. We determined the degree of overlap between pollinator networks on two varieties of apple (Granny Smith and Pink Lady) and co-flowering plant species within orchards and the wider vegetation matrix in two apple-growing regions (Orange and Bilpin) in Australia. We surveyed plant–pollinator interactions at key stages of the cropping cycle: before mass flowering; during king, peak and late blooms; and, finally, once apple flowering had finished. Overall, we found considerable overlap in the flower visitor assemblage on apples and co-flowering species within the orchard. The introduced honeybee (*Apis mellifera*) was the most frequent flower visitor to all three vegetation types at all times in Orange. However, in Bilpin, both a native stingless bee (*Tetragonula carbonaria*) and *A. mellifera* were highly frequent visitors, both on- and off-crop. Numerous native bees, flies and Lepidoptera also commonly visited apple and co-flowering species within orchards in both locations. We found that native-bee and honeybee visitation to apple flowers was positively correlated with co-flowering species richness (within the orchard and the wider matrix); however, visitation by native bees decreased as the area of co-flowering species in the surrounding landscape increased. Our study highlights the importance of maintaining diverse co-flowering plant communities within the local landscape to increase and support a wide variety of pollinators in horticultural production systems.

Keywords: mass-flowering crop; agroecosystems; native bees; cross-habitat spillover; facilitation; introduced pollinator

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1. Introduction

Worldwide, approximately 75% of crops either depend on or benefit from animal pollination [1], with numerous studies having demonstrated that pollinators are integral to optimal fruit set and provide essential pollination services for many crop species [2,3], including apples [4,5]. The important role of wild pollinators in crop pollination is being increasingly realized [6], and, as a result, understanding the requirements of native wild pollinators in terms of floral resources, landscape context [7,8] and nesting opportunities [7] within these systems is paramount.

Mass flowering crops typically offer a bountiful floral resource for both managed and wild pollinators, but only for a short part of the year when the crop is in flower. However, the flowering of other plant species both on the farm and in the wider vegetation matrix may also coincide with this crop flowering period. The impact of one flowering species on another can vary along a continuum, from facilitation (positive) to competition (negative) [9], with the strength and direction of the interaction often being driven by temporal and spatial overlap in flowering between plant species [10] and the degree of pollinator sharing [11]. Facilitation occurs when a flowering species increases the abundance or diversity of pollinators in the local area and co-flowering neighbors benefit through spillover of pollinator activity [12]. In contrast, competition may result if proximity to co-flowering species leads to decreased abundance and/or diversity of pollinators or in fewer visits to specific plants. This may occur if co-flowering species are more attractive to the pollinators [13], or due to pollinator sharing causing interspecific or suboptimal pollen transfer [14,15].

Spillover of pollinators from natural areas into managed cropping systems is common [1,16,17], but it is important to recognize that there may also be spillover from managed systems into the surrounding vegetation matrix [4], especially if honeybee hives are introduced to augment pollination services. This is of particular importance because, in many locations, including Australia, the honeybee is an introduced species and now dominates the pollination networks of many native plants [18–21].

Planting flower strips [22] and maintaining ground cover [23], hedgerows [24] and/or natural/semi-natural vegetation around cropping areas can enhance the pollinator abundance [23], pollinator diversity and pollination success [13,22] of crops. Likewise, pollinators may move from agricultural areas into the surrounding vegetation matrix, and this could affect the pollination of native plants, especially those flowering at the same time as the crop [25]. Therefore, it is important to understand the degree to which crop and non-crop co-flowering species share pollinators and how the pollinator network changes through the flowering season. Such knowledge may help to assist in the design of agri-environment schemes that support crop pollination and promote landscape-scale management and habitat retention for the combined benefits to the crop, wild plants and wild pollinators.

To understand if co-flowering plants facilitate or compete with crop pollination services, we determined the overlap between pollinator networks on two apple varieties (Pink Lady and Granny Smith) and co-flowering species within orchards and the wider matrix in two apple-growing regions of Australia. Specifically, we asked the following questions: (1) How does richness of co-flowering plant species and associated flower visitors change over the apple flowering season within the orchard and surrounding vegetation matrix? (2) To what extent does the flower-visitor assemblage of apple and co-flowering plant species within the orchard and wider vegetation matrix overlap, and how does this change during the apple flowering season? (3) Does the percentage cover and richness of co-flowering plants (within the orchard and wider vegetation matrix) affect the taxonomic richness or number of insect visits to apple flowers?

2. Materials and Methods

2.1. Experimental Design

Two apple-growing regions—Bilpin (33.5000° S, 150.5333° E) and Orange (33.2833° S, 149.1000° E) in New South Wales, Australia—were chosen, as they represent a strong contrast in the amount of native vegetation present and, thus, plant and pollinator habitat diversity in the surrounding areas. Bilpin is surrounded by both the Blue Mountains and Wollemi National Parks, while Orange is situated in a predominantly agricultural landscape with very few patches of remnant native vegetation in the region. The study took place in 2017 and 2018 during the apple flowering season at five orchards in Bilpin and four in Orange, with all orchards growing a range of apple cultivars. Due to the popularity and associated production volume of Granny Smith and Pink Lady apples (for orchard details, see Table 1), these cultivars were selected as study varieties. Orchards ranged in size from approximately 4.8 to 25 ha. The five orchards in Bilpin were separated by a minimum of 700 m and a mean of 3 km ± 0.6; the four orchards in Orange were with a minimum of 860 m and a mean of 2 km ± 0.3 apart. Most of the orchards in both Bilpin (four out of five) and Orange (three out of four) brought in honeybee hives during the apple flowering period, and some also kept honeybee hives permanently throughout the year (three orchards in Bilpin and two in Orange). One orchard in Bilpin also had four native stingless bee (*Tetragonula carbonaria*) hives throughout our study. While it is known that there are feral colonies of honeybees throughout both study regions and in Bilpin, colonies of *T. carbonaria* naturally occur within the area [26,27].

Table 1. Location and specifications of each apple orchard studied.

Location/Orchard	Area of Orchard (ha)	Floral Area within Orchard (ha)	Native Surrounding Floral Area (ha) within 500 m Radius	Apple Cultivar Studied	Approx. Number of Apple Trees
Bilpin					
1	2.7	2.9	42.1	Pink Lady	950
				Granny Smith	490
2	1.9	2.7	32.4	Pink Lady	250
				Granny Smith	450
3	3.2	3.4	27.8	Pink Lady	750
				Granny Smith	250
4	7.8	9.9	46.0	Pink Lady	1800
5	1.5	2.1	47.9	Pink Lady	150
Orange					
1	15.8	12.3	0.7	Pink lady	3500
2	3.2	4.8	0.3	Pink Lady	1320
				Granny Smith	150
3	11.3	8.6	2.7	Pink Lady	1440
				Granny Smith	110
4	4.9	6.4	15.2	Pink Lady	440

The overall flowering phenology stage of the apple bloom (king, peak and late), was determined by counts of the number of buds, and open and dehisced flowers on each of three selected sub-branches on nine apple trees. King bloom was defined as having greater than 60% buds, less than 30% flowering and less than 10% dehisced flowers. Peak bloom was defined by 30% buds, 60% flowering and 10% dehisced flowers. Late bloom was defined by less than 20% buds, at least 40% flowers and at least 20% dehisced flowers.

2.2. Apple Flower Visitor Observations and Sampling

We observed insect visitation to apple flowers in September and October 2017 and 2018 on one day during each of the king (which is often the first central flower within a cluster to bloom), peak and late bloom periods (separately, for both varieties) at all orchards. Nine flowering apple trees per cultivar were randomly chosen, avoiding both consecutive trees and the first five trees of each row, on each of the three observation days (king, peak and late) throughout apple bloom. A sub-branch (a small second order branch from one of the main branches) on each study tree was randomly selected, and, for five minutes, all insects that contacted the reproductive parts of apple flowers were recorded. If an insect could not be identified in the field, the observation was paused while the insect was caught for subsequent microscopic identification, using taxonomic keys [28,29], or to determine if it carried pollen on its body. Captured insects were frozen for later analyses in the jar that they were caught in. Observations of apple flowers were undertaken twice per sampling day, between 08:00 and 11:59 and between 12:00 and 16:00. The temperature and wind speed were also recorded before and after each 5 min flower visitor survey, using a Kestral (2000) anemometer. Observations were only conducted on predominantly sunny days, with no rain, when temperatures exceeded 13 °C and the wind speed was less than 8 $\mathrm{km \cdot h^{-1}}$.

2.3. Do Apple Flower-Visitors Carry Pollen?

To determine if insects caught visiting apple flowers during observations carried apple (Rosaceae) pollen, insect specimens were thawed and examined for pollen by using a dissecting microscope. Upon first examination, if there was pollen present, it was removed by dabbing sticky tape over the body and was then fixed to a microscope slide [30] for closer examination. For corbiculate bees, the legs were removed by using scissors before the whole-body examination to ensure that only pollen available for pollination (i.e., pollen on the body) [31,32] was recorded. Each slide was thoroughly scanned at 400× magnification, and the number of Rosaceae (apple) pollen grains was recorded. Any Rosaceae pollen found on the insects was presumed to be apple, given the overwhelming number of apple flowers present in comparison to the odd rose bush observed within private gardens.

2.4. Flower-Visitor Observations and Sampling of Co-Flowering Species

To assess the diversity and abundance of co-flowering (non-crop) plants and their flower visitors within the orchard, nine 5 × 5 m permanent quadrats were established within each study orchard. Flower-visitor diversity and abundance within the wider vegetation matrix were assessed within nine 10 × 10 m permanent quadrats (Bilpin orchards) or three 5 × 60 m transects (Orange orchards). To reflect differences in the surrounding vegetation matrix and provide a representative assessment of the landscape, we used different observation plots and observation times in Bilpin (complex native vegetation) and Orange (continuous monoculture paddocks). However, the total study area and the amount of time spent observing insect visitors remained consistent (900 m^2 and 1.5 h per observation day, respectively).

The quadrats or transects were positioned to represent the different vegetation types within the orchard and/or the wider landscape. During each survey, plants that were in flower were identified to the species level (or the lowest taxonomic level possible), and the percentage cover of the flowering species within each quadrat was estimated. Five-minute observations of insect visitation to all flowering plants were made for each quadrat, and fifteen-minute observations were undertaken for transects (Orange only); observations were conducted twice per sampling day, between 08:00 and 11:59 and again between 12:00 and 16:00. This amounted to a total of 1.5 h of observations within each habitat type (apple, within orchard (non-crop) and wider matrix) per sampling day. All three habitat types within an orchard were observed on the same day, for each of the three apple-bloom time points. Additionally, quadrats and transects within the orchard and wider matrix were surveyed on two extra occasions, namely six weeks prior to apple flowering and six weeks after apple flowering had ceased; however, six-week-prior data were not collected in 2017 in either Bilpin or Orange.

2.5. Effect of Co-Flowering Plant Area on Apple Visitation

Mean co-flowering plant abundance was calculated as the mean percent coverage (area) of flowers (all flowering species) within a single quadrat for each combination of region and year. The total area of native vegetation within the orchard and surrounding matrix was calculated by using Google Earth Pro©; this was evaluated for a 500 m radius circle (78.5 ha) from the middle of the orchard. For both within-orchard and surrounding-matrix vegetation, floral area was calculated as the mean floral abundance recorded in the respective survey quadrats (see Section 2.4 above), multiplied by the area.

2.6. Data Analysis

2.6.1. Construction of Habitat–Pollinator Networks and Calculation of Indices

Observations of plant–pollinator interactions were pooled across orchards to produce networks by habitat type (within the orchard, wider vegetation matrix and apple cultivar (Pink Lady or Granny Smith)). A time series of matrices encapsulating the different stages of the apple season (before, king, peak, late and after) for habitat type–pollinator observations was prepared for each combination of region, year and apple cultivar. Before and after (apple flowering season) data were collected on the same day at orchards within a region; however, each apple cultivar was sampled on different days for king, peak and late time points in both 2017 and 2018, reflecting differences in crop phenology. Quantitative bipartite networks were constructed in R version 3.6.1, using the igraph package [33], with nodes for all pollinator species and habitats occurring within a region present in each network for easy visual comparison of network interactions (links). Node size was determined by the number of different interactions (degree) and edge thickness, determined as $\ln(a_{ij} + 1)$ where a = the number of interactions for pollinator, i, and, habitat, j.

A number of indices were calculated to describe the bipartite habitat–pollinator networks. These indices included connectance, which is the proportion of realized links out of all possible links between pollinators and habitats (within orchard, wider matrix and apple) within a network. Interaction diversity [34], which is derived from Shannon Diversity and was used to calculate the effective number of links [35], was then used to determine the variation in interaction frequency. The effective number of links is the number of interactions that, if occurring equally, would result in the same interaction diversity and interaction evenness [36]. Other indices commonly used to describe bipartite networks, such as nestedness and modularity, were not used due to their insensitivity to spatial and temporal change [37].

2.6.2. The Effect of Co-Flowering Species' Richness and Abundance on Pollinator Visits to Apple

We followed the same approach as outlined in Reference [38]. Generalized linear mixed effect models were used to determine how the richness and abundance of co-flowering species influenced (1) the total visitation by all flower visitors to apple trees, (2) the abundance of honeybee visits to apple trees, (3) the abundance of native-bee visits to apple trees and (4) the taxonomic richness of all pollinators to apple trees. Visitation, abundance and richness data collected during the morning and afternoon observation periods were totaled across the nine apple trees within each orchard, for each of the key apple bloom periods (king, peak and late). Based on exploratory statistical analyses, it was determined that (1)–(3) were best modeled by using generalized linear mixed effect models, using a negative binomial distribution, and (4) was best modeled by using a Poisson distribution. Two extreme outliers were identified through the examination of diagnostic plots. In both instances, the observations, one which related to honeybee and one to native-bee abundance, were associated with swarming events (i.e., extreme number of visitations). In both cases, the data value was larger than the third quartile plus six times the inter-quartile range ($Q_3 + 6 \times \text{IQR}$) and almost twice as large as the second largest observation. Therefore, one observation was removed from the analysis of (2), one from (3) and two from the analysis of (1).

For all models, the potential fixed effects included apple cultivar, region, year, season (king, peak and late), area of apple trees, area within orchard, area of native vegetation (within a 500 m radius encompassing the orchard), the percentage of co-flowering species within the orchard and the surrounding matrix (calculated as the mean sum of the percentage of open flowers (all species combined) within the orchard or wider matrix), flowering species richness orchard and wider matrix, and floral area within the orchard and wider matrix (area × mean sum of the percentage of open flowers for all plant species across all nine quadrats). The list of potential fixed effects for Models (1)–(3) also included the abundance of the same species of flower visitor within the orchard and wider matrix, and for Models (2) and (3), the abundance of flower visitors of the opposite species to apple trees (i.e., native bees in Model (2) and honeybees in Model (3)); and for Model (4), the flower-visitor richness in the orchard and in the wider matrix was included. Orchard was included as a random effect in all models. In cases of high correlation (greater than 0.7), the respective explanatory variables were always entered into separate models.

We used Akaike's Information Criterion for small sample sizes (AICc) to compare all possible combinations of fixed effects in all candidate models. The top three best-fitting models (with ΔAICc < 2) were further examined (due to correlated predictor variables, model averaging was not undertaken). The significance of fixed effects was tested, and multicollinearity was checked by using variance inflation factors (VIFs) for each of the best-fitting models. The VIFs for each model were found to be below 2. Fixed effects were standardized by centering and scaling.

The packages "lme4", "lmerTest" and "MuMIn" in R version 4.0.4 [33,39–41] were used in all of the analyses.

3. Results

3.1. Pollinator Networks on Granny Smith and Pink Lady Apples and Co-Flowering Plants within the Orchard and Wider Vegetation Matrix

A diversity of non-crop flowering plant species was observed within the orchards at Bilpin (*n* = 19 (2017); *n* = 20 (2018)) and at Orange (*n* = 16 (2017); *n* = 19 (2018)) (see Supplementary Table S1 for a complete list of flowering species observed). Likewise, a diversity of flower-visitor species was observed within the orchards at Bilpin (*n* = 18 (2017); *n* = 18 (2018)) and at Orange (*n* = 16 (2017); (*n* = 16 (2018)) (see Supplementary Table S2 for a complete list of flower visitors observed). Most of the co-flowering plants were introduced forb species (such as clover (*Trifolium repens*), dandelion (*Taraxacum officinale*) and plantago (*Plantago lanceolata*)) that were visited by a diverse array of bees, flies, butterflies and moths (Figures S1 and S2). Across each habitat type (wider matrix and within orchard) and both apple varieties, the honeybee was the most common flower visitor in both Bilpin and Orange. The honeybee was observed throughout the main crop flowering season, and often before and after (Figures S1 and S2). Different native bee species were also commonly observed in Bilpin (a stingless bee, *Tetragonula carbonaria*) and Orange (*Lasioglossum* spp.). These native bees were found to visit multiple non-crop flowers within the orchard but were rarely seen foraging on native Australian flora in the surrounding vegetation matrix. Native bees were observed during and after the apple flowering season but were not recorded prior to crop flowering in 2018 ("before crop flowering" data were not collected in 2017).

Interestingly, the most common native bees observed visiting co-flowering species within orchards in Orange (*Lasioglossum* spp.) were rarely observed visiting either of the apple varieties. Numerous fly species, as well as other native bees (*Exoneura* spp. (Bilpin only) and *Homalictus* spp.), were observed visiting flowering species in all habitat types—typically during and after apple bloom; however, they were generally in lower numbers than the species mentioned above. An analysis of the insects caught visiting apple flowers in both Bilpin and Orange showed that apple pollen was found on the body of the five most common insects recorded during our surveys: *A. mellifera* (*n* = 20/20, average 35 ± SE 12 pollen grains), *T. carbonaria* (*n* = 20/20, 127 ± 31), *Diptera* spp. (other than *Syrphidae* spp.) (*n* = 5/7, 4 ± 1), *Syrphidae* spp. (*n* = 4/6, 6 ± 4) and *Lasioglossum* spp. (*n* = 4/5, 11 ± 4). We thus refer to all insects observed henceforth as pollinators and flower-visitor diversity as pollinator richness. Other insects observed visiting apple flowers were rare visitors and not captured for pollen analysis.

Network connectance, the proportion of realized interactions of all possible interactions within a network, was negatively correlated with pollinator richness. As such, connectance was greater for networks in Orange, where pollinator richness was lower (Table 2). We expected connectance to decrease during the peak apple flowering period, with the crop attracting pollinators from alternative habitats (within the orchard and wider matrix); however, although minor shifts in network connectance across flowering phases were observed, no clear patterns were identified. We found a higher interaction diversity, interaction evenness and effective number of links in 2017 than 2018, because there were more non-dominant pollinators (everything other than *A. mellifera* (Orange) and *T. carbonaria* (Bilpin)) in 2017 (Table 2). In Bilpin, in 2018, 93% of pollinator observations on Pink Lady flowers were of just two species (*A. mellifera* (74%) and *T. carbonaria* (19%)), with corresponding figures of 64% and 33% on Granny Smith flowers. In Orange, most visits were by *A. mellifera*, with 87% of pollinator observations on both Pink Lady and Granny Smith in 2017 and 99% and 98% in 2018, respectively.

Table 2. Bipartite network indices based on observations of plant–pollinator interactions pooled across orchards by habitat type (within orchard, wider matrix and apple cultivar (Pink Lady or Granny Smith)) for two apple-growing regions, Bilpin and Orange, during king, peak and late apple bloom, in 2017 and 2018. The numbers of orchards differed by location and crop variety studied, with three (Bilpin) and two (Orange) orchards for Granny Smith and five (Bilpin) and four (Orange) orchards for Pink Lady.

Region	Apple Cultivar	Year	Season	Connectance	Interaction Diversity	Interaction Evenness	No. of Pollinator Species	Effective Number of Links
Bilpin	**Granny Smith**	**2017**	king	0.500	1.541	0.453	10	4.667
			peak	0.556	1.844	0.559	9	6.322
			late	0.542	1.519	0.478	8	4.568
		2018	king	0.542	1.614	0.507	8	5.020
			peak	0.600	1.252	0.462	5	3.499
			late	0.515	1.436	0.411	11	4.202
	Pink Lady	**2017**	king	0.667	1.804	0.531	10	6.076
			peak	0.564	1.770	0.483	13	5.870
			late	0.533	1.691	0.497	10	5.426
		2018	king	0.542	1.529	0.481	8	4.612
			peak	0.524	1.302	0.428	7	3.676
			late	0.593	1.538	0.467	9	4.656
Orange	**Granny Smith**	**2017**	king	0.667	1.460	0.588	4	4.307
			peak	0.750	1.777	0.715	4	5.913
			late	0.533	1.494	0.552	5	4.456
		2018	king	0.556	1.099	0.500	3	3.000
			peak	0.600	1.113	0.483	5	3.044
			late	0.750	0.213	0.153	2	1.237
	Pink Lady	**2017**	king	0.611	1.521	0.526	6	4.575
			peak	0.619	1.931	0.634	7	6.894
			late	0.667	1.697	0.627	5	5.458
		2018	king	0.429	0.939	0.308	7	2.556
			peak	0.500	0.813	0.327	4	2.254
			late	0.583	0.740	0.298	6	2.095

3.2. Species Richness of Pollinators and Plants

The species richness of pollinators and plants was highly variable among orchards within each region and between years (Figures 1 and 2). For both apple varieties, years and regions, the pollinator species' richness was generally higher for co-flowering species within the orchards than for those in the wider matrix.

We observed more non-crop flowering species within the orchard than in the surrounding matrix, with co-flowering weedy forb species such as dandelions, clover and plantain being the most abundant species within orchards in both regions and years (Figures 1 and 2). In Orange, the total number of non-crop plant species observed in flower was 10 in 2017 and 11 in 2018, while in Bilpin, there were 22 flowering species in 2017 and 15 in 2018 (see Supplementary Table S1 for a complete list of flowering species observed). In Orange, the matrix largely comprised open grassland paddocks with weedy forb species. In contrast, the matrix in Bilpin was mostly native dry sclerophyll woodland.

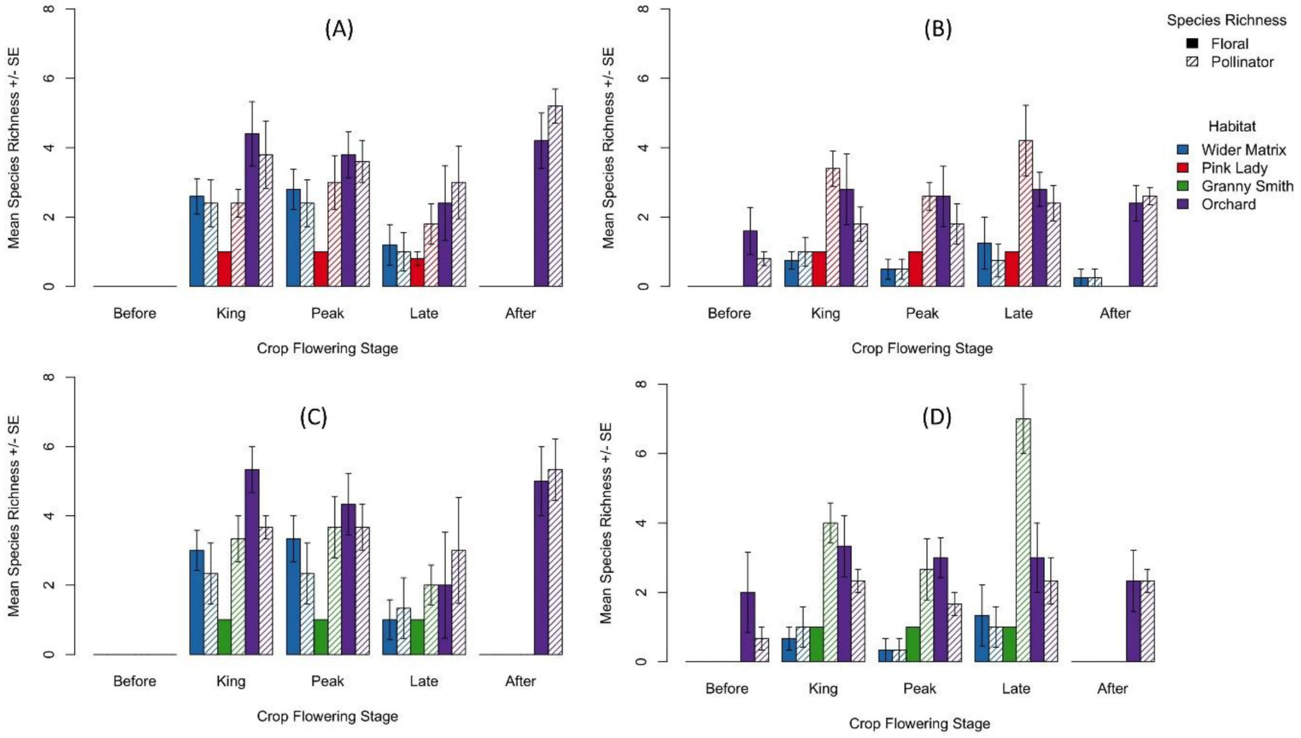

Figure 1. Mean species richness (± standard error) of pollinators (solid fill) and flowering plants (hatching) within the wider matrix (blue) and within orchard (purple) and on Pink Lady apple flowers (red) in 2017 (**A**) and 2018 (**B**) and Granny Smith apple flowers (green) in 2017 (**C**) and 2018 (**D**) (before, king, peak, late and after apple bloom) in Bilpin.

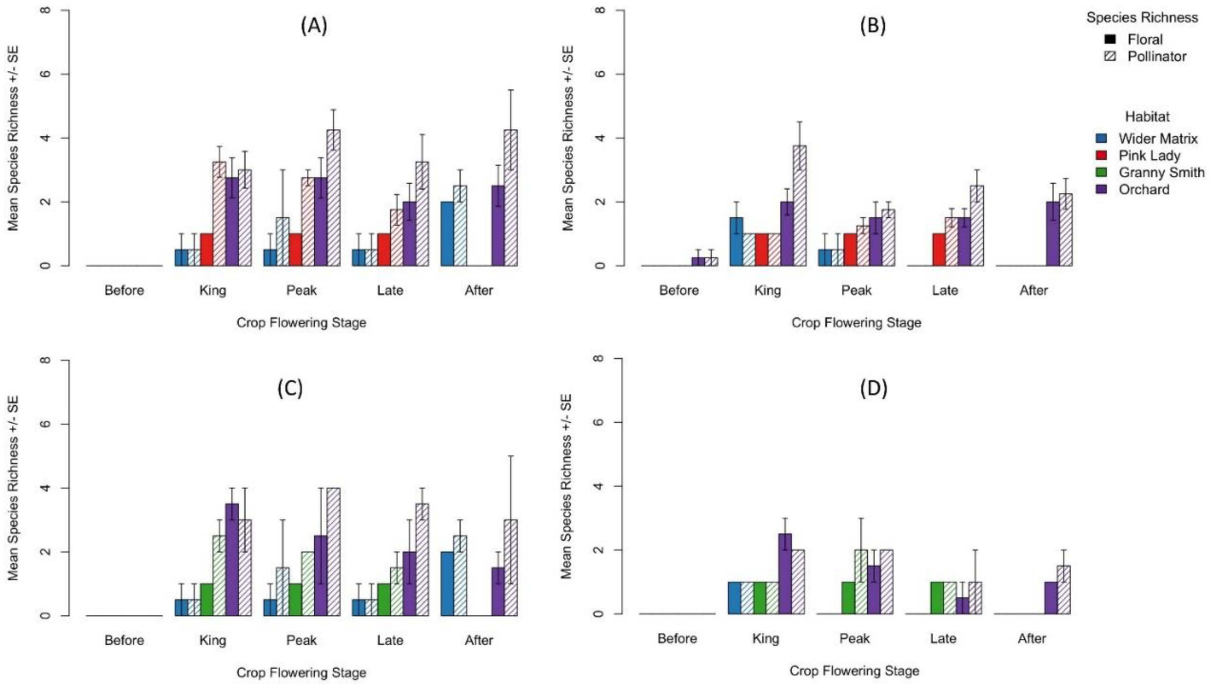

Figure 2. Mean species richness ± standard error of pollinators (solid fill) and flowering plants (hatching) within the surrounding vegetation matrix (blue), within the orchard (purple) and on Pink Lady (red) in 2017 (**A**) and 2018 (**B**) and Granny Smith (green) in 2017 (**C**) and 2018 (**D**) apple flowers (before, king, peak, late and after apple bloom) in Orange.

3.3. Influence of Co-Flowering Species on the Number of Pollinator, Honeybee and Native-Bee Visits to Apple Flowers

The total number of pollinator visits to apple flowers was positively associated with the number of visits to co-flowering species within the wider matrix ($\beta = 0.300 \pm 0.069$, $z = 4.340$, $p < 0.001$). In addition, there were slightly more visits to Pink Lady apple flowers than to Granny Smith ($\beta = 0.231 \pm 0.139$, $z = 1.656$, $p = 0.098$), and there was a significant difference in the total number of pollinator visits to apple flowers between regions, with apple flowers in Orange receiving significantly fewer visits than those in Bilpin ($\beta = -1.109 \pm 0.178$, $z = -6.235$, $p < 0.001$).

There was a significant positive relationship between co-flowering plant richness within the wider matrix and the number of honeybee visits to apple flowers ($\beta = 0.194 \pm 0.088$, $z = 2.214$, $p = 0.027$) (Table 3). Additionally, there were significantly more honeybee visits to Pink Lady apple flowers than to Granny Smith ($\beta = 0.308 \pm 0.143$, $z = 2.144$, $p = 0.032$), and there were significantly less honeybee visits to apple flowers in Orange than in Bilpin ($\beta = -0.628 \pm 0.185$, $z = -3.393$, $p < 0.001$) (Table 3).

Native bees' visits to apple flowers were positively correlated with the number of native-bee visits to co-flowering non-crop species within the orchard ($\beta = 0.508 \pm 0.236$, $z = 2.155$, $p = 0.031$), as well as the richness of co-flowering plants within the orchard ($\beta = 0.573 \pm 0.200$, $z = 2.860$, $p = 0.004$) (Table 3). However, native bees' visits to apple flowers were significantly reduced with the increasing area of flowering vegetation within the wider matrix ($\beta = -0.718 \pm 0.196$, $z = -3.667$, $p < 0.001$) (Table 3), but this trend was not observed for honeybees or when all pollinators (total visits) were combined. We also found that there were less native-bee visits to apple flowers in Orange than in Bilpin ($\beta = -3.292 \pm 0.489$, $z = -6.738$, $p < 0.0001$) (Table 3).

The best fitting model for taxonomic richness of pollinators to apple flowers only contained region, with a significantly lower richness of pollinators observed visiting apple flowers in Orange compared to Bilpin ($\beta = -0.657 \pm 0.148$, $z = -4.423$, $p < 0.0001$) (Table 3).

Table 3. The three best fitting models (with ΔAICc < 2) describing the number and species richness of pollinator visits to apples and co-flowering species within the orchard and the wider matrix. Model (1), total visitation by insect visitors to apple flowers; Model (2), honeybee visitation to apple flowers; Model (3) native-bee visitation to apple flowers; and Model (4), flower visitor richness to apple flowers. Only variables retained in the best fitting models are displayed in the table. The Models (1)–(3) were analyzed by using Generalized Linear Mixed Models with negative binomial distribution, and Model (4) was analyzed 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) [42,43].

	Intercept	SS Abundance Orchard	SS Abundance Wider Matrix	Total VisitsWider Matrix	Pollinator Richness Orchard	Plant Richness Orchard	Area NV	No. of Apple Trees	FA Wider Matrix	Apple Variety	Region	df	AICc	ΔAICc	R^2_m	R^2_c
Model (1): Total visits	4.24			0.30						+	+	6	773.8	0.00	0.64	0.68
	4.39			0.29							+	5	774.1	0.35	0.62	0.68
	3.91			0.31			0.54					5	774.5	0.76	0.61	0.69
Model (2): Honeybees	3.61					0.19				+	+	6	737.5	0.00	0.41	0.45
	3.62		0.13						0.15	+	+	7	737.9	0.42	0.39	0.47
	3.59					0.16			0.10	+	+	7	738.0	0.47	0.41	0.45
Model (3): Native bees	3.05	0.51				0.57			−0.72		+	7	500.4	0.00	0.79	0.8
	1.64	0.39				0.71	1.52		−0.77			7	500.7	0.25	0.78	0.812
	3.18	0.49	0.36					−0.40	−0.56		+	8	500.7	0.25	0.82	0.82
Model (4): Richness	1.22										+	3	294.7	0.00	0.25	0.25
	1.22				0.07						+	4	295.8	1.12	0.26	0.26
	0.94						0.31					3	296.0	1.31	0.23	0.23

SS = same species; NV = native vegetation, FA = floral area; Region = Bilpin and Orange; 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.

4. Discussion

Native-bee and honeybee visitation to apple flowers was found to increase with co-flowering plant species richness within the orchard and wider matrix, respectively. Similarly, a study by Reference [44] found that the frequency of pollinator visits was positively correlated with the number of flowering plant species, which they attribute to increasing floral resource heterogeneity. In contrast to both References [44,45], however, we did not find a significant relationship between pollinator species richness and the apple flower season (availability of food resources). We expected network connectance to decrease during peak apple flowering, with the mass crop flowering drawing pollinators from alternative floral resources—a phenomenon observed in other systems [5,13,46]—but this was not the case. Instead, network connectance was relatively even throughout the apple bloom (king, peak and late), implying that pollinator foraging preferences are not affected by the stage of apple flowering and, presumably, the abundance of apple flowers within these systems. However, these interactions may change depending on the pollinator species, co-flowering plant species, and the relative abundance [47] and evenness of the floral mix [48] within the system.

Despite native-bee visitation to apple flowers increasing with higher levels of within-orchard co-flowering species richness, native-bee visitation was reduced as the area of flowering native vegetation surrounding the orchards increased. This result may be due to lower suitability of the modified orchard landscape for the habitat requirements and nesting preferences of native bees. This includes cavity-nesting social bees such as *Tetragonula carbonaria*, the most common native bee species found in the study, as they rely upon tree hollows for nesting that are largely absent in managed orchards. In addition, structurally diverse understory vegetation (both living and dead) that provides suitable solitary bee habitat, was largely restricted to natural areas outside the orchards. The smaller foraging range of native bees [49] compared to honeybees [50] also restricts the foraging flight distance from nests within the native bushland, resulting in less opportunity for foraging range overlap with the orchards. Although we found evidence of competitive interactions between the crop and area of flowering native vegetation, for native-bee visits, it is likely that the presence of native vegetation surrounding apple orchards leads to many positive benefits in agro-pollination systems.

Without suitable nesting and foraging habitat, the overall population size of native bees would be greatly reduced, with expected corresponding declines to apple visitation [51–53]. For example, the presence of semi-natural habitat [17,54] and the availability of alternative floral resources [55,56] are both important for pollinator diversity and have been shown to influence apple visitation [57], production and quality [5,58,59]. Overall, pollinator richness and total visitation rates to apple flowers were higher in Bilpin than in Orange, which also coincides with greater co-flowering plant richness, greater abundance and larger area of co-flowering species, predominantly due to the presence of large tracts of native vegetation in the National Parks surrounding the orchards in Bilpin. Therefore, management strategies such as retaining or restoring native areas within orchards should be encouraged to promote native-bee visitation within the orchard.

Both pollinator richness and abundance were lower before and after the apple flowering season presumably due to fewer plant species flowering throughout these periods and the typically suboptimal (early spring) temperatures experienced before the apple flowering for native bees such as *T. carbonaria* [60]. In both years, large differences between networks from different regions (Bilpin and Orange) and, to a lesser extent, apple varieties (Granny Smith and Pink Lady) were identified. However, throughout the apple flowering season, networks were similar. This suggests that the number of open apple flowers (i.e., resource abundance) has little effect on the local plant–pollinator networks compared to outside of the crop flowering period and was relatively unaffected by interannual and/or regional variation.

Pollinator-species richness was generally higher within orchards surrounded by a more diverse floral matrix. Numerous studies within agricultural systems have reported declining diversity and abundance of insect crop visitors with increasing distance from native vegetation or non-crop floral resources such as hedgerows (references within References [16,61]), e.g., in grapefruit [62], mango [63] and strawberry [64] farms. Our results align with the findings of Carvalheiro et al. [22], who found that the experimental addition of small patches of native flowers increased the abundance and diversity of flower visitors to mango orchards in close proximity, relative to those farther away, and that the diversity and abundance of mango visitors were highest in orchards located close to natural vegetation [22].

It is known that interactions between co-flowering plants and shared pollinators can either be facilitative, via increased visitation due to improved attraction or maintenance of resident pollinator populations [65,66], or competitive, via heterogenous pollen deposition [67] and competition for pollinator visits [68]. Our study found that the flowering of plant species within the orchard and the matrix overlapped largely with the apple flowering season, with coinciding peaks in flowering events. When co-flowering species richness was sufficiently high, there was increased native-bee (*T. carbonaria*, and to a much lesser extent *Lasioglossum* spp., *Exoneura* spp. and *Homalictus* spp. combined) and honeybee (*A. mellifera*) visitation to apple flowers. Co-flowering plant richness was typically highest within the orchard with introduced weeds such as dandelion, plantago and clover the most commonly visited. The importance of both clover and dandelion in providing nectar for pollinators within farmlands in the United Kingdom has been highlighted by Timberlake et al. [69]. They found that, for bumblebees, clover provided a large amount of nectar, whilst dandelions supplied nectar during periods when other floral resources were limited. Although there are no bumblebees in Mainland Australia, it is highly likely that the resources provided by other exotic weedy species are important for many pollinators within these systems, as well.

There was significant overlap in the assemblage of pollinators to apple and other co-flowering native species within the wider matrix. The potential movement of pollinators between native environments and crops (cross-habitat spillover) can be highly important for crop pollination [1,17], but it can also have effects on the pollinator networks and pollination of wild plants that surround agricultural areas [4,70]. Of particular note, we found that many native plants were most frequently visited by the introduced honeybee *A. mellifera*, and that the most common native bee, *T. carbonaria* (Bilpin only), was rarely seen visiting native plants during the study period, despite showing high abundance on introduced weeds and apple flowers; this could have consequences for native plant reproduction. There is evidence that *A. mellifera* can differ in its foraging behavior, particularly in regard to the number of intra and inter plant movements between flowers, compared to native pollinator species [18,19,71]. However, it is often unclear how differences in honeybee foraging behavior, in turn, can affect seed set [19,72,73]. Understanding the potential for pollinator sharing and spillover between agricultural systems and nearby adjacent native vegetation is particularly important in systems augmented by introduced pollinators and for crops that benefit from native pollinators [24,25,74,75].

5. Conclusions

Plant–pollinator networks are dynamic, and interactions between species can shift from positive to negative depending on the context. We found that native-bee and honeybee visitation to apple flowers increased with co-flowering plant species' richness within the orchard and wider matrix, respectively. Native-bee visitation to apple flowers was, however, lower with increasing area of co-flowering plant species within the wider matrix. Our findings indicate substantial overlap in the pollinator assemblage visiting co-flowering plants and apple flowers, with pollinators dominated by the introduced honeybee, native bees and, to a lesser extent, flies and butterflies. We found higher pollinator richness in the region that had a greater area of native vegetation and higher floral richness. Our study highlights the importance of flowering plant species' diversity and abundance for pollinator diversity within horticultural landscapes. Therefore, conserving or planting flowering species within orchards and their surrounding landscapes are important mechanisms for supporting robust pollinator networks that can provide stable and sustainable pollination services for horticultural crops into the future.

Supplementary Materials: The following supporting information can be downloaded at https://www.mdpi.com/article/10.3390/agriculture12081246/s1. Figure S1: Bipartite plant–pollinator network analysis for each time period (before, king, peak, late and after apple bloom) in Bilpin for co-flowering plants within the orchard (Orchard), the wider vegetation matrix (WM) and on Granny Smith (GS) and Pink Lady apple flowers (PL) in 2017 and 2018. Pollinator species observed are abbreviated as follows: Api = *Apis mellifera*, Coc = *Coccinellidae* spp., Col = *Coleoptera* spp., Cul = *Culicidae* spp., Cur = *Curculionidae* spp., Dip = *Diptera* spp., Exo = *Exoneura* spp., For = *Formicidae* spp., Hom = *Homalictus* spp., Las = *Lasioglossum* spp., Lau = *Lauxaniidae* sp., Lep = *Lepidoptera* spp., Lyc = *Lycenidae* spp., Meg = *Megachilidae* spp., Mer = *Meroglossa* sp., Syr = *Syrphidae* spp. and Tet = *Tetragonula carbonaria*. Figure S2: Bipartite plant–pollinator network analysis for each time period (before, king, peak, late and after apple bloom) in Orange for co-flowering plants within the orchard (Orchard), the wider vegetation matrix (WM) and on Granny Smith (GS) and Pink Lady apple flowers (PL) in 2017 and 2018. Pollinator species observed are abbreviated as follows: Api = *Apis mellifera*, Coc = *Coccinellidae* spp., Dip = *Diptera* spp., Hom = *Homalictus* spp., Las = *Lasioglossum* spp., Lep = *Lepidoptera* spp., Lyc = *Lycaenidae* spp., Meg = *Megachilidae* spp. and Syr = *Syrphidae* spp. Table S1: List of flowering plant species observed during the study period in Bilpin and Orange. Table S2: List of flower visitor species observed throughout the study period in 2017 and 2018 in Bilpin and Orange.

Author Contributions: A.-M.G., S.A.P. and J.M.C. designed the study; A.-M.G. and L.E.B. undertook the field work and collected the data; A.-M.G., C.K. and C.O. analyzed the data; all authors contributed to the writing of the manuscript. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement: The data presented in this study are available on request from the corresponding author.

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