

# Organic dairy farming: impacts on insect–flower interaction networks and pollination

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## Summary

1. Pollination interactions comprise a network of connections between flowers and insect visitors. They are crucial for reproductive success in many angiosperms but are threatened by intensive agricultural practices. Although less intensive approaches, including organic farming, could improve farmland biodiversity, it is not clear whether or not these approaches enhance wild plant pollination and the stability of insect–flower interaction networks.

2. We investigated the effects of organic vs. conventional farming on insect–flower interaction network size and structure, bee and hoverfly diversity, and pollination in 10 pairs of organic and conventional dairy farms in the Republic of Ireland.

3. We found that insect–flower interaction networks on organic farms were larger and more asymmetrically structured than networks on conventional farms. Overall, however, networks contained fewer taxa and niche overlap and plant/animal ratios were relatively low compared with previously documented insect–flower interaction networks. Organic farms did attract higher numbers of bees partly because of higher floral abundances (mainly *Trifolium* sp.). Hoverfly evenness was greater in organic farms but neither abundance, richness nor evenness was related to floral abundance, suggesting organic farms provide additional resources for hoverflies. Pollination of *Crataegus monogyna* hawthorn was higher on organic farms, although pollen deposition was limited.

4. *Synthesis and applications.* Organic dairy farming can increase the size and alter the structure of insect–flower interaction networks. However, network stability was not improved and all networks (organic and conventional) were vulnerable because of their small size, low niche overlap and low plant/animal ratios. Nonetheless, organic farming provided more flowers that attracted more flower visitors and improved pollination of *C. monogyna*. We suggest that strategic management of important flowers for pollinators in hedgerows and pastures should be endorsed in agri-environmental schemes. Sowing *Trifolium* spp., and allowing these plants to flower, could benefit bees, but more research into hoverfly ecology is necessary before realistic conservation recommendations can be made for this group. We conclude that organic farming, although not the solution in its present form, can benefit insect biodiversity, insect–flower interaction networks and insect-mediated pollination.

**Key-words:** agri-environmental schemes, bees, conventional farming, hedgerows, hoverflies, intensive grasslands, network structure, pollen limitation, specialization asymmetry, *Trifolium* sp.

## Introduction

Many wild plant populations and agricultural crops are dependent on pollination services provided by wild pollinators, such as bees, hoverflies and butterflies (Free 1993; Biesmeijer *et al.* 2006). However, wild pollinators have been negatively affected by agricultural intensification and numerous pollinating taxa are now in decline in Europe and North America (Steffan-

Dewenter, Potts & Packer 2005). Bees are considered the most effective pollinators of wild plants but hoverflies have also been shown to provide significant pollination services (Gyan & Woodell 1987a; Sugiura 1996; Vance, Bernhardt & Edens 2004). Few studies have investigated the effects of land-use change on hoverflies (e.g. Jauker *et al.* 2009; Meyer, Jauker & Steffan-Dewenter 2009).

In theory, organic farming (European Union Regulation 2092/91/EEC) should increase biodiversity because it is less intensive than conventional farming (Bengtsson, Ahnstrom &

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Weibull 2005). Beneficial effects of organic farming on plant and pollinator diversity have been reported for arable systems (Bengtsson, Ahnstrom & Weibull 2005; Morandin & Winston 2005), but few studies have compared the biodiversity of organically and conventionally managed grasslands (but see Potts *et al.* 2009). Also, the majority of studies to date on grassland biodiversity relate to species-rich or 'high biological value' grasslands. This is unfortunate given that intensive management is dominant in most lowland grasslands, representing millions of hectares in Europe (Plantureux, Peeters & McCracken 2005). In the Republic of Ireland, more than 80% of agricultural land is permanent grassland, mostly intensively managed (Department of Agriculture, 2009). Intensive grasslands receive high fertilizer application rates and frequent intensive defoliation which optimizes harvested forage quality but results in degraded species pools and structurally homogeneous swards (Vickery *et al.* 2001). Organically managed grasslands would be considered less intensive than conventional grasslands owing to: prohibition of chemical fertilizers and pesticides; encouragement of nitrogen fixation (through planting of *Trifolium* spp. and reduction in manure and slurry fertilizer inputs) and lower grazing intensities. However, both organic and conventional grasslands are still intensive grasslands because they receive anthropogenic disturbance above and beyond the capacity for most disturbance/nutrient sensitive plant species to survive.

This study focused on the role of organically vs. conventionally managed dairy grasslands in supporting wild flower-visitor communities and wild plant pollination. We investigated whether farm management influences insect-flower interaction network size and structure. Insect-flower interaction networks consist of interactions between communities of insects and plants that generally result in mutualistic benefits. In addition to traditional parameters for assessing impacts on biological communities, such as species abundance, richness and diversity indices, network analysis can be used to detect underlying changes to community structure, species interactions and ecosystem function (Tylianakis, Tscharntke & Lewis 2007). Interest in the structure of insect-flower interaction networks has grown in recent years because they allow characterization of the stability of pollination systems (Vázquez *et al.* 2009). We use this methodology to gain understanding of the pollination systems that persist in disturbed grassland habitats.

It is becoming clear that bees and hoverflies respond to habitat change in different ways (Kleijn & van Langevelde 2006; Jauker *et al.* 2009) and conservation actions that encourage bees may not necessarily favour hoverflies. It is not known how both bee and hoverfly assemblages are influenced by farming system in intensive grasslands. Therefore, our second hypothesis was that organic farming positively affects bee and hoverfly abundance, richness and evenness. Our study focused on the farm scale and within the local scale of the farm by comparing field centres with edges.

For plants, inadequate pollination services can lead to pollen limitation which can result in reduced seed/fruit set (Knight *et al.* 2005). For this reason, it is not enough to quantify insect assemblages and their flower visitation rates,

without exploring actual plant reproductive success. Therefore, our third hypothesis was that farm management influences pollination success of a common hedgerow species. This is the first study to investigate relationships between insect-flower interaction networks, insect diversity and pollination in relation to farming system.

## Materials and methods

### STUDY SITES

Ten matched pairs of organic (managed according to the European Union Regulation 2092/91/EEC) and conventional (not managed according to organic regulations) dairy farms in lowland permanent grassland (not ploughed or reseeded for at least 8 years) in the Republic of Ireland were selected (see Table S1, Supporting information). Organic farms were certified for 11.5 years on average (range: 7–20 years), following a 2-year conversion period. Pairs were matched on geology, soil type and climatic similarity. Farms within a pair were 1–4 km apart, in central and southern Ireland (see Fig. S1, Supporting information), which is characterized by well-drained, fertile soils used predominantly for dairy/drystock farming. Average Livestock Units per hectare on organic farms were 1.5, compared with 2.5 on conventional farms.

### SURVEYS OF FLOWER VISITORS AND FLOWERING PLANTS

Two fields from each farm were surveyed three times each between May and July 2009 using standard line transects (Pollard 1977; Westphal *et al.* 2008). Transects 100 × 2 m were walked slowly (10–15 m min<sup>-1</sup>) along the edge (stock-proof hedgerows) and in the centre (30 m from the edge) of every field (12 transects in total per site). All bees (Hymenoptera: Apidae), hoverflies (Diptera: Syrphidae) and butterflies (Lepidoptera) observed within transects were recorded, together with each individual's activity (feeding or not-feeding). If feeding, the respective flower species was noted. In addition to these obligate flower visitors, there may be other facultative flower-visiting taxa which act as pollinators in the study sites (including beetles, flies, etc.). However, we focused on bees and hoverflies because they are the most important and, often, the most effective pollinators of wild plants (Gyan & Woodell 1987a; Sugiura 1996; Vance, Bernhardt & Edens 2004). Specimens that could not be identified on the wing were caught, frozen and identified in the laboratory. Bumblebees (*Bombus* spp.), honeybees *Apis mellifera*, butterflies and solitary bees were identified to species and hoverflies to genus (using: Westrich 1989; Stubbs 2002; Shackleton, Nash & Lewington 2004; Edwards & Jenner 2005) (except for *Bombus terrestris* and *Bombus lucorum*, which were aggregated because of difficulties in distinguishing between them and other cryptic species using morphological methods; Murray *et al.* 2008; Wolf, Rohde & Moritz 2010). Both farms within a pair were visited on the same day and timing of visits within a pair, during the three survey periods, were alternated between morning and afternoon so as to reduce temporal biases. Surveys were conducted between 10:00 and 17:00 on days when ambient temperature was 14 °C or above with no rain or strong winds. Air temperature (°C), wind speed (Beaufort scale) and percentage cloud cover were noted for each transect.

Data on floral abundance and species richness were recorded in every transect in each survey. For every herbaceous flowering plant (excluding grasses, sedges and rushes), species identity (using Stace 2010) and the number of flowering units was estimated in 10 quadrats

per transect (two 1 m<sup>2</sup> quadrats every 20 m along transect). Flowering units were defined as an individual flower or compact inflorescence such that a medium-sized bee has to fly rather than walk between to reach another flowering unit (Dicks, Corbet & Pywell 2002).

Floral unit abundance and abundance, richness and evenness (Shannon Evenness) of bee species (bumblebees and solitary bees combined), hoverfly genera and butterfly species were calculated at the farm level, where edge and, separately, centre transects from three survey periods and two fields surveyed per site were pooled. Species accumulation curves were plotted to ensure the asymptote was reached before evenness was calculated. Butterflies were too rare at sites to be analysed but were included in interaction networks (see next).

#### NETWORK ANALYSIS

A data matrix was constructed for each organic and conventional farm containing the total number of visits observed for each insect–flower interaction over the entire study period. Each matrix was illustrated by a quantitative interaction web (bipartite visitation graph), where a line between two vertices represents an interaction between an insect and a plant species. The interaction webs were then characterized by qualitative and quantitative network parameters using the ‘networklevel’ command in the bipartite package (Dormann *et al.* 2009) in *R* (R Development Core Team 2007). Quantitative parameters weight interactions according to their frequency which makes them less sensitive to sampling intensity and network size. Qualitative parameters included: number of plant and insect taxa in each network and the number of insect–flower interactions. The quantitative parameters calculated were: (i) Generality (weighted mean number of plant species per visitor species). (ii) Vulnerability (weighted mean number of visitors per plant species). (iii) Quantitative connectance (the realized proportion of all possible interactions weighted by the quantitative visitation rate of each species; Bersier, Banasek-Richter & Cattin 2002; Kaiser-Bunbury, Memmott & Müller 2009). (iv) Specialization asymmetry  $d'_i$  (quantification of the imbalance between the interaction strengths of a species pair (Blüthgen *et al.* 2007; Dormann *et al.* 2009) in which singleton species were omitted (Dormann *et al.* 2009) and the effect of variation in observation totals was removed (Blüthgen *et al.* 2007); with 0 indicating high symmetry, and values close to 1 or –1 indicating high asymmetry in terms of specialization by insects or plants, respectively). (v) Niche overlap (mean similarity in interaction pattern between species of the same trophic level; values near 0 indicate no common use of niches, whereas 1 indicates perfect niche overlap; Dormann *et al.* 2009).

#### POLLINATION

Pollination was measured on all organic and conventional farms using *Crataegus monogyna* Jacq., hawthorn, as a model species. *Crataegus monogyna* was chosen because it is visited by bees, hoverflies and butterflies; it is self-incompatible (Grime, Hodgson & Hunt 2007); its flowers were located in field edges so disturbance by livestock was minimized; and it was the only suitable species naturally abundant at all study sites. We verified the reliance of *C. monogyna* on cross pollination: when insects were prevented from visiting 200 flowers using bridal veil netting, only four flowers (2%) produced fruit.

To assess natural levels of pollination, at each site 20 flowers (one per plant) in bud were marked and subsequently examined when fruits were beginning to form. Pollination was determined to have occurred if the hypanthium/ovary had swollen to form an immature

fruit (i.e. the hypanthium had not withered). Fruit set was calculated as the ratio of pollinated vs. unpollinated flowers for each site.

Pollen limitation was investigated by conducting supplemental hand-pollination experiments on an additional 20 flowers per site. Flowers were marked whilst in bud, and once opened were supplementally hand pollinated using the stamens from flowers of different *C. monogyna* individuals along the same hedgerow. Before and after supplemental pollination, flowers were accessible to insects. Fruit set of experimental plants was determined 6 weeks after hand-pollination.

#### STATISTICAL ANALYSIS

Network parameters and fruit set of open/supplementally pollinated flowers were investigated for differences between farming system (organic/conventional), whereas abundance/richness/evenness of bee/hoverfly taxa and floral abundance were tested for differences between farming system and position in field (edge/centre). Network parameters and abundance/richness/evenness of bee/hoverfly taxa and floral abundance were analysed using Linear Mixed Effects Models and fruit set of open/supplementally pollinated flowers was analysed using Binomial GLMM (cbind function). We accounted for spatial autocorrelation by including random terms: farm pair (1–10) and, when applicable, location-within-field (edge/centre). Plant species number (in networks), generality, floral abundance and hoverfly richness were square root transformed [ $\sqrt{(x + 1)}$ ] and bee and hoverfly abundances were log transformed [ $\ln(x + 1)$ ] to achieve normality. In floral abundance and network models: farming system was included as a fixed effect. Floral abundance was included as a fixed effect, interacting with farming system, in the generality and ‘number of insect–flower interactions’ network models. Insect abundance (all bees, hoverflies and butterflies: feeding and non-feeding) was included as a fixed effect, interacting with farming system, in the vulnerability and specialization asymmetry network models. In the bee/hoverfly models: farming system, edge/centre, floral abundance, wind speed, air temperature, percentage cloud cover and bee/hoverfly abundance (see explanation in the following) were included as fixed effects as well as two-way and three-way interactions between farming system, edge/centre and floral abundance. In the richness and evenness models samples containing zero or one individual were removed and abundance was added as a fixed effect to ensure that richness and evenness models were independent from abundance models. Floral species richness was correlated with floral abundance ( $r = 0.257$ ,  $P = 0.001$ ) and so was not analysed further. In the fruit set models: treatment (with four levels: Organic-Open, Conventional-Open, Organic-Supplemental and Conventional-Supplemental) was included as a fixed effect. Models were simplified by removing first non-significant interactions ( $P > 0.05$ ) and then any non-significant main effects (that were not constituent within a significant interaction). For model validation and model adequacy assessment, we followed Zuur *et al.* (2009). Statistical analysis was carried out using nlme (Pinheiro *et al.* 2009) and lme4 (Bates & Sarkar 2006) packages in *R* (R Development Core Team 2007).

#### Results

In total, 504 bees (439 bumblebees, 57 honeybees and 8 solitary bees) were found from five bumblebee species, one honeybee species and three solitary bee species. A total of 832 hoverflies from 17 genera were found. Fewer butterfly individuals were

recorded: 164 individuals of seven species. There were 39 species of flowering plant. *Trifolium repens* L. white clover was the most abundant flowering species in organic farms, with 3382 floral units in field centres, whereas only 177 *T. repens* floral units were counted in conventional centres. *Bellis perennis* L. common daisy was the most abundant flower in conventional farms with 568 floral units counted (compared with 1188 units in organic farms).

#### FLOWER VISITORS AND FARMING SYSTEM

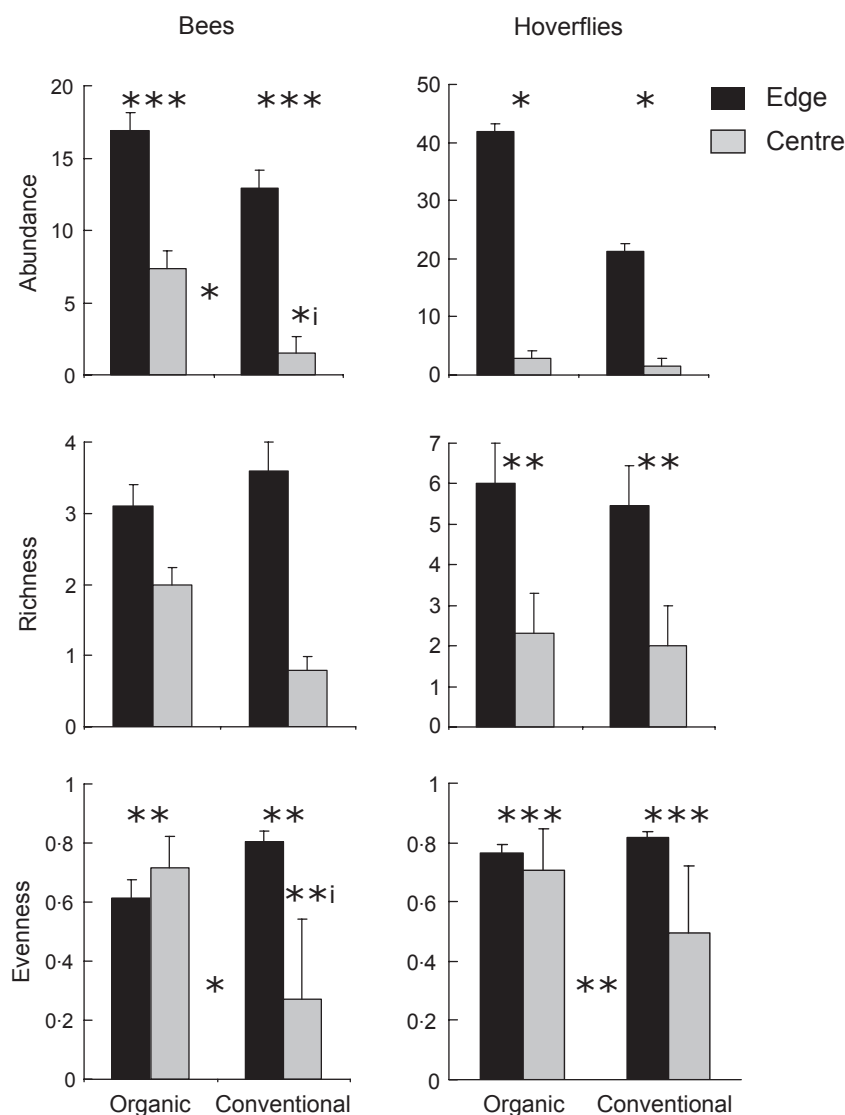
Bee abundance and evenness were significantly higher on organic farms than conventional ones but bee species richness was not (Fig. 1, see Table S2, Supporting information). Independent of farming system, bee abundance and evenness were significantly lower in field centres compared with edges, and this pattern was more pronounced in conventional farms (farm type  $\times$  edge/centre; Table S2, Supporting information, Fig. 1). Bee abundance was positively related to floral abundance, which was higher on organic farms ( $t_9 = 5.52$ ,  $P < 0.001$ ) and particularly high in organic field centres

( $t_{18} = 3.45$ ,  $P = 0.003$ ) compared with conventional centres (Fig. S2, Supporting information). Bee abundance, richness and evenness were not related to environmental conditions.

Hoverfly abundance and richness were independent of farming system, but hoverfly evenness was significantly higher in organic compared with conventional farms (Table S2, Supporting information, Fig. 1). Also, hoverfly abundance, richness and evenness were lower in field centres compared to edges, regardless of farming system. Hoverfly evenness was negatively affected by wind speed (Table S2, Supporting information).

#### INSECT–FLOWER INTERACTION NETWORKS AND FARMING SYSTEM

Organic and conventional insect–flower communities differed in size and composition. Although the number of insect species was similar between organic and conventional networks, significantly more plant species were visited within organic networks and, subsequently, generality was higher in the organic networks (Table 1, Fig. 2, see Figs S3–S11, Supporting infor-



**Fig. 1.** Geometric mean (+SE) abundance, richness and evenness of bees (bumblebees and solitary bee species) and hoverflies (genera) in edges and centres of organic and conventional fields. Significant differences in abundance/richness/evenness between organic and conventional or the edges and centres of all fields (independent of farming system) are illustrated by asterisks (\* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ ). Significant interactions between farm type and edge/centre are shown by '\*i' or '\*e'. Non-significant differences are not included.



**Table 1.** Mean ( $\pm$ SE) network parameter values for organic and conventional farms including significance levels, *t*-values and d.f. for explanatory variables obtained from Linear Mixed Effects Models

Qualitative parameters	Organic Mean $\pm$ SE	Conventional Mean $\pm$ SE	Explanatory variables	<i>t</i> -value	d.f.	<i>P</i> -value
Number of insect taxa	7.80 $\pm$ 0.57	7.4 $\pm$ 0.65	Farm type	–	–	NS
Number of plant species	6.30 $\pm$ 0.67	4.5 $\pm$ 0.37	Farm type	3.32	9	0.009
Number of interactions	14.30 $\pm$ 1.60	10.30 $\pm$ 1.10	Farm type	2.335	9	0.044
			Flower abundance	–	–	NS
			Farm type $\times$ flower abundance	–	–	NS
Quantitative parameters						
Generality	2.07 $\pm$ 0.22	1.61 $\pm$ 0.13	Farm type	–2.151	7	0.067
			Flower abundance	–	–	NS
			Farm type $\times$ flower abundance	2.60	7	0.035
Vulnerability	3.03 $\pm$ 0.21	2.92 $\pm$ 0.32	Farm type	–2.561	8	0.034
			Insect abundance	3.985	8	0.004
			Farm type $\times$ insect abundance	–	–	NS
Connectance	0.19 $\pm$ 0.01	0.19 $\pm$ 0.01	Farm type	–	–	NS
Specialization asymmetry	–0.21 $\pm$ 0.05	–0.20 $\pm$ 0.08	Farm type	2.413	8	0.042
			Insect abundance	–3.496	8	0.008
			Flower abundance	–	–	NS
Insect niche overlap	0.48 $\pm$ 0.04	0.42 $\pm$ 0.09	Farm type	–	–	NS

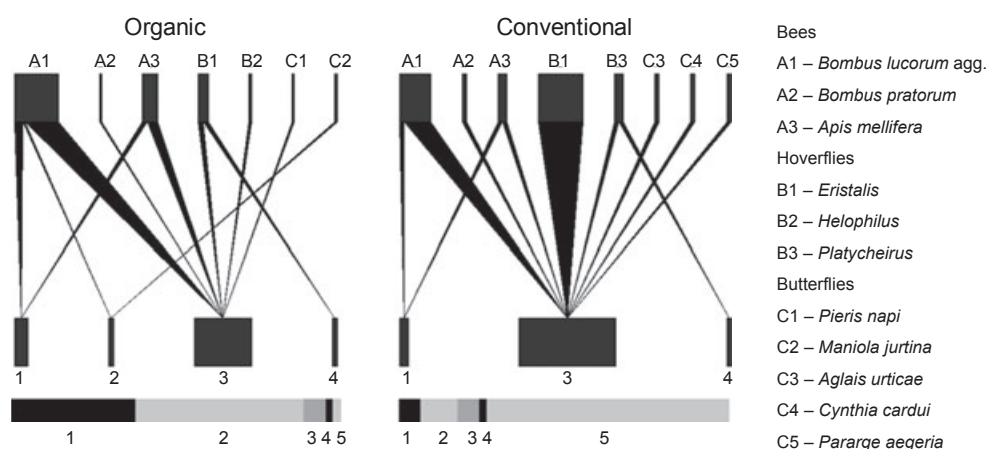
mation). Vulnerability and the number of insect–flower interactions were higher in organic networks but there were no interaction effects between farm type and flower abundance or insect abundance, respectively. Vulnerability was positively related to insect abundance. Insect species out-numbered plants in ratios of 1 : 1.2 for organic networks and 1 : 1.6 for conventional networks.

Organic and conventional networks were quite similar in terms of topology and structure. Quantitative connectance and niche overlap for plants and insects were the same in organic and conventional networks. Niche overlap was high for insects and low for plants. Although the majority of networks (65%)

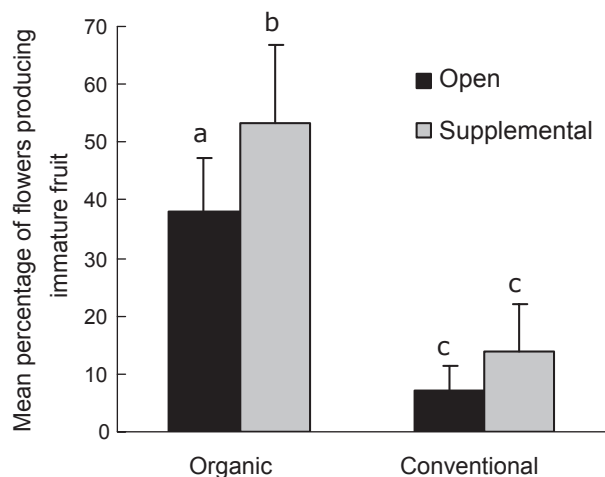
were found to have moderately asymmetrical structures (with plant species being more specialized than insect taxa), organic networks were significantly more asymmetrical than conventional networks which varied widely in structure (ranging from symmetrical to highly asymmetrical). Specialization asymmetry was significantly related to insect abundance on farms.

#### POLLINATION AND FARMING SYSTEM

Fruit set of *C. monogyna* flowers was significantly higher on organic compared with conventional farms for both open pollinated ( $P = 0.002$ ) and supplementally pollinated



**Fig. 2.** One of 10 pairs of organic and conventional insect–flower interaction networks. The bottom levels of each network show plant species (numbered 1–4) visited by insect taxa listed on the top levels. Plant bar thickness is in proportion to the frequency of visitation by insects. The lines between the two levels represent interactions between insect and plant species with line thickness indicating interaction frequency. Floral abundance is displayed in a composite column graph beneath each network as percentage of floral units of the top five most abundant species (representing 98% of total flower abundance at these two farms) in transects. Plant species are: 1 = *Trifolium repens*; 2 = *Ranunculus repens* L.; 3 = *Rubus fruticosus* agg.; 4 = *Heracleum sphondylium* L.; 5 = *Bellis perennis*. Note that full networks (containing bees/butterflies/hoverflies and all their observed interactions with flowers on a farm during the study period) are displayed. Any plant species in the composite column graphs but not in the networks were not observed receiving visits by bees, hoverflies or butterflies in this farm pair.



**Fig. 3.** Mean (+SE) percentage of *Crataegus monogyna* flowers that set fruit after being either supplementally pollinated or left as open pollinated controls on organic and conventional farms. Letters above the bars indicate significant differences among treatments.

( $P < 0.001$ ) flowers (Fig. 3). *Crataegus monogyna* flowers were found to be pollen limited (supplemental fruit set > open fruit set) on organic farms ( $P = 0.006$ ) but not on conventional farms ( $P = 0.423$ ) (Fig. 3).

## Discussion

### INSECT–FLOWER INTERACTION NETWORKS AND FARMING SYSTEM

Insect–flower interaction networks on organic farms were bigger and differed in composition from networks on conventional farms. Insects visited more plant species (had higher generality) as a result of higher floral abundance on organic farms. In addition, plant species received more insect visits (higher vulnerability) on organic farms, which was positively influenced by insect abundance. Intensive grassland networks differed in size and composition, and particularly in floral abundance, depending on management (organic vs. conventional). To date, differences in food web size and structure (plant, herbivore, parasitoid) have been described for organic and conventional mixed arable farms only (Macfadyen *et al.* 2009).

All insect–flower interaction networks had low to moderately asymmetrical structures, with more specialized plant species than insects. This is in accordance with previous work, although our networks are less asymmetric than generally found elsewhere (e.g. Bascompte, Jordano & Olesen 2006; Vázquez *et al.* 2007). Interestingly, networks on organic farms were less variable in structure and more asymmetrical than those on conventional farms. More stable associations between mutualistic communities can be generated by interaction asymmetries (Bascompte, Jordano & Olesen 2006; Kaiser-Bunbury *et al.* 2010) because it is more beneficial for a specialist species to rely on a generalist species (asymmetry) rather than on another specialist (symmetry), in case the other specialist

becomes less reliable and both specialist partners are then vulnerable to co-extinction (Blüthgen 2010). Therefore, the networks on organic farms in our study may be more stable than those on conventional farms. Differences in specialization asymmetries may be partly related to species richness and abundance, for example: floral abundance can influence interaction strength asymmetry (Vázquez *et al.* 2007), and we found more flowers and bees on organic farms.

However, we did not find a relationship between floral abundance and specialization asymmetry (similar to interaction strength asymmetry; Vázquez *et al.* 2007; Dormann *et al.* 2009; Blüthgen 2010), which suggests that floral abundance is not the most important determinant of insect–flower interaction network structure in grasslands. The quality of floral reward (i.e. its nutritional suitability for each consumer or ‘trait complementarity’) and its accessibility (to each consumer, i.e. the presence/absence of ‘exploitation barriers’), may be important as well as quantity (Stang *et al.* 2009). For example, *Rubus fruticosus* agg. flowers were not as abundant as other species, but attracted the highest proportion of insect visits, possibly because its pollen contains high percentages of essential amino acids and protein (Hanley *et al.* 2008), and large volumes of nectar are produced (Gyan & Woodell 1987b) in open flowers that are accessible to a variety of flower visitors (Muller 1881).

As insect (feeding and non-feeding) abundance increased, plants apparently became more specialized. This could be the result of some taxa foraging on previously less-favoured plants when visitor abundance was higher (Fontaine *et al.* 2008) because these plants became relatively rewarding in the presence of increased competition. However, not all insect taxa would be able to do this (because of trait complementarity and exploitation barriers; Stang *et al.* 2009), resulting in apparent increases in plant specialization as new plants are included in the network, but only by those insects that are able to exploit them.

The stability of insect–flower communities is thought to increase with a high degree of redundancy in insects (Memmott, Waser & Price 2004) because if a taxon is redundant in a network (has a similar interaction pattern to other species of the same trophic level) then its loss will not greatly destabilize the system. We found that there was a medium level of overlap (c. 45%), in both farm types, between the niches of insect taxa in our networks and the ratio of plants to insects was lower than that found in other networks (usually 1 : 4; Memmott, Waser & Price 2004; Jordano, Bascompte & Olesen 2006; Vázquez *et al.* 2009) which implies an inadequate level of insect redundancy (Memmott, Waser & Price 2004). All networks in our study were quite small, containing on average only 20 species. Even though our networks contain plant species that can reproduce without pollinators (e.g. *R. fruticosus* agg.), they will not be immune to insect taxa loss because inadequate insect redundancy and small network size may actually facilitate alterations in the system (i.e. changes in floral abundance, insect behaviour or abundance) resulting in increased vulnerability of insect-pollinated plants.

Quantitative connectance on organic and conventional farms was similar with networks dominated by well-connected

generalist taxa, such as *B. lucorum* agg., *Eristalis* hoverflies and *R. fruticosus* agg. Removal of the most highly connected species (plant or insect) can cause rapid network collapse (Memmott, Waser & Price 2004) and is a likely event in intensive grasslands particularly in relation to plant species loss. Management activities such as silage and hedge cutting, topping (standardising grass height by cutting to an acceptable post-grazing height of *c.* 5 cm) and intensive grazing may remove the flowers of many plant species, effectively causing their 'extinction' from the network (at least temporarily). This effect may be exacerbated in our networks as the species pool is small, so the opportunity for insects to switch interaction partners (re-wiring) is low and therefore the networks could be greatly destabilized (Kaiser-Bunbury *et al.* 2010). Although organic farming can increase the size and specialization asymmetry of networks, the differences may be still too small to improve network stability and secure against future perturbations. Therefore, efforts should be made to retain and improve biodiversity by including measures in agri-environmental schemes that seek to maintain a constant floral abundance in intensive farms, particularly in relation to species that yield the highest reward for pollinators.

#### FLOWER VISITORS AND FARMING SYSTEM

As in previous studies (Rundlof, Nilsson & Smith 2008; Potts *et al.* 2009), the higher abundance and evenness of bees on organic farms was probably because of a higher abundance of flowers. The latter is likely to be a result of lower stocking densities, which alleviates grazing pressure and allows time for flowers to emerge. In addition, nitrogen-fixing legumes, such as *Trifolium* species are encouraged in organic systems as an alternative to chemical nitrogen fertilizers (Ledgard, Penno & Sprosen 1999) and were abundant in our organic farms. *Trifolium* species provide important food resources for bees (Pywell *et al.* 2005) as their pollen contains high percentages of essential amino acids and protein (Hanley *et al.* 2008). On conventional farms, *B. perennis* was the most abundant flower species, but it produces small quantities of low-sugar nectar (Schultz & Dlugosch 1999) and is not a valuable food source for bees (Fussell & Corbet 1992).

Hoverflies respond to habitat change differently to bees (Biesmeijer *et al.* 2006; Kleijn & van Langevelde 2006; Jauker *et al.* 2009). Hoverfly genera evenness (but not abundance or richness) was higher on our organic grasslands but, in contrast to previous studies (Kleijn & van Langevelde 2006; Meyer, Jauker & Steffan-Dewenter 2009) and to our findings for bees, there was no relationship between hoverflies and floral abundance, despite adults requiring nectar and pollen as food (Haslett 1989). Since some hoverfly species also feed on graminoid (grasses, sedges, rushes) pollen (Branquart & Hemptinne 2000; Speight 2008), and we did not count graminoid flowers, the lack of association in our study may be misleading. Unlike bees, hoverfly larvae do not require floral resources (Speight 2008). Therefore, the availability of larval microhabitats and food resources may be more important than floral abundance and requires further research.

Bees and hoverflies were significantly more associated with field edges than field centres, despite flower availability in the centres of fields. This may be because bees tend to follow linear features, possibly using them as navigational aids (Cranmer 2004). Wind speed and field boundary height are known to restrict hoverfly movement and cause them to accumulate near field boundaries (Wratten *et al.* 2003), for example, hoverfly evenness was negatively affected by wind speed in the present study. Hedgerows also offer the best food resources over the season (Jacobs *et al.* 2009) and give protection from predators and disturbance by livestock. Efforts to retain existing hedgerows and promote re-planting should be encouraged.

#### POLLINATION AND FARMING SYSTEM

Most pollination network studies have not addressed the links between observed insect assemblages and pollination (Ricketts *et al.* 2008). We used a single model species to gain a better insight into the effects of farm management on pollination. Clearly, pollination success would best be recorded for as many species in the community as possible, but owing to large variations in the presence of suitable plant species among sites, we could only use a single species. Despite this limitation, our study demonstrates farm management effects on pollination. Fruit set of openly pollinated *C. monogyna* flowers was significantly higher on organic farms. Here, we found more insect visitors, which presumably facilitated higher levels of pollination. Similar results have been found for canola crops (*Brassica rapa* and *Brassica napus*) (Morandin & Winston 2005). *Crataegus monogyna* was found to be pollen limited on organic farms, which is in accordance with work in the UK (Jacobs *et al.* 2009). This suggests that pollination levels, although higher than those on conventional farms, are still inadequate in organic grasslands.

In our study, fruit set of supplementally pollinated flowers was significantly lower, and was apparently not pollen limited, on conventional farms indicating that other factors are limiting. Nutrient limitation is possible, but no significant differences in pH, phosphorous, potassium and magnesium levels were found between organic and conventional field edges at the same study sites (E. F. Power, unpublished data). Alternatively, tree damage through cutting, spray drift from or direct application of herbicides (to control weeds) may reduce the fecundity of *C. monogyna* on conventional farms.

#### Summary of recommendations for management and policy

Insect–flower interaction networks in organic grasslands were found to be larger than their conventional counterparts, but overall, the networks in our study (organic and conventional) were small and relatively unstable compared to networks in species-rich habitats. This is likely to be the result of disturbance from intensive management and is concerning because the maintenance of some level of pollination in intensively farmed landscapes is dependent on a network of very few species. However, organic farming was found to provide increased

floral resources that attract more pollinating insects and pollination success was higher on farms under organic management. More research into the interacting effects of landscape and organic dairy farming is required (Gabriel *et al.* 2010), but our findings are an important starting point and have implications for how we perceive intensive grasslands. They are areas with some potential for pro-active conservation. The biodiversity that remains in intensive grasslands performs an essential role in the functioning of agricultural ecosystems and should be conserved and improved upon.

Organic dairy farming should be encouraged and supported particularly where intensive grasslands are widespread. Only 12 organic dairy farms in the Republic of Ireland met our selection criteria in 2008, 10 of which we surveyed, demonstrating the low uptake of organic dairy farming. Certain beneficial organic practices (for pollinators) can also be integrated into conventional farm management plans at little extra cost, for example, sowing *Trifolium* species to increase bee abundance. Strategic management of the flowers of important plant species for pollinators should be introduced into agri-environmental schemes, particularly in relation to hedgerow and pasture management. We confirm the value of hedgerows for pollinators and encourage hedgerow protection and restoration. This study also shows that more research is needed into hoverfly behaviour, dispersal and the influence of larval habitat and food requirements on adult distribution before realistic conservation recommendations can be made for this group. Ultimately, organic dairy farming, although not the solution in its present form, can improve prospects for pollinators in intensive grasslands.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article.

**Fig. S1.** Distribution of the ten farm pairs within Ireland.

**Fig. S2.** Floral units observed in organic and conventional field edge and centre transects.

**Figs. S3–S11.** Organic and conventional insect–flower interaction webs – farm pair 2 to 10.

**Table S1.** Summary of management activities in organic and conventional dairy farms

**Table S2.** Significant variables characterizing bee and hoverfly abundance, richness and evenness in the edges and centres of organic and conventional fields.

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