

Pollinator sharing between mass-flowering oilseed rape and co-flowering wild plants: implications for wild plant pollination

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Abstract Pollinating insects are not only important in wild plant pollination, but also in the production of a large number of crops. Oilseed rape production is increasing globally due to demands for biofuels which may have impacts on pollinating insects which visit the crop and on the pollination services delivered to co-flowering wild plants. In this study, we tested (1) the degree of pollinator sharing between oilseed rape and native wild plants in field margins and hedgerows and (2) the effects of oilseed rape on the quality of pollination service delivered to these wild plants. We found large overlap between flower visitors of wild plants and oilseed rape, but the composition of species overlap differed with respect to each wild plant species. Nearly all individual visitors caught on both

the crop and foraging on wild species carried crop pollen, but more than half the insects also carried pollen from wild plants. However, very little oilseed rape pollen was deposited on wild plant stigmas. This shows that (1) oilseed rape overlaps in pollinator niche with most co-flowering wild plants, and (2) crop pollen deposition on wild plant stigmas is low which may indicate that it is unlikely to cause reductions in seed set of wild plants, although this was not measured here. Furthermore, wild plants in field margins and hedgerows are important sources of alternative forage for pollinating insects even when a crop is mass flowering, and we suggest maintenance and augmentation of field margins and hedgerows to provide alternative forage for pollinator conservation to continue provision of pollination services to both crops and wild plants.

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Introduction

Pollinating insects are important in farmland as pollinators of both crops and wild plants. In these areas, pollinators are often associated with field margins and their associated hedgerows as remnants of semi-natural habitat to provide food, overwintering and/or nesting resources (Morandin et al. 2011;

Hannon and Sisk 2009; Croxton et al. 2002). This can result in pollinator spill-over between semi-natural areas and adjacent crops. Although spill-over is conventionally discussed as movement from semi-natural areas to crops, it can also occur in the opposite direction from the crop to adjacent semi-natural habitats such as field margins and hedgerows (Rand et al. 2006). This spill-over can in turn have consequences for species interactions and the delivery of pollination services (Holzschuh et al. 2011).

Current demands for bioenergy are resulting in increased production of oilseed rape (or canola, *Brassica napus* L.) in Europe and worldwide (EEB 2011). Although partially wind pollinated, oilseed rape increases in yield and market value with insect pollination (Bommarco et al. 2012), and with abundant bright yellow nectar and pollen-producing flowers can be very attractive to pollinating insects (Holzschuh et al. 2013; Stanley et al. 2013). Despite this, pollinating insects are often found more abundantly in field edges than field centres of oilseed rape fields (Stanley and Stout 2013; which is also seen in other mass-flowering crops such as almonds Klein et al. 2012). Previous studies have investigated pollination services within mass-flowering crop fields (Rader et al. 2009; Hayter and Cresswell 2006), and have shown that pollinators are found in both semi-natural and crop habitats (Hannon and Sisk 2009; Holzschuh et al. 2011; Klein et al. 2012). However, whether individuals forage exclusively on mass-flowering crops or supplement their diets with alternative pollen sources from the margins and hedgerows is not yet known. This has implications not only for the persistence of pollinators in agricultural regions, but also for the sustained provision of pollination services to mass-flowering crops.

If pollinators visit both mass-flowering crops and wild plant species in the field margins and hedgerows, there is the potential for the crop to interfere with pollination services to the wild plants (Cussans et al. 2010; Morales and Traveset 2008). As the majority of flowering plant species are limited in reproduction by the amount of pollen they receive (Burd 1994), decreases in pollination services and the resulting effects on plant fecundity could adversely affect plant populations (Aizen et al. 2002). This could have knock-on negative feedback on pollinators through a reduction in forage resources, or impacts on other ecosystem services (Jacobs et al. 2009; Isbell et al.

2011). Plants can affect the pollination of co-flowering species in two ways: firstly by affecting visitation rates, or secondly by affecting how pollen is transferred from one individual to another. One way the latter can occur is when pollen is lost as a result of pollen transfer between species (interspecific pollen transfer, Morales and Traveset 2008). This can be due to loss of pollen through movement on or between flowers of different species, or due to deposition of pollen on heterospecific flowers (Murcia and Feinsinger 1996; Brown and Mitchell 2001; Muchhala and Thomson 2012), with consequences for both male and female fitness.

Previous work investigating the impacts of mass-flowering species (mostly invasive aliens) on pollination services to less abundant species have found predominantly negative effects (Morales and Traveset 2009; Bjerknes et al. 2007). Using plant–pollinator networks, mass-flowering invasive species have been found to play a central role in native plant communities, being visited by high proportions of available pollinator species (Vila et al. 2009). However, previous studies on impacts of mass-flowering crops on pollination services to co-flowering species have been limited to effects on seed set of wild plants (Cussans et al. 2010). One wild hedgerow species, *Lotus corniculatus*, was shown to have increased seed set when grown beside oilseed rape in the UK, while there was no effect on *Glechoma hederacea* (Cussans et al. 2010). *Primula veris* was also shown to have reduced seed set when oilseed rape occurred in low densities in the surrounding landscape (Holzschuh et al. 2011), while no effect of oilseed rape was found on seed set of *Trifolium pratense* (Diekötter et al. 2010). However, the mechanisms behind these changes in seed set are not clear. Although pollen transfer between flowers within the mass-flowering crops has been investigated (e.g. Rader et al. 2009; Hayter and Cresswell 2006), pollen transfer dynamics between mass-flowering crops and wild plants have not been investigated previously, and it is not known if mass-flowering crop pollen can become deposited on wild plant stigmas.

The aim of this study was to investigate whether insects visiting mass-flowering crops also use resources in adjacent margins and hedgerows, and whether this has implications for the pollination services to these wild plants. By intensively sampling all flower-visiting insects on a number of co-flowering wild plant species throughout the entire flowering



Fig. 1 The focal species. From top left to bottom right *Fumaria* spp., *Ulex europeus*, *Vicia sepium*, *Lamium purpureum*, oilseed rape (*Brassica napus*), *Veronica chamedrys*, *Ranunculus repens* and *Stellaria holostea*

period of oilseed rape and constructing highly resolved visitation and pollen transfer networks for each site, we tested (i) whether there is sharing of flower-visiting insects between mass-flowering oilseed rape crops and co-flowering wild plants in terms of both pollinating taxa and individual foragers, and (ii) whether this can affect quality of pollination services in terms of deposition of crop pollen on wild plant stigmas.

Methods

Study sites

Due to the intensive nature of sampling, two winter oilseed rape fields were selected in South-East Ireland, an area where arable, beef and dairy farming are interspersed. Fields, to our knowledge, were not within 500 m of any other mass-flowering entomophilous crops (e.g. field beans or peas), and they were 17 km apart (Field A: Ballyhamilton, Co. Wexford; Field B: Ballymurphy, Co. Carlow; Supplementary Fig. S1). A south facing hedgerow and associated field margin were selected in each field, and along this boundary a 100 m transect with a quadrat placed on both sides every 10 m was used to assess the

abundance and diversity of wild plants co-flowering with oilseed rape (Supplementary Table S1). We aimed to select the four most abundant forbs (non-Brassicaceae) co-flowering with oilseed rape along this transect at the start of the experiment as the focal co-flowering wild plants. In total, seven entomophilous forbs were selected as focal species across the two fields: four species were studied in field A (*Stellaria holostea*, *Lamium purpureum*, *Ulex europeus* and *Fumaria* spp.) and four species in field B (*Ranunculus repens*, *S. holostea*, *Veronica chamedrys* and *Vicia sepium*) (Fig. 1).

Focal observations

Each field was visited seven times between 8th May and 14th June 2010, spanning the period when oilseed rape was in flower. To determine which insect taxa foraged on oilseed rape and on wild plants in the adjacent field margin, six 30 × 30 cm patches of each focal plant species in the field margin, and also six patches of oilseed rape itself, were observed for 5 min on each visit (total observation time = 210 min for each species). Observations in each field were carried out on different days by the same observer. Surveys were limited to warm dry weather conditions (mean temperature 17 °C) to eliminate weather as a potential

confounding factor. The number of floral units (defined as the size of floral area that a medium sized bee has to walk rather than fly in between; Dicks et al. 2002) per patch was counted before each observation period. Any insects visiting flowers were recorded and no a priori decision was made as to which insects were pollinators. Only pollen beetles (*Meligethes aeneus*) were excluded as they were rarely observed to move between flowers. Bumblebees and butterflies were identified to species (except for members of the *Bombus* sensu stricto group, which are impossible to reliably distinguish morphologically, Carolan et al. 2012; Wolf et al. 2010). Hoverflies and solitary bees were identified to genus, and all other flies were grouped.

Insect pollen loads

On each visit to each field, insects were also captured for analysis of pollen loads to identify if the same individuals visited both oilseed rape and wild plant species. For every insect group (bumblebees and honeybee to species, solitary bees and hoverflies to genus) observed in the focal observations visiting a particular plant species, we aimed to catch five individuals performing that same interaction for pollen analyses. Insects were caught straight into clean plastic vials and were cooled immediately and frozen the same day. In the lab, each individual was systematically swabbed with a 2.5 mm³ cube of fuchsin-stained gel (Dafni 1992). Pollen storage areas (i.e. corbiculae) on bees were avoided as pollen stored here is unlikely to be available for pollination. Gel was melted onto a slide, covered with a cover slip and sealed using nail varnish. All pollen grains were then identified and counted on each slide under $\times 400$ magnification, using both a reference collection from each field and other resources (Sawyer 1981; Moore et al. 1999; Chandler and Rennison 2005). Although this method did not give the total pollen load, it gave a measure of relative pollen density. As it is not possible to identify many pollen types to species level, we named pollen grains according to what species were present in the reference collection from the surrounding area, or to broader groupings (e.g. genus or family) when a number of similar species were present. Therefore, it is possible that pollen identified to species level may have come from a closely related species not in the reference collection, and so pollen

identifications are referred to as ‘types’ rather than ‘species’. As insects may pick up heterospecific pollen in the environment without actually visiting that species, we only counted pollen donor species with more than five pollen grains present on a particular insect (this level was set in accordance with work with a monolectic species; Bosch et al. 2009). All swabbed bees and hoverflies were identified to species level; this gave a list of potential hoverfly species that were grouped to genus in the focal observations in the field (*Eristalis* including: *E. abusivus*, *E. arbustorum*, *E. horticola*, *E. interruptus*, *E. pertinax*, *E. tenax* and *Eristalinus sepulchralis*; *Helophilus* including: *H. hybridus* and *H. pendulus*; *Platycheirus/Melanostoma* including: *P. albimanus*, *P. scutatus* and *P. granditarsus*; and *Cheilisia* including: *C. albitarsus*, *C. antiqua* and *C. pagana*).

Stigmatic pollen loads

To quantify heterospecific pollen deposition, twenty stigmas were collected from separate plants of each focal species (ten on each of two visits), at the end of the day to ensure that flowers had been open for at least a full day to allow time for insect visitation. In the laboratory, stigmas were stained using 0.5 % safranin in 50 % alcohol and squashed onto a microscope slide under a cover slip. Pollen grains on the stigmas were then identified as self-pollen, heterospecific pollen or oilseed rape, and abundance counted (counts may not have been comprehensive as some grains may have been obscured under bits of stigmatic tissue). *Stellaria holostea* has three stigmas, and pollen grains were counted on all three. *Ranunculus repens* has many carpels, and two stigmas were examined per individual flower for pollen.

Data analyses

Niche overlap of flower-visitors between oilseed rape and each wild plant species (NO) was calculated from both the visitation data and the pollen data using the following equation (Colwell and Futuyma 1971):

$$NO_{ij} = 1 - 0.5 \sum_k |P_{ik} - P_{jk}|$$

where i and j represent the two plant species under comparison and P_{ik} is equal to V_{ik}/V_{ii} and P_{jk} is equal to V_{jk}/V_{jj} . V_{ik} is the number of visits to plant species i

by insect species k (or the number of pollen grains of plant species i carried by insect species k) and V_{ii} is the total number of visits to plant species i . NO values range from 0 to 1, 0 indicating no overlap in terms of flower-visiting insects and 1 indicating complete overlap. Bumblebees and butterflies were included to species level in NO calculations, hoverflies and solitary bees to genus level, and other flies were grouped.

All analyses were carried out in R version 2.15.2 (R Development Core Team 2011). NO was calculated per sampling visit for the visitation data (resulting in seven measurements for each species), and compared between species using linear mixed effects models with sampling period as a random factor using the nlme package (Pinheiro et al. 2012). For pollen data, due to a small number of insects caught on each sampling visit, NO was only calculated as a total value per field.

To quantify flower visitor sharing in an alternative way, bipartite interaction networks were plotted for both the visitation data and pollen load data from both fields using the bipartite package (Dormann et al. 2008). Visitation networks were created from quantitative matrices containing total counts of the numbers of visits of each observed interaction between flower-visitor group and plant species, and pollen transport networks were constructed from matrices including total counts of pollen grains of each plant species on each insect group. The ‘species level’ command (Dormann et al. 2008) was used to calculate species degree (the sum of interactions per species), strength (the sum of dependencies of each species, Bascompte et al. 2006), partner diversity (Shannon diversity of the interactions of each species) and number of effective partners of oilseed rape and the different focal plant species in the network. All network parameters are measured on a continuous scale and are not bounded by upper values.

To examine pollen loads on native stigmas, we tested for differences in the proportion of oilseed rape pollen found on the stigmas between species of simple and complex morphology, using a non-parametric Wilcoxon signed rank test. Simple flowers were defined as those that were actinomorphic and open in structure and included *R. repens*, *S. holostea* and *V. chamedrys*. Complex flowers were those that were zygomorphic and more closed in structure and included *U. europeus*, *Fumaria* spp. and *V. sepium*.

Results

Across both fields, a total of 1,135 flower visits were recorded (212 to oilseed rape and 923 to wild plant species) in approximately 35 hours of focal observations. For pollen analyses, 236 insects were examined (223 of which carried more than 5 pollen grains) and approximately 296,000 pollen grains counted and identified of 31 pollen types in field A and 25 pollen types in field B (Supplementary Fig. S2; Table S2). Pollen networks were bigger in size than visitation networks with a higher number of links per species, but had lower connectance (Supplementary Fig. S2; Table 1).

Pollinator sharing

Wild plant species all overlapped in flower-visitor niche with oilseed rape (Fig. 2), sharing on average 22 % of a niche. However, niche overlap of flower visitors did not differ between wild species (Linear mixed effects model, field A: $F_{3,9} = 0.69$, $p = 0.58$, field B: $F_{3,9} = 1.97$, $p = 0.19$). Niche overlap, as quantified by pollen carried by insect group, was only calculated per site and so was not tested statistically, but followed a similar pattern to the visitation data with an average of 26 % of the pollinator niche of wild plant species shared with oilseed rape (Fig. 2). However, although each wild species overlapped in pollinator niche with oilseed rape, different visitors overlapped with each wild species. *V. sepium*, *Fumaria* spp. and *L. purpureum* were primarily visited by bumblebees and overlapped mainly in this group with oilseed rape, whereas *S. holostea*, *R. repens* and *V. chamedrys* were visited more frequently by solitary bees and flies, and overlapped in these visitors with the crop (Fig. 3, Supplementary Figs. S3, S4). Of all the focal flowering species, oilseed rape had the highest partner diversity and number of effective partners in pollen and visitation networks from both fields, and also highest species degree and strength in both pollen networks and visitation networks from field A only, confirming oilseed rape was visited by a wide range of insects (Table 1). As a result, oilseed rape was very dominant in networks from both fields (Supplementary Fig. S2).

Pollen data confirmed that the same individuals visited both the crop and wild plants; 59 % of all insect individuals caught foraging on oilseed rape also

Table 1 Network parameters for each species, and overall, in both visitation (*V*) and pollen (*P*) networks for each site

Field A	Oilseed rape		<i>Fumaria</i> spp.		<i>Lamium purpureum</i>		<i>Stellaria holostea</i>	<i>Ulex europaeus</i>		
	<i>V</i>	<i>P</i>	<i>V</i>	<i>P</i>	<i>V</i>	<i>P</i>	<i>V</i>	<i>P</i>	<i>V</i>	<i>P</i>
Partner diversity	2	2.2	0.6	0	1.5	1.6	1	1.3	0.4	1.2
No. effective partners	7.4	8.7	1.9	1	4.6	4.9	2.9	3.7	1.5	3.2
Species degree	11	19	3	1	8	13	6	8	3	5
Strength	6.7	12.7	1.6	0.0004	3.6	1.9	2.2	0.002	0.5	0.05
Field B	Oilseed rape		<i>Ranunculus repens</i>		<i>Stellaria holostea</i>		<i>Veronica chamaedrys</i>		<i>Vicia sepium</i>	
	<i>V</i>	<i>P</i>	<i>V</i>	<i>P</i>	<i>V</i>	<i>P</i>	<i>V</i>	<i>P</i>	<i>V</i>	<i>P</i>
Partner diversity	1.66	1.9	1.45	1.3	1.53	1	1.03	1.2	1.12	0.6
No. effective partners	5.26	6.6	4.27	3.8	4.62	2.8	2.79	3.3	3.08	1.8
Species degree	10	16	10	6	6	8	5	9	7	3
Strength	4.97	8.8	2.94	1	2.78	1.6	2.25	1.8	5.05	0.8

Field A overall network connectance: $V = 0.36$, $P = 0.2$, overall network linkage density $V = 3.64$, $P = 4.7$

Field B overall network connectance: $V = 0.4$, $P = 0.2$, overall network linkage density $V = 2.6$, $P = 3.6$

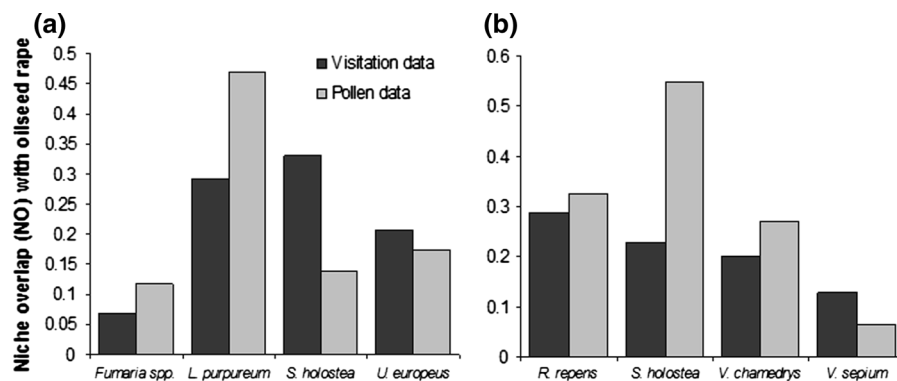


Fig. 2 Niche overlap (NO) of pollinator groups with oilseed rape. 0 = no overlap and 1 = total overlap, (a) field A and (b) field B. Data shown are calculated as totals per field, although analysis of niche overlap for visitation data was carried out on

per sampling visit basis. Bumblebees and butterflies were analysed to species level, hoverflies and solitary bees to genus, and other flies grouped into one category

carried pollen from wild plants, which on average made up 8 % (range 0–83 %) of pollen loads, while 73 % of insects caught foraging on wild plants carried oilseed rape pollen. In general, insects did not specialise on a single flower type, and carried a mean of 2.6 ± 0.12 (standard error) different pollen types, from a range of different wild plant species including trees, shrubs and herbaceous plants (for composition of pollen loads see Supplementary Table S1). Although social bees can pick up small amounts of pollen collected by other individuals in the nest (Paalhaar et al. 2008), we assumed this to be negligible.

Stigmatic pollen loads

Of the 143 stigmas examined of the seven focal wild plant species, nearly all had pollen deposited on them; only six had no pollen grains at all. The vast majority of all pollen (97 %) was con-specific (Fig. 4), with between 1 and 871 grains deposited per stigma. The remainder of pollen loads consisted of a small proportion of oilseed rape pollen and less heterospecific pollen from other species. Combining data from both fields, species differed in the proportion of oilseed rape pollen deposited on the stigma; the more

Fig. 3 The overlap of different pollinator groups between oilseed rape and wild species. The data represented in (a) are proportion of total visits of each pollinator group to each plant species, and (b) is the proportion of total pollen grains of each plant species carried from each pollinator group. Data are from both fields combined

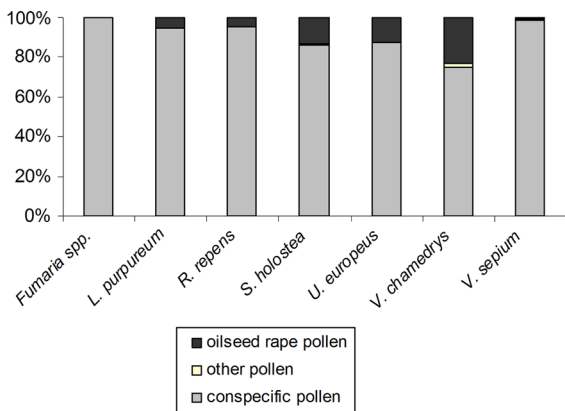
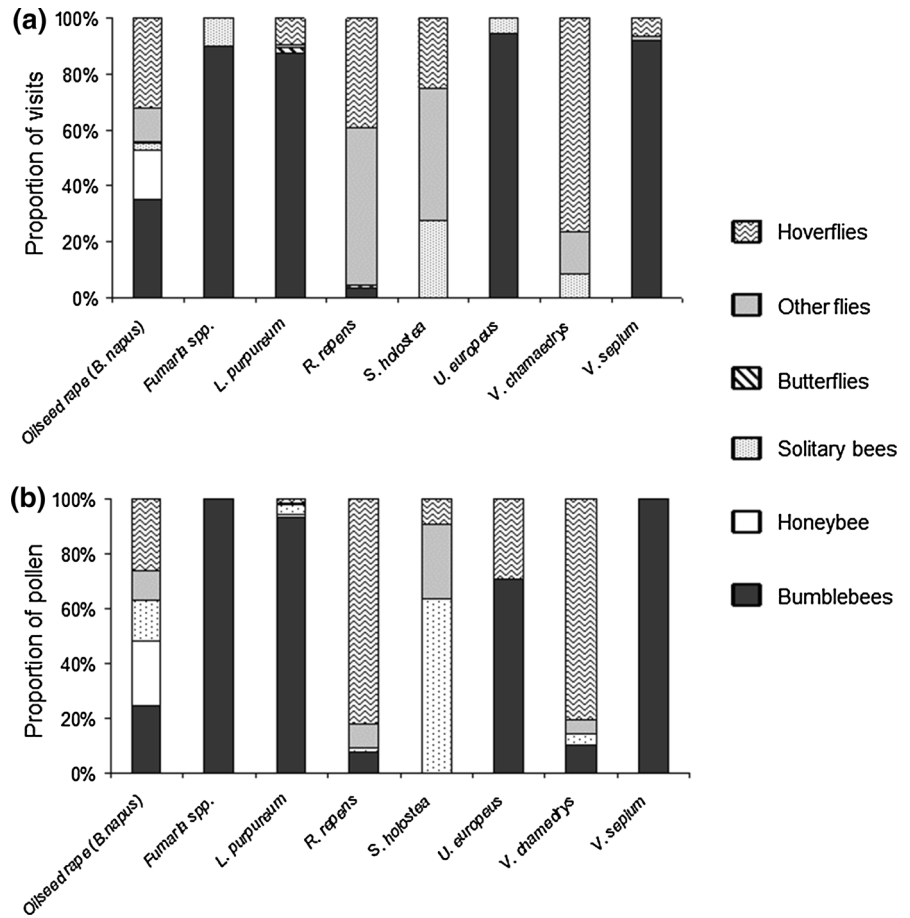


Fig. 4 The mean proportions of conspecific, oilseed rape and other (heterospecific excluding oilseed rape) pollen deposited on the stigmas of wild plant species. Data are from both sites combined, and based on ~20 stigmas per species in each field

closed, complex, zygomorphic flowers *Fumaria* spp., *Lamium purpureum*, *Ulex europaeus* and *Vicia sepium* all had very little oilseed rape pollen on their stigmas

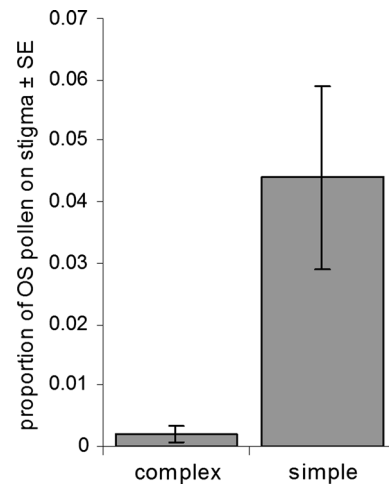


Fig. 5 The mean proportion of oilseed rape (OS) pollen on stigmas of flowers with complex (*Fumaria* spp., *L. purpureum*, *V. sepium* and *U. europaeus*, $n = 68$) and simple (*V. chamedrys*, *S. holostea*, *R. repens*, $n = 94$) morphology

(0, 0.25, 0.7, 0.06 % respectively), whereas the simpler, actinomorphic ones had more (*Stellaria holostea* 7 %, *Ranunculus repens* 0.8 % and *Veronica chamedrys* 6.4 % oilseed rape pollen) (Wilcoxon signed rank test: $W = 2372.5$, $p < 0.01$, Fig. 5). However, the amount of oilseed rape pollen found was overall extremely low (between 1 and 247 grains, 3 % of total pollen deposited on wild plant stigmas).

Discussion

As oilseed rape is increasingly planted around Europe to meet bioenergy targets, the potential for these crops to affect pollinators and the pollination of co-flowering wild plants is increasing. We found that oilseed rape overlaps in terms of species of flower-visitor (pollinator niche), and in terms of individual flower visitors, with co-flowering wild species that grow in the field margins and hedgerows. Oilseed rape also had an important role in plant–pollinator networks with higher species-level network parameters than all wild plants. However, very little oilseed rape pollen was found on the stigmas of wild plants (although there was more on the stigmas of morphologically ‘simple’ flowers in comparison to more complex ones), indicating that the deposition of crop pollen (potentially affecting the quality of conspecific pollen deposition) may not be a mechanism for interference to pollination services. Our data also show that flower-visiting insects in mass-flowering oilseed rape fields do not feed exclusively only on the crop, but also forage simultaneously on wild plants.

All wild plants showed overlap with oilseed rape with respect to the insect species that they were visited by, and oilseed rape was very dominant in both the visitation and pollen transfer networks as it was visited by many insect groups. Similar patterns have been found for mass-flowering non-native invasive species; they are also often highly connected and play central roles in visitation networks (Vila et al. 2009). Furthermore, we found that all insect groups (bumblebees, hoverflies, and solitary bees, except the honeybee) were observed to forage on both the crop and wild plants in the margins and hedgerows, and the majority of individuals also carried pollen from both the crop and wild species. This indicates that the potential for oilseed rape to interfere with wild plant pollination services is high.

Plant forage resources can vary in terms of their nutritional value (Roulston et al. 2000; Baker and Baker 1986). Although experimental studies have shown oilseed rape pollen may be a nutritionally good resource for insects to feed on (e.g. Regali and Rasmont 1995; Cook et al. 2003), insects may still need to supplement mass-flowering crop pollen with alternative forage resources from margins and hedgerows. Alternative forage resources may be especially important to sustain pollinator populations after the flowering on the crop; although bumblebees in field margins of mass-flowering field bean were more abundant when the crop was in flower, they declined after flowering, presumably to exploit alternative resources (Hanley et al. 2011). Interestingly, honeybees were observed to exclusively visit mass-flowering oilseed rape, and honeybee individuals carried high proportions of oilseed rape pollen (although they also carried small amounts from other species). Honeybees are known to be very flower constant (Free 1963); but although honeybees can provide pollination services when wild bees are lacking, services to some crops have been shown to be more stable with visits from other wild pollinator species (Garibaldi et al. 2011; Klein et al. 2012; Brittain et al. 2013). In addition, our data suggest that although honeybees may provide pollination services to crops, they are less likely to provide services to wild plants, to which wild insects provide more visits and carry more pollen.

Although oilseed rape shares flower-visiting insect species with co-flowering wild plants, previous studies have found different responses in seed set of species growing beside the mass-flowering crop (Cussans et al. 2010; Holzschuh et al. 2011; Diekötter et al. 2010). This could be due to differential impacts of the crop on different insect groups, which in turn may impact on plant species (Diekötter et al. 2010). We investigated whether the sharing of flower-visiting insects affected the quality of pollination services to wild plants as a potential explanation for differential effects on seed set. The deposition of foreign pollen on wild plant stigmas has been found in systems with invasive plants (Lopezaraiza-Mikel et al. 2007; Brown and Mitchell 2001), and has been hypothesised to occur in wild plants grown near oilseed rape (Holzschuh et al. 2011). Although we found oilseed rape pollen on the stigmas on native plants, the amount was very low with the majority of pollen being conspecific,

which has also been found in studies with invasive species (Moragues and Traveset 2005; Dietzsch et al. 2011; Bartomeus et al. 2008). The low deposition of crop pollen on wild plant stigmas in our study suggests a low likelihood of interference with wild plant pollination; however, the amount of oilseed rape pollen required to interfere with wild species seed set is currently unknown. Oilseed rape pollen may not have become deposited on stigmas for a number of reasons; pollen may be placed in different places on the bodies of insects in different species (Muchhala and Potts 2007), or the pollen adhesive capability of hetero- and con-specific pollen may differ on the stigmatic surface (Zinkl et al. 1999). However, although oilseed rape pollen misplacement on wild plant stigmas may not occur in abundance, there could still be consequences for male fitness of both the oilseed rape and wild species if con-specific loss of pollen occurs in other ways not measured here (Muchhala and Thomson 2012), or if mass-flowering oilseed rape alters visitation rates to wild plants (Diekotter et al. 2010). Therefore, oilseed rape may influence the *quantity* of pollination (i.e. the visitation rates to the wild species) which was not measured here. In addition, further work on how oilseed rape pollen may affect the seed set of wild plants would also further this area.

We found more oilseed rape pollen grains deposited on the stigmas of open flowers with more simple morphology. This could be due to similarities in morphology, and therefore, pollen placement on insect bodies, between oilseed rape and these flowers (e.g. Gibson et al. 2012; Morales and Traveset 2009), higher susceptibility to pollen deposition by wind which also carries large amounts of oilseed rape pollen on more open flowers (Williams 1984), or the more open flowers may have received less targeted pollen as they are largely pollinated by less specific pollinators (hoverflies and flies). Previous studies on seed set of wild plants beside oilseed rape have investigated long corolla tubed, bee pollinated flowers only (Cussans et al. 2010; Diekotter et al. 2010; Holzschuh et al. 2011); the variable effects seen are therefore unlikely due to crop pollen deposition, and perhaps due to other factors such as visitation rates.

Interestingly, other pollen types of non-focal plant species were also abundant on the bodies of insects, including some hedgerow trees. For example, pollen from *Salix* sp., Horsechestnut (*Aesculus*

hippocastanum) and Rosaceae sp. (mostly Hawthorn, *Craetagus monogyna*) was also found in abundance. This may indicate some other useful species for pollinators in farmland in spring, and highlights not only the importance of herbaceous plants for pollinators in farmland (Pywell et al. 2005), but also the importance of hedgerow trees.

Conclusion

As oilseed rape crops become more frequently planted to satisfy increasing demands for bioenergy, there will be increased potential for the crop to influence pollination services to wild plant species in the surrounding landscape. We found that seven wild plant species, growing in field margins and hedgerows around mass-flowering oilseed rape in Ireland, overlap with the crop in terms of the insects that visit their flowers, and that the same individual insects visit both the crop and wild species. However, very little crop pollen becomes deposited on wild plant stigmas which may suggest this is not a mechanism for interruption to pollination services to wild species, although further work is needed to elucidate the amount of crop pollen needed to influence seed set. The conservation of field margins and hedgerows around mass-flowering crop fields could be beneficial for pollinating insects in the provision of alternative forage which may have a knock-on benefit for crop yields (Carvalho et al. 2012). However, oilseed rape tends to receive high inputs of pesticides (DAFF 2004) which can have negative impacts on bees (Henry et al. 2012; Gill et al. 2012), and can even be found in the nectar of co-flowering wild species (Krupke et al. 2012); therefore, we also suggest that crop management needs to be sensitive to the requirements of pollinating insects, which forage both in the crop and on adjacent wild plants.

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