



Landscape Ecol (2020) 35:513–527  
<https://doi.org/10.1007/s10980-019-00962-0>

## RESEARCH ARTICLE

# Mass-flowering crops have a greater impact than semi-natural habitat on crop pollinators and pollen deposition

Rosalind F. Shaw · Benjamin B. Phillips · Toby Doyle · Judith K. Pell ·  
John W. Redhead · Joanna Savage · Ben A. Woodcock · James M. Bullock ·  
Juliet L. Osborne

Received: 21 November 2018 / Accepted: 27 December 2019 / Published online: 20 January 2020  
© The Author(s) 2020

## Abstract

**Context** Maximising insect pollination of mass-flowering crops is a widely-discussed approach to sustainable agriculture. Management actions can target landscape-scale semi-natural habitat, cropping patterns or field-scale features, but little is known about their relative effectiveness.

**Objective** To test how landscape composition (area of mass-flowering crops and semi-natural habitat) and field-scale habitat (margins and hedges) affect pollinator species richness, abundance, and pollen deposition within crop fields.

**Methods** We surveyed all flower visitors (Diptera, Coleoptera and Hymenoptera) in oilseed rape fields and related them to landscape composition and field

features. Flower visitors were classified as bees, non-bee pollinators and brassica specialists. Total pollen deposition by individual taxa was estimated using single visit pollen deposition on stigmas combined with insect abundance.

**Results** The area of mass-flowering crop had a negative effect on the species richness and abundance of bees in fields, but not other flower visitors. The area of semi-natural habitat in the surrounding landscape had a positive effect on bees, but was not as important as the area of mass-flowering crop. Taxonomic richness and abundance varied significantly between years for non-bee pollinators. Greater cover of mass-flowering crops surrounding fields had a negative effect on pollen deposition, but only when non-bee pollinator numbers were reduced.

**Conclusions** Management choices that result in landscape homogenisation, such as large areas of mass-flowering crops, may reduce pollination services by reducing the numbers of bees visiting fields. Non-bee insect pollinators may buffer these landscape effects on pollen deposition, and management to support their populations should be considered.

**Electronic supplementary material** The online version of this article (<https://doi.org/10.1007/s10980-019-00962-0>) contains supplementary material, which is available to authorized users.

R. F. Shaw (✉) · B. B. Phillips ·  
T. Doyle · J. L. Osborne  
Environment and Sustainability Institute, University of  
Exeter, Penryn, Cornwall TR10 9FE, UK  
e-mail: r.shaw@exeter.ac.uk

J. K. Pell  
J.K. Pell Consulting, Luton, Bedfordshire, UK

J. W. Redhead · J. Savage · B. A. Woodcock · J.  
M. Bullock  
NERC Centre for Ecology and Hydrology, Maclean  
Building, Wallingford, Oxfordshire OX10 8BB, UK

**Keywords** Wild pollinators · Flies · Diptera ·  
Landscape · Pollination services · Bees · Beetles ·  
*Brassica napus* · Field margins

## Introduction

At the global scale, the ecosystem services provided by pollinating insects are estimated to be worth around 7–8% of the total value of agricultural food production (IPBES 2016). Maintaining this service is threatened by declines in pollinating insects over many regions of the world (Biesmeijer et al. 2006; NRC 2007). These declines are generally attributed to anthropogenic influences, with habitat loss being a key factor (Vanbergen and The Insect Pollinators Initiative 2013). Managing landscapes to support pollinating insects is therefore critical, for both conservation of pollinators and to maintain yield of insect-pollinated crops (Garibaldi et al. 2014).

Agricultural landscapes with a higher proportion of semi-natural habitat have been shown to benefit pollinator species richness and abundance (e.g. Kennedy et al. 2013; Woodcock et al. 2013), increase temporal stability of pollinator communities (Garibaldi et al. 2011) and improve the yield of pollinator-dependent mass-flowering crops (Bartomeus et al. 2014; Garibaldi et al. 2013). Mass-flowering crops provide resources during their flowering season that can be important for pollinators (Westphal et al. 2003; Knight et al. 2005; Woodcock et al. 2016), but may result in transient changes in the distribution of pollinators within the landscape; local pollinator numbers may be ‘diluted’ as they respond to the large area of floral resources (Holzschuh et al. 2016). The temporary nature of mass-flowering crops, and spatial separation between different mass-flowering crops in relation to pollinator foraging distances, means that pollinators still need floral resources from other habitats pre- and post-crop flowering (Martins et al. 2018). In addition, semi-natural habitats provide more nest sites such as tussocky grasses, dead wood and undisturbed soil than mass-flowering crops (Lye et al. 2009).

One common field-based intervention to reduce the impacts of habitat loss on pollinator communities has been planting field margins. Field margins are designed to increase insect populations in general or provide additional floral resources for pollinators (e.g. pollinator seed mixes; Isaacs et al. 2009). These interventions have positive effects on wild pollinator populations (Scheper et al. 2013, 2015), but their success is dependent on the landscape context, with greatest benefits seen in landscapes that contain a

minimum threshold of semi-natural habitat rather than very small, or very large, amounts (Scheper et al. 2013). The impact of these changes on crop yield is less clear; some studies show positive effects (Blaauw and Isaacs 2014; Pywell et al. 2015), while others show no effect (Campbell et al. 2017).

The benefits of semi-natural habitat on a landscape scale and field-scale interventions vary in their level of importance for different pollinator groups, although bees are the most commonly studied (Steffan-Dewenter et al. 2002; Rader et al. 2016). Bees are often the most effective pollinators of many plants in terms of pollen deposition or visit rate. However, other insects that are individually less effective pollinators may still provide important levels of pollination due to their high abundance (Rader et al. 2016). Syrphidae (hoverflies) are generally the most recorded group of Diptera, however in agricultural land other Diptera may have greater diversity and abundance, and have similar pollen loads (Orford et al. 2015). It is therefore important that pollination service provision of Diptera is estimated, particularly in crops like oilseed rape which include an abundant Diptera community (Garrett et al. 2014; Phillips et al. 2018). Developing agricultural practices that support a wide range of pollinator groups and species has the potential to maximise yields, particularly under environmentally variable conditions, if pollinator species occupy different temporal or spatial niches (e.g. Hoehn et al. 2008), or respond differently to disturbance (Winfree and Kremen 2009).

To maximise pollination as an ecosystem service, the impacts of landscape composition, including mass-flowering crops, semi-natural habitat and field-scale interventions, on both pollinator populations and pollen deposition need to be assessed, considering the entire flower-visiting community. To do this, we used winter-sown oilseed rape (*Brassica napus*) as a test crop. This is an economically important crop in the UK [approximately 670,000 ha grown in 2015, worth £706 million; DEFRA (2016)] and insect pollination is known to increase yield quantity (Lindström et al. 2016) and quality (Bommarco et al. 2012; Bartomeus et al. 2014). For farming efficiency, this crop is commonly planted in large areas of several fields (‘block cropping’), which may impact pollinator communities. We used an area of the UK which has a mix of arable crops, intensive grassland and high quality semi-natural habitats including species-rich

grassland [see Ridding et al. (2018)], which provides a gradient of mass-flowering crops and semi-natural habitat.

Specifically, we asked the following questions:

- (1) Are mass-flowering crops or semi-natural habitats more important in explaining pollinator species richness and abundance in oilseed rape, and does this vary with pollinator type?
- (2) Is the effect of land use at the landscape scale more or less important than the impact of local-scale interventions such as field margins?
- (3) Do changes to pollinator communities in relation to landscape and local-scale habitat result in changes to pollen deposition in crops?

## Methods

Surveys were done in 2014 and 2015 in southern England (NW corner 51.415482° N, – 2.2892761° E; SE corner 51.087135° N, – 1.5037537° E). This area includes the largest calcareous grassland in Western Europe (Toynton and Ash 2002), and is predominantly mixed arable and livestock farms.

### Landscape composition

We investigated both semi-natural and arable habitat. Grassland was divided into three types according to their relative potential value to pollinators: species rich (greatest potential value), restoring (intermediate potential value) and intensive (least potential value). The area of different types of semi-natural habitat was determined by combining information from several spatial datasets within a GIS (ArcGIS, v10.1, ESRI, Redlands CA) (see Online Resource 1 for detail). Field sites were selected by generating random spatial locations and calculating the area of different grassland types within a 3 km buffer to select approximate locations with a gradient of different habitats. Landowners in these areas were contacted to ask whether they would take part in the project. Twelve fields of winter-sown oilseed rape (OSR) were surveyed in 2014 and twelve different fields in 2015. Semi-natural habitats derived from combining the spatial datasets were verified in the field within a 1 km buffer. Crop species grown within a 1 km buffer each year were recorded during field surveys. For analysis,

the individual areas of species-rich grassland, restoring grassland, intensive grassland, total semi-natural habitat (broad leaved woodland, coniferous woodland, restored grassland, species rich grassland and other grassland, not including intensive grassland), and arable land were calculated in buffers of radii between 0.5 and 3 km at 0.5 km intervals. These radii incorporate the foraging radii of solitary bees, bumblebees and honeybees (Gathmann and Tscharrntke 2002; Knight et al. 2005; Danner et al. 2017). The area of oilseed rape was calculated up to a 1 km buffer radius as this was the limit of the field survey data (more OSR fields will have been present outside this buffer). To account for the size of, and distance to, grassland patches, they were also represented as the area/distance ratio of the nearest patch for each grassland type, and the sum of area/distance ratio for the nearest three grassland patches (see Online Resource 1, Table S1).

### Field-scale habitat

Three 58 m transects were set up in each field, perpendicular to three different field edges. Transects were located using a stratified random selection process to include edges with and without hedges and margins around a single field, where possible. The structure and plant diversity of the field edge adjacent to the transect was assessed by measuring the length of field edge, proportion of field edge with a hedge, proportion of field edge with a field margin and width of field margin. Field margins were assessed for their potential value to pollinators by observing insect pollinated plant [as defined by their pollination vector in Fitter and Peat (1994)] species richness and percent cover in five 1 m<sup>2</sup> quadrats placed at random within 20 m of the transect start during June and July. Species nomenclature followed Stace (1997).

### Flower visitors

Bumblebees (*Bombus* spp.) and honey bees (*Apis mellifera*) were recorded by slowly walking each transect twice on the same day during the oilseed rape flowering season (14/4/2014–17/5/2014 and 20/4/15–27/5/2015) and counting the number of bees visiting flowers within 2 m of the observer (i.e. 58 × 4 m transect). Solitary bees, hoverflies and other flower visitors were assessed using 15 cm diameter

pan traps painted with UV fluorescent yellow paint placed in the crop canopy. On each transect, pan traps were placed at 8 m, 32 m and 58 m into the crop, filled with water and a few drops of scentless detergent and left for 4 days. Where pan traps were knocked over, transects without complete data ( $n = 6$ ) were excluded from any further analysis. Smaller Diptera and Coleoptera were assessed using 1 m<sup>2</sup> quadrats placed next to the pan traps and observed for 5 min. Transects and quadrat surveys were done between 10:00 and 16:00 h, with a minimum temperature of 12 °C and wind speed less than 6–8 m s<sup>-1</sup>. The combined methods were used to maximise detectability of different groups and reduce bias (Westphal et al. 2008). This allows us to observe the relative contribution of groups in different transects or years, but absolute values within or between pollinator groups are difficult to assess.

*Bombus* spp. and *Apis mellifera* were recorded to species and caste when possible; pan trap collected insects were recorded to species level for bees (Hymenoptera: Apoidea) and hoverflies (Diptera: Syrphidae) and to family level for other Hymenoptera and Diptera. Smaller Diptera and Coleoptera visiting quadrats were recorded as morphotypes. Flower visitors were categorised into three functional groups: bees (Apoidea; insects that use pollen as a food source for offspring); brassica specialists that complete their life cycle within a field, including anthomyid flies (*Delia* spp.), pollen beetles (*Meligethes* spp.) and seed weevils (*Ceutorhynchus* spp.), representing species typically considered to be pests of this crop but who also deliver some pollen; and non-bee insect pollinators, predominantly other flies such as Bibionidae, Empididae and Syrphidae.

#### Estimating level of crop pollination

To estimate the level of crop pollination, we used the amount of pollen delivered per transect as a proxy (Kremen et al. 2002). This requires the amount of pollen delivered by different insect species and their visit rate. We used data from Phillips et al. (2018) to divide flower visitors into 11 pollinator groups based on intertegular distance, body size and flower visiting behaviour, which affect pollen deposition (see Online Resource 2, Table S3 for full definitions). Phillips et al. (2018) assessed how many oilseed rape pollen grains deposited on flower stigmas during a single visit

(“single visit pollen deposition”; SVD) by presenting a fresh stigma to pollinators in oilseed rape and counting the number of pollen grains deposited. Control stigmas were prepared in the same way but excluding pollinators to assess the extent of pollen transfer that was not due to insect activity. Flowers with ripe anthers and stamens were used to ensure the results were realistic.

To assess visit rate we calculated the number of flower visits by each pollinator group in each transect (visits m<sup>2</sup> h<sup>-1</sup>) by correcting the pan trap, transect and quadrat data for area and time (for pan traps, pollinators were assumed to be at peak activity for 8 h of each 24 h period). We assumed that pan traps represent a dense area of flowers so were corrected for the area of crop they represented (one pan trap represents 78.5 oilseed rape flowers, assuming an oilseed rape flower is approximately 2.25 cm<sup>2</sup>, divided by the number of receptive flowers/m<sup>2</sup> at the time of survey). To confirm that the calculations resulted in realistic estimates of visit rates, the estimates for anthomyid flies and *Meligethes* spp., which were recorded using all three methods, were compared (see Online Resource S3). The rates did vary between methods, but not in a consistent direction (Mean visit rate m<sup>2</sup> h<sup>-1</sup> per transect ± standard deviation: anthomyid flies quadrats 25.2 ± 46.17; pan traps 39.9 ± 37.09; *Meligethes* spp. quadrats 32.3 ± 25.57; pan traps 7.7 ± 7.96; *Ceutorhynchus* spp. quadrats 0.1 ± 0.69; pan traps 2.7 ± 7.26). The estimates for solitary bees were similar to transect-based estimates in an independent study (Woodcock et al. 2013: solitary bee mean visit rate m<sup>2</sup> h<sup>-1</sup>: 3.2 ± 3.40; this study 4.9 ± 5.29). This variation in estimates means that these relative visit rates can only be used to compare between transects, rather than providing absolute visit rate estimates. The proportion of visits where there was contact with the anthers or stigmas of the flower for each group was calculated using data recorded during the quadrat and transect surveys and from Woodcock et al. (2013). The median number of pollen grains delivered to a stigma (minus the assessed pollen transfer due to experimental methods) per visit was used for each group. If a group delivered more than 160 pollen grains per visit [the estimated number of pollen grains required to fertilise fully one OSR flower; Mesquida and Renard (1984)], then 160 was used. This accounts for some pollinators delivering more pollen grains than required

for full fertilisation. Pollen deposition per transect ( $\text{grains m}^2 \text{h}^{-1}$ ) was calculated by multiplying the visit rate by the proportion of flowers with anther/stigma contact and the number of pollen grains delivered per visit (Kremen et al. 2002).

### Statistical analysis

Analyses were carried out using R v3.4.3 (R Core Team 2016). We analysed the data using a three stage process (1) assessing the impact of landscape factors on pollinator communities at multiple spatial scales (2) using the top landscape model and assessing the impact in combination with local factors on pollinator communities (3) using the resulting models to assess if landscape and local factors affecting the pollinator community had any impact on pollen deposition. We used linear mixed effects models (package lme4; Bates et al. 2015), and checked model assumptions using diagnostic plots (Bates et al. 2015). Models were compared using multi-model inference using AICc (package MuMIn; Bartoń 2016) which allows comparison of multiple models to find the model, or models, which best fit the data (Whittingham et al. 2006). A subset of plausible potential models was considered rather than all possible combinations of variables to avoid biologically unrealistic models, force inclusion of predictors selected a priori (year and functional group) and avoid including highly correlated predictors in the same model. Year was included due to impacts of inter-annual variation on insect populations, weather in different years affecting planting dates and flowering phenology, and because different sites were used in each year (due to crop rotation) which may affect the results. To confirm whether any explanatory variables were different between years, Mann–Whitney U tests were performed (with year entered as a factor; see Online Resource 1, Table S1). In all our interpretation, ‘year’ is considered to be a mix of potential site differences and differences between years. Functional group was included in the models as life history variation means that the impacts on one group could be concealed by impacts (or lack thereof) on others. For the landscape analysis explanatory variables included year and functional group entered individually or as an interaction and then included in all models with landscape variables. Each landscape variable was tested individually, and as second-order interactions with year and

functional group (for full list of candidate models used see Online Resource 4, Table S6). Testing each landscape variable individually allowed us to account for highly correlated landscape variables by never including them in the same model. Landscape variables which were strongly correlated with each other or co-varied in relation to explanatory factors would be expected to result in models with very similar AICc scores. Field and transect identity were entered as random effects. Raw abundance data were used for comparison between transects but log transformed ( $+ 0.001$ ) to meet model assumptions (Ives 2015). Models were ranked by AICc and weight to select the top model, or models. Those with  $\Delta\text{AICc} < 2$  were considered to have similar levels of supporting evidence, and to be the top model or models. The amount of variation explained by each model was assessed using the conditional and marginal  $R^2$  (Nakagawa and Schielzeth 2013). Spatial autocorrelation between fields was tested for using Moran’s I, which were not found to be significantly correlated (Paradis and Schliep 2018).

The top landscape model was used in a further model selection procedure with local habitat factors. The same model structure was used but the fixed effects tested were: species richness of insect-pollinated plants; percent cover of insect-pollinated plants (based on average percent cover of insect pollinated plants in five quadrats multiplied by margin area); margin width (entered as a factor, with the field margin categorised as  $< 1$  m, between 1 and 3 m, between 3 and 6 m and  $> 6$  m); and length of hedge (see Online Resource 1, Table S1). Predictor variables were rescaled to between 0 and 1. Each local habitat factor was assessed individually (in case they had a stronger effect on pollinator communities than landscape factors) and then in combination with the landscape factors as both additive effects and second-order interactions. Although local habitat factors were only tested with the top landscape model, correlation between local habitat factors and landscape factors were tested using Pearson’s correlation coefficient and indicated low correlation ( $< 0.25$ , Online Resource 1, Table S2). The limitation of this two stage approach is that there may be an additive effect of some other landscape factor and local factor which were not tested for, however including all possible models would have resulted in an extremely large set of candidate models.

**Table 1** Results from four separate model selection procedures. Only the top models and next best models shown, unless multiple models had  $\Delta\text{AICc} < 2$ , indicating no clear top model, in which case all models with  $\Delta\text{AICc} < 2$  are shown. Landscape factors were analysed initially and the area of oilseed rape within a 1 km buffer of the transect (OSR1) was in the top model (section a). This model was then used in a second model selection procedure to assess the importance of local factors on taxonomic richness and abundance of flower visitors (section b). Local factors included: the area of insect

pollinated plants in margin ( $\text{m}^2$ ; AreaIP), the species richness insect pollinated plants in margin (IPSpeciesCount), length of hedge on field edge perpendicular to transect (metres; Length Hedge) and the width of margin (margin width). Models were limited to 2nd order interactions only. Full list of potential candidate models is described in methods section and all results are in Online Resource 4 Tables S6, S8, S9, S10. Marginal  $R^2$  ( $R^2\text{m}$ ) and conditional  $R^2$  ( $R^2\text{c}$ ) were calculated according to Nakagawa and Schielzeth (2013)

Model	Model formula	Intercept	df	LogLik	AICc	$\Delta\text{AICc}$	Weight	$R^2\text{m}$	$R^2\text{c}$
(a) Landscape factors									
Taxonomic richness	Year * FG * OSR1	3.402	13	- 384.052	796.083	0.000	0.998	0.38	0.42
	Year + FG * OSR1	4.076	10	- 393.512	808.200	12.117	0.002	0.32	0.36
Abundance	Year * FG * OSR1	6.184	13	- 337.454	702.886	0.000	0.962	0.67	0.68
	Year + FG * OSR1	6.435	10	- 344.080	709.337	6.450	0.038	0.65	0.66
(b) Landscape and local factors									
Taxonomic richness	Year * FG * OSR1 + Area IP	3.451	14	- 388.9	808.094	0.000	0.187	0.36	0.38
	Year * FG * OSR1 + IPSpeciesCount	3.365	14	- 389.05	808.395	0.301	0.161	0.35	0.38
	Year * FG * OSR1 + Length hedge	3.663	14	- 389.102	808.500	0.406	0.153	0.35	0.38
	Year * FG * OSR1 * margin width	2.937	16	- 387.091	809.187	1.093	0.108	0.37	0.38
	Year * FG * OSR1 * length hedge	3.223	18	- 384.839	809.499	1.404	0.093	0.38	0.40
Abundance	Year * FG * OSR1	3.003	15	- 388.532	809.702	1.608	1.608	0.36	0.39
	Year * FG * OSR1 * length hedge	5.842	18	- 323.079	685.979	0.000	0.973	0.72	0.72
	Year * FG * OSR1 + length hedge	6.668	14	- 331.859	694.013	8.033	0.018	0.69	0.69

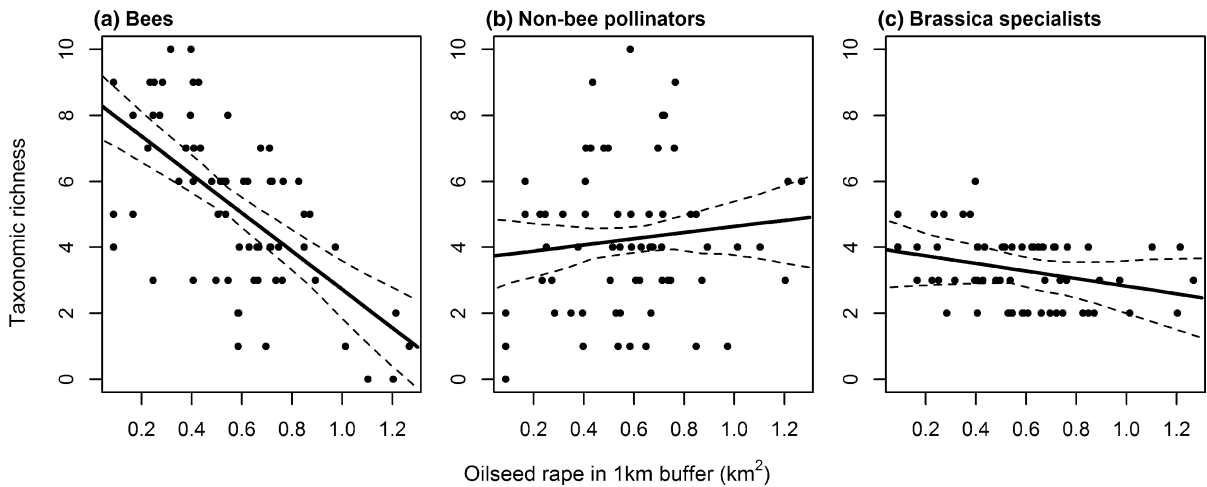
To test whether changes in taxonomic richness and abundance due to landscape or local factors resulted in changes to pollen deposition, the estimated number of pollen grains delivered was log transformed to meet model assumptions and used as the response variable in the selected model.

## Results

The most abundant flower visitors recorded in pan traps were brassica specialists including Anthomyid flies (predominantly *Delia* spp., 67% of total catch 39,023), pollen beetles (*Meligethes* spp., 14%) and weevils (*Ceutorhynchus* spp., 6%). For bees, *Andrena cineraria* were the most commonly caught in pan traps (8%), followed by *Andrena haemorrhoa* (2%). Transect observations were predominantly *Apis mellifera* (74% of 662 total observations) and *Bombus lapidarius* (19%, Online Resource 5).

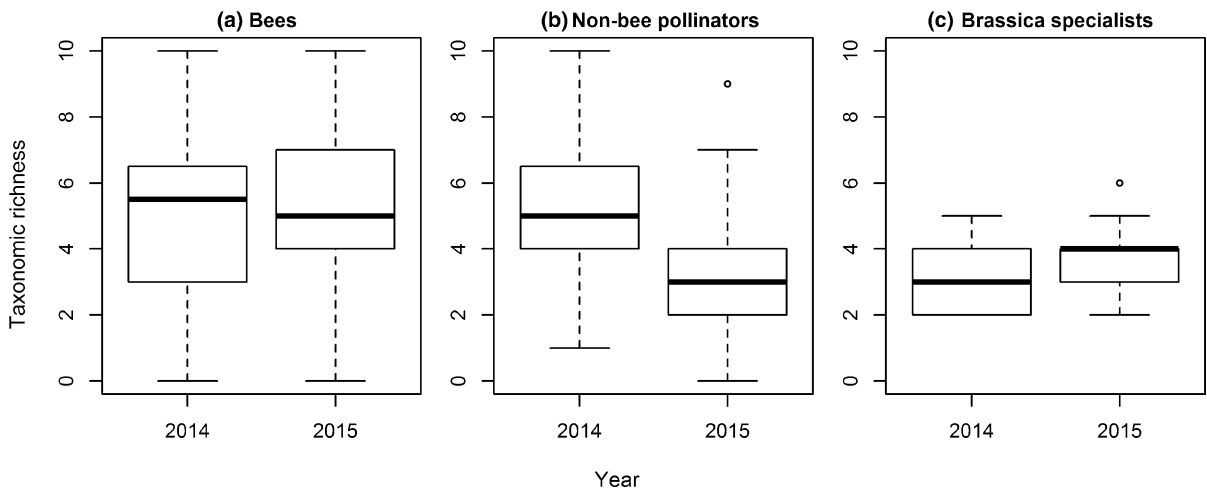
## Taxonomic richness

The top model for taxonomic richness included year, functional group and the area of oilseed rape in a 1 km buffer around the transect (Table 1). There was a significant interaction between the functional group and the area of oilseed rape within a 1 km buffer (Online Resource 4, Table S7): bees had a negative relationship with the area of oilseed rape (effect size  $- 4.64 \pm 1.057$  SE, Fig. 1). There was a significant interaction between year and functional group, with lower taxonomic richness of non-bee pollinators in 2015 (effect size  $- 2.26 \pm 0.570$  SE, Fig. 2). All of the models that included semi-natural habitat had  $\Delta\text{AICc}$  relative to the top model of  $> 38$ , indicating that this explained by far less variation in the data than mass flowering crops (Online Resource 4, Table S6). When local factors were included in the model, the top model included the area of insect-pollinated plants in the margin (Table 1), which was positively related to the taxonomic richness of flower visitors, although the effect size was close to zero (effect size  $0.81 \pm 0.700$  SE, Online Resource 4, Table S7). The next best



**Fig. 1** Taxonomic richness of flower-visiting insects in oilseed rape transects (n = 66) in relation to the area of oilseed rape in a 1 km radius buffer around each transect, for each functional group. Flower visiting insects were divided into three functional groups **a** bees (Hymenoptera: Apoidea), **b** non-bee pollinators

(Diptera, Hymenoptera: Tenthredinoidea) and **c** brassica specialists (Diptera: Anthomyiidae, Coleoptera). Solid lines represent predicted values from linear mixed effects analysis (Table S7), dashed lines represent 95% confidence intervals calculated via boot strapping of 200 simulations



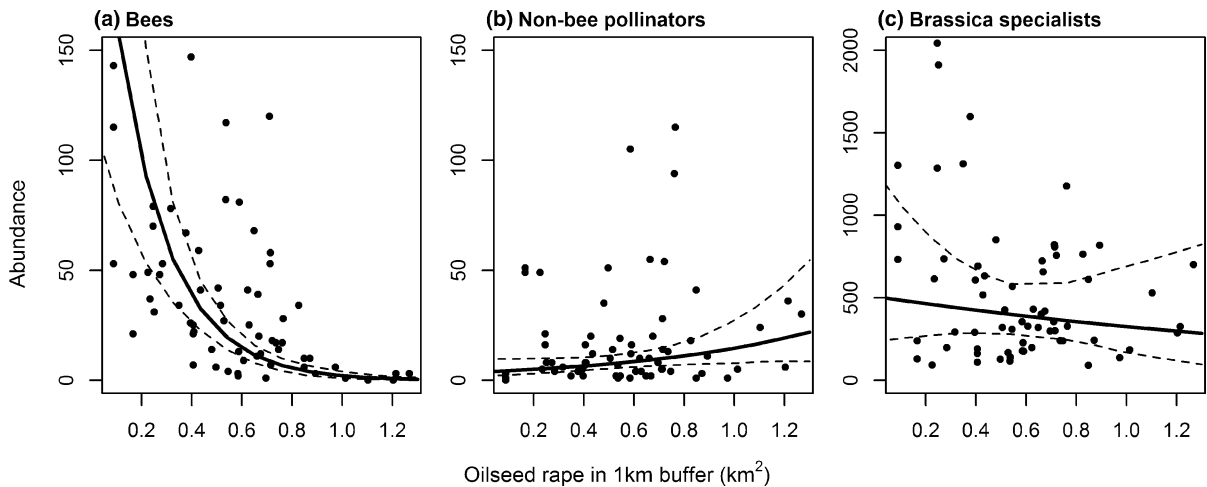
**Fig. 2** Boxplots (median, interquartile range, outliers) showing the interaction between study year and functional group on the taxonomic richness of flower-visiting insects in oilseed rape

fields (Table S7). Flower visitors were divided into three functional groups **a** bees, **b** non-bee pollinators and **c** brassica specialists

models had  $\Delta AICc$  of  $< 2$  and all included parameters relating to margin resources; but also included the original landscape model without any additional local factors indicating that there was little increase in explanatory power (Table 1).

**Abundance**

For pollinator abundance, the top landscape only model also included year, functional group and the area of oilseed rape in a 1 km buffer around the transect (Table 1). The abundance of bees had a negative relationship with the area of oilseed rape (effect size  $-4.40 \pm 0.845$  SE, Fig. 3, Online Resource 4 Table S7), and the abundance of non-bee

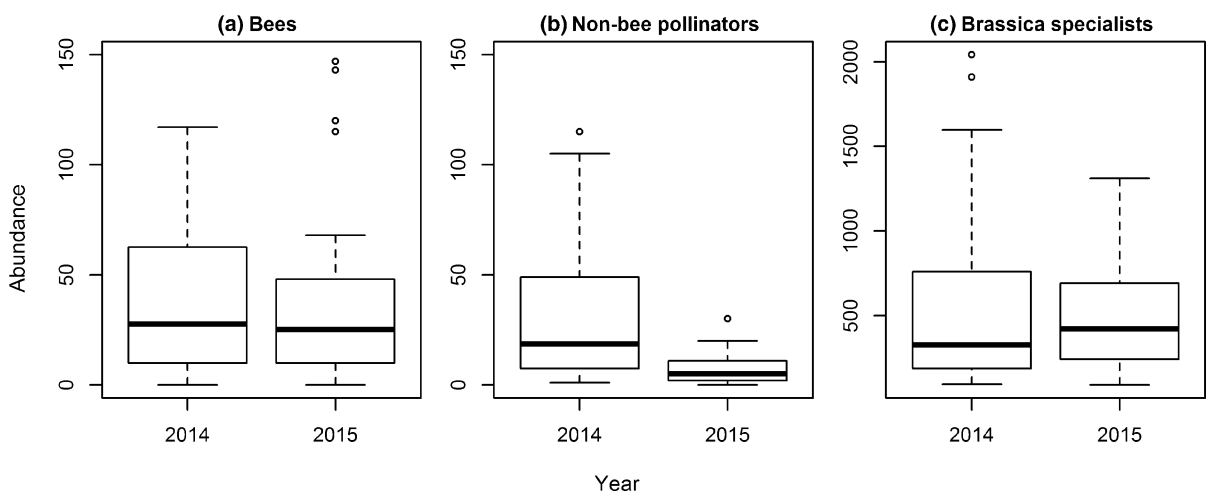


**Fig. 3** Abundance (no. of individuals) of flower-visiting insects in oilseed rape transects ( $n = 66$ ) in relation to the area of oilseed rape in a 1 km radius buffer around each transect. The interaction between each functional group and oilseed rape are plotted separately to aid visual interpretation. Flower visitors were divided into three functional groups **a** bees, **b** non-bee

pollinators and **c** brassica specialists (used as the baseline reference level). Solid lines represent back transformed predicted values from linear mixed effects analysis (Table S7), dashed lines represent 95% confidence intervals calculated via bootstrapping of 200 simulations

flower visitors was lower in 2015 (effect size  $-1.45 \pm 0.456$  SE, Fig. 4, Online Resource 4 Table S7). The best model that included semi-natural habitat had a  $\Delta\text{AICc}$  of  $> 48$  (Online Resource 4 Table S8) when compared with the top model, again indicating that mass flowering crop area explained more variation in the pollinator community than semi-natural habitat. When local habitat variables were included, the top model included the landscape model

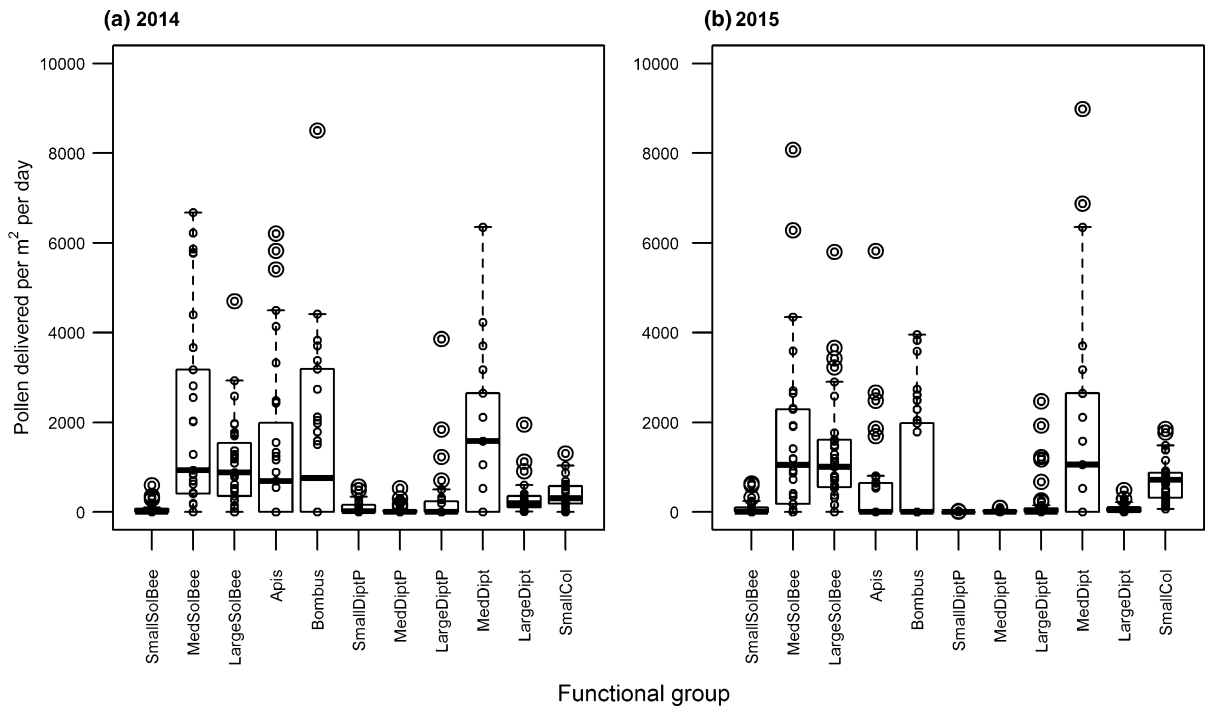
(year, functional group, area of OSR in 1 km and their interactions) and the length of hedge next to the field edge, which had a significant negative interaction with the area of oilseed rape within 1 km (effect size  $-5.52 \pm 1.461$  SE, Online Resource 4 Table S7). This model had substantially more supporting evidence than the initial landscape model only ( $\Delta\text{AICc}$  14.34, Online Resource 4, Table S10).



**Fig. 4** Boxplots (median, interquartile range, outliers) showing the interaction between study year and functional group on the abundance of flower-visiting insects in oilseed rape fields

(Table S7). Flower visitors were divided into three functional groups **a** bees, **b** non-bee pollinators and **c** brassica specialists (plotted on a different y axis scale for ease of interpretation)





**Fig. 5** Estimated total number of pollen grains delivered per  $m^2$  per day for each transect, by different visitor types. Pollinator groups as follows, with their functional group in brackets—SmallSolBee, small solitary bee (bee); MedSolBee, medium solitary bee (bee); LargeSolBee, large solitary bee (bee); Apis, *Apis mellifera* (bee); Bombus, *Bombus* spp. (bee); SmallDiptP, small probing fly (non-bee pollinator); MedDiptP, medium

sized probing fly (non-bee pollinator); LargeDiptP, large probing fly (non-bee pollinator); MedDipt, medium sized Diptera (brassica specialist); LargeDipt, large Diptera (non-bee pollinator). Outliers of  $> 10,000$  pollen grains per  $m^2$  per day ( $n = 16$ ) were removed to aid visual interpretation. For definitions of pollinator groups see Online Resource 2 Table S3

### Impacts of landscape on pollination

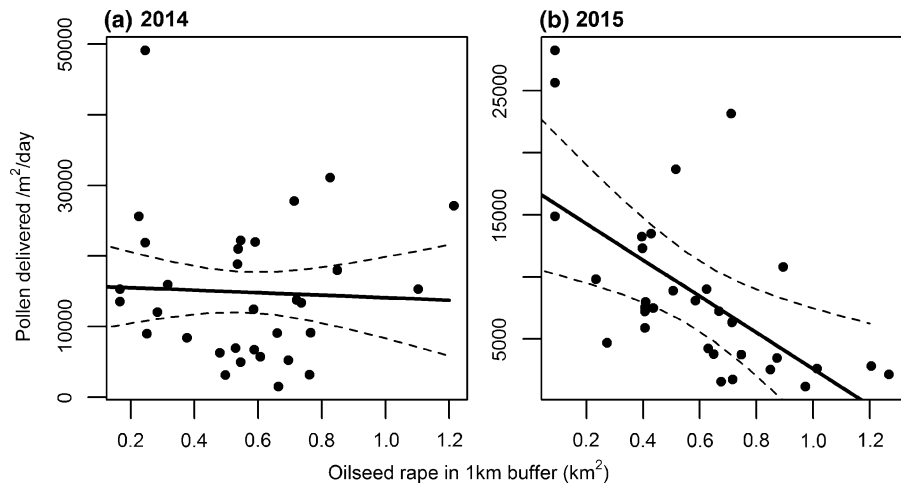
From the 11 pollinator groups, 198 individuals were used to assess pollen deposition [see Phillips et al. (2018); Online Resource 2 Table S3]. The four groups with the highest single visit deposition were medium-sized solitary bees, bumblebees, large solitary bees and honey bees (median SVD 457, 331, 326 and 193, respectively; Online Resource 2 Table S3). However, when the number of pollen grains was capped at 160 pollen grains per visit and multiplied by the effective visit rate, the groups that delivered most pollen, were medium-sized flies, medium-sized solitary bees and large solitary bees (median number of pollen grains delivered per  $m^2$  per hour 198, 161 and 131 respectively; Online Resource 2 Table S3). Estimated pollen delivery per transect varied depending on both the effectiveness and abundance of visitors (Fig. 5). The area of OSR within 1 km had no significant effect on pollen deposition (effect size  $0.19 \pm 0.709$  SE,  $df =$

36,  $t = 0.26$ ,  $P = 0.79$ ); neither did the year (effect size 2015  $0.39 \pm 0.532$  SE,  $df = 22$ ,  $t = 0.74$ ,  $P = 0.47$ ) or hedge length (effect size  $0.0007 \pm 0.00071$  SE,  $df = 36$ ,  $t = 0.98$ ,  $P = 0.33$ ) but there was a significant interaction between year and area of OSR within 1 km, with a reduction in oilseed rape pollen deposition in transects surrounded by more oilseed rape in 2015 (effect size OSR: Year 2015  $-1.93 \pm 0.823$  SE,  $df = 36$ ,  $t = -2.34$ ,  $P = 0.025$ ; Fig. 6).

### Discussion

Our study was the first to look at landscape factors, local factors, and pollen deposition in oilseed rape using the full pollinator community. The results indicate that the area of mass-flowering crop can have a negative impact on bee diversity and abundance in the crop, but not other flower-visitors, and explained

**Fig. 6** The impact of year and surrounding land use (area of oilseed rape) on the estimated number of pollen grains delivered per  $\text{m}^2$  per transect per day (8 h) ( $n = 32$  due to missing data). Pollen deposition calculated based on the number of pollen grains delivered per single visit for each pollinator group multiplied by the visit rate of each pollinator group on that transect



more variation than semi-natural habitat. Landscape-mediated changes to the pollinator community affected pollen deposition. The area of oilseed rape had a negative effect on pollen deposition, but only when there were low numbers of non-bee pollinators.

#### Impacts of landscape composition

Transects with a greater proportion of oilseed rape in the surrounding landscape had lower bee species richness and abundance in the crop. This reduction was only seen for bees and not for species that can complete their entire life cycle within the crop, or for other non-bee pollinators. Mass-flowering crops such as oilseed rape have been shown to have contrasting effects on different pollinators, for example decreasing the number of long-tongued bumble bees (Diekötter et al. 2010) and increasing the species richness and abundance of cavity-nesting bees (Diekötter et al. 2014). In our system, there were high numbers of solitary bees, particularly the genus *Andrena*. Solitary bees have a smaller foraging range (Gathmann and Tscharrnke 2002) and respond to landscape changes at a smaller scale than bumblebees or honeybees (Stefan-Dewenter et al. 2002). Lower species richness and abundance of pollinators may be due to two main mechanisms—(1) dilution of pollinators resulting in fewer visitors per  $\text{m}^2$  crop or (2) landscape-scale reduction in abundance or species richness of the pollinator community overall due to less semi-natural habitat resulting in fewer floral resources overall and lower nest site availability (Holzschuh et al. 2016). Previous experiments investigating the influence of

mass-flowering crops on dilution vs population growth of pollinators have indicated that dilution is the stronger effect (Holzschuh et al. 2016). However, while most bee species were found in fewer transects surrounded by large areas of oilseed rape, eleven bee species were never found in these transects. This reduction in bee species richness as well as abundance indicates that some species require additional resources that are not provided by crops and associated edge habitats, as suggested by Martins et al. (2018). The species never found in oilseed rape dominated areas were smaller bees such as *Lasioglossum* species, which need all their foraging requirements within a smaller range (Müller et al. 2006).

Previous studies have shown a positive impact of semi-natural habitat on species richness and abundance of pollinators in multiple crops (Ricketts et al. 2008) and for oilseed rape specifically (Bommarco et al. 2012; Woodcock et al. 2013; Bartomeus et al. 2014). We analysed both different types of semi-natural habitat with potential impact and total semi-natural habitat. While models that included semi-natural habitat did demonstrate a positive effect on species richness of bees (the best model that included semi-natural habitat had a positive relationship between bees and total semi-natural habitat within 0.5 km (effect size  $3.98 \pm 2.506$  SE, see Online Resource 6), the  $\Delta\text{AICc}$  was 38 and marginal  $R^2$  0.24, indicating this factor explained far less variation than the amount of oilseed rape. For abundance, the best model that did not include the area of oilseed rape included the total area of arable habitat within 1 km, which had a negative impact on bees (effect size

–  $1.10 \pm 0.490$  SE,  $\Delta AICc$  45.83, marginal  $R^2$  0.57). The total area of surrounding arable land was negatively correlated with total semi-natural habitat (Pearson's  $r$  – 0.37). Our results may contrast with previous studies because few of the earlier studies tested the area of semi-natural habitat and mass-flowering crops simultaneously (but see Bommarco et al. 2012; Holzschuh et al. 2016); or they had a different pollinator community; or they studied bees only. For example, very few flower visits in Bommarco et al. (2012) or Bartomeus et al. (2014) were made by solitary bees. Both landscape-scale support of bees by semi-natural habitat and dilution of bees in crops due to block cropping are likely to be happening in tandem (Diekötter et al. 2014). In our study, the area of mass-flowering crop had the strongest impact on pollen deposition within fields.

Non-bee pollinators are often less sensitive to landscape variables, although there are fewer studies than on bees (Rader et al. 2016). Studies on groups that are predominantly predatory but also include flower visitors (such as Empididae) have indicated that landscape variables, particularly woodland and wet habitats, can be important (Pfister et al. 2017). Larval stages of non-bee pollinators in this study are commonly soil dwelling and consume plant detritus (Bibionidae) or other soil invertebrates (Empididae: Empis). In contrast, many hoverflies (Diptera: Syrphidae) in agricultural systems have above-ground aphidophagous larvae. Habitat does impact the distribution of these groups (e.g. Burel et al. 1998), but they are not central place foragers. Therefore they probably migrate to OSR fields as adults and remain there, potentially reducing the impacts of landscape variables.

Field edge habitat appeared to have little impact on the abundance and species richness of pollinators. The presence of a weak interaction indicated that in landscapes with large areas of oilseed rape there were more bees in the crop when there was no hedge, suggesting that bees were foraging in hedges as an alternative when available in these landscapes. The field margins were either grass dominated or contained plants that flowered later than OSR; the most common insect-pollinated plants were *Heracleum sphondylium* and *Trifolium repens*. The hedges may be providing more nectar resources in spring via species such as *Crataegus monogyna*, *Salix* spp. and *Prunus spinosa* which often overlap in flowering time with winter-

sown oilseed rape. Previous studies have found that the presence of field edge habitat has a positive effect on wild bee abundance and diversity (Kennedy et al. 2013). In our study all but nine field edges had a margin of > 1 m width and of those, three had a hedge, indicating that some minimum requirements for semi-natural habitat were being met. Other studies have shown that an increase in the number of flowering species in sown grasslands and wildflower mixes can increase flower visitation (Ebeling et al. 2008) and pollinator abundance (Scheper et al. 2013), but these are more likely to have a positive impact than grass-dominated margins. For non-bee pollinators, local interventions also have varying effectiveness; several groups have greater larval aggregations near to non-crop habitat (e.g. Benefer et al. 2016), and woody edge habitats have a positive effect on Empididae (Pfister et al. 2017). The most common Dipteran pollinator in this study, anthomyid flies, complete their life cycle within the crop. The larvae feed on oilseed rape roots, without causing any significant economic damage if plants are at low density (Doddall et al. 1998). Agricultural practices such as zero tillage increase emergence (Doddall et al. 1998) which may also benefit other pollinators with soil-dwelling larvae (Stinner and House 1990) and ground nesting bees (e.g. Ullmann et al. 2016).

#### Impacts on pollination

The contribution of different groups of insects to pollen deposition is a combination of the single visit pollen deposition, visit rate, and their abundance in the field. Flower visitors such as anthomyid species are often not considered as pollinators, but do deposit pollen when visiting flowers. Despite their low individual visit rate, when highly abundant they deliver relatively large numbers of pollen grains (Fig. 5). Our method for estimating pollen deposition was conservative as we used the median number of pollen grains delivered per single visit, and accounted for proportion of visits with stigma or anther contact. While honey bees and bumblebees delivered large numbers of pollen grains in a single visit, not all these pollen grains are likely to be required for full fertilisation. The low abundance of bumblebees and honey bees during the crop flowering period means that they delivered less pollen overall than medium-sized flies or medium-sized solitary bees. While we

observed these groups using different methods, had we only used pan trap data bumblebees and honey bees would have contributed even less pollen as they were rarely recorded. Our method does not take into account the quality of the pollen delivered, for example the amount of outcrossed pollen (Patchett et al. 2017), although oilseed rape varieties are commonly self-fertile to some degree (Hudewenz et al. 2013).

The impact of landscape-level simplification caused by increases in the area of mass-flowering crops sown has the potential to reduce pollen deposition. We found that this effect varied in the two years of our study. The number of pollen grains deposited was reduced in landscapes with large areas of oilseed rape in the year when there were fewer non-bee pollinators. This suggests that the reduction in the number of flower visits by bees in relation to the area of oilseed rape in 2014 was mitigated for by non-bee pollinators, whereas in 2015 when the numbers of non-bee pollinators were low this was not the case. The pollination service provision was therefore resilient in some years but not in others. This may have been due to inter-annual variation in weather, asynchrony in emergence times and OSR flowering times, or another unspecified factor that varied between years or sites (see Online Resource 1 Table S1 for list of variables considered) which had a stronger impact on non-bee pollinators than other groups. Winfree and Kremen (2009) found little evidence for density compensation between bee species, but instead contrasting responses by different bee species. In contrast, we found different responses between bees, non-bee pollinators and brassica crop specialists.

## Conclusions

Alterations to landscape and local resources have contrasting impacts on pollinating taxa (Westphal et al. 2003; Diekötter et al. 2010). In this study we found that the impacts of mass-flowering crops were stronger than the impact of semi-natural habitat, but only for bees. Non-bee pollinators were relatively insensitive to landscape composition but numbers varied between the two years of study. Reductions in both the taxonomic richness and abundance of bees in landscapes with large areas of oilseed rape indicates some bee species require additional resources

provided by semi-natural habitat, although the effect was swamped by the effect of the mass-flowering crop. This suggests that practices such as growing mass flowering crops in large, contiguous areas may lead to a dilution of bee foraging density and therefore a reduction in pollen deposition in crops. By looking at the entire pollinator community, we found that the impact of landscape changes on the pollination service in oilseed rape was buffered by non-bee insect pollinators, but only when these were abundant. This highlights the need to understand the impacts of landscape, local habitat and cropping practices on non-bee insect pollinators, and the importance of considering the full flower-visiting community when assessing variation in ecosystem service delivery.

**Acknowledgements** Thanks to Carly Benerfer, Richard Comont, Emma Higgins, Ciara McGinley, James Duffy, Andrew Suggitt, Stefano Casalegno, Ivan Wright and the RSPB and farmers for allowing site access. The manuscript was substantially improved by two anonymous referees. Funded by the UK Natural Environment Research Council as part of Wessex BESS (Ref. NE/J014680/1).

**Funding** Funded by the UK Natural Environment Research Council as part of Wessex BESS (Ref. NE/J014680/1).

**Data availability** Datasets available in the NERC Environmental Information Data Centre repository <https://doi.org/10.5285/6128a4f7-d2ac-43c5-b492-af4c654e89b8>.

## Compliance with ethical standards

This study was approved by the University of Exeter Ethics Committee 2014/622.

**Conflict of interest** The authors declare that they have no conflict of interest.

**Open Access** This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

## References

- Allen-Wardell G, Bernhardt P, Bitner R, Burquez A, Buchmann S, Cane J, Cox PA, Dalton V, Feinsinger P, Ingram M, Inouye D, Jones CE, Kennedy K, Kevan P, Koopowitz H, Medellin R, Medellin-Morales S, Nabhan GP, Pavlik B, Tepedino V, Torchio P, Walker S (1998) The potential consequences of pollinator declines on the conservation of biodiversity and stability of food crop yields. *Conserv Biol* 12(1):8–17
- Bartomeus I, Potts SG, Steffan-Dewenter I, Vaissière BE, Woyciechowski M, Krewenka KM, Tscheulin T, Roberts SPM, Szentgyörgyi H, Westphal C, Bommarco R (2014) Contribution of insect pollinators to crop yield and quality varies with agricultural intensification. *PeerJ* 2:e328
- Bartoń K (2016) MuMIn: multi-model inference, R package version 1.15.6
- Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. *J Stat Softw* 67(1):1–48
- Baude M, Kunin WE, Boatman ND, Conyers S, Davies N, Gillespie MAK, Morton RD, Smart SM, Memmott J (2016) Historical nectar assessment reveals the fall and rise of floral resources in Britain. *Nature* 530(7588):85–88
- Benefier CM, D’Ahmed KS, Blackshaw RP, Sint HM, Murray PJ (2016) The distribution of soil insects across three spatial scales in agricultural grassland. *Front Ecol Evol* 4:41
- Biesmeijer JC, Roberts SPM, Reemer M, Ohlemüller R, Edwards M, Peeters T, Schaffers AP, Potts SG, Kleukers R, Thomas CD, Settele J, Kunin WE (2006) Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science* 313(5785):351–354
- Blaauw BR, Isaacs R (2014) Flower plantings increase wild bee abundance and the pollination services provided to a pollination-dependent crop. *J Appl Ecol* 51(4):890–898
- Bommarco R, Marini L, Vaissiere BE (2012) Insect pollination enhances seed yield, quality, and market value in oilseed rape. *Oecologia* 169(4):1025–1032
- Burel F, Baudry J, Butet A, Clergeau P, Delettre Y, Le Coeur D, Dubs F, Morvan N, Paillat G, Petit S, Thenail C, Brunel E, Lefeuvre JC (1998) Comparative biodiversity along a gradient of agricultural landscapes. *Acta Oecol Int J Ecol* 19(1):47–60
- Campbell AJ, Wilby A, Sutton P, Wäckers FL (2017) Do sown flower strips boost wild pollinator abundance and pollination services in a spring-flowering crop? A case study from UK cider apple orchards. *Agr Ecosyst Environ* 239:20–29
- Danner N, Keller A, Härtel S, Steffan-Dewenter I (2017) Honey bee foraging ecology: season but not landscape diversity shapes the amount and diversity of collected pollen. *PLoS ONE* 12(8):e0183716
- DEFRA (2016) Agriculture in the United Kingdom 2015. DEFRA, London
- Diekötter T, Kadoya T, Peter F, Wolters V, Jauker F (2010) Oilseed rape crops distort plant–pollinator interactions. *J Appl Ecol* 47(1):209–214
- Diekötter T, Peter F, Jauker B, Wolters V, Jauker F (2014) Mass-flowering crops increase richness of cavity-nesting bees and wasps in modern agro-ecosystems. *GCB Bioenergy* 6(3):219–226
- Dosdall LM, Florence LZ, Conway PM, Cowle NT (1998) Tillage regime, row spacing, and seeding rate influence infestations of root maggots (*Delia* spp.) (Diptera: Anthomyiidae) in canola. *Can J Plant Sci* 78(4):671–681
- Ebeling A, Klein A-M, Schumacher J, Weisser WW, Tschamtk T (2008) How does plant richness affect pollinator richness and temporal stability of flower visits? *Oikos* 117(12):1808–1815
- Fitter AH, Peat HJ (1994) The ecological flora database. *J Ecol* 82(2):415–425
- Garibaldi LA, Carvalheiro LG, Leonhardt SD, Aizen MA, Blaauw BR, Isaacs R, Kuhlmann M, Kleijn D, Klein AM, Kremen C, Morandin L, Scheper J, Winfree R (2014) From research to action: enhancing crop yield through wild pollinators. *Front Ecol Environ* 12(8):439–447
- Garibaldi LA, Steffan-Dewenter I, Kremen C, Morales JM, Bommarco R, Cunningham SA, Carvalheiro LG, Chacoff NP, Dudenhoefler JH, Greenleaf SS, Holzschuh A, Isaacs R, Krewenka K, Mandelik Y, Mayfield MM, Morandin LA, Potts SG, Ricketts TH, Szentgyörgyi H, Viana BF, Westphal C, Winfree R, Klein AM (2011) Stability of pollination services decreases with isolation from natural areas despite honey bee visits. *Ecol Lett* 14(10):1062–1072
- Garibaldi LA, Steffan-Dewenter I, Winfree R, Aizen MA, Bommarco R, Cunningham SA, Kremen C, Carvalheiro LG, Harder LD, Afik O, Bartomeus I, Benjamin F, Boreux V, Cariveau D, Chacoff NP, Dudenhöfner JH, Freitas BM, Ghazoul J, Greenleaf S, Hipólito J, Holzschuh A, Howlett B, Isaacs R, Javorek SK, Kennedy CM, Krewenka KM, Krishnan S, Mandelik Y, Mayfield MM, Motzke I, Munyuli T, Nault BA, Otieno M, Petersen J, Pisanty G, Potts SG, Rader R, Ricketts TH, Rundlöf M, Seymour CL, Schüepp C, Szentgyörgyi H, Taki H, Tschamtk T, Vergara CH, Viana BF, Wanger TC, Westphal C, Williams N, Klein AM (2013) Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *Science* 339(6127):1608–1611
- Garratt MPD, Coston DJ, Truslove CL, Lappage MG, Polce C, Dean R, Biesmeijer JC, Potts SG (2014) The identity of crop pollinators helps target conservation for improved ecosystem services. *Biol Conserv* 169:128–135
- Gathmann A, Tschamtk T (2002) Foraging ranges of solitary bees. *J Anim Ecol* 71(5):757–764
- Hoehn P, Tschamtk T, Tylianakis JM, Steffan-Dewenter I (2008) Functional group diversity of bee pollinators increases crop yield. *Proc R Soc B Biol Sci* 275(1648):2283–2291
- Holzschuh A, Dainese M, González-Varo JP, Mudri-Stojnić S, Riedinger V, Rundlöf M, Scheper J, Wickens JB, Wickens VJ, Bommarco R, Kleijn D, Potts SG, Roberts SPM, Smith HG, Vilà M, Vujić A, Steffan-Dewenter I (2016) Mass-flowering crops dilute pollinator abundance in agricultural landscapes across Europe. *Ecol Lett* 19(10):1228–1236
- Hudewenz A, Pufal G, Bögeholz AL, Klein AM (2013) Cross-pollination benefits differ among oilseed rape varieties. *J Agric Sci* 152(5):770–778
- IPBES (2016) Summary for policymakers of the assessment report of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services on pollinators, pollination and food production. In: Potts SG, Imperatriz-Fonseca VL, Ngo HT et al (eds) Secretariat of the

- Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. IPBES, Bonn
- Isaacs R, Tuell J, Fiedler A, Gardiner M, Landis D (2009) Maximizing arthropod-mediated ecosystem services in agricultural landscapes: the role of native plants. *Front Ecol Environ* 7(4):196–203
- Ives AR (2015) For testing the significance of regression coefficients, go ahead and log-transform count data. *Methods Ecol Evol* 6(7):828–835
- Kennedy CM, Lonsdorf E, Neel MC, Williams NM, Ricketts TH, Winfree R, Bommarco R, Brittain C, Burley AL, Cariveau D, Carvalho LG, Chacoff NP, Cunningham SA, Danforth BN, Dudenhöffer J-H, Elle E, Gaines HR, Garibaldi LA, Gratton C, Holzschuh A, Isaacs R, Javorek SK, Jha S, Klein AM, Krewenka K, Mandelik Y, Mayfield MM, Morandin L, Neame LA, Otieno M, Park M, Potts SG, Rundlöf M, Saez A, Steffan-Dewenter I, Taki H, Viana BF, Westphal C, Wilson JK, Greenleaf SS, Kremen C (2013) A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. *Ecol Lett* 16(5):584–599
- Kiehl K, Thormann A, Pfadenhauer J (2006) Evaluation of initial restoration measures during the restoration of calcareous grasslands on former arable fields. *Restor Ecol* 14(1):148–156
- Kleijn D, Winfree R, Bartomeus I, Carvalho LG, Henry M, Isaacs R, Klein A-M, Kremen C, M'Gonigle LK, Rader R, Ricketts TH, Williams NM, Lee Adamson N, Ascher JS, Baldi A, Batary P, Benjamin F, Biesmeijer JC, Blitzer EJ, Bommarco R, Brand MR, Bretagnolle V, Button L, Cariveau DP, Chifflet R, Colville JF, Danforth BN, Elle E, Garratt MPD, Herzog F, Holzschuh A, Howlett BG, Jauker F, Jha S, Knop E, Krewenka KM, Le Feon V, Mandelik Y, May EA, Park MG, Pisanty G, Reemer M, Riedinger V, Rollin O, Rundlöf M, Sardinias HS, Scheper J, Sciligo AR, Smith HG, Steffan-Dewenter I, Thorp R, Tschamtk T, Verhulst J, Viana BF, Vaissiere BE, Veldtman R, Westphal C, Potts SG (2015) Delivery of crop pollination services is an insufficient argument for wild pollinator conservation. *Nat Commun* 6:7414
- Knight ME, Martin AP, Bishop S, Osborne JL, Hale RJ, Sanderson A, Goulson D (2005) An interspecific comparison of foraging range and nest density of four bumblebee (*Bombus*) species. *Mol Ecol* 14(6):1811–1820
- Kremen C, Williams NM, Thorp RW (2002) Crop pollination from native bees at risk from agricultural intensification. *Proc Natl Acad Sci USA* 99(26):16812–16816
- Kreyer D, Oed A, Walther-Hellwig K, Frankl R (2004) Are forests potential landscape barriers for foraging bumblebees? Landscape scale experiments with *Bombus terrestris* agg. and *Bombus pascuorum* (Hymenoptera, Apidae). *Biol Conserv* 116(1):111–118
- Lindström SAM, Herbertsson L, Rundlöf M, Smith HG, Bommarco R (2016) Large-scale pollination experiment demonstrates the importance of insect pollination in winter oilseed rape. *Oecologia* 180(3):759–769
- Lye G, Park K, Osborne JLO, Holland J, Goulson D (2009) Assessing the value of Rural Stewardship schemes for providing foraging resources and nesting habitat for bumblebee queens (Hymenoptera: Apidae). *Biol Conserv* 142:2023–2032
- Martins KT, Albert CH, Lechowicz MJ, Gonzalez A (2018) Complementary crops and landscape features sustain wild bee communities. *Ecol Appl* 28(4):1093–1105
- Mesquida J, Renard M (1984) Etude des quantités de pollen déposées sur les stigmates dans différentes conditions de pollinisation; influence sur la production de graines chez le colza d'hiver mâle-fertile. Vème Symposium International sur la Pollinisation. In: *Compte Rendu du Vème Symposium International sur la Pollinisation*, Versailles, France 1984. INRA, pp 351–356
- Müller A, Diener S, Schnyder S, Stutz K, Sedivy C, Dorn S (2006) Quantitative pollen requirements of solitary bees: implications for bee conservation and the evolution of bee-flower relationships. *Biol Conserv* 130(4):604–615
- Nakagawa S, Schielzeth H (2013) A general and simple method for obtaining R<sup>2</sup> from generalized linear mixed-effects models. *Methods Ecol Evol* 4(2):133–142
- NRC (2007) Status of pollinators in North America. The National Academies Press, Washington, DC
- Orford KA, Murray PJ, Vaughan IP, Memmott J (2016) Modest enhancements to conventional grassland diversity improve the provision of pollination services. *J Appl Ecol* 53(3):906–915
- Orford KA, Vaughan IP, Memmott J (2015) The forgotten flies: the importance of non-syrphid Diptera as pollinators. *Proc R Soc B* 282(1805):20142934
- Paradis E, Schliep K (2018) ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics*. <https://doi.org/10.1093/bioinformatics/bty633>
- Patchett RB, Ballantyne G, Willmer PG (2017) Estimating pollinator performance of visitors to the self-incompatible crop-plant *Brassica rapa* by single visit deposition and pollen germination: a comparison of methods. *J Pollinat Ecol* 21(3):78–85
- Pfister SC, Sutter L, Albrecht M, Marini S, Schirmel J, Entling MH (2017) Positive effects of local and landscape features on predatory flies in European agricultural landscapes. *Agric Ecosyst Environ* 239:283–292
- Phillips BB, Williams A, Osborne JL, Shaw RF (2018) Shared traits make flies and bees effective pollinators of oilseed rape (*Brassica napus* L.). *Basic Appl Ecol*. <https://doi.org/10.1016/j.baae.2018.06.004>
- Pywell RF, Heard MS, Woodcock BA, Hinsley S, Ridding L, Nowakowski M, Bullock JM (2015) Wildlife-friendly farming increases crop yield: evidence for ecological intensification. *Proc R Soc B*. <https://doi.org/10.1098/rspb.2015.1740>
- R Core Team (2016) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Rader R, Bartomeus I, Garibaldi LA, Garratt MPD, Howlett BG, Winfree R, Cunningham SA, Mayfield MM, Arthur AD, Andersson GKS, Bommarco R, Brittain C, Carvalho LG, Chacoff NP, Entling MH, Foully B, Freitas BM, Gemmill-Herren B, Ghazoul J, Griffin SR, Gross CL, Herbertsson L, Herzog F, Hipólito J, Jaggard S, Jauker F, Klein A-M, Kleijn D, Krishnan S, Lemos CQ, Lindström SAM, Mandelik Y, Monteiro VM, Nelson W, Nilsson L, Pattemore DE, de O. Pereira N, Pisanty G, Potts SG, Reemer M, Rundlöf M, Sheffield CS, Scheper J, Schüepp C, Smith HG, Stanley DA, Stout JC, Szentgyörgyi H, Taki

- H, Vergara CH, Viana BF, Woyciechowski M (2016) Non-bee insects are important contributors to global crop pollination. *Proc Natl Acad Sci* 113(1):146–151
- Ricketts TH, Regetz J, Steffan-Dewenter I, Cunningham SA, Kremen C, Bogdanski A, Gemmill-Herren B, Greenleaf SS, Klein AM, Mayfield MM, Morandin LA, Ochieng A, Viana BF (2008) Landscape effects on crop pollination services: are there general patterns? *Ecol Lett* 11(5):499–515
- Ridding LE, Redhead JW, Oliver TH, Schmucki R, McGinlay J, Graves AR, Morris J, Bradbury RB, King H, Bullock JM (2018) The importance of landscape characteristics for the delivery of cultural ecosystem services. *J Environ Manag* 206:1145–1154
- Scheper J, Bommarco R, Holzschuh A, Potts SG, Riedinger V, Roberts SPM, Rundlöf M, Smith HG, Steffan-Dewenter I, Wickens JB, Wickens VJ, Kleijn D (2015) Local and landscape-level floral resources explain effects of wild-flower strips on wild bees across four European countries. *J Appl Ecol* 52(5):1165–1175
- Scheper J, Holzschuh A, Kuussaari M, Potts SG, Rundlöf M, Smith HG, Kleijn D (2013) Environmental factors driving the effectiveness of European agri-environmental measures in mitigating pollinator loss—a meta-analysis. *Ecol Lett* 16(7):912–920
- Stace C (1997) *New flora of the British Isles*. Cambridge University Press, Cambridge
- Steffan-Dewenter I, Munzenberg U, Burger C, Thies C, Tschamtké T (2002) Scale-dependent effects of landscape context on three pollinator guilds. *Ecology* 83(5):1421–1432
- Stinner BR, House GJ (1990) Arthropods and other invertebrates in conservation-tillage agriculture. *Annu Rev Entomol* 35:299–318
- Toynton P, Ash D (2002) Salisbury plain training area—the British steppes? *Br Wildl* 13:335–343
- Ullmann KS, Meisner MH, Williams NM (2016) Impact of tillage on the crop pollinating, ground-nesting bee, *Peploponapis pruinosa* in California. *Agric Ecosyst Environ* 232:240–246
- Vanbergen AJ, The Insect Pollinators Initiative (2013) Threats to an ecosystem service: pressures on pollinators. *Front Ecol Environ* 11(5):251–259
- Westphal C, Bommarco R, Carré G, Lamborn E, Morison N, Petanidou T, Potts SG, Roberts SPM, Szentgyörgyi H, Tscheulin T, Vaissière BE, Woyciechowski M, Biesmeijer JC, Kunin WE, Settele J, Steffan-Dewenter I (2008) Measuring bee diversity in different European habitats and biogeographical regions. *Ecol Monogr* 78(4):653–671
- Westphal C, Steffan-Dewenter I, Tschamtké T (2003) Mass flowering crops enhance pollinator densities at a landscape scale. *Ecol Lett* 6(11):961–965
- Whittingham MJ, Stephens PA, Bradbury RB, Freckleton RP (2006) Why do we still use stepwise modelling in ecology and behaviour? *J Anim Ecol* 75(5):1182–1189
- Winfree R, Kremen C (2009) Are ecosystem services stabilized by differences among species? A test using crop pollination. *Proc R Soc B* 276(1655):229–237
- Woodcock BA, Edwards M, Redhead J, Meek WR, Nuttall P, Falk S, Nowakowski M, Pywell RF (2013) Crop flower visitation by honeybees, bumblebees and solitary bees: behavioural differences and diversity responses to landscape. *Agric Ecosyst Environ* 171:1–8
- Woodcock BA, Isaac NJB, Bullock JM, Roy DB, Garthwaite DG, Crowe A, Pywell RF (2016) Impacts of neonicotinoid use on long-term population changes in wild bees in England. *Nat Commun* 7:12459

**Publisher's Note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.