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Bees increase oilseed rape yield under real field conditions

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ABSTRACT

Oilseed rape (OSR, *Brassica napus* L.) is a common crop found in many European agricultural landscapes. It is pollinated by a wide variety of insects, but the reported contribution of pollinators to yield varies widely between studies (from 0 to 50%). Moreover, such a contribution has seldom been estimated at the field scale in real farming conditions. We analysed OSR yields in response to insect pollination; over four years, at two different scales: farm fields and individual plants. We used both empirical and experimental approaches along a gradient of pollinator diversity and abundance. The empirical approach was based on farm surveys (151 fields) while the experimental approach used various pollination exclusion methods (570 plants in 101 fields) to estimate the relative contributions of insect, wind, and self-pollination. The OSR yields were positively correlated to total bee abundance and bee genera diversity, through improved fruiting success and plant seed mass (after adjusting for plant biomass). Hoverfly diversity and abundance, and bumblebee abundance did not have any effect. The main OSR pollinators in our study were honeybees (*Apis mellifera*) and wild bees (*Lasioglossum* spp.). Yields were increased, on average, by up to 37.5% (27.7% – 47.5%) at field scale when bee genera diversity increased from a single genus to more than 10 genera (pan-trap data). Insect pollination contributed about 30% of plant yield. Self-pollination and wind pollination accounted for the remaining 70%, with self-pollination being the major contributor. Our study demonstrates that pollinator diversity and abundance, at least at very high levels, have a major effect on OSR yields. This suggests that establishing a monetary value for pollination services in OSR farming systems could be used to balance the cost of managing semi-natural habitats or meadows to maintain bees and other pollinators.

1. Introduction

In most angiosperms, pollen transfer depends on animals (Ollerton et al., 2011), and this holds true for both wild and domesticated plant species, of which 70% are pollinator dependent (Klein et al., 2007). The economic value of pollination service has been estimated at 10% (€149 billion) of yearly global world agricultural production (Gallai et al., 2009), being particularly important for the yield of many small farms (Garibaldi et al., 2016). The dependence of crop yields on insect pollination, however, varies widely between crops, from independent to obligate (Klein et al., 2007). Pollinators not only increase yields by increasing seed set, but they may also enhance crop quality (Bartomeus et al., 2014), and stabilise food production either in time (Garibaldi et al., 2011) or space (Deguines et al., 2014). However, despite the global importance of pollinators for food production, pollination is

rarely taken into account in the development of farming systems or practices (Breeze et al., 2014), partly because it is difficult to disentangle pollination by insects from other factors that affect yield (Marini et al., 2015). Additionally, there may be an order of magnitude variation in the effect of insect pollination on yields within a particular crop (Gallai et al., 2009). This variability is explained by the spatial variation of pollinator communities, leading to a spatial variation of pollination potential and pollen limitation (Gómez et al., 2010), reducing agricultural production (Wilcock and Neiland, 2002).

Oilseed rape (OSR, *Brassica napus* L.) is the fourth largest oil crop in terms of production in the world and the most common in the European Union (FAOSTAT, 2014). OSR is not only pollinated by insects but also by wind and self-pollination (Becker et al., 1992; Mesquida and Renard, 1982). Wind pollination is the transfer of pollen from one plant to another by passive wind transport, while self-pollination is the direct

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passage of pollen between the male and female parts of the same flower or between two flowers on the same plant. There is huge uncertainty in estimates of the relative importance of insect pollination for OSR yields, with reported values ranging from negligible (Sammegard et al., 2016) to 50% (Araneda Durán et al., 2010) with a range of values in between (Bartomeus et al., 2014; Bommarco et al., 2012; Lindström et al., 2016; Stanley et al., 2013; Zou et al., 2017). There is no accepted explanation for such a high variability, which may result from farming practices (Marini et al., 2015), plant varieties (Hudewenz et al., 2014), or variation in pollinator communities (Rader et al., 2015). The major pollinators also depend strongly on the study being honeybees (*Apis mellifera*), bumblebees, wild bees or hoverflies (Garratt et al., 2014; Lindström et al., 2016; Zou et al., 2017b). Factors affecting OSR yields include pollinator visitor rate (Bartomeus et al., 2014; Woodcock et al., 2013), nearby honeybee hives (Lindström et al., 2016), and bee diversity (Zou et al., 2017). In addition, the measurements used to estimate the effects on OSR yields varied between studies, from being a small part of the OSR plant (Stanley et al., 2013), total seed production per plant (Hudewenz et al., 2014; Zou et al., 2017), or a set of OSR plants from either small (< 2 m², Araneda Durán et al., 2010; Bommarco et al., 2012; Bartomeus et al., 2014) or large (> 50m², Lindström et al., 2016) field section (in this latter study, only the contribution by honeybees was investigated). So far, to our knowledge, no study has ever quantified the effect of pollinators on yield at field scale for oilseed rape.

Here, we use, for the first time, a systemic approach by quantifying the effect of insect pollination on OSR yields, at both field scale and individual plant scale, combining field scale yields and field scale assessments of pollination. We used both empirical data obtained for 151 fields and experimental manipulation of pollination in 101 fields. The yield estimates from both methods were compared with pollinator abundance and diversity, obtained by trapping in the fields. The OSR focus fields were distributed along gradients of landscapes with varying concentration of meadows, semi-natural habitats and organically farmed fields, which are all known to affect pollinator abundance and diversity (Holzschuh et al., 2008; Kennedy et al., 2013; Steffan-Dewenter et al., 2002; Woodcock et al., 2013). By using landscape gradients, we aimed to maximise the variation in the pollinator community to be able to quantify its effects on yield and identify the main pollinators involved. By measuring various fecundity traits of the OSR plants, such as the fruiting success, seeds per pods, seed unit weight and seed mass, we also identified the traits that were most affected by pollinators. Finally, we quantified the relative contributions of insects (large *versus* small), wind and self-pollination at plant level. Our experimental design, changing pollinator abundances using landscape variations as well as using pollinator exclusion, allowed us to i) quantify the effect of pollinator rich landscapes on pollination rate, and ii) quantify the contribution of pollination by insects at plant (grain biomass per plant) and field (yield) scales.

2. Material and methods

2.1. Study site, experimental fields and landscape context

Pollinator exclusion experiments and farming surveys were conducted between 2013 and 2016 in the LTSER “Zone Atelier Plaine & Val de Sèvre”, a 450 km² study site located in the south of Deux-Sèvres district (Fig. 1a), central western France (Fig S.A, <http://www.za.plainevalsevre.cnrs.fr/>, Bretagnolle et al., 2018). Only winter OSR is grown in the LTSER, representing about 8% of the agricultural area (Fig. 1a). Experiments were conducted directly in commercial farm fields. Since we were interested in quantifying insect pollination in OSR fields under normal conditions, we did not request any modification of the farming practices. We used a moving window to randomly select 1 km² squares (Fahrig et al., 2011) that represented density gradients of three environmental features: semi-natural habitats (hedgcs and forest

fragments), meadows, and organically farmed fields (obtained from the French parcel register 2014). All these landscape features are known to strongly influence the abundance of pollinators (Kennedy et al., 2013) and were mapped in the GIS LTSER (Bretagnolle et al., 2018). Within the selected squares, an OSR focus field was then chosen, if present (usually, there was only one OSR field). On average, OSR fields were at 365 m (48 to 1152 m) from the nearest OSR neighbour. Field size ranged from 0.65 ha to 28.5 ha (mean 6.3 ha). The selected fields had similar soil types according to the IGCS soil map (available at <https://www.geoportail.gouv.fr/>). In 93% of the fields the soil was calcareous and in the rest the soil was red (with some clay).

A first set of 151 OSR fields (27 in 2013, 45 in 2014, 48 in 2015, and 31 in 2016) was used for an empirical assessment of the effects of pollinator abundance and diversity on crop yield at the field scale. No field was used twice in the four years. We interviewed the farmers, owners of the fields, to collect information on practices (fertilizer, pesticides, and OSR variety) and yield at the end of each cropping season (during winter). A second set of 101 fields (15 in 2013, 29 in 2014, 27 in 2015, and 30 in 2016) was used for pollinator exclusion experiments, of which 66 were also in the first set. The two sets differed because some farmers refused the survey or refused permission for the exclusion experiment. There were 28 varieties of OSR, mainly restored hybrid (88.7%) and conventional (11.1%). All OSR varieties in this study could be self-pollinated or cross-pollinated.

2.2. Experimental treatments

Six individual OSR plants were selected in each field at two positions: one at the field edge and one at 20 m from the edge in the field core. These two positions were selected to assess whether the distance from semi-natural habitats affected the pollination by insects (Woodcock et al., 2016). For each individual OSR plant, three (2013), two (2014) and four (2015–16) secondary branches were selected for pollinator exclusion treatments (Fig. 1c). There were different numbers of branches in each year because we tested different exclusion treatments. The branches were selected so as to be at the same flowering stage and adjacent or opposite to each other. The various exclusion treatments allowed self-pollination (SF), wind-pollination (W), small-bodied (SP) and large-bodied (LP) insect pollinators. One of the branches was used as a control (570 branches in total) where all flowers could be pollinated in any way (insects, wind and self-pollination, “LP + SP + W + SF”). A second branch was enclosed in a small mesh bag (0.6 mm mesh size, 517 branches), for which the flowers could only be self-pollinated or wind pollinated (“W + SF”). In 2013, 2015 and 2016, a third branch was enclosed in large mesh bag (3 mm mesh size, 403 branches), allowing self-pollination and pollination by wind and small insects (“SP + W + SF”). Finally, in 2015 and 2016, a fourth branch was enclosed in a gas-permeable Osmolux bag (Pantek, France) (272 branches), excluding all except self-pollination (“SF”). In 2013 only, each treatment was replicated for each plant (*i.e.* two controls, two large and two small mesh treatments per plant). The branches were bagged before onset of flowering and plants were visited weekly to adjust the bags, lifting them upwards to cover new or future flowers while releasing those flowers that had faded. The bags were completely removed after the last flower had faded. The operations were carried out gently to avoid as far as possible any effect on pod development (Wragg and Johnson, 2011). Branches were collected five days before the harvest. In 2015 and 2016, the rest of plant was also collected to estimate the total plant biomass and total seed biomass. In 2016, six further OSR plants were collected, three from the edge and three at 20 m from the edge, from each of the 44 fields monitored that year, to estimate the effect of pollinators on the total plant production (see Appendix A in Supplementary material for sample sizes and treatments for each year).

All insects caught were identified in the laboratory by professional entomologists, at genera level for wild bees and species level for hoverflies. Bee species were identified in 2015 and 2016. As large numbers were caught in 2013 and 2014 (about 70% of the whole sample) and identifying the species is very time consuming given that there are almost 300 species in the LTSER (Rollin et al., 2013) the species were not identified these years. Four guilds of pollinators were targeted: honeybees (*Apis mellifera*), bumblebees (genus *Bombus*), wild bees (Hymenoptera: Apoidea) and hoverflies (Diptera: Syrphidea). Abundance for each genus was obtained by a nested averaging procedure, starting with mean count per bowl colour and position in the field (core vs. edge), then averaging per position in field, and finally per field (in 2016, pan traps were set twice in each field, and were thus further averaged). For each focal field, this final average per genus was averaged with all other fields within a radius of 1250 m and within a time window spanning from day 90 (30/31 March) to day 170 (18/19 June), thus covering the full OSR flowering period every year (see Appendix B in Supplementary material for a sensitivity analysis of window size and time period). The total pollinator abundance was the sum of all individuals caught. The total number of genera caught was used as a proxy for the diversity. A similar procedure was used for the sweep net samples.

2.5. Statistical analyses

We used a linear model to analyse the effect of farming practices on the crop yield of 151 OSR fields, including the main fertilizers (nitrogen, phosphorus, potassium and sulphur), pesticides (frequency of insecticide, herbicide, and fungicide treatments) and OSR type (restored hybrid versus conventional). Only main effects were included (no interactions), and stepwise selection (backward and forward) was used to select only those variables with significant or marginally significant effects on yield ($P < 0.1$). We then used linear models to test the effects of total pollinator diversity, bee diversity, hoverfly diversity as well as total pollinator abundance, bee abundance and hoverfly abundance on yields, accounting for the farming practice variables selected at the previous step. Significant farming practice variables were added as covariates as well as their two-way interactions with pollinator metrics. The year and its interactions with pollinator metrics were also included. The models were fitted independently for pan trap and sweep net abundance data. In addition, stepwise multiple regression was used to find those pollinator genera that most affected the yield among the nine most common genera caught with pan traps or the eight most common genera caught with sweep nets, corresponding to genera with abundances greater than 1% of the total abundance. This help to account for collinearity between pollinator metrics by starting with a null model and adding, step by step (forward selection), pollinators with the largest effect on OSR yield (all pollinators with a significant or marginally significant effect were kept in the model). Correlations between pollinator's genera are given in Fig S.C.3.

We then investigated, at plant scale, the plant fecundity traits that were affected by insect pollinators. The traits were: the fruiting success, the average number of seeds per pod, the averaged seed unit weight measured on control branches, for all four years, as well as the total seed biomass per plant, only available in 2015 and 2016. Total seed biomass per plant was strongly correlated to plant biomass (Appendix D, Zhang and Flottmann, 2016), thus we adjusted the seed biomass for the plant total biomass using a linear regression between seed biomass and plant biomass, both of which were $\log(x+1)$ transformed (Appendix D). Positive residuals of this model showed those OSR plants that produced more seed biomass than expected for their total biomass. The residuals (the seed biomass adjusted for plant biomass) of the model were then used in further analyses. All these traits were averaged for each position in the field. Then we used mixed linear models to explain fecundity traits as a function of bee abundance estimated by pan traps, accounting for year (four values), and plant position in the

field (edge vs. core), and their two-way interactions with bee abundance, all as fixed factors, and field ID as a random factor.

To quantify the relative contributions of the different pollination processes (i.e. insect, wind and self-pollination), we used paired branch comparisons of OSR fecundity traits (Wragg and Johnson, 2011), using fruiting success as the trait for calculation since this was shown to be positively affected by pollinators (see results below). Fruiting success was hierarchically averaged per treatment and then per field to obtain contributions at field level. The contribution of wind pollination was estimated as the difference between the traits for “W + SF” (“W”: Wind pollination, “SF”: self-pollination) and “SF” treatments while the contribution of self-pollination was based on “SF” alone ($N = 57$). In 2013 and 2014, there was no Osmolux treatment so the contribution of wind plus self-pollination was based on “W + SF” ($N = 44$). The contribution of pollination by small insects was estimated as the difference between “SP + W + SF” (“SP”: Small-bodied pollinators) and “W + SF” ($N = 72$) and for large insects by the difference between “LP + SP + W + SF” (“LP”: Large-bodied pollinators) and “SP + W + SF” ($N = 72$). In 2014, there was no large mesh treatment, hence the contribution of all insects was estimated as the difference between “LP + SP + W + SF” and “W + SF” ($N = 29$). The relative contributions of each of the pollination processes were then obtained as the % of the traits measured for the control branches (Bartomeus et al., 2014; Bommarco et al., 2012). In some cases, the difference in fecundity traits between treatments was negative, when, for example, fruiting success was higher in “W + SF” than in “SF”. Since a negative contribution cannot theoretically exist, negative values were arbitrarily set to 0 where such negative contributions exceeded -5% (16.5% of 332 fruiting success values, see Appendix E). Additionally as the fruiting success could be biased by the treatment protocol (e.g., mechanical effects), we also adjusted for this bias (as detailed in Appendix E) and checked for the difference between unadjusted (uncorrected data, underestimating self-pollination) and adjusted values (corrected data, Appendix E).

In all analyses, pollinator abundance was $\log(x+1)$ transformed and fruiting rate was arcsine transformed to ensure that the distributions were normal and homoscedastic. All analyses were performed using R (R Core team, 2015). The “stats” package was used for linear modelling, predicting values, model selection and stepwise multiple regression. The “lmerTest” package was used for linear mixed model (Kuznetsov et al., 2014).

3. Results

3.1. Pollinator diversity

A total of 23,744 pollinators were caught over the four years in pan traps (average 6.7 in./trap, range 0–136) within or near the focal fields. As expected, there was a strong variation between fields in the number of pollinators caught, from 0.33 to 43.19 individuals per pan trap, a 131-fold variation. Similarly, there was a ten-fold variation in genera diversity. Wild bees were the main guild caught (81.3%), followed by hoverflies (14.4%), honeybees (3.2%) and bumblebees (1.1%). The most abundant pollinator genera were *Lasioglossum* (62.9%), *Halictus* (9.2%) and *Andrena* (7.8%). The complete list is given in Appendix C. In all, 19 genera of bees and 23 genera of hoverflies were caught. The sweep net method captured 1110 pollinators (average 6.5 in./transect, range: 0–68) in 2015 and 2016 ($n = 71$ fields), with mainly honeybees (73.5%), hoverflies (19.3%), wild bees (4.6%) including, *Lasioglossum* (1.34%), *Andrena* (2.6%) and *Halictus* (0.25%), and Bumblebees (2.5%), see Appendix C. The capture profiles of the pan traps and the sweep nets were completely different and gave uncorrelated results (Appendix C). They were, therefore, considered separately.

3.2. Effect of fertilizers and pesticides inputs on OSR yield

The OSR yield at field scale (as declared by the farmers) was, on

Table 1

Linear models of OSR yield as a function of pollinator diversity or pollinator abundance (obtained by pan traps in 151 fields or sweep nets in 44 fields), year, phosphorus fertilizer and their two way interactions with pollinator metrics. All abundances are $\log(x + 1)$ transformed. Significant effects ($P > 0.05$) are in bold.

	Pan trap		Sweep net			Pan trap		Sweep net	
	F	P	F	P		F	P	F	P
Total diversity	3.99	0.048	1.40	0.25	Total abundance	7.75	0.006	4.52	0.042
Year	6.93	< 0.001	0.01	0.92	Year	4.85	0.003	0.01	0.92
Phosphorus fertilizer	7.07	0.009	7.09	0.011	Phosphorus fertilizer	7.28	0.008	8.04	0.007
Total diversity x year	0.24	0.87	4.68	0.037	Total abundance x year	0.35	0.79	3.07	0.088
Total diversity x phosphorus fertilizer	0.70	0.4	0.13	0.72	Total abundance x phosphorus fertilizer	0.54	0.47	0.03	0.85
Bee diversity	14.93	< 0.001	0.17	0.68	Bee abundance	12.06	0.001	5.63	0.023
Year	4.55	0.004	0.02	0.88	Year	3.58	0.016	0.01	0.9
Phosphorus fertilizer	10.20	0.002	6.84	0.013	Phosphorus fertilizer	7.54	0.007	6.72	0.013
Bee diversity x year	0.18	0.9	6.97	0.012	Bee abundance x year	0.12	0.95	3.58	0.066
Bee diversity x phosphorus fertilizer	0.48	0.49	1.02	0.32	Bee abundance x phosphorus fertilizer	0.38	0.54	0.20	0.66
Hoverfly diversity	0.01	0.99	1.85	0.18	Hoverfly abundance	3.76	0.055	0.40	0.53
Year	6.96	< 0.001	0.01	0.91	Year	5.49	0.001	0.03	0.87
Phosphorus fertilizer	6.73	0.010	7.94	0.008	Phosphorus fertilizer	7.98	0.005	9.71	0.003
Hoverfly diversity x year	0.14	0.94	0.37	0.55	Hoverfly abundance x year	2.07	0.11	0.78	0.38
Hoverfly diversity x phosphorus fertilizer	0.19	0.66	0.00	0.96	Hoverfly abundance x phosphorus fertilizer	0.01	0.93	2.81	0.1

average, 3.14 tons/ha (range 1.9–5.2, $n = 151$) and varied between years ($F_{3,147} = 6.39, p < 0.001$). Yield was significantly affected by phosphorus fertilizer ($F_{1,149} = 6, p = 0.015$), while the other fertilizers (nitrogen, potassium and sulphur), pesticides (herbicides, insecticides and fungicides), and OSR type (see Appendix G, for interaction with pollinator metrics), had no significant effect on OSR yield (all $P > 0.11$, see Appendix F for model selection).

3.3. Contribution of pollinators at field scale

Once the main farming practices had been identified, we found that OSR yield was significantly and positively correlated with pollinator diversity measured using pan traps (Table 1), especially bee diversity

(Table 1, Fig. 2a), but not with hoverfly diversity (Table 1). There were no significant interactions between farming practices and pollinator metrics in any of our models (Table 1). An increasing the number of bee genera from 1 to 10, was associated with an increase in yield of 37.5% (range: 27.7–47.5%), about 1 t ha^{-1} . Each additional genus was, therefore associated with an average increase of 0.11 t ha^{-1} in OSR yield. Restricting the analysis to years 2015 and 2016, when bees were identified at species level, species richness had a similar, but non-significant effect (Appendix G). The number of genera was, therefore, a better predictor of OSR yield than species richness. Total pollinator abundance also increased the yield (Table 1), with bee abundance having a greater effect than hoverfly abundance (Table 1, Fig. 2b). Bee abundance had slightly less effect (slope 0.16 ± 0.05) than bee

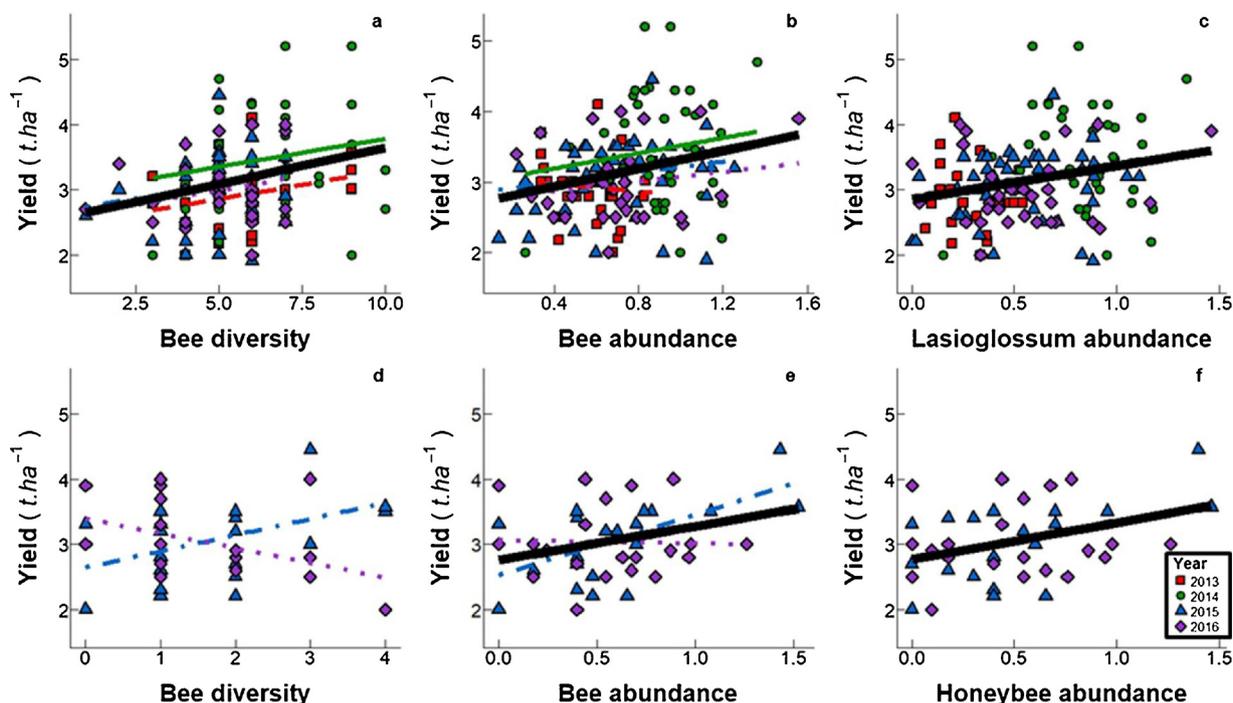


Fig. 2. Effect of pollinator community metrics estimated from pan traps (a–c) and sweep nets (d–e) on OSR crop yield. All abundances are $\log(x + 1)$ transformed. The colour lines indicate the linear regressions between yield and pollinator for 2013 (red, square dot, dashed line), 2014 (green, round dot, solid line), 2015 (blue, triangle dot, dot-dashed line) and 2016 (purple, diamond dot, dotted line). The black line shows the relationship averaged over the four years. The black line is not drawn where the regressions are not significant (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

diversity (slope 0.18, ± 0.05): i.e. an increase of yield of one ton/ha would require nine more genera but 29.4 more bees. Multiple stepwise regression using the nine most abundant genera indicated that *Lasioglossum* was the probable main contributor ($F_{1,147} = 10.27$, $P = 0.0016$, Fig. 2c), followed by bumblebees ($F_{1,147} = 3.44$, $P = 0.066$) and the hoverfly *Euweodes* ($F_{1,147} = 2.83$, $P = 0.095$).

There was also a significant positive correlation between yield and bee abundance measured using sweep nets (Table 1) with an overall increase of 0.8 ton ha^{-1} (28.6%, range: 15.6–41.6%, Fig. 2e), but the effect of bee diversity (species or genus level) was far less pronounced and varied with the year (Table 1, Fig. 2d, Appendix G). Multiple stepwise regression suggested that honeybees were the main contributor to yield ($F_{1,42} = 6.51$, $P = 0.015$, Fig. 2f), rather than *Lasioglossum* as found for pan traps. This is likely to be an artefact of the low effectiveness of pan traps for catching honeybees: honeybees and *Lasioglossum* accounted for 3.2% and 62.9% of catches in pan traps, and 73.5% and 1.3% of catches in sweep nets. Restricting the analyses to fields where exclusion experiments were carried out (66 fields instead of 151) did not change any of the conclusions (see Appendix G).

3.4. Effect of pollinators on OSR fecundity traits at plant scale

For the control branches, a model taking into account bee abundance, plant position and year (and their two-way interactions with bee abundance), showed that bee abundance measured by pan traps increased fruiting success ($F_{1,184} = 10.67$, $P = 0.002$, Fig. 3a) while the year had an equally strong effect ($F_{3,184} = 10.02$, $P < 0.001$; see Appendix H for additional statistical models). The number of seeds per pods was negatively correlated ($F_{3,184} = 5.98$, $P = 0.016$, Fig. 3b) with bee abundance, but seed unit weight was not affected ($F_{3,184} = 0.003$, $P = 0.96$, Fig. 3c). However, the increase in fruiting rate was sufficient to increase the seed biomass adjusted for plant biomass ($F_{1,130} = 6.86$, $P = 0.011$, Fig. 3d). In addition the seed biomass adjusted for plant biomass averaged per field was positively correlated to yield ($r_s = 0.31$, $P = 0.04$, $n = 43$). This suggested that OSR plants increase their investment in grain production in preference to vegetative biomass production in presence of pollinators. No significant interaction was found between bee abundance and plant position or year ($P > 0.19$ for both interactions) for any fecundity trait. The results were the same when farming practices were taken into account in the models (Appendix H).

3.5. Experimental quantification of insect pollination

Insect pollinators were estimated to have contributed 30% of the

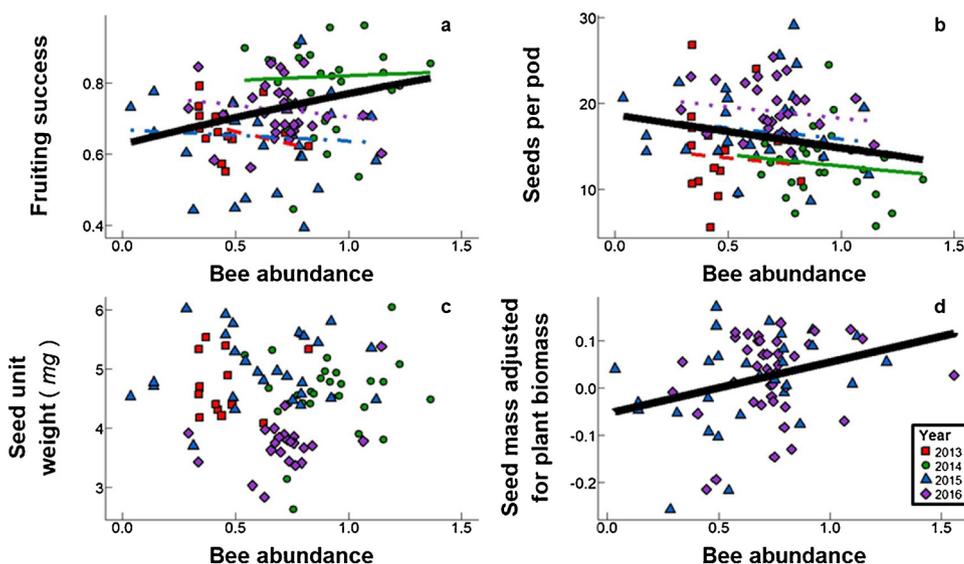


Fig. 3. Effect of bee abundance estimated from pan traps on different OSR fertility traits, averaged at field scale. The traits were measured for the control branch (a–c) and whole plant (d). The coloured lines show the linear regressions between OSR fertility traits and bee abundance ($\log(x+1)$ transformed) for 2013 (red, square dot, dashed line), 2014 (green, round dot, solid line), 2015 (blue, triangle dot, dot-dashed line) and 2016 (purple, diamond dot, dotted line) where these are significant. The black line shows the relationship averaged over the four years. Lines are not drawn where the regressions are not significant (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

fruiting success (Fig. 4a) and this contribution increased with increasing bee abundance (Table 2, Fig. 4b). Wind and self-pollination accounted for 70% of fruiting success (Fig. 4a). In 2015 and 2016, wind and self-pollination rates were separated and self-pollination was found to have a far greater contribution (66%) than wind (4.2%) (Fig. 4). A positive correlation between pollinator contribution and yield ($r_s = 0.24$, $P = 0.05$, $n = 66$) confirmed that an increase in pollinators increased the yield at field scale. We found that large-bodied insect species (abdomen wider than 3 mm) had a similar contribution (15.6%) to small-bodied insects (12%). Bee diversity (for both pan traps and sweep nets), *Lasioglossum* (pan traps), and honeybee (sweep net) abundances all had a significant positive effect on the contribution of insects to pollination (Fig. 4b, Table 2), confirming that honeybees were the main large pollinators while *Lasioglossum* were the main wild bee pollinators genus.

4. Discussion

Determining the role of insect pollinators is a central question for managing pollination services in crop production (Kremen, 2005). Previous studies have already emphasised the role of insect pollinators in OSR yields, usually in fields with or without pollinators (Araneda Durán et al., 2010; Bommarco et al., 2012; Hudewenz et al., 2014; Marini et al., 2015; Stanley et al., 2013) or correlating OSR yields with pollinator abundance (Bartomeus et al., 2014; Woodcock et al., 2016; Zou et al., 2017). In most studies however, the contribution of pollinators was calculated for small area (except Lindström et al., 2016) which may have under-estimated pollinator contribution, especially for OSR, a plant that shows high ability to compensate for flower loss (Pinet et al., 2015). Here we combined empirical and experimental data collected over four years in farm fields to estimate pollinators' contribution at two different scales, field and plant. Our study shows that bees have a major effect on OSR yields, with 35.7% higher yields in pollinator rich landscapes than in landscapes with almost no pollinators.

4.1. Contribution of insect pollination to OSR yield

Oilseed rape is a crop showing a modest dependence on pollinators, between 10% and 40% (Klein et al., 2007), and self-pollination is dominant in OSR (Becker et al., 1992). Using genetic inheritance tests, self-crossing has been shown to be 53% to 87% depending on the field (Becker et al., 1992). In our study, we found that self-pollination accounted for approximately 66% of total pollination, but varied between

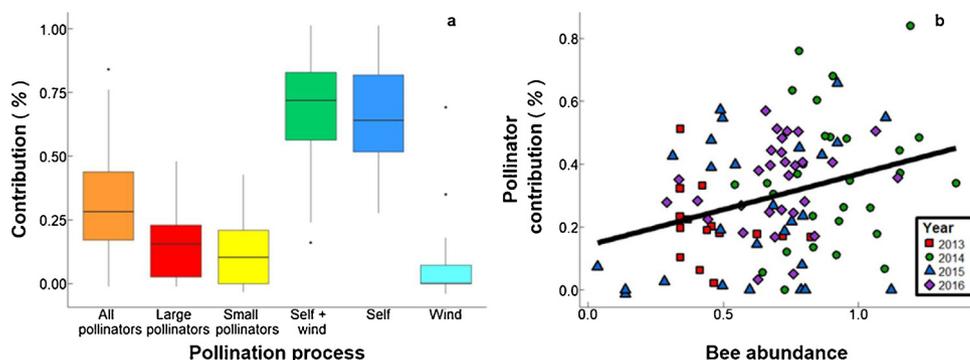


Fig. 4. (a) Relative contributions of different pollination processes over the four years on fruiting success. Boxes show upper and lower quartiles, horizontal line is the median. (b) Effect of bee abundance ($\log(x+1)$ transformed) on contribution of pollinators. The black line is the linear regression. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

Table 2

Effect of bee diversity, bee abundance and *Lasioglossum* caught by pan traps and sweep nets on the contribution of all pollinators, large pollinators and small pollinators, respectively, to fruiting success. A linear model was used. All abundances are $\log(x+1)$ transformed. Significant effects ($P < 0.05$) are in bold.

		Pollinator contribution			Large pollinators contribution			Small pollinators contribution		
		Value	F	P	Value	F	P	Value	F	P
Pan trap	Bee diversity	0.033	7.52	0.007	0.01	0.89	0.37	0.026	5.03	0.028
	Bee abundance	0.23	10.47	0.0017	0.14	5.3	0.024	0.073	1.27	0.26
	<i>Lasioglossum</i>	0.2	10.93	0.0013	0.11	3.78	0.056	0.087	2.14	0.15
	Sample size (Field)	101			72			72		
Sweep net	Bee diversity	0.057	5.62	0.021	0.066	20.88	< 0.001	-0.009	0.026	0.61
	Bee abundance	0.11	2.8	0.01	0.15	13.61	< 0.001	-0.039	0.71	0.44
	Honeybee	0.1	2.27	0.14	0.13	11.45	0.0019	-0.035	0.59	0.45
	Sample size (Field)	55			55			55		

fields (95% CI = 30.8% to 100%). Self-pollination and self-crossing are not directly comparable and we cannot infer whether an increase in the contribution by pollinators replaced or supplemented the contribution of self-pollination, although pollinators have been shown to increase the out-crossing rate (Brunet and Weet, 2006). Wind pollination contributed about to 4.2%. Only one other study has quantified wind pollination in OSR and the values ranged from 3% to 12% (Mesquida and Renard, 1982). Weak wind pollination in OSR has been linked to both the pollen and the flower structures, which are more adapted to insect dispersal than wind dispersal (Hayter and Cresswell, 2006). Using pollinator exclusion, we estimated that pollinator contribution was 30%, close to the 37.5% increase in yield at field scale corresponding to the highest pollinator diversity in our study site. Pollinator contribution was independent of plant variety or farmer's practices. Conventional OSR has been shown to be more dependent on pollinators than hybrid OSR (Lindström et al., 2016; Marini et al., 2015), but Hudewenz et al. (2014) analysed a large number of varieties and found that the contribution of pollinators depend more on the OSR varieties themselves rather than the OSR type (conventional versus hybrid). Studies including farming practices have not agreed on whether farming practices affect the contribution of pollinators: some authors found no interaction with pollinators (van Gils et al., 2016), as in our study, while others found interactions between practices and pollinators (Marini et al., 2015).

Our results therefore clearly demonstrate that insect pollinators are an important component of OSR yield for farmers in our study area, increasing yields by up to 0.8 to 1 ton ha^{-1} , depending on the method used to sample the pollinators (pan traps or sweep nets). The net effect of pollinators in our study is thus slightly higher than that found in other studies (Lindström et al., 2016; Woodcock et al., 2016), from 0.4 to 0.6 ton ha^{-1} , but far less than the 2.5 tons ha^{-1} found by Araneda Durán et al. (2010). In our study, the increase in yield, between 29% and 37.5%, depending on the method for sampling pollinators and the scale (plant versus field), is generally higher than increases reported so far: between 12% and 20% (Bartomeus et al., 2014; Bommarco et al., 2012; Samnegard et al., 2016; Zou et al., 2017) up to 30% (Stanley

et al., 2013). This discrepancy may arise from differences in the pollinator communities, since our study site has a very rich wild bee community, with more than 250 species (Rollin et al., 2015). Bartomeus et al. (2014) and Woodcock et al. (2016) found that OSR seed production was positively correlated with pollinator visiting rate, a parameter that we did not measure here. It should also be noted that we used partial plant bags rather than entire caged plants (Bartomeus et al., 2014; Zou et al., 2017), which may also account for part of the differences between this and other studies.

We were able to identify which fecundity traits were affected by pollinators, and at which scale (branch or plant), and were thus responsible for the increase of yield at the field level. Two main traits benefited from insect pollinators: fruiting success and seed biomass adjusted for plant biomass. As expected, pollinators increased fruiting success, potentially due to more pollen brought by pollinators (Hayter and Cresswell, 2006) and better pollen transfer that may increase out-crossing rates (Brunet and Weet, 2006) compared to wind or self-pollination. We also detected a trade-off between the number of seeds per pod and the fruiting rate, the number of seeds per pods decreasing with increasing presence of pollinators, suggesting that the plant may not maximise all fecundity traits simultaneously. Other trade-offs have already been identified, e.g. seed unit weight vs. number of pods per plant (Araneda Durán et al., 2010), or number of seeds per pod vs. seed unit weight (Zou et al., 2017). Interestingly, total seed mass per plant adjusted for plant biomass was positively correlated with the presence of pollinators and field yield. Zou et al., 2017 found a very similar result: plant yield divided by straw (similar to plant biomass) was correlated with wild bee abundance. Our adjusted seed biomass per plant is actually fairly close to the harvest index (ratio of seed total biomass divided by plant biomass), which has been found to be more closely correlated with OSR field yield than with OSR plant yield (Degenhart and Kondra, 1984). We found no effect of the position in the field on the pollination by insects, however the distance into the field tested in our study was relatively small. Woodcock et al. (2016), for instance, the effect of the position with a higher distance (maximum of 200 m), and found that visits to OSR flowers strongly decreased with distance but

only for bumblebee and hoverflies (no effects were found for wild bees and honeybees). Interestingly, bumblebee and hoverflies were not identified as main pollinators in our study.

4.2. Which insects contribute to OSR pollination?

We found that higher bee diversity (genus level) resulted in higher OSR yields, possibly as a result from niche complementarity since bees show different foraging temporal preferences, or forage on different flowers according to the position of the flower on the plant (Hoehn et al., 2008). The effect of bee species diversity on OSR yield has been reported recently (Zou et al., 2017) and 20 of the most common bee species were found to forage in OSR (Kleijn et al., 2015). Large bees, such as honeybees, are known to pollinate OSR and visit more flowers than any other pollinators (Garratt et al., 2014). We found that honeybees were the most important pollinators, but unlike other studies, did not find that bumblebees had any effect (Garratt et al., 2014). This is perhaps because bumblebees were scarce during oilseed rape blooming in our site, as already reported by Rollin et al. (2013). Although wild bees are usually less abundant than honeybees in OSR (Rollin et al., 2013), they spend longer on flowers (Woodcock et al., 2013) and, therefore, transfer more pollen during flower visits than honeybees. Among wild bees, *Lasioglossum* (from *Halictidae* family) had a fairly strong effect, which is surprising since, unlike *Osmia*, this genus has never been identified as an important OSR pollinator, (Garratt et al., 2014). *Lasioglossum* is however known to forage extensively on OSR (Le Féon et al., 2013; Woodcock et al., 2013). Hoverflies were also present in our pollinator community, however we did not find that hoverflies had any effect. This can be explained by the fact that hoverflies are less effective pollinators for OSR (Garratt et al., 2014).

5. Conclusions

We show here that OSR fields in our study area are pollinator limited, both in terms of bee (genus) diversity, and honeybee and wild bee abundances. Given the increase of OSR fields worldwide and the pollination service supply limitations that have already been identified (Breeze et al., 2014) and with the current decline in pollinators (Potts et al., 2010) improving pollinator richness or abundance in general is becoming urgent, though problematic (Bretagnolle and Gaba, 2015). Simplification of agricultural landscapes leads to poor pollination services (Connelly et al., 2015), intensive farming practices are either directly (Henry et al., 2012) or indirectly (Requier et al., 2015) harmful to bees, and the maintenance of semi-natural habitats in the landscape is critical for wild bees (Kennedy et al., 2013). However, plans for reducing pesticide use, improving or restoring semi-natural habitats in farming landscapes and establishing wild flower strips (Blaauw and Isaacs, 2014) have, so far, remained limited. All these measures, whether they are implemented through Agri-environmental Schemes or as greening components of direct payments under the Common Agriculture Policy, still have costs. The merit of our study is that it demonstrates that increasing pollinator abundance at landscape level also has financial benefits for farmers, since increase in production can be directly translating into gross margins or revenue. By accurately quantifying the yield increase as a function of pollinator abundance, we pave the way for a monetary evaluation of the pollination service in OSR farming systems that can be balanced against the cost of managing landscapes to maintain bee diversity and pollinator abundance within a land sharing framework, *i.e.* at the cost of reducing the area under crops. Most public policies targeting wild bees aim to exchange crop area for semi-natural habitats, and use, therefore land sharing strategies (Green et al., 2005). However, sharing land for bees may not necessarily mean that farmer's revenue will decrease, since crop yields (hence income) will increase as shown by our study and another recent study (Pywell et al., 2015).

Authors' contributions

M. Roncoroni, J-L Gautier and T. Perrot collected the field data; V. Bretagnolle and S. Gaba designed the study. V. Bretagnolle, S. Gaba and T. Perrot designed the methodology, analysed the data and wrote the manuscript.

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Appendix A-H. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.agee.2018.07.020>.

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