Pollination efficiency of wild bees and hoverflies provided to oilseed rape

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Abstract

1 Declining numbers in honeybees and various wild bee species pose a threat to global pollination services. The identification and quantification of the pollination service provided by different taxa within the pollinator guild is a prerequisite for the successful establishment of nature conservation and crop management regimes.

2 Wild bees and hoverflies are considered to be valuable pollinators in agricultural and natural systems. Although some information on pollination efficiency of individual pollinator species is available, comparative studies of both taxa at different densities are rare. In the present study, the efficiency of the solitary mason bee *Osmia rufa* and two hoverfly species (*Eristalis tenax* and *Episyrphus balteatus*) as pollinators of oilseed rape *Brassica napus* was examined in a standardized caged plant breeding regime. Honeybee *Apis mellifera* colonies were used as a reference pollinator taxon.

3 Yield parameters responded differently to pollinator density and identity. Fruit set and number of seeds per pod increased with increasing pollinator density, although these were stronger in the mason bee than the hoverfly treatment. Weight per 1000 seeds did not respond to any pollinator treatment, indicating that seed quality was not affected. Oilseed rape yield in the highest tested densities of both pollinator taxa resulted in yield values close to the efficiency of small honeybee colonies.

4 Hoverflies required approximately five-fold densities of the red mason bees to reach a similar fruit set and yield. Thus, mason bees are more efficient in plant breeding and managed pollination systems. Both natural pollinator taxa, however, are of potential value in open and closed crop production systems.

Keywords Apidae, *Brassica napus*, cage experiments, density dependence, ecosystem services, plant breeding, pollinators, syrphidae, yield.

Introduction

The pollination of arable crops and wild flowers is an important ecosystem service and function with great economic and ecological relevance (Kearns *et al.*, 1998; Klein *et al.*, 2007). The contributing insect species are manifold and pollination efficiency is likely to differ between pollinator species (Strickler, 1979; Buchmann & Nabhan, 1997; Daily, 1997; Hoehn *et al.*, 2008). For example, a decline in wild plant diversity was mirrored by a decline in wild bee diversity in the U.K. and the Netherlands, whereas such a consistent pattern between plant and pollinator diversity was not found for hoverflies (Biesmeijer

et al., 2006). Wild bees are fairly well studied with respect to their pollination efficiency and are generally considered the most important pollinator group in most ecosystems (LaSalle & Gauld, 1993). Hoverflies are also traditionally placed within the pollinator guild and sometimes are considered to represent the second most important pollinators after wild bees (Larson *et al.*, 2001). The potential importance of hoverflies for wild plant reproduction is primarily based on flower visitation observation (Goulson & Wright, 1998) and conspecific pollen load count (Sugiura, 1996; Vance *et al.*, 2004), although it has also been shown experimentally (Fontaine *et al.*, 2006). Regarding arable crops, empirical field data linking yield gain specifically to one pollinator taxon are scarce. It is a general consensus that honeybees and wild bees contribute most to crop pollination (McGregor, 1976). Recently, however, both honeybees

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and wild bees have been reported to decline in numbers regionally (Kluser & Peduzzi, 2007). At the same time, agriculture has become more pollinator-dependent because of a stronger increase in the area cultivated with flowering crops compared with nonflowering crops (Aizen *et al.*, 2008, 2009; Aizen & Harder, 2009). Consequently, to estimate the risk of a global 'pollination crisis', the role of alternative pollinators needs to be identified and ultimately implemented into agro-environmental schemes for enhancing pollination services at the landscape scale.

Oilseed rape *Brassica napus* L. is the dominant flowering field crop in the European Union, especially as a result of the recent increase in cultivated area because of an increased demand for energy crops (van der Velde *et al.*, 2009). It is a well established plant system in pollination studies (Hayter & Cresswell, 2006; Hoyle *et al.*, 2007) and yield components have been shown to vary with specific pollination treatments (Steffan-Dewenter, 2003). The pollination efficiency of wild bees for oilseed rape and other crops has been demonstrated, where they may economically substitute for honeybees in agricultural plantations and in plant breeding schemes within enclosed environments (Steffan-Dewenter, 2003; Slaa *et al.*, 2006, Sheffield *et al.*, 2008). Information on the crop pollination efficiency of hoverflies is rare. In germplasm regeneration studies, both wild bees (*Osmia rufa* L.) and hoverflies (*Eristalis tenax* L.) have been used for carrot, onion and turnip rape associations (Schittenhelm *et al.*, 1997). Insect densities, however, differed vastly between species in these experiments and the examined pollinator species showed different plant preferences. Because the specific plant assemblage was not included in the statistical analysis, the pollination efficiency of one specific pollinator taxon on one specific plant species is difficult to disentangle. *Eristalis tenax* has also been suggested as an adequate pollinator of sweet pepper in greenhouses (Jarlan *et al.*, 1997) and for apple trees (Kendall *et al.*, 1971).

In self-compatible oilseed rape, *Episyrphus balteatus* (De Geer) enhanced the number of seeds per pod, although the study design did not allow for a direct assessment of effects on overall yield (Jauker & Wolters, 2008). There are also cultivars of different morphs available (i.e. male sterile lines that do not produce pollen). In these lines, pollinated flowers must have received pollen from a male fertile 'donor' plant nearby. In such systems, benefits to the seed set by pollinators must result from cross pollination. By contrast to specialist pollinators, generalist species such as hoverflies without distinct floral fidelity are considered to facilitate self-fertilization rather than cross pollination (Moeller, 2006). This is often considered as unfavourable and might ultimately lower seed set and reproductive success as a result of genetic fitness factors such as inbreeding depression (Takebayashi & Morrell, 2001). In a male-sterile crop system, however, low selectivity for floral traits might be advantageous. In the present study, male sterile oilseed rape as target plants and male fertile plants as pollen donors were used in flight cages, excluding any insects other than the pollinator target species. Two different pollinator taxa, the wild bee *Osmia rufa* and the hoverflies *E. balteatus* and *E. tenax*, were used at a gradient of similar densities to allow for comparison of pollination efficiency. Although *O. rufa* is generally not considered as a specialist pollinator species within the wild bees, the degree of specialization is considered larger compared with the hoverfly species. The present study aimed to assess the potential of alternative pollinator species in closed environments, including professional plant breeding systems, and to determine their role in natural environments.

Materials and methods

Experimental design

The present study was carried out at the research station Klostergut Reinshof of the Georg August University Göttingen, Germany. Two near-isogenic lines of spring oilseed rape *B. napus* were used for the experiment: the male fertile MSL 501 B line and the male sterile MSL 501 C line (Norddeutsche Pflanzenzucht, Hans Georg Lembke KG, Germany). The male sterile line has reduced stamens that do not produce pollen and is therefore completely dependent on pollen transport from the donor plants by insects or wind.

The rape seeds were sown mechanically in 30 plots with six rows each in mid April 1998. In each plot, the two centre rows contained seeds of the male fertile line, whereas the two rows at each side contained seeds of the male sterile line. The spacing between rows of the same line was 30 cm and the spacing between rows of different lines was 50 cm. Spacing between plants within rows was 10 cm. The ten plants per row with six rows on a $1 \times 1.9 \times$ m area resulted in a plant density of approximately 31.5 plants/m². All plots were sown after regular soil cultivation and standard fertilizer applications: two fertilizer applications in March 1998 with 90 kg N/ha and April 1998 with 70 kg N/ha, two herbicide applications with 0.2 l/ha Butisan (BASF, Germany) and 0.8 l/ha Fusilade (Syngenta, Sweden) in September 1997 and two pesticide applications with 150 g/ha Karate (Syngenta, Sweden) and 0.1 l/ha Fastac (BASF, Germany) in April 1998. In mid June, at the beginning of oilseed rape flowering, all plots were caged with iron frames covered by fine mesh plastic gauze (cage length 3 m, width 2.5 m, height 2 m; cage area 7.5 m²; mesh size approximately 1 mm).

Pollinator treatments

Pollinators were distributed into 26 cages in mid June 1998. Females of the red mason bee *O. rufa* were used in 14 cages; individuals of the hoverfly species *E. tenax* and *E. balteatus* were used in 12 cages. The bee densities in the cages were $n = 1, 2, 3, 4, 6, 8, 10, 16, 24$ and 36 individuals. Nesting traps were placed in the cages, consisting of approximately 150 internodes of common reed *Phragmites australis* (Cav.) in a plastic tube (diameter 10.5 cm). One nesting trap was used in the cages with $n = 1, 2, 3$ and 4 bees, two traps in the cages with $n = 6$ and 8 bees, three traps in cages with $n = 10$ and 16 bees, five traps in cages with $n = 24$ and 36 bees. The mason bees were taken from hibernated cocoons from trap nest that had been exposed at the experimental field of the Agroecology group in the previous year. Each six female bee cocoons were reared in a climate chamber at 25 °C together with ten male cocoons to allow copulation. After observed copulation, females were separated from males and used for the cage experiment.

The hover fly densities in the cages were $n = 1, 4, 8, 18, 22, 28, 52, 68$ and 96 individuals. The ratios of *E. tenax* to *E. balteatus* were $1 : 0, 4 : 0, 8 : 0, 9 : 9, 8 : 14, 16 : 12, 36 : 16, 46 : 22$ and $66 : 30$, respectively. Individuals of *E. tenax* were reared at the institute. Because the number of individuals obtained was not sufficient, individuals of *E. balteatus* caught on site were used in similar ratios to restock the hoverfly densities. Although interspecific competition cannot be excluded in the hoverfly treatment, intraspecific competition as a result of the large density gradient within all treatments was considered the more relevant factor. Additionally, two cages without any pollinators (negative control) and two cages with a small honeybee colony (*Apis mellifera* L., approximately 200 individuals) (positive control) were established. All treatments were distributed randomly among the cages. Cages with low pollinator density treatments (bees: $n = 1, 2, 3, 4$; hoverflies: $n = 1, 4, 8$) were replicated once to account for stochastically induced fluctuations. One plot within each low pollinator species treatment (bees: three individuals, hoverflies: four individuals), however, was omitted from the analyses because oilseed rape plants did not develop properly. Although it was not possible to track all pollinators individually, all cages contained alive and active pollinators throughout the experiment, with the exception of the control cages.

Pollinator observations

Pollinator observations were conducted during the flowering of oilseed rape in cages of the five highest density treatments of each pollinator taxon. Only the highest density treatments were chosen to minimize the comparing of repeated measurements of single individuals in low densities with averaged measurements of various individuals in high densities. Observations took place in a randomized order under favourable climatic conditions (i.e. on sunny days with a temperature of above 15 °C, little wind, and in direct sunshine). On 14 occasions between June 26 and July 10 1998, one individual per cage was observed for 5 min and the duration of each flower visitation was measured. Flower visitation was defined as the events when insects collected either pollen or fed on nectar. Mean flower visitation time per observation unit was calculated and used for further analyses. The same observation procedure was applied in cages containing honeybee colonies.

Yield components

At the end of August, ten randomly chosen plants of the male sterile line in each plot were harvested before pods dehisced (280 plants in total). Plants were transferred to the laboratory and dried at 25 °C for 12 h in a drying chamber. The pods and unfertilized flowers of each plant were counted and the ratio of both was used to calculate the fruit set, whereas the sum of both refers to the number of flowers per plant. The seeds were separated from the pods, counted for each plant using a seed counter (Contador E; Baumann Saatzuchtbedarf, Germany) and weighed. The dry mass of each plant was measured, whereas the weight per 1000 seeds and the number of seeds per pod was calculated for each plant. For all parameters, the mean values of the ten examined plants per plot were calculated and used for further analyses. Additionally, the seed weight obtained from plants within 1 m^2 was estimated by multiplying the average seed weight per plant by the average number of plants/m^2. This parameter reflects the yield and is the integration of the aforementioned ecological subparameters reflecting the economic interest of farmers.

Statistical analysis

General linear models (GLM) were used to examine effects of pollinator species, pollinator density and the interaction of both on different yield components of oilseed rape (fruit set, seeds per pod, seed weight, yield). Rather than the number of individuals placed into the cages, ratios of pollinators per 100 flowers per plant (derived from the mean values per plot) were used for pollinator densities to account for natural variability in the morphology of the examined plants. The two negative controls (cages without pollinators) were included twice in the models, assigned to each pollinator species (wild bees and hoverflies). The two positive controls (cages with small *A. mellifera* colonies) were not included in the statistical models but were used to estimate pollination efficiency in relation to the expected optimal pollination by honeybees. Each yield component was analyzed separately. Yield components were expected to be affected differently by pollinator factors and Type III GLMs were used to ensure the same test for all components and to account for unequal sample size. All analyses were carried out using STATISTICA, version 7.1 (StatSoft Inc., Tulsa, Oklahoma). All continuous factors used in the statistical analyses were checked for normal distribution and homogeneity of variances. Fruit set was arcsin-transformed and yield was log-transformed to meet assumptions. Values are reported as the mean $\pm$ SE.

Before analyses, biotic factors were checked for collinearity to exclude statistical bias. Plant dry mass was not correlated with pollinator density (product moment correlation: $r = 0.152$, $P = 0.438$, $n = 28$) and did not differ between the two pollinator treatments (t-test: $F = 0.258$, $P = 0.616$, $n = 28$). However, plant dry mass was included into the models to account for variability explained by plant factors, possibly blurring pollinator effects.

Pollinator observation data was available in small sample sizes only (i.e. $n = 5$ for each taxon). Thus, a conservative nonparametric approach was selected for examining density dependence of flower visitation time. Spearman rank correlations with the variables 'pollinator density' and 'mean flower visitation time' were conducted for each taxon.

Results

Yield parameters

The overall mean fruit set for both tested pollinator taxa without honeybees was $20.78 \pm 1.36\%$ (arcsin-transformed) (range 11–35%). The mean number of seeds per pod was 5.6 ± 0.25 (range 3.25–8.0). The mean seed weight per 1000 seeds was 3.38 ± 0.16 g (range 1.32–4.96 g). The seed yield per m^2 averaged on 70.61 ± 13.84 g of seeds (range 5.67–287 g). The

Table 1 Mean values of dependent variables in relation to main treatments

	Bees	Hoverflies	Negative control	Positive control
Fruit set	22.03 ± 0.96	19.33 ± 1.02	11.85/14.14	50.17/55.79
Seeds per pod	5.85 ± 0.41	5.36 ± 0.28	3.25/5.25	7.70/9.63
Seed weight	3.42 ± 0.22	3.33 ± 0.24	1.32/3.24	3.00/3.10
Yield	89.06 ± 22.86	49.33 ± 12.43	5.67/23.31	245.70/412.36

Fruit set is arcsin-transformed, other data are original values. Values for bee and hoverfly treatments (total $n = 28$) include the SE. For the negative control (no pollinators) and positive control (honeybee colonies), the values of both established cages are given. Fruit set denotes the percentage of developed pods in relation to number of flowers, seed weight (g) was measured for 1000 seeds, yield denotes the weight (g) of seeds obtained from oilseed rape plants/m^2 (31.5 plants).

Table 2 Results of the general linear models (Type III)

|	d.f.	Fruit set	Seeds per pod	Seed weight	Yield
Pollinator species	1,19	NS	NS	NS	NS
Pollinator density	1,19	$F = 39.99$ $P < 0.001$	$F = 17.53$ $P < 0.001$	NS	$F = 17.02$ $P < 0.001$
Pollinator species × density	1.19	$F = 13.89$ $P = 0.001$	$F = 11.84$ $P = 0.002$	NS	$F = 6.45$ $P = 0.018$
Plant weight	1,19	NS	NS	NS	$F = 8.13$ $P = 0.009$
Adjusted R^2		0.73	0.46	—	0.64

F- and *P*-values are given for significant effects. NS, not significant. Yield components (columns) have been tested separately for effects of pollinator species, pollinator density, interaction of pollinator species and pollinator density and plant weight (rows). For transformations of factors, see Table 1. Numerator and denominator degrees of freedom (d.f.) and adjusted R^2 values are given for each model.

positive control with the two honeybee cages exceeded the mean values of fruit set, number of seeds per pod and yield for the other pollinator treatments considerably (Table 1). Seed weight per 1000 seeds, however, was slightly lower than in the average mason bee and hoverfly treatment (Table 1).

Effects of pollinator densities

Fruit set was positively affected by pollinator density. The significant interaction term between pollinator species and pollinator density indicated an effect of pollinator species on the fruit set–pollinator density relationships (Table 2). Thus, fruit set increased considerably stronger with increasing bee density than with hoverfly density (Fig. 1). The pattern for number of seeds per pod was similar, with a significant interaction term between pollinator species and pollinator density (Table 2). Thus, the number of seeds per pod also increased stronger with increasing bee density than hoverfly density (Fig. 2). Both factors, fruit set and number of seeds per pod, were not influenced by plant weight and no effect of any explanatory variable on weight of a 1000 seeds could be established (Table 2). Yield, measured as seed weight/m^2, was affected by both pollinator factors and plant weight (Table 2). The pollinator effect was similar to the effects on fruit set and number of seeds per pod: yield increased stronger with increasing wild bee density than hoverfly density (Fig. 3).

Mean flower visitation time was 2.63 ± 0.32 s for mason bees and 7.58 ± 2.08 s for hoverflies. Flower visitation time correlated positively with the density of mason bees ($r = 0.90$, $P = 0.037$, $n = 5$). No density effect could be established for hoverflies ($r = 0.50$, $P = 0.391$, $n = 5$).
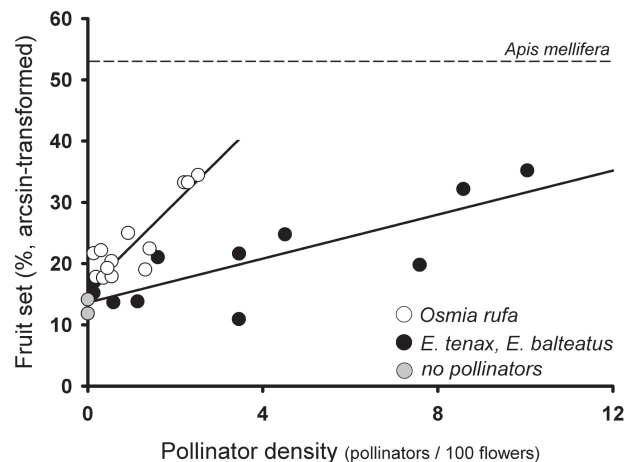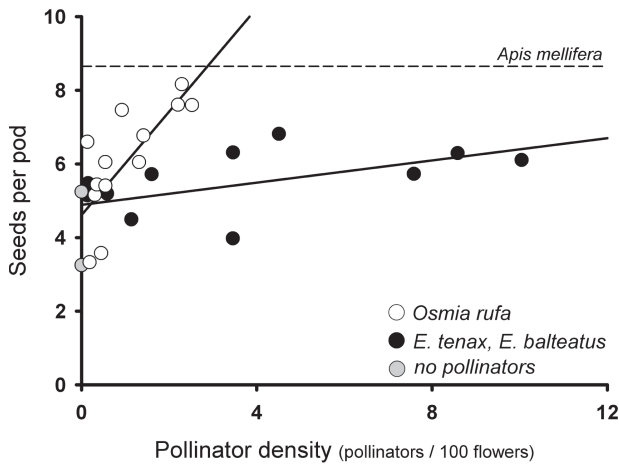

Figure 1 Relationship between pollinator density and fruit set of oilseed rape plants as a percentage (arcsin-transformed) for wild bees (*Osmia rufa*) and hoverflies (*Episyrphus balteatus* and *Eristalis tenax*), including cages without pollinators. The slopes for wild bees and hoverflies differ significantly (see significant interaction term in Table 2). Single correlations for both species are significant (Spearman correlations; wild bees: $r = 0.79$, $P < 0.001$, $n = 15$; hoverflies: $r = 0.72$, $P = 0.006$, $n = 13$). The dashed line indicates the mean fruit set of oilseed rape in the two cages with honeybee colonies (53%).

Discussion

As soon as the flowers appear on a plant, pollinators considerably influence reproductive processes at the single-flower level, both in wild plants (Larson & Barrett, 2000) and crop plants (Bos *et al.*, 2007). Accordingly, increasing densities of

Figure 2 Relationship between pollinator density and number of seeds per pod of oilseed rape plants for wild bees (*Osmia rufa*) and hoverflies (*Episyrphus balteatus* and *Eristalis tenax*), including cages without pollinators. The slopes for wild bees and hoverflies differ significantly (see significant interaction term in Table 2). Single correlations for both species are significant (Spearman correlations; wild bees: $r = 0.80$, $P < 0.001$, $n = 15$; hoverflies: $r = 0.70$, $P = 0.007$, $n = 13$). The dashed line indicates the mean number of seeds per pod in the two cages with honeybee colonies (8.66).
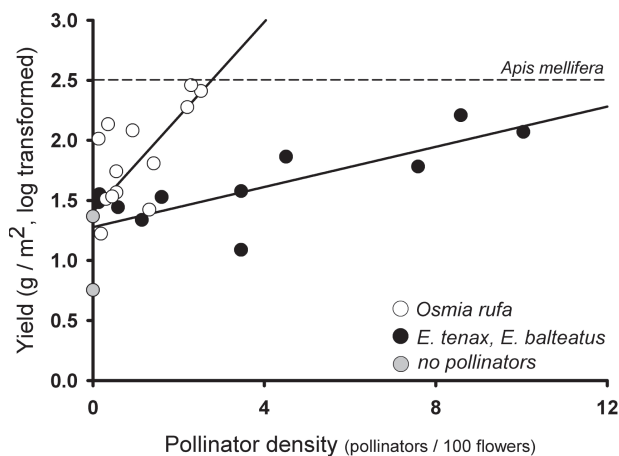
Figure 3 Relationship between pollinator density and yield of oilseed rape plants (log-transformed) for wild bees (*Osmia rufa*) and hoverflies (*Episyrphus balteatus* and *Eristalis tenax*), including cages without pollinators. Yield relates to the weight of seeds obtained from oilseed rape plants/1 m² (i.e. 31.5 plants). The slopes for wild bees and hoverflies differ significantly (see significant interaction term in Table 2). Single correlations for both species are significant (Spearman correlations; wild bees: $r = 0.70$, $P = 0.003$, $n = 15$; hoverflies: $r = 0.78$, $P = 0.002$, $n = 13$). The dashed line indicates the mean yield (log-transformed) in the two cages with honeybee colonies (2.62).

pollinators have been shown to increase yield of oilseed rape in the field (Morandin & Winston, 2005, 2006). These studies, however, show a very coarse taxonomic resolution (i.e. potentially include all flower visiting insects in the study area). The causal mechanism of the increased pollination success remains unclear and the contribution of generalist versus specialist

pollinators cannot be distinguished. Although pollinator density *per se* was also an important predictor for pollination success in the present study, it also highlights the need for a more accurate distinction between the pollination efficiency of mason bees and hoverflies with regard to their degree of specialization.

Although hoverflies are considered less specialized pollinators than wild bees and more effective in open than tubular flowers (Fontaine *et al*., 2006), no differences between the two examined pollinator species in the pollination of oilseed rape independent from their density could be established. There was, however, a significant interaction between pollinator density with pollinator species for all yield components analyzed, indicating differences in pollination efficiency between the two taxa. An approximately five-fold greater density of hoverflies is needed to reach the same fruit set as that provided by the highest tested densities of mason bees. Unexpectedly, both species only achieved approximately 35% fruit set compared with the more than 50% fruit set in cages with honeybees. Because the target plants in the present study were male-sterile, the differences between these three taxa most likely represent the 'foraging effort' (i.e. the number of flowers visited per time unit). The social honeybee foragers visited more flowers for provisioning the brood than the solitary mason bees, most probably because of the vast differences in their densities. Hoverflies, also exceeding the densities of mason bees, appear to visit fewer flowers per individual to meet their own resource requirements without any need for foraging for their offspring. This assumption is supported by the observation, that flower visitation time of hoverflies exceeded the flower visitation time of mason bees. The fact that flower visitation time was density-independent in hoverflies suggests that the available resources were sufficient for their own energy demands. The increasing handling time in wild bees, in turn, suggests a greater foraging effort at high densities, possibly as a result of resource depletion (Ishii *et al*., 2008). This greater foraging effort, however, does not necessarily lead to pollination effectiveness similar to honeybees because pollen removal and deposition rates vary generally among pollinator species with distinct foraging behaviours and stochastically during dispersal by individual pollinators (Goodell & Thomson 2007, Richards *et al*., 2009). Nevertheless, handling time in wild bees was considerably shorter than in hoverflies in most cases, suggesting that foraging behaviour and the degree of specialization might be of greater importance for differences in pollination efficiency between these two taxa (Larsson, 2005).

In turn, the number of seeds per pod is dependent on the amount of pollen deposited during visitation rather than the number of flowers visited in one foraging bout that increases fructification probability in male sterile plants. At this single-flower level, the gap between honeybees and wild bees is less prominent. Indeed, mason bees are similarly effective at much lower densities (approximately 10%) compared with small honeybee colonies. This indicates a greater effectiveness of mason bees at the single flower, although fewer flowers might be visited during foraging, as was observed for apple trees and other fruits (Vicens & Bosch, 2000). Hoverflies performed rather poorly, showing the lowest increase in number of seeds per pod with increasing densities compared with their efficiency regarding fruit set or yield. Furthermore, flowers pollinated by

hoverflies developed less seeds per pod than flowers pollinated by mason bees in the respective maximum densities, despite the fact that the hoverfly maximum considerably exceeded the wild bee maximum. Thus, the quantity of pollen delivered to each flower appears to differ substantially between specialist and generalist species (Larsson, 2005).

Considering yields in g/m^2 solitary mason bees are equally effective as small honeybee colonies, although at much lower densities (16–36 mason bees versus 200 honeybees), indicating that lower fruit set was compensated by higher seed weight per pod. Unexpectedly, the gap between yields in the hoverfly treatment at maximum densities and honeybees is less prominent than the differences in numbers of seeds per pod would suggest. Again, this might be explained by plant compensation at the level of individual seed weight. Thus, from an economic point of view, both wild pollinators likely comprise valuable agents of a pollination service in enclosed plant breeding regimes, even at much lower densities than honeybees. Because of the differences in pollination efficiency, however, more hoverflies are needed for optimal yield gain. Yield was also the only parameter responding to plant weight. Because plant weight did not vary systematically among treatments, the most likely explanation is that plant weight is predominantly determined by the number of pods and seeds. Thus, plants exposed to a high pollination service produce more pods and seeds and are heavier. Although the general trend of the shown differences between the density dependence in pollination efficiency of pollinator taxa is likely valid in the field, a direct translation of the experimental density gradient into natural abundances is difficult. Recent studies have shown, however, that pollinator abundances tend to differ vastly between oilseed rape fields, in the range 25–86 bees within 48 h in pan traps (Morandin & Winston, 2005; Morandin et al., 2006) and 0–40 wild bees and 83 hoverflies in observation transects of 5–8 min for an area of 67.5 m^2 (Arthur et al., 2010).

Because self-fertilization was omitted by using male-sterile plants, the predominance of wild bees with respect to providing outcrossing in plants compared with hoverflies becomes obvious. Although the long-term benefits of outcrossing might not apply for crops, the results suggest general differences between pollinator taxa in successfully transferring viable pollen between conspecific flowers (Brunet & Sweet, 2006). Because of their different susceptibility to agricultural management (Jauker et al., 2009), however, generalist pollinators such as hoverflies might compensate for the loss of specialist pollinators such as wild bees in agroecosystems, in accordance with the insurance hypothesis (Ives et al., 2000). The influence of pollinator diversity (i.e. both pollinator taxa in one treatment) on crop yield was not explicitly tested, although the immediate benefits of multiple pollinator taxa to crop yield have been demonstrated in other recent studies (Klein et al., 2003; Hoehn et al., 2008; Winfree & Kremen, 2009). Nevertheless, the hoverfly treatment with two pollinator species did not perform equally well to the one species treatment of wild bees. Differences in the ratio of tested hoverfly species might have affected overall pollination effectiveness (Rader et al., 2009) because among-pollinator differences in effectiveness are key drivers of the diversity–function relationship of plant–pollinator interactions (Perfectti et al., 2009). Future studies need to consider the agriculturally-induced alterations in pollinator assemblages and the impact of these alterations on the pollination service with regard to compensatory effects among and within pollinator taxa (Jauker & Wolters, 2008; Meyer et al., 2009; Winfree & Kremen, 2009; Gomez et al., 2010).

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