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PLANT-ANIMAL INTERACTIONS - ORIGINAL PAPER

Hover flies are efficient pollinators of oilseed rape

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Abstract Understanding the consequences of declining diversity and abundance of pollinators for crops and floral biodiversity is a major challenge for current conservation ecology. However, most studies on this issue focus on bees, while other invertebrate taxa are largely ignored. We investigated the pollination efficiency of the globally abundant hover fly *Episyrphus balteatus* on the common crop, oilseed rape (*Brassica napus*). The study was conducted over a period of 2 consecutive years by means of enclosure experiments at an agricultural site located in Central Hesse (Germany). *E. balteatus* significantly increased both seed set and yield. This effect was very constant in the 2 years, despite considerable interannual differences in total seed numbers and seed mass. It highlights the important role of hover flies as pollinators of arable crops under varying environmental conditions. In contrast to bees, the effect of *E. balteatus* was lower at high pollinator densities than at low pollinator densities. This suggests adverse effects of density-dependent factors on pollination efficiency at high densities. Thus, models ignoring the modulating effect of biotic interactions by generally assuming a simple positive relationship between pollinator density and pollination efficiency might not apply to a vital component of the pollinator community.

Keywords Syrphidae · Canola · Pollination · Generalists · *Brassica napus*

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Introduction

Ecosystem services, such as pollination, are essential to human welfare (Daily 1997) and are of substantial economic value (e.g., Costanza et al. 1997). A general linkage of pollinator diversity and increased crop yield has been discussed ambiguously (Richards 2001; Ghazoul 2005; Steffan-Dewenter et al. 2005), but high abundances of pollinators have generally been proven to be beneficial to yields of numerous crops (Goodman et al. 2001; Kremen et al. 2002, 2004; Ricketts 2004; Klein et al. 2007). Yet, only one pollinator taxon has been thoroughly considered in this context: the bees (Apidae).

Alarming declines in wild bee populations have been reported for various European countries and elsewhere (e.g., Westrich 1989; Buchmann and Nabhan 1997; Allen-Wardell et al. 1998). Investigations in the UK and in the Netherlands suggest that the decline in the diversity of wild bees is mirrored by a decline in the diversity of insect-pollinated plants, whereas such a correlative pattern was less consistent in hover flies (Biesmeijer et al. 2006). Hover flies are probably the most significant anthophilous Diptera, and yet their importance as pollinators has not been investigated sufficiently (Larson et al. 2001). According to some early references, the hover fly *Eristalis tenax* potentially is an efficient pollinator of various fruit crops such as apple trees (Solomon and Kendall 1970) or strawberries (Kendall et al. 1971; Nye and Anderson 1974). However, syrphid genera other than *Eristalis* and crops other than fruit plants have received little but theoretical attention in the literature. It thus remains unclear whether the results of Biesmeijer et al. (2006) based on the investigation of a broad range of insect-pollinated plants really imply that hover flies are inefficient pollinators (Sahli and Conner 2006), or could also be explained by masking effects of confounding variables such as a differential response to environmental disturbance (Kearns 2001).

In the study reported here, we quantified the pollination service provided by *Episyrphus balteatus* (Syrphidae) to oilseed rape (Brassicaceae, *Brassica napus*). *E. balteatus* is one of the most common hover fly species worldwide. It predominantly occurs in agricultural landscapes (e.g., Bargen et al. 1998; MacLeod 1999; Sutherland et al. 2001), because its larvae feed on aphids. *B. napus* is an important oilseed crop in temperate regions. In Germany, for example, the acreage of oilseed rape recently increased from 1.2 million in 2003 to 1.35 million hectares in 2005 (Statistisches Bundesamt 2005). *B. napus* is mainly self-pollinated, yet pollen transport by invertebrate vectors has been shown to result in higher seed set and yield (see Steffan-Dewenter 2003 for a review). We hypothesized that: (1) *E. balteatus* has a positive effect on seed set of *B. napus*, and (2) this effect is more prominent at high as compared to low numbers of hover flies.

Materials and methods

Design

The experiment was carried out in 2004 and 2005 at the experimental field station of the Justus-Liebig-University Giessen in Rauischholzhausen (Hesse, Germany). Each year seeds of spring-sown *B. napus* (cultivar Licosmos, Deutsche Saatveredelung, Lippstadt, Germany) were mechanically drilled in 12 plots (1.5 × 1.5 m). Four rows of 1.25 m length with 62 seeds per row were planted at each plot. All plots were sown after regular soil cultivation at the end of April (2004) and in early May (2005). In mid June, before flowering, all plots were caged with fine-mesh plastic gauze (mesh size ca. 1 mm) using iron frames of 2 m height and enclosing an area of approximately 4 m^2.

The plots were arranged in three rows of four replicates each according to the following treatments: (1) no pollinators; (2) low hover fly density (12 individuals per cage, corresponding to 3 individuals m^{-2}); (3) high hover fly density (25 individuals per cage, corresponding to 6.25 individuals m^{-2}). To reduce the impact of microspatial conditions on pollinator activity, the experimental sites differed between the 2 years (distance: approximately 1.2 km) and row orientation was shifted by 90°. Approximately 1 week after caging, when about 5% of the oilseed rape flowers had opened, waterproof roofed plastic boxes containing pupae of *E. balteatus* (Katz Biotech, Welzheim, Germany) were placed inside the cages. All hover flies emerged within the next 3 days and remained alive and active for the entire flowering period.

Sampling

In each of the 2 years, all plants were harvested at once in order to avoid effects of unequal growing periods on seed set. Because of asynchronous fruit ripening, most plants carried both dehisced pods and unripe green pods. Only dry and closed pods of each plant were used for determining seed set. Furthermore, plants carrying less than ten dry and closed pods were excluded from the analysis. A total of 240 plants were analyzed in 2004 and 208 plants in 2005. The number of pods sampled amounted to 12,617.

Seeds were separated from the pods and cleaned by hand. The number of seeds per plant was measured using a seed counter (Contador E; Baumann Saatzuchtbedarf, Waldenburg, Germany). The number of seeds per pod was calculated to account for differences in number of pods per plant within treatments. Additionally, seed mass per plant was measured and converted to seed mass of individual seeds in milligrams to account for differences in total number of seeds per plant.

Data analysis

All data were tested for normality and homogeneity of variances within and between treatments. No transformation of data was necessary. Mean values of seeds per pod and seed mass were calculated for each replicate and these values were used as dependent variables for further analyses. Since one cage of the control plots had been destroyed in 2005, the sample size (n) was 23. Differences among treatments (control, low density of syrphids, high density of syrphids) were analyzed using a fixed factor one-way ANOVA (type III sums of squares to account for unequal n). The factor Year (2004 and 2005) was added to account for spatiotemporal differences relating to the shift of experimental sites described above. All statistical analyses were conducted using STATISTICA 7.1 (StatSoft, Tulsa, Okla.).

Results

The results of the ANOVA on both the number of seeds per pot and seed mass are summarized in Table 1. The main effects of the factor Year reflect the significant increase of the former parameter and the significant decrease of the latter parameter in 2005 (Fig. 1). However, no significant interaction with treatment could be established, indicating that the effect of the hover flies was not confounded by spatiotemporal variations (Table 1).

Hover flies significantly increased the mean number of seeds per pod from 17.75 in the control to 22.25 in the low-density treatments and to 20.5 in the high-density treatments (Table 1; Fig. 2). The number of seeds per pod was

Table 1 Differences in number of seeds per pod and seed mass (mg) of spring-sown *Brassica napus*, based on ANOVA performed with the fixed factor treatment (control, low and high *Episyrphus balteatus* density) and including the covariable Year (2004 vs. 2005) ($n = 23$)

	df	Number of seeds per pod		Seed mass (mg)	
		F	*P*	*F*	*P*
Treatment	2	30.0	<0.001	3.1	0.071
Year	1	6.3	0.023	34.4	<0.001
Treatment × Year	2	1.4	0.275	0.3	0.760
Adjusted R^2		0.75		0.62	

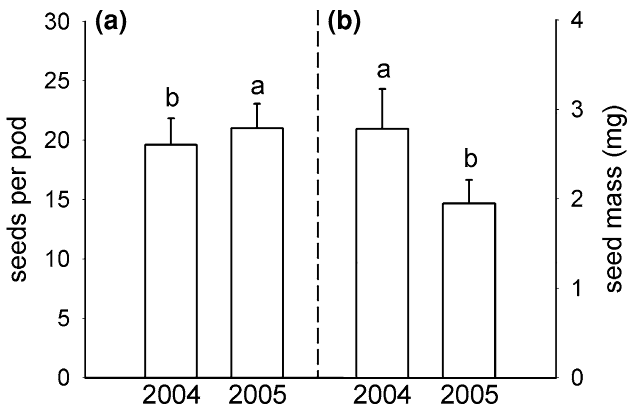

Fig. 1 Differences between years (2004 and 2005) in **a** number of seeds per pod ($F_{1,17} = 6.26$, $P = 0.027$) and **b** seed mass ($F_{1,17} = 34.37$, $P < 0.001$) of spring-sown *Brassica napus*. Significant differences are indicated by *different letters*. Data are means with SD ($n = 23$)

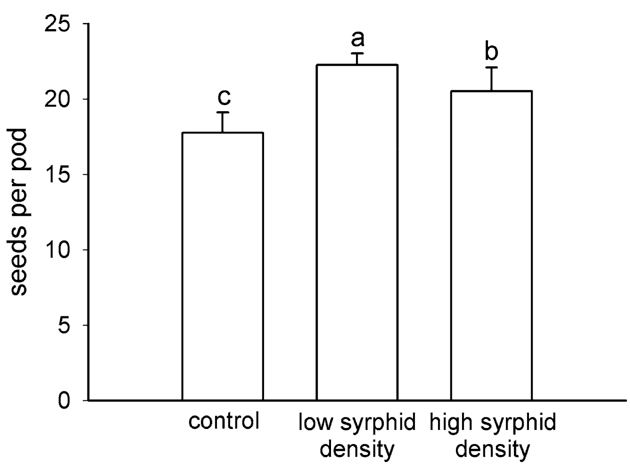

Fig. 2 Differences between treatments in number of seeds per pod of spring-sown *B. napus*. Pods were sampled from caged plants exposed to no pollinators (control), 12 individuals of *Episyrphus balteatus* (low syrphid density), and 25 individuals of *E. balteatus* (high syrphid density). Significant differences are indicated by *different letters* (Tukey's honestly significant difference test for unequal *N*, $P_{\text{control versus low}} < 0.001$, $P_{\text{control versus high}} < 0.001$, $P_{\text{low versus high}} < 0.05$). Data are means with SD ($n = 23$)

significantly greater in the low- than in the high-density treatment. No impact of hover flies on seed mass could be established.

The average number of plants per cage did not differ among treatments (ANOVA, $F_{2,19} = 2.80$, $P = 0.086$) and years ($F_{1,19} = 0.29$, $P = 0.595$). The mean number of pods per plant was 27.8 in the first (minimum 15; maximum 40) and 28.6 (minimum 21; maximum 33) in the second year, without being affected by treatment or year (ANOVA: treatment, $F_{2,19} = 1.85$, $P = 0.184$; year, $F_{1,19} = 0.07$, $P = 0.796$). The mean seed mass was 2.4 mg, with no correlation to the number of seeds per pod (Pearson product-moment correlation, $n = 23$, $R = 0.04$, $P = 0.855$).

Discussion

Flowers of oilseed rape produced significantly more seeds per pod when *E. balteatus* was present. Thus, hover flies are not only important biological control agents in agricultural systems (Tenhumberg and Poehling 1995; Pineda et al. 2007), but can also be efficient pollinators of arable crops. So far, little is known about hover fly densities on oilseed rape in the field. Concerning the aphidophagous guild, Frank (1999) reports an average density of 4 individuals m^{-2}, with *E. balteatus* being among the most common species. We thus assume the densities of 3 ("low") and 6.25 individuals m^{-2} ("high") chosen for our experiment to realistically reflect the natural range of hover fly abundance. Parallel studies using the same experimental setting but focusing on different pollinator taxa suggest that caging did not affect growth or productivity of the plants (Kristen 2008). Although the seed mass did not reach the "standard" of the Licosmos cultivar announced by the seed company (2.9 mg), the mean number of seeds per pod closely resembled the values given for winter-sown oilseed rape (Diepenbrock 2000).

According to Morandin and Winston (2006), pollinators increase the number of seeds by 1.8 seeds per pod, corresponding to a yield gain of oil seed by about 10%. Our experiment revealed a much higher increase by 4.5 (low density) and 2.75 seeds per pod (high density) for hover flies alone. As seed mass was not affected by the number of seeds per pod and treatment, it can be calculated that hover flies may augment yield gain by 15–25%. The fact that the effect of the syrphids, in contrast to other spatiotemporal effects on seed number and seed mass, remained remarkably constant over the years, suggests that hover fly pollination is quite resistant to fluctuating environmental conditions. Though our finding of a comparatively strong effect of hover flies on seed set of rape is supported by studies on wild flowers (Vance et al. 2004; Fontaine et al. 2006), such extrapolations should be handled with care, as

B. napus might be very variable in seed mass, but could be quite conservative for overall yield, due to its considerable compensatory capacity (Westcott and Nelson 2001). Since we do not have data on the total amount of flowers within the cages, for example, we cannot exclude that plants could compensate for pollination deficit by producing more flowers.

Admittedly, our experiment was conducted with self-compatible plants, whereas bees have been shown to primarily affect self-incompatible rape cultivars (Steffan-Dewenter 2003). It might thus be speculated that syrphid pollination is of particular importance for self-compatible oilseed rape. Evidence supporting this conclusion is provided by investigations on both the flower constancy (Goulson and Wright 1998) and the conspecific pollen load of hover flies (Sugiura 1996) suggesting that hover flies may considerably affect self-compatible plants via cross pollination. The fact that *E. balteatus* usually touches the flower heads several times with its tarsi before settling down (F. Jauker, personal observation) suggests that supported self pollination may also be involved.

Studies on various *B. napus* cultivars revealed a positive correlation between bee abundance and seed set or yield (Morandin and Winston 2005, 2006). Steffan-Dewenter (2003) was able to directly link seed set to the numbers of honey bees and mason bees. Thus, the fact that the pollination efficiency of *E. balteatus* was significantly greater at low than at high densities contradicts our initial hypothesis that pollination efficiency should be positively correlated to pollinator abundance (cf. Hayter and Cresswell 2006; Hoyle and Cresswell 2006). Some indications of a negative relation between the seed set of spring turnip rape and abundance of fly taxa other than syrphids have been found by Schittenhelm et al. (1997), while Jarlan et al. (1997) report an increased seed set in sweet pepper at higher densities of the drone fly *Eristalis tenax* under greenhouse conditions. However, our results suggest that pollination efficiency of *E. balteatus* is adversely affected by density-dependent factors. A potential explanation is that hover flies of the aphidophagous guild are not central place foragers and thus might respond to high densities by shifting from small-scale movements between neighboring flowers to large-scale dispersal activities. This might particularly apply to *E. balteatus* even under caged conditions, since this species is considered to be highly migratory (Speight 2006) and thus probably is very sensitive to the facilitation of stress induced by factors such as intraspecific competition or male harassment (Enfjäll and Leimar 2005). A much better understanding of both specific habitat requirements and behavioral response patterns is needed to substantiate this argument.

To conclude, our findings clearly show that hover flies (and other generalists) should not be neglected in future studies on the ecological services provided by pollinators in agroecosystems (see also Waser et al. 1996; Kearns et al. 1998). Moreover, the negative relationship between the density of *E. balteatus* and pollination efficiency indicates that modeling approaches that ignore the modulating effect of biotic interactions by simply assuming a positive relationship between pollinator density and pollination efficiency might not apply to a vital component of the pollinator community. Future studies have to resolve whether adverse effects of increasing density also occur among other species. Considering the current concern about pollinator decline, investigations addressing potential synergetic, compensatory, or even adverse effects of environmentally induced changes in species composition and density are urgently needed.

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