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RESEARCH ARTICLE

Flower fields and pesticide use interactively shape pollen beetle infestation and parasitism in oilseed rape fields

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Abstract

1. Pollen beetles (*Brassicogethes* spp.) are the main pests of oilseed rape (OSR, *Brassica napus*) in Europe and responsible for massive yield losses. Upcoming pesticide resistances highlight the need for other means of crop protection, such as natural pest control. Sown flower fields aim to counteract the decrease of insect biodiversity in agricultural landscapes by providing resources to ecosystem service providers. However, the optimal age and size of flower fields to increase natural pest control is still unclear.
2. We conducted experiments on 31 OSR fields located along a gradient of landscape-scale semi-natural habitat (SNH). OSR fields were located adjacent to flower fields which differed in age, continuity and size, or adjacent to crop fields or calcareous grasslands. Pesticide-free areas were established to examine interactive effects of pesticide use and flower field characteristics. The abundance of pollen beetle adults and larvae, parasitism and superparasitism rates in OSR were recorded at increasing distances to the adjacent sites.
3. Flower fields and calcareous grasslands increased pollen beetle parasitism when compared to OSR fields neighbouring crop fields. The threshold for effective natural pest control of 35% could be reached in the pesticide-free areas of OSR fields adjacent to calcareous grasslands and flower fields maintained continuously for at least 6 years. In pesticide-sprayed areas, pollen beetle parasitism and superparasitism declined with increasing distance to the adjacent field. Furthermore, flower fields larger than 1.5 ha were able to improve pollen beetle parasitism more than smaller fields.
4. *Synthesis and applications*. To promote natural pest control in oilseed rape (OSR), large flower fields should be maintained for several years, to create stable habitats for natural enemies. The continuous maintenance of flower fields should be preferred, as ploughing and resowing after 5–6 years decreased the positive effects of the flower fields on natural pest control in adjacent OSR fields. However, pesticide use can abrogate positive effects of flower fields on pollen beetle parasitism. This study highlights that sown flower fields have the potential to increase natural

pest control in OSR, but this potential is depending on its age, continuity and size and can be hindered by pesticide use.

KEYWORDS

agri-environment scheme, *Brassicogethes* spp., distance-decay function, ecosystem services, natural pest control, oilseed rape, sown flower field age and size

1 | INTRODUCTION

Natural pest control agents such as arthropod predators and parasitoids have high potential to suppress insect pest populations and lower pest damage (Bianchi et al., 2006; Bommarco et al., 2011). However, natural pest control is threatened by agricultural intensification, including loss and fragmentation of natural areas and pesticide use (Bianchi et al., 2006). Pesticides can alter the physiology and behaviour of beneficial arthropods and influence their orientation, fecundity and longevity negatively (Desneux et al., 2007), to the extent of being lethal (Tillman & Mulrooney, 2000). Arthropods can encounter pesticides, such as insecticides, in different ways: by direct contact with the spray mist, by contact to chemical residues on the surface of plants or by the consumption of contaminated material (Longley & Jepson, 1996a; Ulber, Klukowski, et al., 2010). Additionally, insecticides may exhibit repellent effects on parasitoids (Longley & Jepson, 1996a). Insecticide use can even lead to reduced predator–prey ratios in crop fields, if predators and parasitoids are more negatively affected than their prey, thereby deteriorating natural pest control and increasing pest damage (Bommarco et al., 2011; Krauss et al., 2011).

Agri-environmental schemes aim to enhance ecosystem services in intensively used agricultural landscapes and often include the preservation of remaining semi-natural areas (Bommarco et al., 2013). Semi-natural habitats (SNH) such as field margins, permanent grasslands and hedgerows provide resources and habitats to insects while enabling spillover into agricultural fields (Bianchi et al., 2006; Tscharntke et al., 2007). Complex landscapes with high amounts of SNH can therefore enhance natural pest control and ultimately reduce crop damage (Bianchi et al., 2006). Agri-environment schemes can include the implementation of flower fields (Haaland et al., 2011), which qualify as refuge habitats from the pesticide-sprayed crop fields (Schellhorn et al., 2008). The dense vegetation cover creates a favourable microclimate for parasitoids and arthropod predators, thereby prolonging the longevity of these natural enemies (Dyer & Landis, 1997). Furthermore, flower fields can provide alternative hosts and nectar (Gillespie et al., 2016). Most of the adult parasitoids need sugar resources, to cover their energetic needs (Bianchi & Wäckers, 2008). Therefore, floral resources can enhance the longevity and oviposition rate of parasitoids in the field (Lee & Heimpel, 2008) and ultimately lead to higher parasitism rates in their vicinity (Tylianakis et al., 2004).

Nevertheless, effects of flower fields on crop pests are ambiguous, with studies showing neutral effects or even an increase in pest populations and crop damage, since pests might also benefit from the additional resources (Winkler et al., 2010). For successful enhancement of natural pest control, flower field traits like age and size might be important, but their effects on pest control are not well understood. Knowledge gaps must be closed, to provide specific management recommendations concerning these traits. Additionally, pesticides are widely used and their utilization is expected to increase even further (Delcour et al., 2015). Therefore, it is important to know whether pesticide use might counteract positive effects of flower fields on natural pest control.

Pollen beetles (*Brassicogethes* spp.) are the main pests of oilseed rape (OSR, *Brassica napus*) in Europe (Williams, 2010). They have become increasingly resistant to widely used pyrethroid insecticides (Slater et al., 2011) with significant yield losses despite pesticide application (Schneider et al., 2015), highlighting the need for effective natural pest control (Skellern & Cook, 2018). Pollen beetles have several specialist and generalist natural enemies, attacking at different life stages (Büchs & Alford, 2003), which might benefit from close-by flower fields and the resources they provide. If the parasitism rate of pollen beetles exceeds a certain threshold, approximately of 35%, they can be effectively controlled by parasitoids (Thies et al., 2008). Here, we examine the effects of sown flower fields with differing ages and sizes, the surrounding landscape and interactions with pesticide use on adult and larval pollen beetle infestation and parasitism as well as superparasitism rates in OSR fields. We predict the following:

1. Flower fields decrease both larval and adult pollen beetle infestation in OSR fields and increase pollen beetle parasitism compared to fields with adjacent crop fields.
2. High amounts of SNH in the surrounding landscape decrease pollen beetle infestation by increased pollen beetle parasitism and natural pest control in general.
3. Effects of flower fields on pollen beetle infestation and parasitism decrease with growing distance into the OSR field.
4. Pesticide use decreases pollen beetle infestation, but also parasitism rates and counteracts positive effects of flower fields or SNH on natural pest control.
5. OSR fields next to large flower fields or calcareous grasslands have lower infestation and higher parasitism rates than OSR fields next to small flower fields.

2 | MATERIALS AND METHODS

2.1 | Study sites

Experiments were conducted on 31 conventionally managed winter OSR fields in the district of Lower Franconia in Germany in 2016. The OSR fields were located adjacent to five different sites: Three types of sown flower fields ('new flower field', 'refreshed flower field' and 'continuous flower field'), calcareous grasslands and conventionally managed crop fields. The different site types were either directly adjacent to the OSR or divided by grassy field margins or gravel farm roads. At the time of the study, flower fields were or had been part of an agri-environment scheme ('Kulturlandschaftsprogramm'). They were sown with specific seed mixtures and managed according to state regulations: (a) flower fields ploughed and sown the previous year ('new flower field'; $n = 8$), (b) flower fields established in 2009–2010, ploughed and resown the previous year ('refreshed flower field'; $n = 8$) and (c) flower fields established in 2009–2010, and mown with shredding and distribution of the plant material on the field (mulched) yearly since 2015 ('continuous flower field'; $n = 7$; Figure S1). Calcareous grasslands ($n = 4$) were used for comparison with the sown flower fields. Additionally, OSR fields next to conventional crop fields (adjacent conventional crop fields included three winter cereal fields, one OSR field; size 2.33 ± 0.16 ha [mean ± *SE*]) were chosen as negative control fields. Flower fields and calcareous grasslands were assigned to the two size categories 'small' (<1.5 ha) and 'large' (>1.5 ha), with half of the flowering fields of each type and half of the grasslands being small and the other half large (New flower fields: 4 small/4 large; 1.32 ± 0.41 ha. Refreshed flower fields: 4 small/4 large; 1.14 ± 0.32 ha. Continuous flower fields: 3 small/4 large; 1.27 ± 0.26 ha. Calcareous grassland: 2 small/2 large; 4.86 ± 3.40 ha [mean ± *SE*]). The size of the OSR focus fields, where the experiments were conducted, was 3.07 ± 0.42 ha (mean ± *SE*).

We assessed forb species richness and flower cover in the flower fields and calcareous grasslands in May and June 2016 on four 4 m^2 squared plots with a distance of 25 m to each other in the small flower fields and calcareous grasslands, and on six 4 m^2 plots in the large ones to account for the difference in field size. The different flowering as well as non-flowering plant species were identified to species level if possible (Table S4). Of the flowering plants, the number of flower units was multiplied with the respective mean surface area and then divided by the plot area. For each field, the flower cover was averaged over all plots. The overall flower cover was 17.88 ± 6.87% for new flower fields, 6.45 ± 2.90% for refreshed flower fields, 1.35 ± 0.33% for continuous flower fields and 0.47 ± 0.26% for calcareous grasslands (mean ± *SE*).

The landscape in 1 km radius around the fields and calcareous grasslands featured differing amounts of SNH (3.6%–31.6%). The study sites were at least 2.1 km apart from each other, to avoid landscape overlapping. SNH consisted of forest edges, field margins, bank borders, roadside vegetation, small wood groves, hedgerows, orchard meadows and extensive pastures as well as semi-natural calcareous grasslands and grasslands taken out of agricultural production. SNH was assessed using satellite images and land-cover maps, which were provided by the Bavarian State Ministry of Nutrition, Agriculture and Forestry and computed using ArcMap (ESRI v. 10.3).

2.2 | Study system

Pollen beetles (*Brassicogethes* spp.) are the most important pest species of (OSR, *Brassica napus*). The females lay their eggs into the flower buds, where the hatched larvae feed on pollen (Williams, 2010) and feeding of both adults and larvae can lead to bud abscission (Skellern & Cook, 2018). After maturing in the bud, the larvae drop to the ground, pupate in the soil and new beetles emerge in summer (Williams, 2010).

In our study, we could only find eggs of *Tersilochus heterocerus*, which is among the most abundant parasitoids of pollen beetles (Rusch et al., 2013). *Tersilochus heterocerus* predominantly lays eggs in second instar larvae feeding in open buds and flowers (Nilsson, 2003). The parasitoid larvae hatch shortly before the host larvae drop to the ground to complete their life cycle in the soil, thereby killing their host, and the parasitoid larvae overwinter in their pupal cocoon (Ulber, Williams, et al., 2010). *Tersilochus heterocerus* can exhibit high parasitism rates often exceeding the threshold value of 35% for effective pollen beetle control (Thies et al., 2008). Superparasitism occurs if parasitoids of the same species lay more than one egg into the same host and is common with *T. heterocerus* and pollen beetle larvae (Ulber, Williams, et al., 2010). Superparasitism can have beneficial effects in natural pest control by increasing the number of emerging parasitoids while reducing the survival rate of the host (Khafagi & Hegazi, 2008). Furthermore, *T. heterocerus* was found to feed on sugar, supposedly nectar, during foraging in the field (Rusch et al., 2013).

2.3 | Data collection

In the OSR fields, eight experimental plots of 4 m^2 size were located along two parallel transects (7.5 m distance from each other) in growing distance (0–124.7 m) to the adjacent site (flower field, calcareous grassland or crop field, Figure S1). To have evenly distributed data points over the whole distance of 124.7 m, experimental plots were established at varying distances with adjustments to tractor lanes. If possible, plots were located 25 m away from other field edges of the OSR field. In very narrow OSR fields ($n = 3$), 5 m to other field edges was ensured. Areas without pesticide spraying were established the winter before the field season on one of the transects with a size of 25 m^2 located around each of the 4 m^2 plots. Farmers were advised to refrain from spraying all kinds of pesticides (insecticides, herbicides and fungicides) within these 25 m^2 areas. All farmers sprayed at least once against pollen beetles on the rest of the field (for additional information on pesticide application, see Table S3).

Adult pollen beetles were counted on the main raceme of three randomly chosen flowering OSR plants within each plot (24 plants per field; BBCH growth stage 63–64; Meier et al., 2009). To assess pollen beetle larvae infestation and parasitism, three randomly chosen plants within each of the 4 m² plots were cut during blooming (24 plants per field, BBCH growth stage 64–65) and frozen until further analysis. Subsequently, all pollen beetle larvae in open flowers and the number of open flowers per frozen plant were counted. Pollen beetle parasitism was quantified by dissecting collected second instar larvae larger than 3 mm and counting eggs of *T. heterocerus*. Superparasitism by *T. heterocerus* was defined by pollen beetle larvae infested with more than one egg and noted down. Larvae smaller than 3 mm were disregarded, because other studies showed very low parasitism rates (Thies et al., 2003).

2.4 | Statistical data analysis

Adult pollen beetle abundance on the main raceme of the OSR plants ('pollen beetle abundance'), the infestation with pollen beetle larvae of the whole OSR plant ('larvae infestation'), the pollen beetle larvae parasitism rate ('parasitism') and the superparasitism rate ('superparasitism') by *T. heterocerus* were chosen as response variables. Data analyses were performed using generalized mixed effects models (GLMM) with the LME4 package (Bates et al., 2015) in R Version 3.4.1 (R Core Team, 2019). GLMMs with negative binomial error distribution were used for the 'pollen beetle abundance' and 'larvae infestation' models, to account for overdispersion. The number of flowers per plant was used as an offset term in the 'larvae infestation' model, to set the number of larvae in relation to plant size. A binomial distribution using the 'cbind' command was used for the 'parasitism' and 'superparasitism' rate models, with the number of parasitized, respectively, superparasitized larvae as the 'successes' and the number of larvae without parasitism, respectively, the number of parasitized larvae without superparasitism as 'failures'. The random effects '*Plot identity*' nested in '*Field identity*' were included in all models to account for pseudoreplication. The following fixed effects were tested according to the study design: (a) *Type:* type of adjacent site (new flower field, refreshed flower field, continuous flower field, calcareous grassland, crop field), (b) *SNH:* amount of SNH, (c) *Distance:* within OSR field distance to adjacent field edge and (d) *Treatment:* Sprayed pesticide treatment (+ Pesticide: pesticides applied according to regular farming scheme, − Pesticide: No pesticides applied in this area). We tested two-way interactions between *treatment* and the other fixed effects. Additionally, the fixed effect (e) *Size:* size category of flower fields and calcareous grasslands (small <1.5 ha, large >1.5 ha) was tested in a subset model including only OSR fields adjacent to flower fields or calcareous grasslands, as well as the interaction of size with treatment. We did additional LMMs for an analysis of the relationship between pollen beetle infestation and parasitism rate and the relationship between the pesticide treatment and the number of flowers per plant. Residual plots were used to check model assumptions. Wald chi-square tests (Type II sums of squares) using the function 'ANOVA' from the package CAR (Fox & Weisberg, 2018) were used to calculate *p*-values. Subsequent post-hoc analyses were conducted by calculating estimated marginal means by using the package EMMEANS (Lenth, 2018).

3 | RESULTS

3.1 | Pollen beetle abundance

The abundance of adult pollen beetles on the main raceme of OSR plants during flowering decreased with increasing distance to the field edge (Table 1; Figure S2a). Additionally, mean pollen beetle abundance was around 15% higher in pesticide-treated than in pesticide-free areas of the OSR field (Table 1; Figure S2b). The type and size of the adjacent field, the amount of SNH and interactions with treatment did not significantly influence adult pollen beetle abundance in the OSR fields.

3.2 | Larvae infestation

The plants next to continuous flower fields had overall lower numbers of pollen beetle larvae than plants next to refreshed flower fields and partly next to crop fields, where untreated plants had the same numbers as untreated plants next to continuous flower fields (Table 1; Table S1; Figure 1a). The pesticide treatment reduced larvae infestation in OSR fields next to the continuous flower fields and the calcareous grasslands by around 36% and 14%. Larvae infestation on pesticide-treated plants increased by around 16% when the amount of SNH in the surrounding landscape increased from 3.6% to 31%, whereas infestation on untreated plants remained almost constant (1% decrease, Table 1; Figure 2a). The number of open flowers per plant was higher on plants in the pesticide-treated areas ($\chi^2 = 23.01$, χ^2 *df* = 1, *p*-value <0.001). The size of the flower fields and calcareous grasslands had no significant effect on larvae infestation (Table 1).

3.3 | Parasitism

Parasitism rates in OSR were lower on the pesticide-treated plants next to the crop control than on all plants next to refreshed and continuous flower fields as well as on the untreated plants next to the calcareous grasslands (Table 1; Table S2; Figure 1b). Furthermore, the parasitism rate was lower on untreated plants next to the crop control than on untreated plants next to continuous flower fields. The threshold parasitism rate for effective control of pollen beetles of 35% (Thies et al., 2008) was reached on the untreated plants next to the continuous flower fields and calcareous grasslands. Parasitism rates declined with increasing amount of SNH in the surrounding landscape (Table 1; Figure 2b). A stronger decline was observed on untreated plants (65%) compared to pesticide-treated plants (48%) when the amount of SNH in the surrounding landscape increased from 3.6% to 31%. Furthermore, a 40% decline of parasitism was observed with increasing distance into the OSR fields on the pesticide-treated plants,

TABLE 1 Wald chi-square tests of GLMMs for the different pollen beetle response variables in oilseed rape fields next to the three types of flower fields and the two types of control fields. Separate models were performed for the fixed effect *size* and its interaction with *treatment*, excluding the OSR fields adjacent to crop fields (model 2). *Type*: adjacent site type (new flower field, refreshed flower field, continuous flower field, calcareous grassland and crop field); *SNH*: amount of semi-natural habitat in 1 km radius; *Distance*: distance to the adjacent field edge within OSR fields; *Treatment*: Sprayed pesticide treatment of the OSR plants (+ pesticide: pesticides applied according to regular farming scheme, − pesticide: no pesticides applied); *Size*: size category of flower fields and calcareous grasslands (small <1.5 ha, large >1.5 ha). Significance levels: $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$

Model response variable	Fixed effects	χ^2	χ^2 *df*	*p*-value
Pollen beetle abundance				
Model 1	Type	3.044	41	0.551
	SNH	0.054	1	0.816
	Distance	34.972	1	**<0.001*****
	Treatment	5.751	1	**0.016***
	Type × Treatment	4.556	4	0.336
	SNH × Treatment	2.535	1	0.111
	Distance × Treatment	0.246	1	0.620
Model 2	Size	0.360	1	0.549
	Treatment	7.081	1	**0.008****
	Size × Treatment	0.206	1	0.650
Larvae infestation				
Model 1	Type	15.309	4	**0.004****
	SNH	0.185	1	0.667
	Distance	1.765	1	0.184
	Treatment	17.153	1	**<0.001*****
	Type × Treatment	23.437	4	**<0.001*****
	SNH × Treatment	6.627	1	**0.010***
	Distance × Treatment	0.067	1	0.796
Model 2	Size	0.576	1	0.448
	Treatment	26.381	1	**<0.001*****
	Size × Treatment	0.031	1	0.861
Parasitism				
Model 1	Type	10.908	4	**0.028***
	SNH	1.509	1	0.220
	Distance	10.388	1	**0.001****
	Treatment	24.931	1	**<0.001*****
	Type × Treatment	10.955	4	**0.027***
	SNH × Treatment	5.584	1	**0.018***
	Distance × Treatment	5.624	1	**0.018***
Model 2	Size	4.805	1	**0.028***
	Treatment	16.470	1	**<0.001*****
	Size × Treatment	1.192	1	0.275
Superparasitism				
Model 1	Type	6.702	4	0.152
	SNH	0.821	1	0.365
	Distance	0.738	1	0.390
	Treatment	15.673	1	**<0.001*****
	Type × Treatment	3.309	4	0.507
	SNH × Treatment	0.446	1	0.504
	Distance × Treatment	4.119	1	**0.042***
Model 2	Size	3.978	1	**0.046***
	Treatment	18.074	1	**<0.001*****
	Size × Treatment	0.400	1	0.527

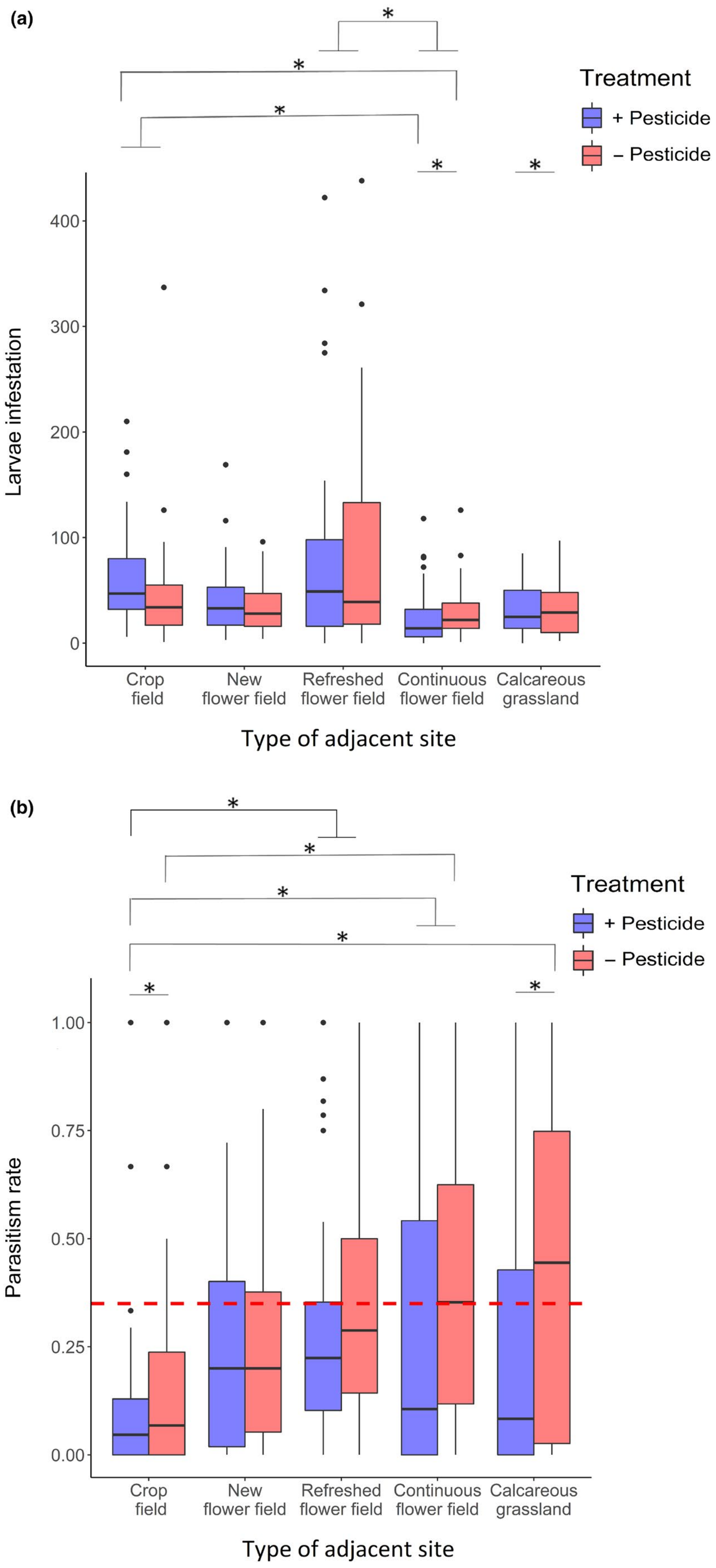

FIGURE 1 Pollen beetle larvae (a) infestation per plant and (b) parasitism rate in oilseed rape (OSR) plants adjacent to different types of sites and with different pesticide treatments. Boxplots show median and the 1st and 3rd quartiles, circles show outliers. Whiskers represent 1.5 interquartile range (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$; Tables S1 and S2). The red dashed line in plot (b) indicates the threshold for effective natural control of a parasitism rate of 0.35. New flower field: newly established the previous year, ploughed and sown with a flower mixture and then left without further management. Refreshed flower field: established 5–6 years prior to this study and left without further management, ploughed and resown the previous year and left without further management. Continuous flower field: established 5–6 years prior to this study, left without management until the previous year and since mown yearly. Treatment: + Pesticide: pesticides applied according to regular farming scheme, – Pesticide: no pesticides applied

whereas the parasitism rate on untreated plants decreased less (17%) over the whole tested distance of 124.7 m (Table 1; Figure 3a). In general, the parasitism rate was higher in OSR fields next to large flower fields compared to OSR fields next to small flower fields (Table 1; Figure S3a). Additionally, we examined the relationship between pollen beetle larvae infestation and the parasitism rate and found that the parasitism rate increases with the infestation ($\chi^2 = 12.465$, χ^2 $df = 1$, p-value <0.001; Figure S4).

3.4 | Superparasitism

Superparasitism declined by 47% with growing distance into the field on pesticide-treated plants compared to untreated plants, where it increased slightly (2%) over the tested distance (124.7 m; Table 1; Figure 3b). Additionally, the superparasitism rate was higher in OSR fields next to large flower fields compared to small flower fields (Table 1; Figure S3b).

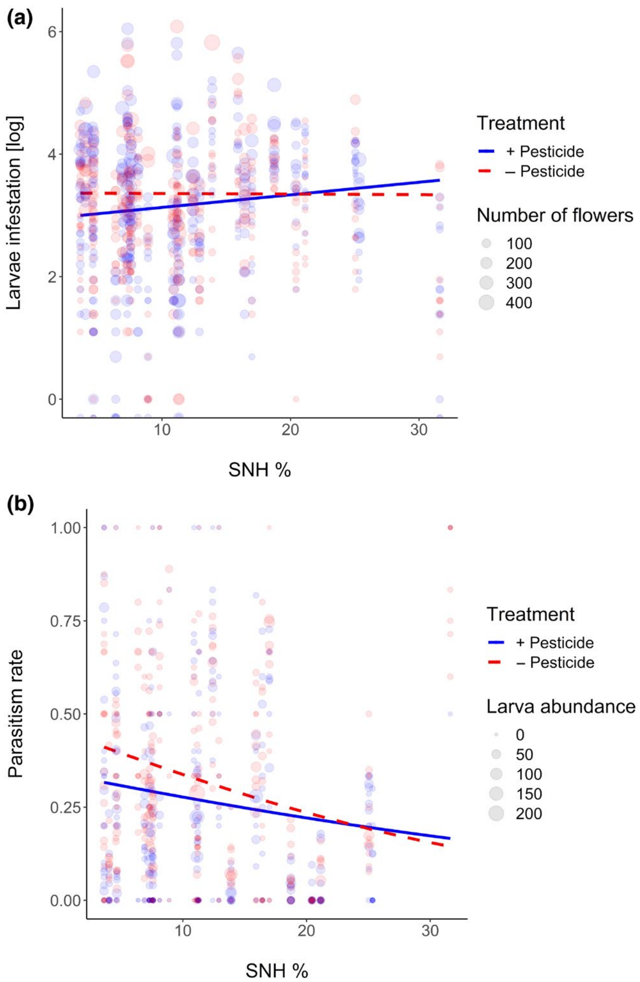

FIGURE 2 Pollen beetle larvae (a) infestation per plant (log e transformed) and (b) parasitism rate in oilseed rape (OSR) in landscapes along a semi-natural habitat (SNH) gradient in 1 km radius with different pesticide treatment on the OSR plants. Fitted lines show model predictions. Treatment: + Pesticide: pesticides applied according to regular farming scheme, – Pesticide: no pesticides applied

4 | DISCUSSION

We found that old and continuous flower fields can decrease pest infestation and increase pollen beetle parasitism in OSR. SNH in the surrounding landscape did not decrease infestation or improve parasitism, and parasitism and superparasitism decreased with increasing distance into the field. Furthermore, we found that pesticide use interacts negatively with positive effects of flower fields by keeping parasitism rates below the threshold for effective natural pest control and by displaying a stronger distance decay within OSR fields.

Continuous flower fields and calcareous grasslands led to the lowest larval infestation numbers and the highest parasitism rates in adjacent OSR fields. Older wildflower strips often show increased insect diversity and abundance compared to younger ones (Haaland et al., 2011) and were shown to have higher predator species richness and abundance (Frank et al., 2007). Many arthropod predators are active in the crop canopy of OSR, for example larvae of several rove beetle species (Felsmann & Büchs, 2006) and soldier beetles (Büchs & Alford, 2003). Higher abundances of predators next to continuous flower fields and calcareous grasslands are a possible explanation for the lower numbers of larvae, whereas the number of adult beetles did not differ between the types of flower fields. Effects of pollen beetle parasitism on OSR infestation will be mainly visible the following year, due to reduced pollen beetle emergence of the next generation. Therefore, and due to crop rotation, increased pollen beetle parasitism observed in our experimental OSR fields would benefit other nearby OSR fields the following year (Schneider et al., 2015). This also means that infestation by adult pollen beetles on our experimental fields was influenced by the landscape composition of the previous year, which makes it difficult to detect benefits of flower fields on crop infestation at the field level. In our study, the pollen beetle parasitism rate was higher in OSR next to flower fields and calcareous grasslands compared to OSR next to crop fields, except for the new flower fields which were implemented the previous year. Flower fields can improve as habitats with age (Frank et al., 2007) and the new flower fields apparently did not yet support parasitoid populations.

We expected lower pollen beetle infestation and higher parasitism rates in landscapes with high amounts of SNH due to higher levels of natural pest control in complex landscapes (Tscharntke et al., 2007). Parasitism rates decreased with increasing SNH in our landscapes, even though earlier studies showed higher parasitism rates by *T. heterocerus* in landscapes with high amounts of SNH (Rusch et al., 2011). However, SNH can benefit pests as well as natural pest enemies (Tscharntke et al., 2016). The parasitism rate increased with increasing pest infestation in our study, so a dilution effect is unlikely. Earlier studies showed, that host density can affect parasitism levels independent of landscape complexity (Costamagna

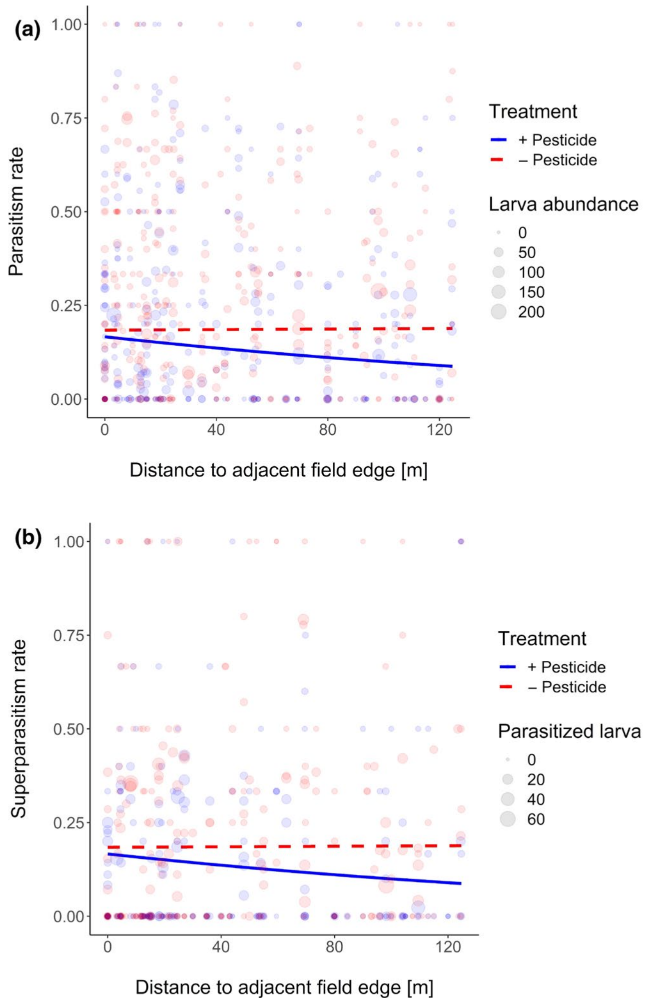

FIGURE 3 Distance decay (in meters) of pollen beetle larvae (a) parasitism rate and (b) superparasitism rate in oilseed rape (OSR) fields with different pesticide treatment on the OSR plants. Fitted lines show model predictions. Treatment: + Pesticide: pesticides applied according to regular farming scheme, − Pesticide: no pesticides applied

et al., 2004). However, landscape configuration and local habitat characteristics affect natural enemies interactively with landscape composition (Martin et al., 2019). Calcareous grasslands, which are SNH, in our study supported parasitism in the adjacent OSR field while the amount of SNH in the landscape did not, indicating that other semi-natural habitat types were less beneficial for pest control than calcareous grasslands. Population dynamics interplaying with annual turnovers in landscape composition due to crop rotations might interfere with effects of SNH and non-crop habitat in general, therefore displaying no consistent trend regarding the responses of pest and enemy abundance as well as predation rates (Karp et al., 2018; Scheiner & Martin, 2020).

Adult pollen beetles decrease with increasing distance into the field since they colonize OSR fields from the edges (Schneider et al., 2015). However, larva abundance can be as high or even higher in the centre of the fields (Schneider et al., 2015), because female beetles avoid intraspecific competition by venturing further into the fields for oviposition (Cook et al., 2006). In our study, the abundance of pollen beetle larvae did not decrease with increasing distance into the field. Parasitoids are often more abundant at field edges compared to field centres, due to their limited dispersal abilities (With et al., 1999). We found a general distance decay of pollen beetle parasitism, but it was more pronounced in the pesticide-treated areas, where also a distance decay of superparasitism was apparent. As mentioned, superparasitism can make natural pest control of pollen beetles more efficient (Khafagi & Hegazi, 2008). Encapsulated eggs of *T. heterocerus* have been found in the fat body of adult pollen beetles that survived parasitism by single eggs (Osborne, 1960), while superparasitism decreases pollen beetle survival (Khafagi & Hegazi, 2008). Apparently, pesticides diminish the dispersal abilities of parasitoids even further, probably by influencing their vitality negatively, and stronger distance decay of parasitism and superparasitism in the presence of pesticides might therefore decrease natural pest control particularly in OSR field centres.

We found higher abundances of adult pollen beetles in the pesticide-sprayed areas compared to the pesticide-free areas. OSR plants in general had higher numbers of flowers in the pesticide-treated areas and plant size was not accounted for in this analysis. Therefore, higher numbers of adult pollen beetles in the pesticide-treated areas could simply be due to higher numbers of flowers on the main raceme. However, repellent effects of pesticides (Longley & Jepson, 1996a) and higher survival may have lead crop canopy predators to accumulate on the pesticide-free plants and higher predation rates might explain lower pollen beetle abundance in pesticide-free areas. Furthermore, we found higher parasitism rates in the areas without pesticide spraying. Pesticides applied during OSR flowering can harm parasitoids and reduced the abundance of pollen beetle parasitoids in field trials (Ulber, Klukowski, et al., 2010). Higher parasitism rates could therefore be explained by higher survival of parasitoids in the areas without pesticide spraying. Already the contact to chemical residues on sprayed plants is sufficient for pesticide uptake by parasitoids and can have negative effects on their behaviour (Longley & Jepson, 1996b). Additionally, aggregation of parasitoids on the untreated plants inside of the pesticide-free areas is likely, since pesticides can have repellent effects (Longley & Jepson, 1996a). The threshold parasitism rate for effective natural pest control of pollen beetles lies at approximately 35% (Thies et al., 2008). In our study, this proportion of parasitized larvae could only be reliably achieved inside the pesticide-free areas in OSR next to the continuous flower fields and calcareous grasslands. Flower fields can help to mitigate the negative effects of pesticides on parasitoids, but in our study were not successful to push the parasitism rate above the critical threshold, indicating that natural pest control is prevented by pesticide application.

Large flower fields and calcareous grasslands supported higher parasitism and superparasitism rates than small ones and the natural pest control threshold could only be reliably reached in OSR next to large sites. Natural enemy density, richness and diversity can increase with the size of flower plantings, due to more resources and habitat (Blaauw & Isaacs, 2014). Therefore, the establishment of large flower fields might be beneficial to promote pollen beetle parasitism in OSR.

In our study, the provision of flower fields improved pollen beetle parasitism rates in adjacent OSR fields. This effect was depending on the flower field age and size. Newly established fields did not improve parasitism yet, and large sites over 1.5 ha promoted parasitism better than smaller ones. Therefore, perennial flower fields should be preferred over annual flower fields, and the perennial flower fields should be maintained continuously with as little disturbance as possible. Ploughing and resowing after 5–6 years decreased the positive effects of the flower fields on natural pest control of pollen beetles in OSR. Large fields might be preferable over smaller ones. However, we could not test several small flower fields compared to a single large flower field. Furthermore, the local management is important for successful ecological intensification: Pesticide use not only poses the risk of resistances, it also diminished positive effects of flower fields on pollen beetle parasitism. Our study highlights the negative side effects of pesticides on parasitoids and the need for alternative measures to promote natural pest control in conventional farming.

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CONFLICT OF INTERESTS

The authors declare that they have no conflict of interest.

AUTHORS' CONTRIBUTIONS

E.K., E.A.M., A.H., J.K. and I.S.-D. conceived and designed the study; E.K. collected and analysed the data; E.K., E.A.M. and I.S.-D. interpreted the results; E.K. wrote the first draft of the manuscript. All authors contributed substantially to manuscript revision and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.1zcrjdfqv (Krimmer et al., 2020).

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