Agri-environment schemes and ecosystem services:

The influence of different sown flower field characteristics on pollination, natural pest control and crop yield.

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“Man darf nie an die ganze Straße auf einmal denken, verstehst du?

Man muß nur an den nächsten Schritt denken, an den nächsten Besenstrich. Und immer wieder nur an den nächsten.

Dann macht es Freude; das ist wichtig, dann macht man seine Sache gut.“

-Michael Ende, Momo

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Zusammenfassung

Insekten sind für einen Großteil der Ökosystemdienstleistungen Bestäubung und natürliche Schädlingskontrolle zuständig. Schwinden die Insekten, so können diese Dienstleistungen nicht mehr zuverlässig gewährleistet werden. Als Ursachen für den Rückgang an Insekten wurde unter anderem die Intensivierung der Landwirtschaft und damit einhergehend der Verlust und die Fragmentierung von Lebensraum identifiziert. Ökologische Intensivierung hat das Ziel, alternative und nachhaltige Bewirtschaftungsmethoden in der Landwirtschaft zu fördern und beispielsweise den Einsatz von Spritzmitteln zu verringern. Agrarumweltmaßnahmen entschädigen Landwirte, wenn sie ökologisch wertvolle Maßnahmen in ihren Betrieb integrieren und können dadurch ökologische Intensivierung unterstützen. Die Bandbreite an Agrarumweltmaßnahmen ist groß, beinhaltet aber häufig das Anlegen von Blühflächen auf Ackerflächen. Blühflächen liefern Nahrungsressourcen und Lebensraum für eine Vielzahl von Insekten und sollten daher in der Lage sein Insektenpopulationen zu unterstützen und Ökosystemdienstleistungen auf angrenzenden Feldern zu verstärken. Jedoch ist das ökologische Potential von Blühflächen von einer Vielzahl von Faktoren abhängig. Unter anderem können das Alter und die Größe der Blühfläche entscheidend beeinflussen, inwiefern

unterschiedliche Insektengruppen profitieren. Zusätzlich hat die Landschaftskomplexität der direkten Umgebung, und damit die potentiell vorhandene Biodiversität, großen Einfluss auf die Fähigkeit von Blühflächen Ökosystemdienstleistungen lokal zu erhöhen. In dieser Studie geht es darum zu entschlüsseln, wie sich diese verschiedenen Faktoren sich auf die beiden Ökosystemdienstleistungen Bestäubung und natürliche Schädlingskontrolle auswirken und ob sie sich gegenseitig beeinflussen. Zusätzlich soll untersucht werden, inwiefern Blühflächen und Ökosystemdienstleistungen Erträge beeinflussen können. Weitere in dieser Studie untersuchte Einflussfaktoren sind die Distanz zur Blühfläche und der Einsatz von Pestiziden. Die Abundanz von Nützlingen kann mit der Distanz zu geeigneten Habitaten stark abnehmen. Der Einsatz von Spritzmitteln wiederum könnte die positiven Einflüsse der Blühflächen auf Nützlinge aufheben.

Um diese verschiedenen Aspekte zu untersuchen und letztendlich Empfehlung für die Etablierung von Blühflächen geben zu können, wurden Feldversuche auf Blühflächen mit unterschiedlicher Beschaffenheit und auf angrenzenden Rapsflächen durchgeführt. Die Blühflächen unterschieden sich hierbei in ihrem Alter und ihrer Kontinuität. Zusätzlich wurden Blühflächen mit unterschiedlicher Größe getestet. Außerdem wurden die Blühflächen und ihre benachbarten Rapsfelder so ausgewählt, dass sie sich in Landschaften mit unterschiedlichem Anteil an halbnatürlichen Habitaten befinden. Rapsflächen neben Kalkmagerrasen und Äckern mit konventionellen Feldfrüchten dienten als Kontrollflächen. Auf den Rapsflächen wurden Bestäuberbeobachtungen sowie Aufnahmen von Rapsglanzkäferbefall und deren Parasitierung durchgeführt. Zusätzlich wurden verschiedene Ertragsparameter von Raps aufgenommen. Die

Untersuchungen fanden jeweils in unterschiedlichen Distanzen zur Blühfläche innerhalb des Rapsfeldes statt, um Distanz-Abnahme Funktionen zu untersuchen. Spritzfenster wurden etabliert, um den Einfluss von Pestiziden auf Ökosystemdienstleistungen und Erträge zu untersuchen. Für die statistische Auswertung wurden lineare gemischte Modelle verwendet.

Die Ergebnisse haben zum einen gezeigt, dass frisch angelegte Blühflächen mit hoher Blütendeckung sehr attraktiv für Bestäuber sind. Jedoch blieben die Bestäuber in den Blühflächen, wenn diese eine gewisse Größe hatten (> 1.5ha) und verteilten sich nicht auf die umgebenden Flächen. Ein hoher Anteil an halbnatürlichen Habitaten in der umgebenden Landschaft erhöhte den Wert von kleinen Blühflächen als Ausgangspunkt für Bestäuber und ihren anschließenden Übergang auf Ackerflächen. Hohe Mengen an halbnatürlichen Habitaten verringerten außerdem den Rückgang der Bestäuber mit steigender Entfernung zur Blühfläche. Auf Grundlage dieser Ergenisse wäre es zu empfehlen, kleine Blühflächen in Landschaften mit viel halbnatürlichem Habitat und große Blühflächen in Landschaften mit wenig halbnatürlichem Habitat anzulegen. Außerdem ist anzumerken, dass Blühflächen keinen adequaten Ersatz für dauerhafte halbantürliche Habitate darstellen. Diese müssen weiterhin aktiv geschützt und erhalten werden, um Bestäubung auf Ackerflächen zu fördern. Des Weiteren wurde auf Rapsflächen neben kontinuierlichen Blühflächen mit einem Alter über 6 Jahre der niedrigste Befall mit Rapsglanzkäferlarven festgestellt. Blühflächen und Kalkmagerrasen erhöhten die Parasitierung von Rapsglanzkäfern in benachbarten Rapsflächen im Vergleich zu Rapsflächen die neben Ackerflächen liegen. Der Schwellenwert für eine effektive natürliche Schädlingskontrolle wurde nur in den pestizidfreien Bereichen in

Rapsflächen neben kontinuierlichen Blühflächen und Kalkmagerasen erreicht. In mit Pestiziden behandelten Bereichen nahmen Parasitismus und Superparasitismus mit zunehmender Entfernung zum benachbarten Feld ab. In den Spritzfenstern ohne Pestizide blieben sie jedoch auf dem gleichen Niveau. Große Blühflächen erhöhten Parasitismus und Superparasitismus mehr als kleine. Insgesamt können Blühflächen die Parasitierungsraten von Rapsglanzkäfern auf Rapsflächen erhöhen, jedoch können Pestizide diese positiven Effekte aufheben.

Zuletzt wurden die Effekte von Blühflächen und Ökosystemdienstleistungen auf den Rapsertrag untersucht. Hier stellte sich heraus, dass Bestäubung keine positiven Effekte auf den Rapsertrag hatte. Alte und kontinuierliche Blühflächen erhöhten die natürliche Schädlingskontrolle in den Rapsfeldern, welche wiederrum den Samenansatz und das absolute Samengewicht erhöhten. Die Behandlung mit Pestiziden hatte negative Asuwirkungen auf natürliche Schädlingskontrolle, aber positive Auswirkungen auf den Ertrag. Bestäubung und natürliche Schädlingskontrolle nahmen mit der zunehmenden Entfernung zum Feldrand ab, aber der Fruchtansatz nahm leicht zu. Die Feldqualität hatte keine Auswirkungen auf die im Modell untersuchten Rapsertrag Messwerte. Ertragsbildung bei Rapspflanzen ist ein komplexer Vorgang an dem viele Faktoren beteiligt sind. Mehrjährige Blühflächen können ökologische Intensivierung fördern indem sie den Ertrag durch natürliche Schädlingskontrolle erhöhen. Diese Studie leistet einen wertvollen Beitrag zum besseren Verständnis der Auswirkungen von unterschiedlich beschaffenen Blühflächen auf Bestäubung, natürliche Schädlingskontrolle und Rapsertrag.

Summary

Insects are responsible for the major part of the ecosystem services pollination and natural pest control. If insects decline, these ecosystem services can not longer be reliably delivered. Agricultural intensification and the subsequent loss and fragmentation of habitats has among others been identified to cause insect decline. Ecological intensification aims to promote alternative and sustainable management practices in agricultural farming, for example to decrease the use of external inputs such as pesticides. Agri-environment schemes make amends for farmers if they integrate ecologically beneficial measures into their farming regime and can therefore promote ecological intensification. There is a wide variety of agri-environment schemes, but the implementation of sown flower fields on crop fields is often included. Flower fields offer foraging resources as well as nesting sites for many different insect species and should be able to support insect populations as well as to increase ecosystem services to adjacent fields. However, the potential of flower fields to exhibit these effects is depending on many factors. Among others, the age and size of the flower field can influence if and how different insects profit from the measure. Additionally, the complexity of the surrounding landscape and therefore the existing biodiversity is influencing the potential of flower fields to increase ecosystem services locally. The goal of this study is to disentangle to which degree these factors influence the ecosystem services pollination and natural pest control and if these factors interact with each other. Furthermore, it will be examined if and how flower fields and ecosystem services influence crop yield. Additional factors examined in this study are distance decay and pesticide use. The abundance of beneficial insects can decrease strongly with increasing distance to suitable habitats. Pesticide use in turn could abrogate positive effects of flower fields on beneficial insects.

To examine these different aspects and to be able to make recommendations for flower field implementation, field experiments were conducted on differently composed sown flower fields and adjacent oilseed rape fields. Flower fields differed in their age and continuity as well as in their size. Additionally, flower and oilseed rape fields were chosen in landscapes with different amounts of semi-natural habitat. Oilseed rape fields adjacent to calcareous grasslands and conventional crop fields served as controls. Pollinator observations and pollen beetle and parasitism surveys were conducted in the oilseed rape fields. Additionally, different yield parameters of the oilseed rape plants were recorded. Observations were conducted and samples taken in increasing distance to the flower fields to examine distance decay functions. Spray windows were established to inspect the influence of pesticides on ecosystem services and crop yields. Linear mixed models were used for statistical analysis.

The results show, that newly established flower fields with high amounts of flower cover are very attractive for pollinators. If the flower fields reached a certain size (> 1.5ha), the pollinators tended to stay in these fields and did not distribute into the surroundings. High amounts of semi-natural habitat in the surrounding landscape increased the value of small flower fields as starting points for pollinators and their subsequent spillover into crop fields. Additionally, high amounts of semi-natural habitat decreased the decay of pollinators with increasing distance to the flower fields. Based on these results, it can be recommended to establish many small flower fields in landscapes with high amounts of semi-natural habitat and large flower fields in landscapes with low amounts of semi-natural habitat. However, it is mentionable that flower fields are no substitute for perennial semi-natural habitats. These still must be actively conserved to increase pollination to crop fields.

Furthermore, the lowest amount of pollen beetle infestation was found on oilseed rape fields adjacent to continuous flower fields aged older than 6 years. Flower fields and calcareous grasslands in general increased pollen beetle parasitism in adjacent oilseed rape fields compared to conventional crop fields. The threshold for effective natural pest control could only be reached in the pesticide free areas in the oilseed rape fields adjacent to continuous flower fields and calcareous grasslands. Parasitism and superparasitism declined with increasing distance to the adjacent fields in pesticide treated areas of the oilseed rape fields. However, they remained on a similar level in spray windows without pesticides. Large flower fields increased parasitism and superparasitism more than small flower fields. Flower fields generally have the potential to increase pollen beetle parasitism rates, but pesticides can abrogate these positive effects of flower fields on natural pest control.

Last but not least, effects of flower fields and ecosystem services on oilseed rape yield were examined. No positive effects of pollination on oilseed rape yield could be found. Old and continuous flower fields increased natural pest control in oilseed rape fields, which in turn increased seed set and total seed weight of oilseed rape plants. The pesticide treatment had negative effects on natural pest control, but positive effects on crop yield. Pollination and natural pest control decreased with increasing distance to the field edge, but fruit set slightly increased. The quality of the field in terms of soil and climatic conditions did not influence the yield parameters examined in this study. Yield formation in oilseed rape plants is a complex process with many factors involved, and it is difficult to disentangle indirect effects of flower fields on yield. However, perennial flower fields can promote ecological intensification by increasing crop yield via natural pest control. This study contributes to a better understanding of the effects of differently composed flower fields on pollination, natural pest control and oilseed rape yield.

Chapter I: General introduction

The importance of sustainable ways to promote agricultural productivity by increasing biodiversity-based ecosystem services.

I.1 Loss of insect biodiversity

The bumblebee species *Bombus cullumanus* was first described in Britain in the early 19th century as *Apis cullumana*, named in honour of Sir Thomas Gery Cullum who was a local historian and naturalist (KIRBY, 1802). The males are yellow banded while the females are red tailed and therefore difficult to distinguish from females of *Bombus lapidarius* (WILLIAMS ET AL., 2013). In the beginning of the 20th century, *B. cullumanus* could still be observed in England, the south of Sweden, northern Germany and the Netherlands (RASMONT ET AL., 2005). Since the 1950s however, *B. cullumanus* has become extinct in these countries and whole central Europe (KOSIOR ET AL., 2007). Single specimens could still be found at the Pyrenees and the Central Massif in France, but the total population is estimated to consist only of a few dozen remaining queens (RASMONT ET AL., 2005).

However sad, the fate of *Bombus cullumanus* is not an individual one. A study using historical records for their analysis showed, that after 1980 wild bee species declined in Britain by 52% and in the Netherlands by 67% (BIESMEIJER ET AL., 2006).

Another analysis of longterm data in Britain showed a decline of biomass, but mostly for large flying insects (SHORTALL ET AL., 2009). In recent years, a drastic loss of insect biodiversity is becoming more visible, and temperate regions are affected as well as tropical ones. In nature protection areas in Germany, a 75% decrease of total flying insect biomass was detected over the last 27 years (HALLMANN ET AL., 2017). In the Luquillo rainforest of Puerto Rico, arthropod biomass declined between 98% and 78% for ground and canopy dwelling predators (LISTER AND GARCIA, 2018). There are massive population declines worldwide and a horrifying amount of 40% of all insect species might be on the edge of extinction (SÁNCHEZ-BAYO AND WYCKHUYS, 2019). Recent extinction rates exceed the background extinction rate by a magnitude of 1000 (PIMM ET AL., 2014) and earth is recently experiencing a sixth major mass extinction event (CEBALLOS ET AL., 2017) with insects declining seemingly more rapidly than other groups (THOMAS ET AL., 2004).

I.2 Importance of insects and ecosystem services

Estimates of total insect species range from 5-50 million, with estimated 750 thousand species being described so far (GASTON, 1991). Insects are manifold and numerous, and they are crucial for the functioning and stability of ecosystems worldwide (SÁNCHEZ-BAYO AND WYCKHUYS, 2019). Resilient ecosystems consist of a variety of species that feature specific traits and can replace each other in case of deficiencies, for example if environmental conditions change (WILLIS ET AL., 2018). However, if the most functionally efficient species decline, the ecosystem function can be altered in a negative way (LARSEN ET AL., 2005). Insects are often among the most abundant species in terrestrial ecosystems and perform several important roles in the complex ecosystem structure. Insects are an important source of nutrients for higher trophic levels: Around 60% of all bird species are insectivorous, as are many amphibians, reptiles and mammals (Hallmann et al., 2017; Morse, 1971). If Insects vanish, there will be severe cascading consequences for other animal groups and entire foodwebs (Sánchez-Bayo and Wyckhuys, 2019). They are involved in many ecosystem functions like herbivory and detrivory, thereby transforming huge amounts of biomass which is crucial for nutrient cycling and decomposition (Yang and Gratton, 2014). Furthermore, insects play crucial roles in plant pollination and natural pest control (Bommarco et al., 2011; Ollerton et al., 2011).

If the human population benefits directly or indirectly from ecosystem functions like decomposition or pollination, they are called ecosystem services (Costanza et al., 1997). Ecosystem services can be grouped into different categories, with nutrient cycling and soil formation being 'supporting services', while pollination and natural pest control are 'regulating services' (Bommarco et al., 2013). Additional services are 'provisioning services', such as food and water, and 'cultural services', which includes aesthetic and recreational values (Bommarco et al., 2013). The ecosystem services are always connected to an ecosystem function. For pollination, the function is the movement of the gametes, for natural pest control the trophic-dynamic regulation of populations (Costanza et al., 1997). The actual values of these services worldwide was estimated with US$117 billion for pollination and US$417 billion for natural pest control in 1997 (Costanza et al., 1997). A more recent estimation suggested a much higher number for pollination of between US$235-577 (Ipbes 2017). Natural pest control can stabilize yields and promote resilience in agricultural production systems (Bommarco et al., 2013), especially since resistances against pesticides are emerging for major crop pests such as the pyrethroid resistance of the oilseed rape pollen beetle (SLATER ET AL., 2011). There is real value in the provisioning of these services, but the loss of insects to provide them, for example pollinators, puts them at risk (POTTS ET AL., 2010). For pollination, the common species are the biggest service providers (KLEIJN ET AL., 2015) and their decline will lead to a pollinator shortage (AIZEN ET AL., 2008), which ultimately puts the ecosystem service pollination at risk (OLIVER ET AL., 2015). This is especially worrying, as pollination is not only important for many wild plants (OLLERTON ET AL., 2011), but also for a wide variety of crops used for human consumption (KLEIN ET AL., 2007) and the amount of pollinator dependent crops grown is increasing worldwide (AIZEN ET AL., 2008).

I.3 Causes of the insect biodiversity decline

The fact, that specialist as well as common generalist species are affected by the species and population declines suggests, that the declines are not tied to a particular habitat but instead affect common insect traits (GASTON AND FULLER, 2007). Land-use change from natural habitats to crop land and agricultural intensification with high fertilizer and pesticide input are often identified as the main causes of the recent insect decline (BIANCHI ET AL., 2006; HALLMANN ET AL., 2017; NEWBOLD ET AL., 2015; TSCHARNTKE ET AL., 2005). Land-use change includes habitat conversion, habitat degradation and habitat fragmentation (TITTENSOR ET AL., 2014). Habitat fragmentation is often defined as the transformation of large and connected habitat patches into smaller and disconnected ones, which can have negative effects on biodiversity (FAHRIG, 2003). Habitat fragmentation and the replacement of Leguminosae with chemical fertilizer has been identified as responsible for the decline of the earlier mentioned bumblebee *Bombus cullumanus* (Rasmont et al., 2005, 1993). Furthermore, habitat fragmentation is often associated with habitat loss, but the consequences of habitat loss are more visible and severe (Fahrig, 2003). Habitat loss, for example the conversion of grassland into arable land or the removing of hedgerows in agricultural landscapes (Fuller, 1987; Robinson and Sutherland, 2002), has negative effects on species richness and abundance (Best et al., 2001; Guthery et al., 2001; Steffan-Dewenter et al., 2002) as well as genetic diversity (Gibbs, 2001). It also severely decreases population growth rates and declining species are often found in areas where habitat loss occurred (Donovan and Flather, 2002).

Agricultural intensification includes land conversion and crop land expansion as well as the intensification of cultivation methods, for example fertilization, irrigation and pesticides (Matson et al., 1997). Pesticide use is one of the most important tools to improve food production (Matson et al., 1997). Their usage increased immensely in the last decades and is expected to increase even further (Delcour et al., 2015; Tilman et al., 2002), but they should not be used unscrupulous. It was shown, that pesticide exposure can have strong negative effects on human health (Guillette and Iguchi, 2012). Pesticides are also known to play a role in the decline of aquatic organisms (Beketov et al., 2013) and birds (Mineau and Whiteside, 2013). Furthermore, they can have detrimental effects on non-target arthropods and other animals (Ekström and Ekbom, 2011). Pesticides are known to have effects on the physiology and behaviour of potentially beneficial arthropods (Desneux et al., 2007). They have negative effects on arthropod orientation, fecundity and longevity (Desneux et al., 2007) to the extent of being lethal (Tillman and Mulrooney, 2000). Pesticide use can lead to reduced predator-prey ratios, thereby decreasing natural pest control efficiency and increasing pests in the long term (KRAUSS ET AL., 2011). To maintain high crop yields while at the same time counteracting the species and population declines, new and sustainable ways of crop production with high agricultural outputs and minimal impact on the environment are needed (PRETTY, 2008).

I.4 Ecological intensification and agri-environment schemes

Ecological intensification aims to enhance agricultural outputs by implementing alternative and sustainable management practices that support ecosystem service providing organisms (BOMMARCO ET AL., 2013), thereby decreasing the necessity of anthropogenic inputs such as fertilizer and pesticides (DORÉ ET AL., 2011). Ecological intensification is an alternative to conventional intensification and aims to close the yield gap between the potential and the actual yield, its measures are ecologically beneficial and may help to restore the biodiversity in the agricultural landscape (BOMMARCO ET AL., 2013). Ecological intensification includes on-field measures by changing management procedures to biodiversity friendly ones, such as conservation tillage, integrated pest management or the expansion of organic farming, as well as off-field measures by enhancing or preserving semi-natural habitats, such as the restoration of hedgerows (BOMMARCO ET AL., 2013; GARIBALDI ET AL., 2014; ÖSTMAN ET AL., 2001; RUSCH ET AL., 2010). To aid realizing ecological intensification and restore biodiversity in the agricultural landscape, agri-environment schemes are implemented by the EU (BATÁRY ET AL., 2015).

Agri-environment schemes (AES) are meant to compensate farmers for income losses derived from using environmentally friendly management practices

(Hodge et al., 2015). They aim to enhance the diversity of agro-ecosystem types and decrease the negative impact agricultural food production has on the environment (Batáry et al., 2015). First implemented to protect natural habitats, their main application soon became the mitigation and prevention of biodiversity losses in agricultural landscapes (Batáry et al., 2015). Nowadays, their focus shifted towards the improvement of ecosystem service delivery, mainly pollination and natural pest control (Ekroos et al., 2014). AES are widely implemented, but their actual contribution to ecological intensification can be variable. Many AES schemes seem to lack positive effects on biodiversity (Kleijn and Sutherland, 2003).

Their effectiveness is depending on their objective, with successful schemes often focusing on the conservation of specific rare species (Ekroos et al., 2014; Kleijn et al., 2006). A clear distinction between biodiversity conservation and the promotion of ecosystem services is often missing but would be necessary to optimize AES measures (Scheper et al. 2013). Non-targeted schemes that generally aim to enhance biodiversity at best benefit common species or at worst have no impact at all (Kleijn and Sutherland, 2003). Furthermore, off-field measures targeting areas out of production such as hedgerow restoration seem more effective at enhancing biodiversity than on-field measures on arable fields or grasslands (Batáry et al., 2015). Hedgerow restoration or an increase in the amount of floral resources in agricultural landscapes can help to establish stable populations of beneficial insects instead of just transiently attracting or redistributing individuals (M'Gonigle et al., 2015; Wood et al., 2015).

Another important factor is the landscape surrounding the AES focus fields (Kleijn et al., 2011). There are several hypotheses concerning AES effectiveness: the hypothesis on the relationship between effectiveness and landscape structure, on effectiveness and land-use intensity and on effectiveness and ecological contrast (BATÁRY ET AL., 2011; SCHEPER ET AL., 2013). AES could have most impact in landscapes with intermediate amounts of natural areas, since in simple landscapes the necessary species pool to benefit from AES measures is missing and in complex landscapes the overall biodiversity is already high and does not benefit as much (SCHEPER ET AL., 2013; TSCHARNTKE ET AL., 2012). On the other hand, the biodiversity gain compared to the loss in agricultural landscapes could be highest in complex landscapes (WHITTINGHAM, 2011). However, several meta-analyses showed, that AES are most effective in simple compared to intermediate or complex landscapes (BATÁRY ET AL., 2011; SCHEPER ET AL., 2013). For example, organic farming was shown to have a larger positive impact on biodiversity in landscapes with high amounts of cropland compared to landscapes with small amounts (TUCK ET AL., 2014).

To draw conclusions on the relationship between effectiveness and land-use intensity is difficult, since many studies are conducted in countries with intensive farming regimes such as Germany or the United Kingdom, and are often missing an intensification gradient (DICKS ET AL., 2014). Concerning ecological contrast, it is argued that in intensively farmed landscapes with poor foraging resources and pollination deficits the implementation of AES might improve ecosystem services the most, since they are mainly provided by mobile and generalist species (DEGUINES ET AL., 2014; KLEIJN ET AL., 2015). The way of implementation and a clear goal of either an increase of rare species conservation or ecosystem services is important for the effectiveness of agri-environment schemes.

I.5 Study system and research question

Sown flower fields are implemented as on-field AES measure in many European Countries (HAALAND ET AL., 2011). They increase the biodiversity in the agricultural landscape by providing key resources and habitat for many species that serve as ecosystem service providers (LANDIS ET AL., 2000; SCHEPER ET AL., 2015). They provide rich floral resources and thereby nectar and pollen to different groups of pollinators and natural enemies that also benefit from floral nectar, such as parasitoids (BIANCHI AND WÄCKERS, 2008; GRASS ET AL., 2016). Low disturbance levels make them suitable as nesting, refuge and overwintering habitat (SCHEID ET AL., 2011; SCHELLHORN ET AL., 2008; SCHEPER ET AL., 2015). They provide a beneficial microclimate and alternative prey to natural pest control agents (DYER AND LANDIS, 1997; ÖSTMAN, 2004). Overall, earlier studies showed, that sown flower fields can have positive effects on pollination and natural pest control services (BLAAUW AND ISAACS, 2014; BÜCHI, 2002; FELTHAM ET AL., 2015; TSCHUMI ET AL., 2016).

However, their effectiveness seems to be influenced by many factors, among others flower field characteristics such as size and age. Restoring floral resources in the agricultural landscape was shown to be able to support new and persistent pollinator populations instead of just redistributing pollinators (WOOD ET AL., 2015). Since populations need time to develop, an increase in population size over time can be expected (HÄUSSLER ET AL., 2017). Actually, an increase in wild bee abundance could be observed 3 to 4 years after flower field establishment (BLAAUW AND ISAACS, 2014) and older flower fields often show an increase in biodiversity compared to younger ones (HAALAND ET AL., 2011). Older flower fields harbor higher predator species richness and abundance (FRANK ET AL., 2007). The size may also play an important role.

Small flower fields were shown to be sufficient to enhance flower visits to fruits (FELTHAM ET AL., 2015), but natural enemy density and diversity can increase with the size of the flower field (BLAAUW AND ISAACS, 2012). Larger flower fields provide more resources and habitat, which can be important for certain species (BLAAUW AND ISAACS, 2012). Depending on the examined ecosystem service, the effect of a certain flower field characteristic can be differing. In this study, three types of sown flower fields of different ages and continuity and their effects on ecosystem services in adjacent oilseed rape fields were examined (Fig. I.1, Fig. I.2). The sown flower fields had different sizes, to see if larger or smaller fields are more beneficial. Additionally, the flower fields were chosen along a semi-natural habitat gradient. Furthermore, oilseed rape fields adjacent to conventional crop fields served as negative and oilseed rape fields adjacent to calcareous grasslands as positive control fields. Observations were done and samples taken in the oilseed rape fields, whereas transects were conducted in the sown flower fields and calcareous grasslands. This study design allowed to not only examine effects of age, size and surrounding landscape individually, but combined effects of these three parameters on ecosystem services. Effects on pollination and natural pest control as well as crop yield were examined.

Knowledge gaps exist on how the quality and quantity of green infrastructure such as sown flower fields can influence benefits to crops. This study is part of the European BiodivERsa FACCE-JPI Project ECODEAL (Enhancing biodiversity-based ecosystem services to crops through optimized densities of green infrastructure in agricultural landscapes) which was coordinated from Lund, Sweden and had project partners in Austria, France, the Netherlands and Spain. Ecodeal aimed to gain more insight into how green infrastructure enhances ecosystem services to crops. So far, farmers often decide themselves how to implement flower fields within a certain framework. The goal of this project is to provide recommendations on how sparing land can enhance food production, biodiversity preservation and overall farm economic performance across European agricultural systems (CLOUGH 2017). This study contributes to the understanding of how size, age and the surrounding landscape of sown flower fields implemented as agri-environment scheme influences the ecosystem services pollination, natural pest control and ultimately oilseed rape yield.

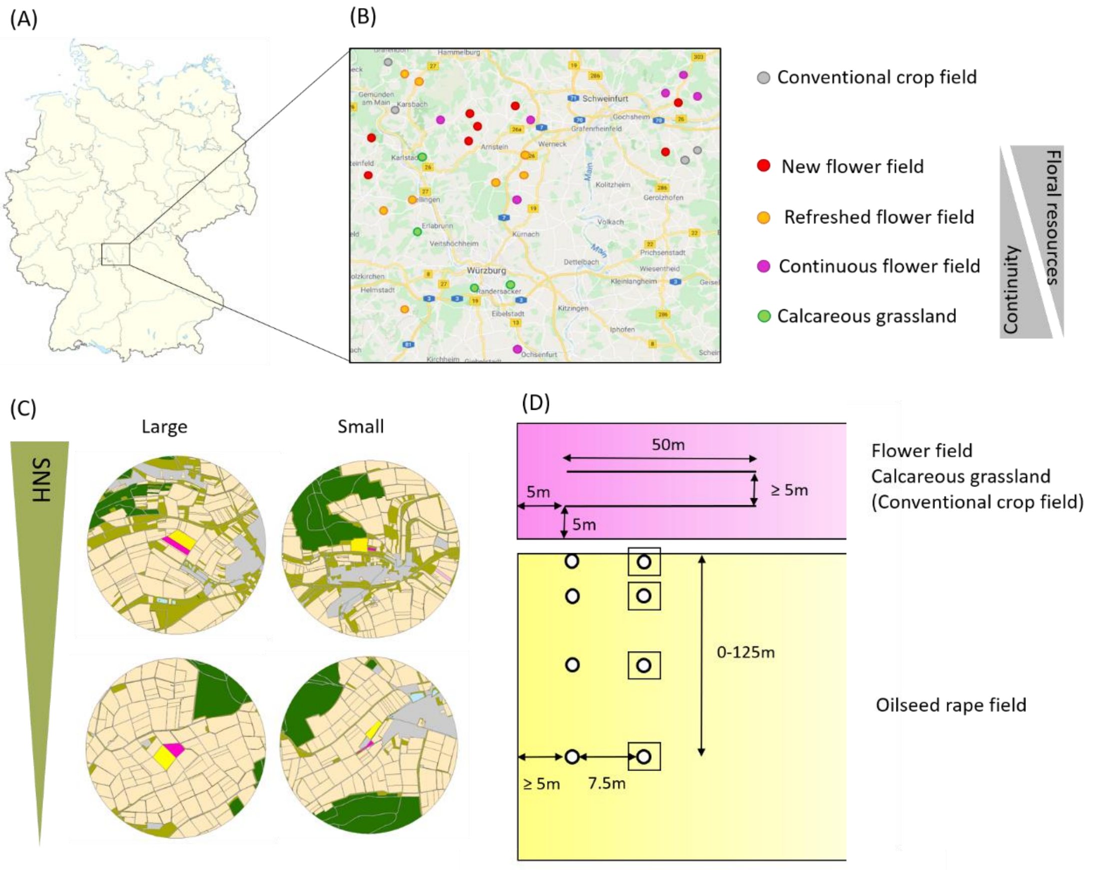


Fig. I.1. Overall study design on landscape and field level. (A) Experiments were conducted in Germany in 2016 in (B) the area of Lower Frankonia around Würzburg. Three different kind of sown flower fields (explained in more detail in the material and methods of chapter II,III and IV) and calcareous grasslands were chosen for the experiment and show opposing gradients of floral resources and continuity. Oilseed rape (OSR) fields adjacent to conventional crop fields were added as controls. (C) Flower fields and adjacent OSR were selected in landscapes along a semi-natural habitat (SNH) gradient (1km radius). Two sizes of flower fields were chosen: Large (>1.5 ha) and small (<1.5ha). (D) Observation and sample points (circles) were located in the OSR fields at various distances. Transects were conducted in the flower fields and calcareous grasslands. Spray windows (25m²) were established around half of the sample points.

Fig. I.2. The three different types of sown flower fields used in this study. (A) Refreshed flower fields adjacent to an oilseed rape field divided by a grassy field margin. (B) New flower field and (C) continuous flower field in spring 2016. Flower field types are explained in more detail in chapter II,III and IV.

Chapter II: Pollination

Size, age and surrounding semi-natural habitats modulate the effectiveness of flower-rich agri-environment schemes to promote pollinator visitation in crop fields.

Animal pollination is of major importance to wild plants and a wide variety of crops, yet agricultural intensification has led to pollinator declines and yield gaps in agroecosystems. Agri-environment schemes (AES) aim to restore biodiversity and ecosystem services by providing suitable habitats and key resources. Sown flower fields are often implemented as AES and are assumed to partly compensate for the lack of semi-natural habitats (SNH). But the combined effects of local management, size and landscape context on the effectiveness of flower fields remain unclear. We studied five pollinator groups (honey bees, bumble bees, other wild bees, hover flies and other flies) in three types of AES flower fields differing in age, size, and local management along a SNH gradient. We use calcareous grasslands as control sites. Further, we examined distance decay functions of flower visitation rates in adjacent oilseed rape (OSR) fields. Young flower fields in the first year after establishment characterised with high flower cover were very attractive for pollinators, however pollinators tended to remain in these fields when they were large (>1.5ha). High

amounts of SNH in the surrounding landscape enhanced the value of small flower fields as starting points for pollinators and their subsequent movement into crops. Distance decay of pollinators was reduced in the presence of high amounts of SNH in the surrounding landscape. Based on our results, we recommend establishing smaller sown flower fields in landscapes with high amounts of SNH and larger flower fields in landscapes with low amounts of SNH. Importantly, sown flower fields were no substitute for perennial semi-natural habitats, underpinning the importance of SNH conservation in agricultural landscapes to maintain pollinators visiting flowers in crops.

II.1 Introduction

Pollination provided by wild and managed animals is essential for the successful reproduction of a wide variety of wild plants (Biesmeijer et al., 2006; Ollerton et al., 2011) and is important to numerous world crops (Klein et al., 2007). Pollination by unmanaged insects in particular is beneficial to various crops (Garibaldi et al., 2013). In recent years, a severe decline in both wild and managed pollinators has been observed in many parts of the world (Potts et al., 2010), while the global production of pollinator dependent crops is further increasing (Aizen et al., 2008), which leads to pollination deficits and yield gaps in intensively managed agricultural landscapes (Deguines et al., 2014).

Ecological intensification has been proposed to conserve and restore biodiversity in agricultural landscapes while maintaining high outputs from crops. Ecological intensification is based on the enhancement of ecosystem service-providing organisms via implementation of biodiversity-friendly agricultural management practices (Bommarco et al., 2013). To realize this, agri-environment schemes (AES) are implemented by the European Union (Batáry et al., 2015). AES can include on-field measures, like the reduction of agro-chemicals and expansion of organic farming as well as off-field measures that improve the quality and/or quantity of semi-natural habitats (SNH) like hedgerows and field boundaries (Bommarco et al., 2013; Garibaldi et al., 2014). Restoring hedgerows and floral resources at the farm level can not only redistribute pollinators within the landscape or generate a temporary local increase of pollinators, but also lead to new stable and persistent pollinator populations (M'Gonigle et al., 2015; Wood et al., 2015).

A major contributor to pollinator decline is presumably the decline of suitable host plants (SCHEPER ET AL., 2014). Hence, adding floral resources into landscapes with low floral resources and thereby creating an ecological contrast might be most effective to enhance pollination (SCHEPER ET AL., 2015). Perennial sown flower fields are a common on-field measure to enhance biodiversity in the agricultural landscape by increasing floral resources and providing nesting habitats for many species (SCHEPER ET AL., 2015) and have been implemented in several European countries, among others Germany, Austria and the United Kingdom (HAALAND ET AL., 2011). Sown wildflower fields attract different groups of pollinators (GRASS ET AL., 2016) and can increase pollinators in the wider agricultural landscape (JÖNSSON ET AL., 2015). Their impact however largely depends on the way they are implemented and how the effectiveness is influenced by the surrounding landscape (CARVELL ET AL., 2011; SCHEPER ET AL., 2013). It is argued, that AES have most impact in intermediate landscapes: in cleared landscapes, the insect pool to colonize the AES is missing, while in complex landscapes the AES do not improve the already high biodiversity (SCHEPER ET AL., 2013; TSCHARNTKE ET AL., 2012). To promote ecosystem services mainly provided by mobile generalist species, it might be most beneficial to implement AES in intensively farmed landscapes with poor foraging resources and largest pollination deficits (DEGUINES ET AL., 2014; KLEIJN ET AL., 2015). The amount of SNH in a specified area is a good measure for landscape complexity (CHAPLIN-KRAMER ET AL., 2011), and its impact can be assessed by placing study sites in areas with varying amount of SNH, thereby creating a SNH gradient (STEFFAN-DEWENTER ET AL., 2002).

Sown flower fields can undergo severe changes in the years after establishment, especially considering succession of the sown flowering plant species

(Carvell et al., 2007). Wildflower plantings in Michigan, USA increased wild bee abundance 3 to 4 years after their establishment compared to the first year, due to an increase of floral resources and nesting sites (Blaauw and Isaacs, 2014). Pollinators need time to build persistent populations and a growth in population size over time is expected as a result of flower strip establishment (Häussler et al., 2017). Seed mixtures including forb flowers could consistently enhance floral resources and pollinator abundances in intensively used grasslands over a period of four years (Woodcock et al., 2014). Small patches (0.25ha) of high quality forage are sufficient to attract and promote bumble bees (Carvell et al., 2011). Small flower patches of 0.03ha also seem sufficient to increase the number of flower visits in nearby strawberry crops (Feltham et al., 2015). However, precise instructions regarding flower field establishment are often missing in AES guidelines and practitioners themselves choose size and location within a certain framework. Significant knowledge gaps exist concerning the interplay of age, size, and the surrounding landscape of sown flower fields in terms of improving ecosystem services. We aim to disentangle these interactions to see if it would be beneficial to provide more precise specifications for flower field establishment.

For ecosystem service delivery, the amount and distance of the movement of beneficial insects from the source habitat into arable crops is crucial (Woodcock et al., 2016). Generally, the distance decay of pollinator richness and flower visitation rate from SNH into fields is very pronounced in tropical, but slightly less in temperate regions (Ricketts et al., 2008). Positive effects on pollinator abundances of restored hedgerows were only observable up to 10m into crop fields (Morandin and Kremen, 2013). Wildflower plantings can enhance pollination service to close-by blueberries

(Blaauw and Isaacs, 2014) and pollinator visits to strawberries (Feltham et al., 2015). On longer distances, high-quality SNH was shown to promote pollinator spillover more effectively than small flower-rich patches (Kohler et al., 2008).

In our study, we observed flower visits of pollinators in oilseed rape (OSR) fields next to differently composed sown flower fields distributed along a semi-natural habitat (SNH) gradient. We examined how age, which was associated with the abundance of floral resources, flower field size, and availability of SNH in landscapes surrounding the fields affected pollinator abundances. We particularly asked if the composition of flower fields alters the abundance of pollinators in OSR fields and thereby influences flower visitation. We test the following predictions:

(1) Old age, large size and high amount of surrounding SNH interactively increase pollinator abundance in sown flower fields.

(2) These factors and their interactions also increase flower visitation in adjacent OSR crops.

(3) The distance decay of flower visits within oilseed rape fields can be reduced by old and large-sized sown flower fields as well as by increasing amounts of SNH in the surrounding landscape.

II.2 Material & methods

II.2.1 Study region and sites

This study was conducted in 2016 in the vicinity of Würzburg, Germany. In the study area 27 field pairs were chosen, consisting of a conventionally managed oilseed rape fields (OSR) and adjacent either a sown flower field (23 fields) or a calcareous grassland (4 fields). Oilseed rape (*Brassica napus* L.) is the most important oilseed crop in Europe and gained importance over the last decades driven mainly by the expansion of biodiesel (CARRÉ AND POUZET, 2014; WITTKOP ET AL., 2009). It is partly self-fertile and wind pollinated, but benefits from additional insect pollination, especially by wild bees, with increased seed set, weight and quality in terms of oil and chlorophyll content (BOMMARCO ET AL., 2012; MORANDIN AND WINSTON, 2005), depending on the variety (HUDEWENZ ET AL., 2014). Winter OSR attracts honey bees and bumble bees, but also hover flies and other wild bees (STANLEY ET AL., 2013), which are valuable pollinators of OSR (JAUKER ET AL., 2012).

We chose three types of flower fields for our study, that at the time of the study were or have been part of an AES called Kulturlandschaftsprogramm and followed state regulations concerning seed mixtures and management practices (Table II.1; Table II.S1): (1) flower fields that were newly established the previous year, ploughed and sown with a flower mixture and then left without further management ('new flower fields'; 8 field pairs), (2) flower fields that were established 5 years prior to this study and left without further management, they were ploughed and re-sown the previous year and left without further management ('refreshed flower fields'; 8 field pairs), and (3) flower fields that were established 5 years prior to this study, left without management until the previous year and since then are mown, with shredding and distribution of the plant material, yearly ('continuous flower fields'; 7 field pairs; Table II.1). The different flower field types therefore differ in their age, continuity and dependent on that in flower cover (Fig. II.1; Table II.1). Four calcareous grasslands adjacent to OSR fields were chosen as control sites for comparison with the AES sown flower fields. Calcareous grasslands belong to the most species rich habitats in central Europe. They often represent the last remains of semi-natural flower-rich grasslands in the agricultural landscape and contain numerous rare plant and insect species (STEFFAN-DEWENTER AND TSCHARNTKE, 2002). This study design provides the possibility to examine the effectiveness of differently aged flower fields in the same year, thereby avoiding inter-annual fluctuations in bee abundances altering the results (WILLIAMS ET AL., 2001).

Field size of the sown flower fields varied between 0.29ha and 3ha (Mean ± SE. New flower fields: 1.32 ± 0.41ha, refreshed flower fields: 1.14 ± 0.32 ha, continuous flower fields: 1.27 ± 0.26ha, 3ha being the maximum size funded by government). Field size of the calcareous grasslands was 4.88 ± 3.40ha (Mean ± SE). Half of the fields per type were larger than 1.5ha and half of them smaller, therefore being assigned to two categories (small/large). Flower fields and OSR fields were either directly adjacent or separated by grassy field margins and small farm roads.

Table II.1. Parameters of the different flower field types adjacent to oilseed rape. Size, SNH, flower cover: Mean ± SE; Range. SNH: semi-natural habitat.

	New flower field	Refreshed flower field	Continuous flower field	Calcareous grassland
Age (years)	1	≥6	≥6	unknown
Year with ploughing and sowing	2015	2009/2010 2015	2009/2010	None
Management	None	None	Yearly mulching since 2015	None/seasonal grazing
Size (ha)	1.32 ± 0.41 0.29 - 3	1.14 ± 0.32 0.19 - 2.07	1.27 ± 0.26 0.47 - 2.43	4.875 ± 3.40 0.41 - 14.99
SNH (%)	10.21 ± 1.94 3.63 - 18.73	10.88 ± 2.46 3.64 - 25.04	8.25 ± 1.09 4.04 - 12.41	23.77 ± 3.12 16.99 - 31.62
Flower cover (%) in May/June	17.88 ± 6.87 1.50 - 56.34	6.45 ± 2.90 0.28 - 23.74	1.35 ± 0.33 0.36 - 2.98	0.47 ± 0.26 0.06 - 1.20
Replicates	8	8	7	4

The four fields of a specific type size combination were each located in landscapes with differing amounts of semi-natural habitat (SNH) (3.6-31.6%) in 1km radius around the flower field. The minimum distance between the flower fields was 2.1km to avoid overlapping of landscape areas. SNH provided nesting and foraging sites for pollinators and included 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. The amount of SNH in the landscapes did not correlate with the amount of OSR. SNH was assessed using satellite images and land-cover maps.

Land-cover maps and data on field identity were provided by the Bavarian State Ministry of Nutrition, Agriculture and Forestry and processed using ArcMap (ESRI v. 10.3, Redlands, CA, USA).

II.2.2 Sampling methods

In the flower fields, transect walks were conducted on two parallel transects of 50m length and 2m width (Fig. II.1). Pollinators were caught along the transect by sweep netting for 10min, which adds up to 20 minutes catching time per sampling round. One transect was located at the edge of the flower field (5m to field edge), whereas the other was located in the middle of the flower field or 25m into the field, depending on field size. Pollinator abundance of five pollinator groups (honey bees, bumble bees, other wild bees, hover flies and other flies) was counted. Species identification was acquired for honey bees, bumble bees, other wild bees and hover flies (Table II.S4-II.S7). General differences in their interaction with OSR flowers exist between these five pollinator groups, regarding the time spent on flowers and the probability to transport and transfer pollen to stigmas (WOODCOCK ET AL., 2013). We therefore consider the classification into these broad groups meaningful and sufficient for the aim of our study. Flower cover was assessed in May/June 2016 on four 4m^2 quadrats at intervals of 25m located along the two transects on small fields, and on six 4m^2 quadrats on big fields to account for the difference in field size. The total number of flower units was multiplied with the respective mean surface area for every flowering plant species. The resulting flower surface area was divided by the quadrat area to get the flower cover. The flower cover for each field was averaged over all quadrats.

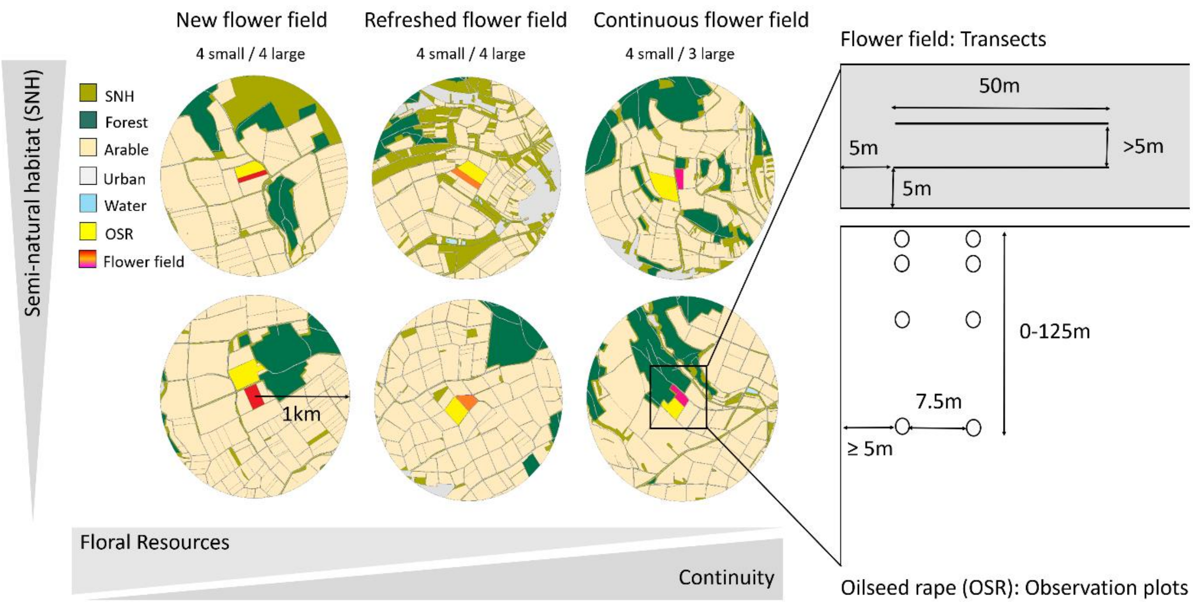


Fig. II.1. Experimental design on landscape and field level. Landscapes differ in the amount of semi-natural habitat (SNH) in 1km radius. Different types of flower fields show opposing gradients of floral resources and continuity (Table II.1). Observation plots and transects were located in the fields at various distances. Red: New flower field, newly established the previous year, ploughed and sown with a flower mixture and then left without further management. Orange: Refreshed flower field, established 5 years prior to this study and left without further management, ploughed and re-sown the previous year and left without further management. Pink: Continuous flower field, established 5 years prior to this study, left without management until the previous year and since mulched yearly. Small: flower fields <1.5ha; Large: flower fields >1.5ha.

Pollinators were observed in the OSR fields for 5 minutes on eight 4m² observation plots at varying distances to the field edge of the flower field (0-124.7m) located along two parallel transects (Fig. II.1). This adds up to a total of 40 minutes observation time per sampling round and field. Pollinator abundance and flower visitation of the five pollinator groups were recorded.

For flower visitation, we counted every flower visit of every pollinator of the five pollinator groups that involved contact to the OSR flower stigma within the observation area and time. Four sets with four within field distance classes were applied randomly to each flower field type and size combination with slight aberrations due to in-field tractor lane locations: (1) 0m, 8m, 30m, 80m; (2) 0m, 10m, 40m, 100m; (3) 0m, 15m, 55m, 105m; (4) 0m, 20m, 65m, 120m. Earlier studies showed, that the distance of 120m is reasonable to observe distance decay in bees and hover flies (KOHLER ET AL., 2008; MORANDIN AND KREMEN, 2013). These four sets were applied to the design to have evenly distributed data points over the whole tested distance. The observation plots were at least 5m away from other field edges in very narrow fields, but if possible located 25m inside the OSR fields. The distance between the parallel plots was 7.5m, with one transect being inside pesticide spray windows of 25m². Spray windows had no effects on pollinator abundance and flower visits. Abundance of pollinators visiting flowers and total flower visits were noted. Since we did not catch pollinators during observation time, we afterwards walked slowly along the observation plots back to the field edge for ten minutes per transect and caught all pollinators visiting flowers by sweep netting, to make a rough assessment of pollinator species present in the OSR field (Table II.S4-II.S7). Two rounds of transect walks in the flower fields and subsequent observations and catches in the OSR were conducted during the short period of OSR flowering in late April/May 2016 under standardized weather conditions of at least 15°C, no rain, low or no cloud cover and low wind speeds between 9am and 6pm.

II.2.3 Statistical data analysis

Data analyses for pollinator abundances in the flower fields and flower visits in the OSR fields 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). Models were performed for overall abundances in the flower fields and overall flower visitation in the OSR fields. We chose flower visitation as response variable in the OSR field models, because it is a more accurate measurement of pollination services than pollinator abundance (VÁZQUEZ ET AL., 2005). We tested the following fixed effects and all possible two-way interactions on overall pollinator abundance in the flower fields and on flower visits in OSR fields according to the study design: (1) *Type:* different types of flower fields (new flower field, refreshed flower field, continuous flower field, calcareous grassland, reflecting the age/continuity of the fields), (2) *Size:* size category of flower fields (small <1.5ha, large>1.5ha), (3) *SNH:* amount of semi-natural habitat in 1km radius around the flower fields, and additionally in the OSR models (4) *Distance:* distance to the flower field edge within OSR fields. The continuous fixed effects *Distance* and *SNH* were standardized using the function 'rescale' from the package 'arm' to facilitate model convergence (GELMAN, 2008). We also tested if the size of the OSR fields and the amount of OSR in the surrounding landscape affected flower visitation in the OSR fields, but we did not find any significant effect and therefore excluded it from our analysis. To account for pseudoreplication, the crossed random effects '*Field identity'* and *'Date'* were included in the two models. For the overall flower visitation in OSR fields model, the parallel transects containing the observation points were summed together. A GLMM with poisson distribution and log link function was used for the flower field model and a GLMM with negative binomial distribution and log link function was used in the OSR field model, to account for overdispersion. Residual plots were used to check model assumptions. To assess fixed effect importance, we performed a hybrid model fitting approach on the full model (all fixed effects and tested interactions) using the Akaike Information Criterion (AIC) to select the best model (with lowest AIC) in combination with an analysis of variance (ANOVA) of the best model to calculate p-values. These were obtained by Wald chisquare tests (Type II sums of squares) using the function ‘Anova’ from the package ‘car’ (FOX AND WEISBERG, 2018). Subsequent post-hoc analyses with false discovery rate correction (FDR) (BENJAMINI AND HOCHBERG, 1995) were conducted by calculating estimated marginal means by using the package ‘emmeans’ (LENTH, 2018).

II.3 Results

II.3.1 Pollinator abundance in sown flower fields

During the period of oilseed rape flowering, 773 individuals of the five pollinator groups were observed on the different flower fields. Of these, 34% were honey bees (263 individuals), 22.1% bumble bees (171 individuals), 15.3% other wild bees (118 individuals), 13.6% hover flies (105 individuals) and 15% other flies (116 individuals). There were no effects of any of the tested two-way interactions or semi natural habitat (SNH) on overall pollinator abundance and only a marginal effect of size (χ^2 =3.532, χ^2 df=1, p-value=0.060). However, there was a clear effect of the type of flower field on pollinator abundance (χ^2=16.402, χ^2 df=3, p-value <0.001) and a post-hoc analysis showed that new flower fields (13.0 ± 3.5) and refreshed flower fields (7.1 ± 1.3) had significantly higher abundances of pollinators than continuous flower fields (2.5 ± 0.4) and calcareous grassland (3.6 ± 3.5; mean ± SE; Fig. II.2; Table II.S2).

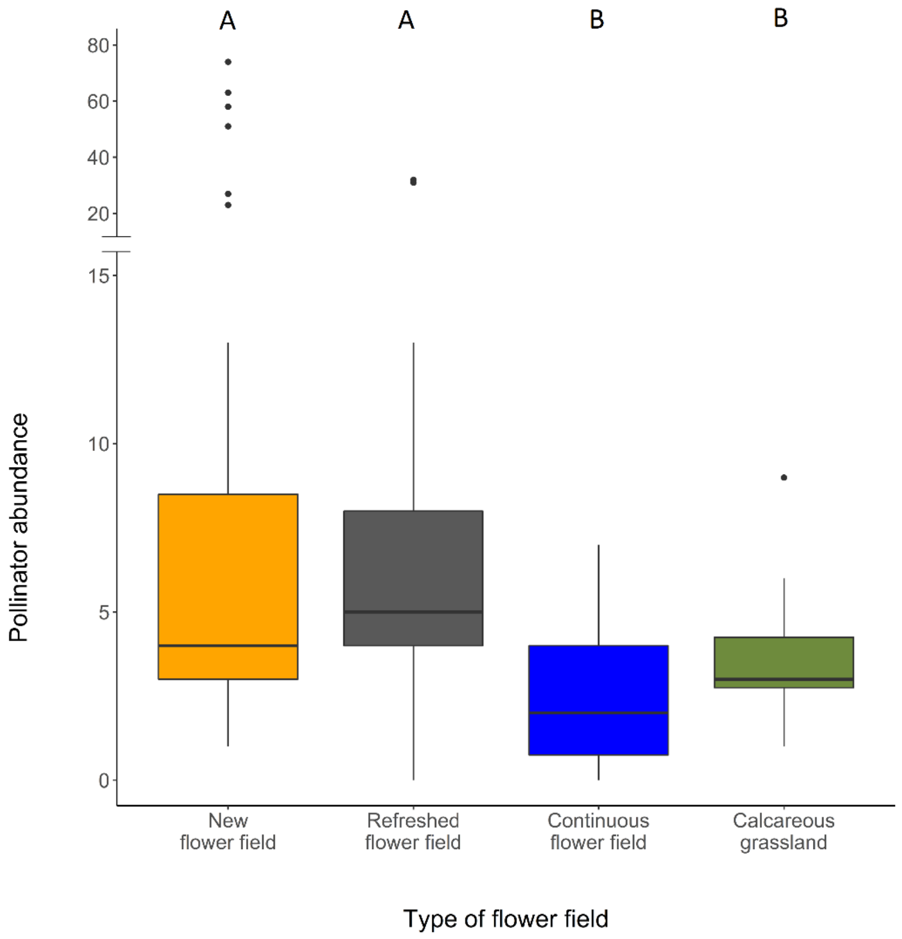


Fig. II.2. Overall pollinator abundance in different types of flower fields. Boxplots show median and the 1st and 3rd quartiles, circles show outliers. Whiskers represent 1.5 interquartile range. Letters display significant differences in post-hoc analysis (*P* < 0.05; Table II.S2). The y-axis contains a gap and adjusted scaling. 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 years prior to this study and left without further management, ploughed and re-sown the previous year and left without further management. Continuous flower field: established 5 years prior to this study, left without management until the previous year and since mulched yearly.

II.3.2 Flower visits in in oilseed rape (OSR) fields

A total of 5541 flower visits were observed on OSR flowers in the two observation rounds during flowering. In detail, 63.1% (3497) of flower visits were conducted by honey bees, 6.7% (372) by bumble bees, 8% (441) by other wild bees, 1.4% (77) by hover flies and 20.8% (1154) by other flies. Overall flower visitation was influenced by the type of flower field, their size, the amount of SNH in the surrounding landscapes and their interactions (Table II.2).

Table II.2. Wald chi-square tests of GLMMs for overall flower visits in oilseed rape fields next to the four different types of flower fields. Significance levels: **p* < 0.5, ***p* < 0.1, ****p* < 0.01.

Model Fixed effects		χ^2	χ^2 df	p-value	
Overall flower visits					
	Type	13.689	3	0.003	**
	Size	0.337	1	0.562	
	Distance	36.402	1	<0.001	***
	SNH	2.574	1	0.109	
	Type * Size	11.103	3	0.011	*
	Size * SNH	6.553	1	0.010	*
	Distance * SNH	4.903	1	0.027	*

A post-hoc analysis on the type-size interaction showed that there were significantly less visits in OSR fields next to large new flower fields, than next to refreshed flower fields, continuous flower fields and large calcareous grasslands (Fig. II.3; Table II.S3). Additionally, next to small flower fields, flower visitation in OSR increased with increasing amount of SNH in the landscape, while flower visitation was not affected by SNH next to large flower fields (Fig. II.4). Distance decay of overall flower visits in the OSR fields over the maximum tested distance (124,7m) was less pronounced in landscapes with high amounts of SNH (25% SNH) within 1km radius from the OSR field, than in landscapes with low to intermediate amounts of SNH (4-12.5% SNH), where pollinator visits decreased stronger with growing distance into the OSR field (Fig. II.5).

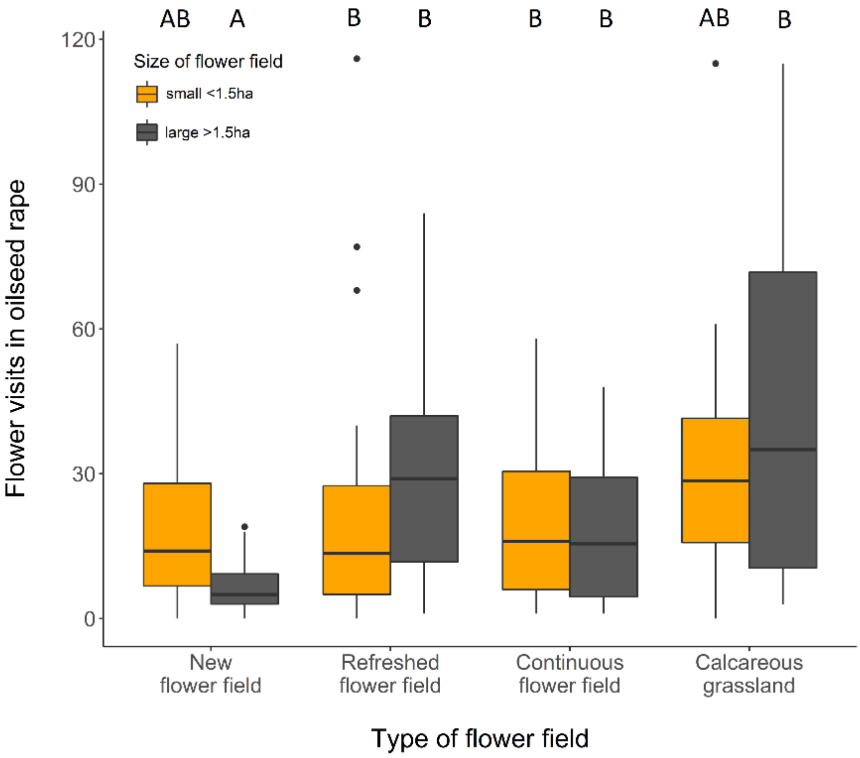


Fig. II.3. Overall flower visits in oilseed rape (OSR) adjacent to different types of flower fields in two size categories. Boxplots show median and the 1st and 3rd quartiles, circles show outliers. Whiskers represent 1.5 interquartile range. Letters display significant differences in post-hoc analysis (*P* < 0.05; Table II.S3). 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 years prior to this study and left without further management, ploughed and re-sown the previous year and left without further management. Continuous flower field: established 5 years prior to this study, left without management until the previous year and since mulched yearly.

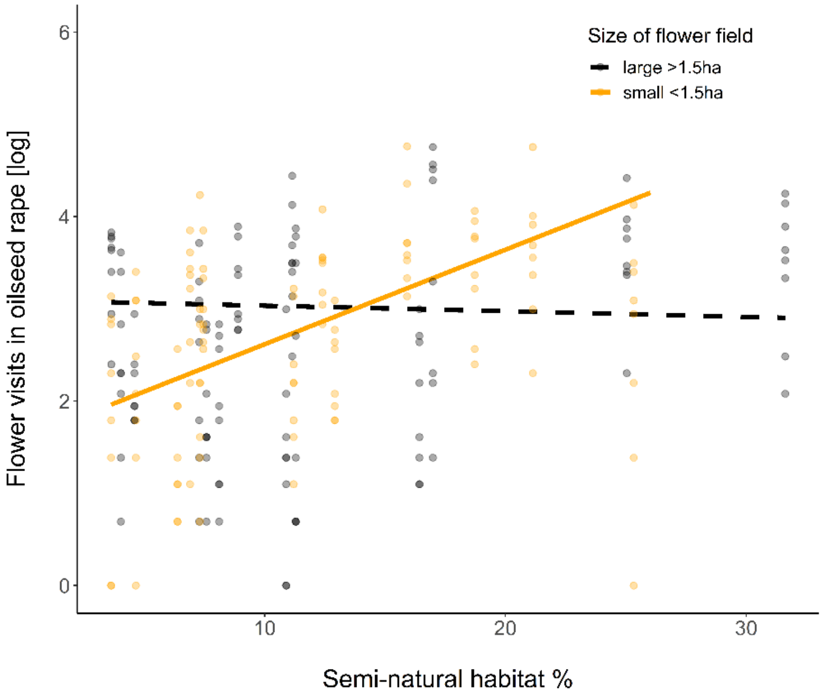


Fig. II.4. Overall flower visits in oilseed rape (OSR) fields next to differently sized flower fields in landscapes along a semi-natural habitat (SNH) gradient in 1km radius. Fitted lines show model predictions for the two different sizes of flower fields (small <1.5ha, large >1.5ha).

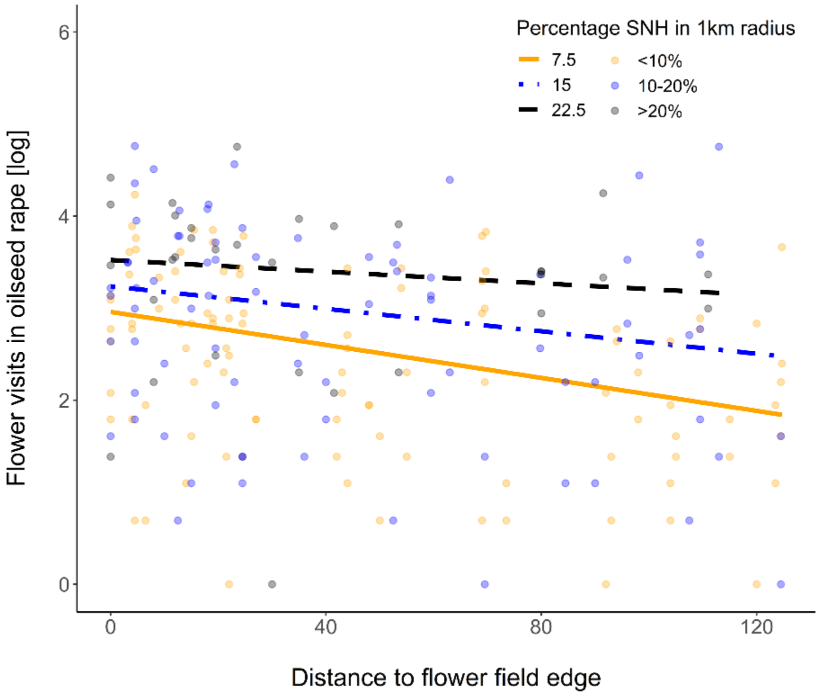


Fig. II.5. Distance decay of overall flower visits in oilseed rape (OSR) fields with different amounts of semi-natural habitat (SNH) in 1km radius. Fitted lines show model predictions for the different amounts of SNH (7.5%, 15%, 22.5%).

II.4 Discussion

Landscape and size dependent modulation of flower field effectiveness to promote pollination services to crops emphasises the need for more targeted implementation and management recommendations in this regard.

II.4.1 Pollinator abundance in sown flower fields

Pollinator abundance in the sown flower fields and calcareous grasslands strongly depended on the type, but only marginally on its size and not on the amount of semi-natural habitats (SNH) in the surrounding landscape. New flower fields and refreshed flower fields had higher abundances of pollinators than continuous flower fields and calcareous grasslands during the period of oilseed rape (OSR) flowering. New flower fields and refreshed flower fields offered high numbers of floral resources in spring (Table II.1), making them very attractive to pollen and nectar collecting insects (KOHLER ET AL., 2008). In contrast, the amount of flowering plants in early spring was low in continuous flower fields and calcareous grasslands (Table II.1), making them less attractive to pollinators compared to OSR, a mass flowering crop offering rich pollen and nectar resources. Mass-flowering crops like OSR can temporarily dilute pollinator densities in the agricultural landscape, thereby leading to a decrease of bumble bees in nearby SNH (HOLZSCHUH ET AL., 2016), which can ultimately lead to a pollination deficit in wild plants (HOLZSCHUH ET AL., 2011). Wild plants depending on insect pollination are susceptible to pollinator declines, which will directly reduce their reproductive success (CLOUGH ET AL., 2014).

Continuous flower fields are extensively managed and relatively unperturbed and might therefore be suitable for nesting sites and hibernation of insects. This continuity led to similar carabid beetle assemblages in continuous flower fields and calcareous grasslands (Boetzl et al., 2018). Calcareous grasslands are among the most species-rich areas in Europe, maintaining stable pollinator populations in the agricultural landscape (Steffan-Dewenter and Tscharntke, 2002). Additionally, beekeepers often place their hives next to semi-natural areas like calcareous grasslands (Steffan-Dewenter et al., 2002). Floral resources in calcareous grasslands are present also after OSR flowering and gain importance as alternative foraging resources throughout the year. These high quality habitats therefore serve as source habitats for low quality ephemeral habitats such as crop fields, which may lead to underestimating their value as foraging habitats for pollinators especially during mass flowering of crops (Kleijn et al., 2011). Differences in pollinator abundance in flower fields demonstrate differences in the value of the different flower field types as pollen and nectar sources, but provide limited insight into the potential variation in the quality as nesting sites which might be higher for continuous, though flower-poor flower field types like continuous flower fields and calcareous grasslands.

II.4.2 Flower visits in oilseed rape fields

While new flower fields had high numbers of pollinators in the flower field itself, flower visits in the OSR fields adjacent to large new flower fields were low. Two mechanisms could be responsible for this phenomenon: (1) temporal changes in foraging patterns due to the high flower cover of new flower fields, which makes them very attractive and prevent pollinators to venture into the OSR fields and (2) pollinator populations on the new flower field itself did not have time to grow yet. Most likely, a mixture of both is responsible for the observed patterns. As stated above, new flower fields feature high flower cover already in spring. The 'Circe Principle' proposes, that habitats could be so attractive, for example by offering rich floral resources, that they tempt individuals to linger and not distribute as they would without them (LANDER ET AL., 2011). Large new flower fields apparently kept pollinators from distributing into the surrounding landscape and acted as pollinator concentrators (MORANDIN AND KREMEN, 2013). Nonetheless, the capability of flower fields to increase pollinator visits in adjacent crop fields depends on their constancy and continuity as well as on the nesting opportunities they provide and is likely to improve with age (MORANDIN AND KREMEN, 2013). Young and newly established flower fields were shown to have a negative effect on pollinator abundance and richness in the direct farmland vicinity around fields (KOHLER ET AL., 2008). Population growth is a process that takes time, therefore delays in population restoration are possible after habitat restoration (ILES ET AL., 2018). However, a strong ramp-up in effectiveness of flower fields has been shown over the years to supply ecosystem services to surrounding crop fields (BLAAUW AND ISAACS, 2014). This is in accordance with our findings, because the OSR next to the refreshed flower fields had higher numbers of flower visits than the OSR next to new flower fields. Importantly, the negative effect of the new flower fields on flower visits in the OSR depended on the size of the flower field. Only OSR fields next to large new flower fields had significantly lower amounts of flower visits, while this effect was not visible next to small new flower fields. Our results indicate that below a certain size new flower fields do not decrease pollinator abundances in adjacent crop fields. However, Kohler et al. (2008) found negative effects on bee abundance already in fields next to flower patches of only 0.01ha size, suggesting that these effects depend on multiple factors of flower field composition, age, and regional landscape context.

Size also mattered in interaction with the landscape structure surrounding the fields. In OSR fields next to small flower fields, the amount of flower visits increased with the amount of SNH. In contrast, in OSR next to large flower fields, the flower visits were not affected by increasing SNH. SNH generally increases the abundance of pollinators in the landscape (ÖCKINGER AND SMITH, 2007). Apparently, if large flower fields were available, OSR did not benefit from the higher abundance of pollinators in the SNH rich landscape. Instead, pollinators might have preferred to forage on the floral resources offered by the flower field. If flower fields are small, they might not offer enough resources to exhibit this concentration effect and OSR receives more flower visits. Patch sizes ranging from 0.06ha to 1.01ha were sufficient to increase pollination to blueberries (BLAAUW AND ISAACS, 2014) and even smaller patches of 0.03 ha were able to increase pollination to nearby strawberries (FELTHAM ET AL., 2015). In general, small patches of suitable habitat can promote diverse pollinator communities (ALBRECHT ET AL., 2007), while large sown flower fields might promote competition for pollinators in the agricultural landscape. At least if the flower field is newly established or in landscapes with high amounts of SNH. Nonetheless, large flower fields are to be preferred in landscapes with low amounts of SNH, where they can partly supplement for the missing SNH and increase overall flower visits in OSR compared to small fields.

However, even large flower fields did not influence distance decay of pollinator flower visits in OSR as a less steep distance decay was only observed when the amount of SNH in the landscape was high. As stated before, high amounts of SNH increase wild pollinator abundance in the agricultural landscape (ÖCKINGER AND SMITH, 2007). Therefore, in landscapes with high amounts of SNH pollinators can find forage and nesting sites in many parts of the landscape and venture into vast crop fields from all sides. In comparison, in simple landscapes with low amounts of SNH, the importance of flower fields as starting points for pollinator spillover into OSR fields might be more pronounced, hereby explaining a stronger flower visit distance decay from the flower fields into the crop fields. This result shows, that flower fields can only locally enhance pollination and highlights the importance of restoring and conserving semi-natural habitats in agricultural landscapes to provide widespread pollinator visits to crops.

II.4.3 Management recommendations

Agri-environment schemes can help to create starting points for pollinators to spillover into adjacent crop fields in agricultural landscapes (ALBRECHT ET AL., 2007), but their effectiveness depends on the way they are implemented. Based on our results for sown flower fields, we recommend a mixture of continuous and refreshed flower fields, which provide habitats offering rich floral resources as well as undisturbed areas suitable for nesting and hibernation. We would advise to establish smaller sown flower fields in landscapes with high amounts of SNH and larger flower fields in landscapes with low amounts of SNH. Further, our results indicate that in landscapes with low amounts of perennial SNH, flower fields can be important starting points for pollinator spillover into crops. Sown flower fields do not only support crop pollination, already newly established flower fields also contribute to biological pest control (BOETZL ET AL., 2018). Ideally, the succession of sown flower fields could be linked to crop rotation schemes. Young flower fields could be established adjacent to non-flowering crops, for example cereal fields, where they contribute to biological pest control. Flowering crops like OSR or sun flowers instead should preferably be grown adjacent to older, less flower-rich fields with established pollinator populations. However, establishing a few sown flower fields is no alternative to conserving species-rich SNH areas in the agricultural landscape if the goal is to enhance pollinator visits over the whole surface of vast crop fields. We conclude that a targeted spatial management of sown flower fields for crop pollination services, taking into account size, area and spatial arrangement in relation to landscape structure, could be a relevant component of ecological intensification.

II.5 Supplementary material

Table II.S1. Seed mixtures used for the flower fields in the agri-environment scheme Kulturlandschaftsprogramm.

Name	Used for sowing in year	Wild plants		Cultivated plants	
		Percentage	Number of species	Percentage	Number of species
Lively Field – dry / Lebendiger Acker - trocken	2015	38.2	35	61.8	9
Lively Field – fresh / Lebendiger Acker - frisch	2015	37.2	29	62.8	9
Lively Forest – dry / Lebendiger Waldrand – trocken	2015	31.3	23	68.7	10
Lively Forest – fresh / Lebendiger Waldrand - frisch	2015	31.1	21	68.9	10
Habit1 / Lebensraum1	2009/2010	29.9	36	70.1	11
Bee Meadow / Bienenweide	2009/2010	40	31	60	11

Table II.S2. Post-hoc analysis of pollinator abundance on the different types of flower fields (p-values).

p-value	Refreshed flower field	Continuous flower field	Calcareous grassland
New flower field	0.814	**0.003 ****	**0.032 ***
Refreshed flower field		**0.003 ****	**0.024 ***
Continuous flower field			0.599

Table II.S3. Post hoc analysis on flower visits in oilseed rape fields next to different types and sizes of flower fields (p-values).

p-value	New flower field Large	Refreshed flower field Small	Refreshed flower field Large	Continuous flower field Small	Continuous flower field Large	Calcareous grassland Small	Calcareous grassland Large
New flower field Small	0.054	0.776	0.236	0.821	0.776	0.776	0.238
New flower field Large		**0.011** **	**<0.001** ***	**0.032** *	**0.007** **	0.402	**0.007** **
Refreshed flower field Small			0.315	0.938	0.980	0.663	0.315
Refreshed flower field Large				0.315	0.315	0.238	0.776
Continuous flower field Small					0.938	0.744	0.315
Continuous flower field Large						0.661	0.331
Calcareous grassland Small							0.238

Table II.S4. Distribution of the honey bee species *Apis mellifera* among the different types of flower fields, calcareous grasslands and adjacent oilseed rape fields. CG: Calcareous grassland; C: Continuous flower field; N: New flower field; R: Refreshed flower field. L: Large flower field; S: Small flower field.

Field code	Species	Flower field Abundance	Oilseed rape Abundance
CG_L_1	Apis mellifera	7	52
CG_L_2	Apis mellifera	16	53
CG_S_1	Apis mellifera	22	45
CG_S_2	Apis mellifera	27	93
C_L_1	Apis mellifera	15	
C_L_2	Apis mellifera	61	28
C_L_3	Apis mellifera	1	16
C_L_4	Apis mellifera	3	18
C_S_1	Apis mellifera	51	22
C_S_2	Apis mellifera		20
C_S_3	Apis mellifera	3	4
N_L_1	Apis mellifera	11	1
N_L_2	Apis mellifera	10	
N_L_3	Apis mellifera	31	
N_L_4	Apis mellifera	7	7
N_S_1	Apis mellifera	98	74
N_S_2	Apis mellifera	27	19
N_S_3	Apis mellifera	44	40
N_S_4	Apis mellifera	69	16
R_L_1	Apis mellifera	148	69
R_L_2	Apis mellifera	87	84
R_L_3	Apis mellifera	9	1
R_L_4	Apis mellifera	27	25
R_S_1	Apis mellifera	9	104
R_S_2	Apis mellifera	20	56
R_S_3	Apis mellifera	34	5
R_S_4	Apis mellifera	62	18

Table II.S5. Distribution of bumble bee species among the different types of flower fields, calcareous grasslands and oilseed rape fields. CG: Calcareous grassland; C: Continuous flower field; N: New flower field; R: Refreshed flower field. L: Large flower field; S: Small flower field.

Field code	Species	Flower field Abundance	Oilseed rape Abundance
CG_L_1	Bombus lapidarius	3	
	Bombus pascuorum	7	
	Bombus pratorum	1	
	Bombus sylvestris	1	
	Bombus terrestris		1
CG_L_2	Bombus lapidarius	3	5
	Bombus pascuorum	1	
	Bombus sylvarum	2	
	Bombus terrestris	5	2
CG_S_1	Bombus lapidarius	1	
	Bombus pascuorum	6	
	Bombus terrestris	13	2
CG_S_2	Bombus lapidarius	1	
	Bombus pascuorum	1	
	Bombus pratorum	1	
	Bombus terrestris	4	
C_L_1	Bombus hortorum	1	
	Bombus lapidarius	3	
	Bombus pascuorum	3	
	Bombus pratorum	1	
	Bombus terrestris	8	
C_L_2	Bombus lapidarius	30	2
	Bombus sylvarum	2	
	Bombus terrestris	11	3
	Bombus vestalis	1	
C_L_3	Bombus lapidarius	6	
C_L_4	Bombus lapidarius	5	1
	Bombus terrestris	4	1
C_S_1	Bombus lapidarius	1	1
	Bombus terrestris	25	4
C_S_2	Bombus pascuorum	1	
C_S_3	Bombus pascuorum	2	
	Bombus terrestris	1	
N_L_1	Bombus lapidarius	1	
	Bombus pascuorum	1	
	Bombus pratorum	1	
	Bombus sylvarum	1	
	Bombus terrestris	15	2
N_L_2	Bombus lapidarius	3	
	Bombus pascuorum	3	
	Bombus sylvarum	1	
	Bombus terrestris	11	
N_L_3	Bombus lapidarius	11	1
	Bombus pascuorum	2	
	Bombus terrestris	3	
N_L_4	Bombus hortorum	1	
	Bombus lapidarius	10	2
	Bombus pascuorum	3	

	Bombus pratorum	5	
	Bombus terrestris	29	1
N_S_1	Bombus hypnorum	2	
	Bombus lapidarius	8	
	Bombus pascuorum	2	
	Bombus pratorum	3	
	Bombus sylvarum	1	
	Bombus terrestris	15	
N_S_2	Bombus pratorum	1	
	Bombus terrestris	6	
N_S_3	Bombus lapidarius	5	
	Bombus pratorum	7	1
	Bombus terrestris	15	3
N_S_4	Bombus hortorum	7	
	Bombus lapidarius	12	
	Bombus pratorum	15	
	Bombus terrestris	32	1
R_L_1	Bombus lapidarius	6	
	Bombus pascuorum	1	
	Bombus terrestris	6	2
R_L_2	Bombus hortorum	1	
	Bombus lapidarius	15	
	Bombus pascuorum	1	
	Bombus pratorum	7	
	Bombus terrestris	26	
R_L_3	Bombus lapidarius	10	
	Bombus sylvarum	1	
	Bombus terrestris	25	2
R_L_4	Bombus lapidarius	9	
	Bombus pratorum	12	2
	Bombus terrestris	5	7
R_S_1	Bombus hypnorum	1	
	Bombus lapidarius	4	
	Bombus pascuorum	1	
	Bombus terrestris	1	1
R_S_2	Bombus hypnorum	2	
	Bombus lapidarius	2	
	Bombus pascuorum	1	
	Bombus pratorum	5	
	Bombus sylvarum	1	
	Bombus terrestris	22	3
R_S_3	Bombus hortorum	1	
	Bombus lapidarius	1	1
	Bombus pascuorum	1	2
	Bombus terrestris	3	2
R_S_4	Bombus lapidarius	7	1
	Bombus pascuorum	3	
	Bombus pratorum	1	
	Bombus sylvarum	1	
	Bombus terrestris	33	

Table II.S6. Distribution of other wild bee species among the different types of flower fields, calcareous grasslands and oilseed rape fields. CG: Calcareous grassland; C: Continuous flower field; N: New flower field; R: Refreshed flower field. L: Large flower field; S: Small flower field.

Field code	Species	Flower field Abundance	Oilseed rape Abundance
CG_L_1	Andrena fulvicornis	1	
	Andrena subopaca	1	
	Eucera nigrescens	1	
	Halictus tumolorum	2	
	Lasioglossum calceatum	2	
	Lasioglossum fulvicorne	1	
	Lasioglossum leucozonium	4	
	Lasioglossum pauxillum	2	
	Megachile willughbiella	1	
CG_L_2	Andrena cineraria	1	2
	Andrena flavipes		2
	Andrena nitida	1	
	Andrena subopaca	1	
	Anthophora plumipes		1
	Eucera nigrescens		1
	Lasioglossum interruptum	1	
	Osmia bicolor		1
	Unidentified solitary bee		2
CG_S_1	Andrena cineraria		1
	Andrena ovatula wilkella	1	
	Colletes cunicularius		2
	Osmia bicolor	4	
CG_S_2	Andrena flavipes		1
	Andrena nigroaenea	2	
	Colletes cunicularius		1
	Osmia bicolor	1	
C_L_1	Andrena cineraria	1	
	Andrena haemorrha		2
	Eucera nigrescens	1	
C_L_2	Andrena flavipes	6	
	Andrena haemorrha	2	3
	Andrena nitida		1
	Anthophora plumipes		1
	Lasioglossum glabriusculum	1	
	Lasioglossum pauxillum	1	
	Lasioglossum villosulum	1	
	Osmia bicolor	1	
C_L_3	Andrena flavipes	2	
	Andrena haemorrha		2
	Hylaeus annularis	1	

	Lasioglossum pauxillum	3	
C_L_4	Andrena carantonica	1	
	Andrena flavipes	6	1
	Andrena nitida	1	
	Anthophora plumipes	2	
C_S_1	Andrena flavipes		2
	Andrena haemorrha	1	
	Anthophora plumipes	3	
	Lasioglossum pauxillum	1	
C_S_3	Andrena haemorrha		1
N_L_1	Andrena chrysosceles	1	1
	Andrena flavipes	17	
	Andrena haemorrha	2	5
	Halictus symplex	1	
	Lasioglossum xanthopus	1	
N_L_2	Andrena cineraria		1
	Andrena flavipes	7	
	Andrena fulvicornis	1	
	Anthophora plumipes	4	
	Eucera nigrescens	5	
N_L_3	Andrena dorsata	1	
	Andrena flavipes	4	
	Andrena haermorrha		1
N_L_4	Andrena chrysosceles	1	
	Andrena cineraria		1
	Andrena dorsata		1
	Andrena flavipes	4	
	Andrena fulva		1
	Anthophora plumipes	1	
	Lasioglossum calceatum	1	
	Lasioglossum pauxillum	1	
	Lasioglossum punticolle		1
N_S_1	Andrena cineraria	1	
	Andrena flavipes	3	1
	Andrena florivaga		1
	Andrena haemorrha		2
	Andrena ovatula wilkella	3	
	Anthidium oblongatum	2	
	Anthophora plumipes	2	
	Eucera nigrescens	2	
	Lasioglossum interruptum	1	
	Megachile rotundata	1	
N_S_2	Andrena flavipes	14	
	Andrena fulvicornis	1	
	Andrena haemorrha		1
	Andrena proxima	1	
	Halictus tumolorum	1	
	Lasioglossum lativentre	1	

	Sphecodes gibbus	1	
N_S_3	Andrena cineraria		1
	Unindentified solitary bee		1
R_L_1	Andrena flavipes	2	
	Andrena fulvicornis	1	
	Andrena haemorrhoa		4
	Andrena nitida		1
	Anthophora plumipes	1	1
	Halictus scabiosae	2	
	Halictus symplex	1	
	Lasioglossum malachurum	2	
R_L_2	Andrena cineraria		1
	Andrena flavipes	10	
	Andrena nigroaenea	1	
	Anthophora plumipes	2	
	Eucera nigrescens	1	
	Lasioglossum xanthopus	1	
	Osmia bicolor	1	
R_L_3	Andrena cineraria	1	1
	Andrena decipiens	1	
	Andrena flavipes	15	2
	Andrena haemorrha	2	1
	Anthophora plumipes	1	2
R_L_4	Andrena cineraria		1
	Andrena flavipes	2	2
	Andrena fulva	1	1
	Andrena haemorrha		1
	Andrena minuta		1
	Andrena nitida	2	
	Halictus rubicundus	1	
	Halictus symplex	1	
	Lasioglossum calceatum	1	
	Lasioglossum malachurum	2	3
R_S_1	Andrena decipiens	2	
	Andrena flavipes	5	2
	Andrena fulvicornis	1	
	Lasioglossum malachurum	1	
	Lasioglossum pauxillum	1	
R_S_2	Andrena cineraria		1
	Andrena flavipes	5	
	Andrena haemorrha		1
	Andrena minutula	1	
	Anthophora plumipes	6	
	Hylaeus signatus	1	
R_S_3	Andrena cineraria	1	2
	Andrena fulva		5
	Andrena haemorrha	1	3
	Andrena lathyri	1	

	Andrena nitida		1
	Lasioglossum xanthopus		1
R_S_4	Andrena cineraria	1	
	Andrena flavipes	1	
	Andrena haemorrha	1	
	Andrena labiata	1	
	Andrena nigroaenea		1
	Lasioglossum pauxillum	1	

Table II.S7. Distribution of hover fly species among the different types of flower fields, calcareous grasslands and oilseed rape fields. CG: Calcareous grassland; C: Continuous flower field; N: New flower field; R: Refreshed flower field. L: Large flower field; S: Small flower field.

Field code	Species	Flower field Abundance	Oilseed rape Abundance
CG_L_1	Eristalis tenax	1	
	Melanostoma mellinum agg.	1	
	Sphaerophoria scripta	1	
	Xanthogramma citrofasciatum	1	
CG_L_2	Chrysotoxum vernale c.f.	2	
	Melanostoma mellinum agg.	2	
	Sphaerophoria scripta	7	
	Eupeodes corollae		1
CG_S_1	Episyrphus balteatus	1	
	Melanostoma mellinum	3	
CG_S_2	Chrysotoxum vernale c.f.	1	
	Melanostoma mellinum	1	
	Xanthogramma citrofasciatum	1	
C_L_1	Episyrphus balteatus	1	
	Melanostoma mellinum	1	
	Sphaerophoria scripta	10	
C_L_2	Episyrphus balteatus	1	
	Eristalis tenax	1	
	Helophilus trivitattus	1	
	Sphaerophoria scripta	3	
C_L_3	Episyrphus balteatus	6	
	Eristalis tenax	1	
	Sphaerophoria scripta	2	
	Syrphus vitripennis	1	
C_L_4	Episyrphus balteatus	6	
	Melanostoma mellinum	1	
	Platycheirus albimanus	1	
	Parasyrphus punctulatus		1
C_S_1	Episyrphus balteatus	1	
	Sphaerophoria scripta	7	1
	Syrphus vitripennis	1	
C_S_2	Sphaerophoria scripta	2	
	Cheilosia nebulosa	1	
	Episyrphus balteatus	6	
	Melanostoma mellinum agg.	3	
	Pipiziella sp.	1	
	Sphaerophoria scripta	4	
N_L_1	Eristalis tenax	1	
	Melanostoma mellinum agg.	1	
	Sphaerophoria scripta	3	
N_L_2	Episyrphus balteatus	1	
	Eristalis arbastorum	1	
	Eristalis tenax	1	
	Melanostoma mellinum agg.	1	1

	Melanostoma mellinum		2
	Sphaerophoria scripta	6	
N_L_3	Episyrphus balteatus	6	
	Eristalis tenax	3	
	Melanostoma mellinum	1	
	Pipiziella sp.	1	
	Sphaerophoria scripta	11	
	Syrphus ribesii	1	
N_L_4	Episyrphus balteatus	2	
	Sphaerophoria scripta	5	
N_S_1	Eristalis tenax	1	
	Melanostoma mellinum agg.	1	
N_S_2	Chrysotoxum verralli c.f.	1	
	Episyrphus balteatus	1	
	Sphaerophoria scripta	3	
N_S_3	Myathropa florea	1	
	Sphaerophoria scripta	2	
N_S_4	Eristalis arbastorum	1	
	Eristalis tenax	1	1
	Eupeodes corollae	1	
	Sphaerophoria scripta	12	
R_L_1	Melanostoma mellinum	1	1
	Sphaerophoria scripta	4	
R_L_2	Eristalis arbastorum	1	
	Melanostoma mellinum	1	
	Melanostoma mellinum agg.	1	
	Sphaerophoria scripta	3	
R_L_3	Eristalis tenax	2	
	Melanostoma mellinum	1	
	Sphaerophoria scripta	3	
R_L_4	Eristalis tenax	1	
	Melanostoma mellinum	2	
	Melanostoma mellinum agg.	1	
	Myathropa florea	1	
	Sphaerophoria scripta	7	
R_S_1	Melanostoma mellinum agg.	1	
	Sphaerophoria scripta	6	
R_S_2	Eristalis tenax	4	
	Melanostoma mellinum	2	1
	Melanostoma mellinum agg.	1	1
	Platycheirus pelatus	3	1
	Sphaerophoria scripta	3	
R_S_3	Episyrphus balteatus	1	
	Eristalis arbastorum	1	
	Eristalis tenax	4	2
	Platycheirus albimanus	1	
	Sphaerophoria scripta	1	
R_S_4	Episyrphus balteatus	1	
	Melanostoma mellinum	2	1
	Melanostoma mellinum agg.	3	
	Sphaerophoria scripta	6	

Chapter III: Natural pest control

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

The pollen beetle *Brassicogethes spp.* is the main pest of oilseed rape (OSR) in Europe and responsible for massive yield losses. Pesticides often do not provide sufficient protection due to resistances, underpinning the need for other means of protection such as natural pest control. Sown flower fields aim to counteract the decrease of insect biodiversity in the agricultural landscape by providing nesting and foraging sites to ecosystem service providers such as parasitoids. However, the optimal composition of flower fields to effectively increase natural pest control is still unclear. We conducted experiments in 31 OSR fields located along a gradient in 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 and calcareous grasslands. In the OSR fields, areas without pesticide application were established to reveal interactive effects of pesticide use and flower fields. The abundance of adult pollen beetles, pollen beetle larvae, parasitism and superparasitism rates in OSR were analysed at growing distances to the adjacent fields. Our results show that OSR next

to flower fields maintained continuously for >6 years had the lowest numbers of pollen beetle larvae. Flower fields and calcareous grasslands increased pollen beetle parasitism in adjacent OSR fields compared to OSR fields neighbouring crop fields. However, the threshold for effective natural pest control could only be reached in the pesticide free areas of OSR fields adjacent to calcareous grassland and continuous flower fields. In pesticide-sprayed areas, pollen beetle parasitism and superparasitism declined with increasing distance to the adjacent field, but they remained on the same level in spray windows without pesticides. Large flower fields (>1.5ha) increased parasitism and superparasitism more than small ones. In general, flower fields enhance parasitism rates in OSR, but pesticide use can abrogate positive effects on natural pest control.

III.1 Introduction

Natural pest control has proven to be effective and profitable to control pest damage in field crops (BOMMARCO ET AL., 2011). Predators and parasitoids have high potential to suppress insect pest populations (RIGGI ET AL., 2017; ZALLER ET AL., 2009). However, natural pest control is threatened by agricultural intensification, including excessive pesticide use and the loss and fragmentation of natural areas (BIANCHI ET AL., 2006; TSCHARNTKE ET AL., 2005). Pesticides can have detrimental effects on human health and non-target animals (GUILLETTE AND IGUCHI, 2012). Arthropods can encounter pesticides 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 AND JEPSON, 1996A; ULBER ET AL., 2010A). Pesticides can alter the physiology and behaviour of beneficial arthropods and influence their orientation, fecundity and longevity negatively (DESNEUX ET AL., 2007). Additionally, pesticides may exhibit repellent effects on parasitoids (LONGLEY AND JEPSON, 1996A). Excessive pesticide use can lead to reduced predator-prey ratios in crop fields, thereby deteriorating natural pest control and increasing pest damage (BOMMARCO ET AL., 2011; KRAUSS ET AL., 2011).

Ecological intensification aims to enhance ecosystem services in intensively used agricultural landscapes by implementation of management practices supporting ecosystem service providing organisms (BOMMARCO ET AL., 2013). Agri-environmental schemes can promote ecological intensification and often include the preservation of remaining semi-natural areas in agricultural landscapes (BOMMARCO ET AL., 2013). Semi-natural habitats (SNH) like field margins, permanent grasslands and hedgerows provide resources and habitats to insects, while at the same time enabling spillover into agricultural fields (BIANCHI ET AL., 2006; TSCHARNTKE ET AL., 2007). Complex landscapes with high amounts of semi-natural habitats can therefore enhance natural pest control and may ultimately reduce crop damage (Bianchi et al., 2006; Rusch et al., 2016).

Agri-environment schemes can include the implementation of flower fields (Haaland et al., 2011), which offer several key resources to natural enemies in agricultural landscapes (Landis et al., 2000). Low disturbance levels qualify flower fields as refuge habitats from the pesticide-sprayed crop fields (Schellhorn et al., 2008). The dense vegetation cover creates a favourable microclimate for parasitoids and predators, thereby prolonging their longevity (Dyer and Landis, 1997). Furthermore, flower fields can provide alternative prey (Östman, 2004) and nectar (Gillespie et al., 2016). Most of the adult parasitoids need additional sugar resources, to cover their energetic needs (Bianchi and Wäckers, 2008). Floral resources can enhance the longevity and oviposition rate of parasitoids in the field (Lee and Heimpel, 2008) and ultimately lead to higher parasitism rates in their vicinity (Tylianakis et al., 2004). Positive effects of flower patches on natural pest control were already shown in cereals (Tschumi et al., 2016) and oilseed rape (Büchi, 2002).

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 (Hausammann, 1996; Winkler et al., 2010). For successful enhancement of natural pest control, flower field traits like age and size might be playing an important role. Additionally, pesticide use increased immensely over the last decades and is expected to increase even further (Delcour et al., 2015). It is therefore important to know if excessive pesticide use might counteract positive effects of flower fields on natural pest control.

The pollen beetle *Brassicogethes* spp. is the main pest of oilseed rape (OSR) in Europe and is responsible for massive yield losses in spring and winter OSR (HANSEN, 2004). It has 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 AND COOK, 2018). The pollen beetle has several specialist and generalist natural enemies, attacking at different life stages (BÜCHS AND ALFORD, 2003; NILSSON, 2003), which might benefit from close-by flower fields and the resources they provide. Here we examine effects of differently composed sown flower fields, the surrounding landscape and interactions with pesticide use on adult and larval pollen beetle infestation and parasitism as well as superparasitism rates. We predict the following:

(1) Flower fields decrease both larval and adult pollen beetle infestation and increase pollen beetle parasitism compared to fields with adjacent crop fields. This is especially true for OSR next to old and continuously maintained flower fields as well as calcareous grasslands.

(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 on pollen beetle infestation and parasitism decrease with growing distance into the OSR field.

(4) OSR fields next to large flower fields or calcareous grasslands have lower infestation and higher parasitism rates.

(5) Pesticide use decreases pollen beetle infestation, but also parasitism rates and counteracts positive effects of flower fields or SNH on natural pest control.

III.2 Material and Methods

III.2.1 Study sites

Experiments were conducted on 31 conventionally managed oilseed rape (OSR) fields in Germany in 2016. The OSR fields were located adjacent to five field types: Three different types sown flower fields (‘new flower fields’, ‘refreshed flower fields’, ‘continuous flower fields’), calcareous grasslands and conventionally managed crop fields. The fields were directly adjacent or divided by grassy field margins and 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: (1) flower fields ploughed and sown the previous year (‘new flower fields’; n=8), (2) flower fields established 5 years prior to this study, ploughed and re-sown the previous year (‘refreshed flower fields’; n=8), and (3) flower fields established 5 years prior to this study, and mulched yearly since 2015 (‘continuous flower fields’; n=7; Fig. III.1). Calcareous grasslands (n=4) were used for comparison with the flower fields sown as part of an AES, since they are among the most species-rich habitats in Europe and harbour many rare plant and insect species (STEFFAN-DEWENTER AND TSCHARNTKE, 2002). Additionally, OSR fields next to conventional crop fields (n=4) were chosen as negative control fields (3 winter cereal fields, 1 OSR field). Flower fields and calcareous grasslands were assigned to two size categories: ‘small’ (<1.5 ha) and ‘large’ (>1.5 ha) (new flower fields: 1.32 ± 0.38ha, refreshed flower fields: 1.05 ± 0.30 ha, continuous flower fields: 1.12 ± 0.25ha, calcareous grassland: 4.86 ± 3.40ha (mean ± SE)).

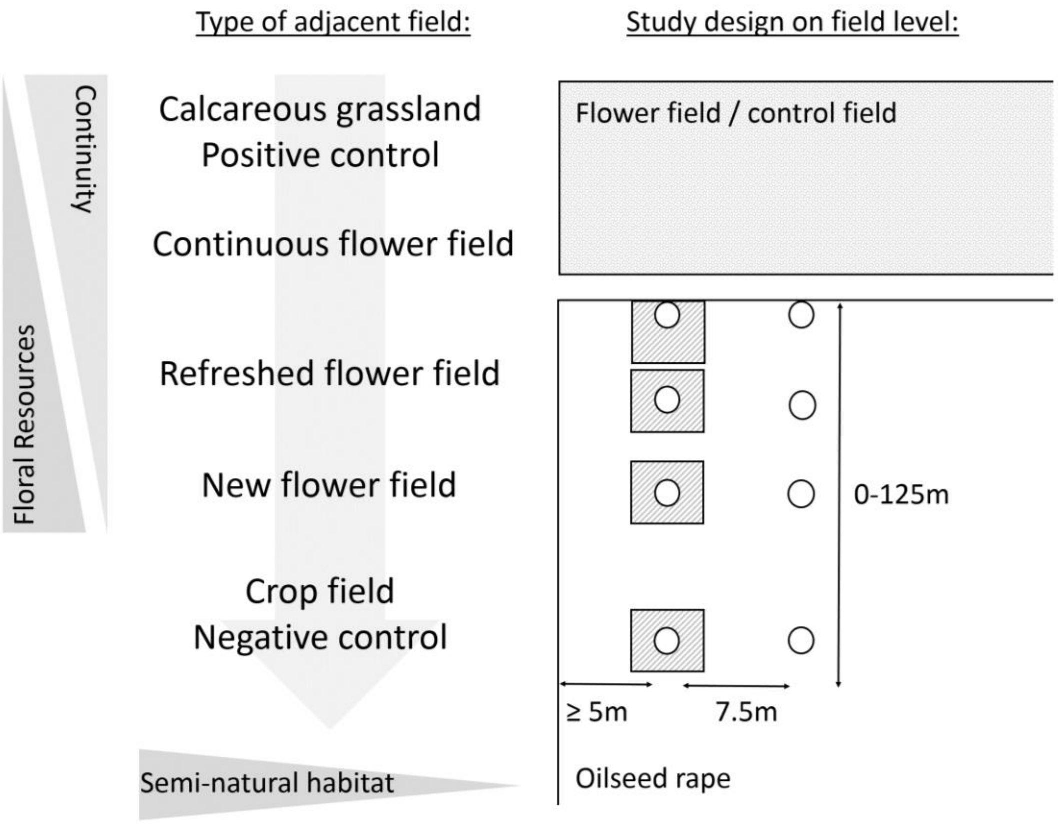


Fig. III.1. Experimental design on field level. The different types of sown flower fields and the positive control show opposing gradients of floral resources and continuity and all fields are placed along a gradient in landscape-scale semi-natural habitat (SNH) in 1km radius. Observation plots (circles) were located in the fields at increasing various distances in the Oilseed rape field and half of them were placed in spray windows of 25m² size (striped squares). 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 years prior to this study and left without further management, ploughed and re-sown the previous year and left without further management. Continuous flower field: established 5 years prior to this study, left without management until the previous year and since mulched yearly.

The landscape in 1km radius around the fields featured differing amounts of semi-natural habitat (SNH) (3.6-31.6%). Fields were at least 2.1km 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 grassland 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, REDLANDS, CA, USA).

III.2.2 Study system

Oilseed rape (*Brassica napus* Linneaus) is an important oilseed crop in Europe (WITTKOP ET AL., 2009). The pollen beetle (*Brassicogethes* spp. syn. *Meligethes* spp.) is one of the most important pest species of OSR, despite frequent use of pesticides (RICHARDSON, 2008). The beetles overwinter mainly in winter OSR fields and forest edges (SUTTER ET AL., 2018) and start colonising OSR plants in spring to feed on flower buds (WILLIAMS, 2010). The females lay their eggs into the flower buds where the hatched larvae feed on pollen (WILLIAMS, 2010) and feeding of adults and larvae can lead to bud abscission (SKELLERN AND COOK, 2018). After maturing in the bud, the larvae drop to the ground, pupate in the soil and new beetles emerge (WILLIAMS, 2010).

Tersilochus heterocerus (Thomson) is among the most abundant parasitoids of pollen beetles (BÜCHI, 2002; RUSCH ET AL., 2013). In our study, we could only find eggs of *T. heterocerus*, which often dominates in winter OSR and is the most abundant pollen beetle parasitoid in the study region (NILSSON, 2003; SCHNEIDER ET AL., 2015). *T.*

heterocerus predominantly lays eggs in second instar larvae feeding in open buds and flowers (Williams and Cook, 2010). The larvae hatch shortly before the host larva drops to the ground to complete their life cycle in the soil, thereby killing their host, and overwinter in their pupal cocoon (Nilsson, 2003; Ulber et al., 2010b). *T. heterocerus* can exhibit high parasitism rates often exceeding the threshold value of 30-40% for effective pollen beetle control (Thies et al., 2008). Superparasitism commonly occurs with *T. heterocerus* and pollen beetle larvae (Williams, 2006). Superparasitism can have beneficial effects in natural pest control by increasing the number of emerging parasitoids while at the same time reducing the survival rate of the host (Khafagi and Hegazi, 2008). Higher parasitism rates by *T. heterocerus* were found for landscapes with high amounts of SNH (Rusch et al., 2011). Furthermore, *T. heterocerus* was found to feed on sugar, supposedly nectar, during foraging in the field (Rusch et al., 2013). Since *T. heterocerus* is also present at the end of OSR flowering, Rusch et al. (2013) propose that it might be beneficial for natural pest control of pollen beetles to provide alternative floral resources in the direct vicinity of OSR fields.

III.2.3 Data collection

In the OSR fields, eight experimental plots of 4m² size were located along two parallel transects (7.5m distance from each other) in growing distance (0-124.7m) to the adjacent site (flower field, calcareous grassland or crop field (Fig. III.1)). Four varying within field distance sets were assigned randomly to the different fields with adjustments to in-field tractor lanes, to have evenly distributed data points over the whole distance: (1) 0m, 8m, 30m, 80m; (2) 0m, 10m, 40m, 100m; (3) 0m, 15m, 55m, 105m; (4) 0m, 20m, 65m, 120m. If possible, plots were located 25m away from other field edges of the OSR field. In very narrow OSR fields (n=3) a distance of 5m to other field edges was ensured. Spray windows were established on one of the transects with a size of 25m² located around each of the 4m² plots. Farmers were advised to refrain from spraying pesticides within these 25m² areas. Pesticides used against pollen beetle populations are applied as spray (THIEME ET AL., 2010). Therefore, spray windows are an effective measure to avoid pesticide application.

Adult pollen beetles were counted on the main raceme of 3 randomly chosen flowering oilseed rape plants within each plot (24 plants per field; BBCH growth stage 63-64, see Federal Biological Research Centre for Agriculture and Forestry 2001 for details on the universal BBCH code for growth stages; MEIER ET AL. 2009). To assess pollen beetle larva infestation and parasitism, three randomly chosen plants within each of the 4m² plots were cut during blooming (BBCH growth stage 64 – 65) and frozen until further analysis, which adds up to 24 plants per field. 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 3mm 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 3mm were disregarded, because other studies showed very low parasitism rates (THIES ET AL., 2003).

III.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 for the different response variables 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 error distribution was used for the 'parasitism' and 'superparasitism' rate models. 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: (1) *Type:* type of the adjacent field (new flower field, refreshed flower field, continuous flower field, calcareous grassland, crop field), (2) *SNH:* amount of semi-natural habitat in 1km radius around the fields, (3) *Distance:* within OSR field distance to the adjacent field edge and (4) *Treatment:* Sprayed pesticide treatment of the OSR plants (+ Pesticide: pesticides applied according to regular farming scheme, - Pesticide: No pesticides applied in the spray window). To examine the dependency of effects on pesticide use, we tested two-way interactions between *treatment* and the other fixed effects. Additionally, the fixed effect (5) *Size:* size category of flower fields (small <1.5ha, large>1.5ha) 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 an additional LMM for an analysis of the relationship between pollen beetle infestation and parasitism rate. We standardized the continuous fixed effects *SNH* and *distance* using the function 'rescale' from R package 'arm' to facilitate model convergence (GELMAN, 2008). Residual plots were used to check model assumptions. Wald chisquare tests (Type II sums of squares) using the function 'Anova' from the package 'car' (FOX AND WEISBERG, 2018) were used to calculate P-values. Subsequent post-hoc analyses with false discovery rate correction (FDR) (BENJAMINI AND HOCHBERG, 1995) were conducted by calculating estimated marginal means by using the package 'emmeans' (LENTH, 2018).

III.3 Results

III.3.1 Pollen beetle abundance

The abundance of adult pollen beetles on the main raceme of oilseed rape (OSR) plants during flowering decreased with increasing distance to the field edge (Table III.1, Fig III.2A). Additionally, mean pollen beetle abundance was around 15% higher in pesticide-treated than in pesticide-free areas of the OSR field (Table III.1, Fig. III.2B). The type and size of the adjacent field, the amount of semi-natural habitat (SNH) and interactions with treatment did not influence adult pollen beetle abundance in the OSR fields.

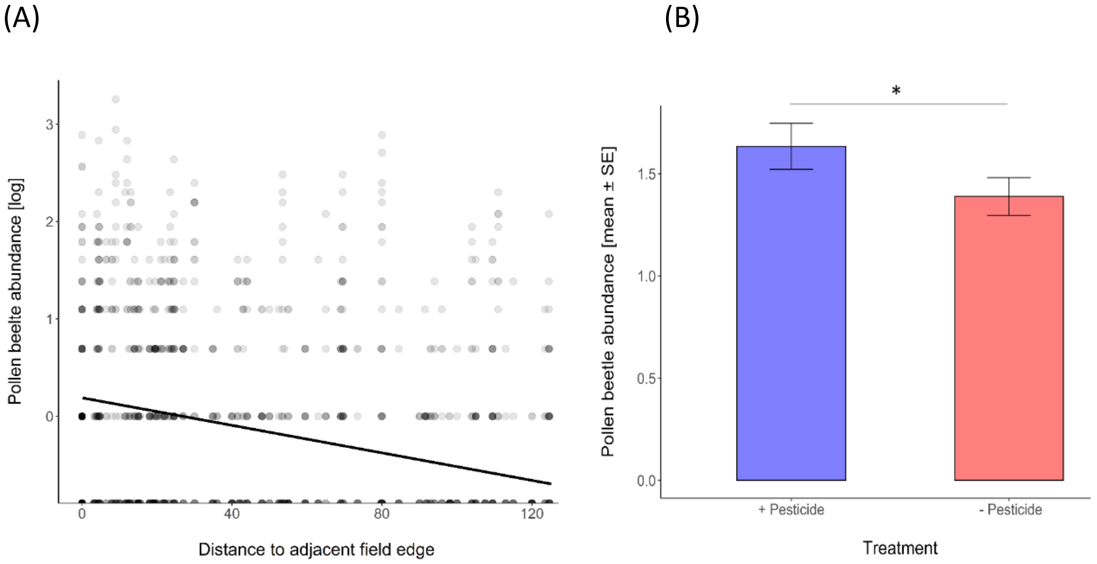


Fig. III.2. (A) Distance decay of pollen beetle abundance and (B) pollen beetle abundance in relation to different pesticide treatments in oilseed rape (OSR) fields. Fitted lines show model predictions. Columns show mean adult pollen beetle abundance ± standard error. (* $P < 0.05$; Table III.S1; + Pesticide: pesticides applied according to regular farming scheme, - Pesticide: No pesticides applied).

Table III.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, calcareous grasslands and crop 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 field type (new flower field, refreshed flower field, continuous flower field, calcareous grassland, crop field); *SNH:* amount of semi-natural habitat in 1km 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 (small <1.5ha, large>1.5ha). Significance levels: **p* < 0.5, ***p* < 0.1, ****p* < 0.01.

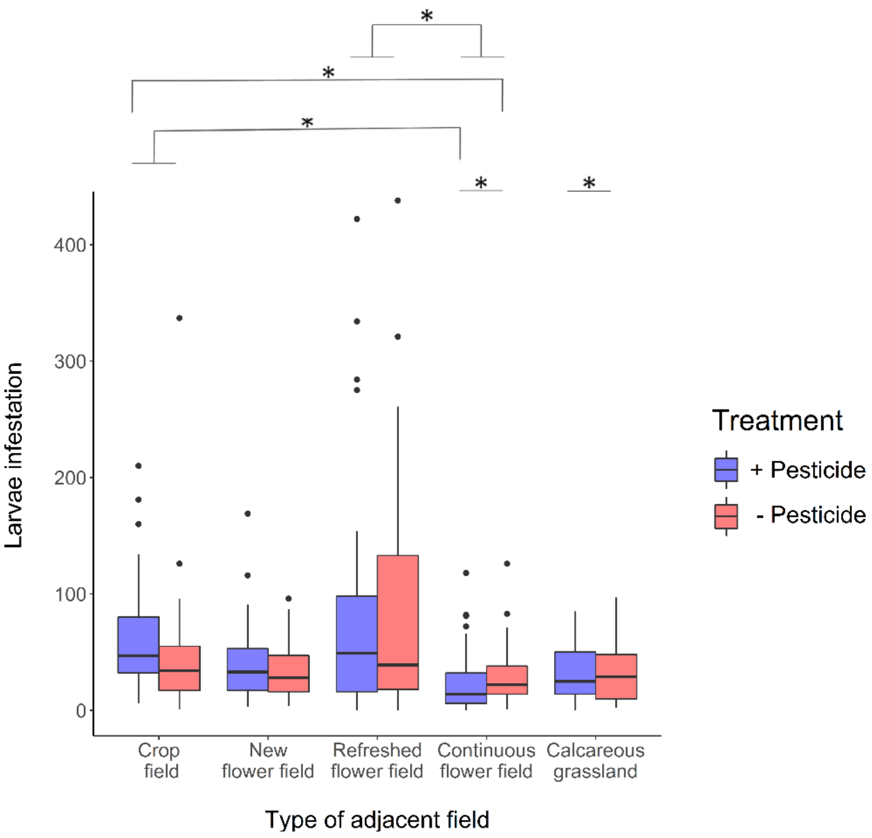
Model Response variable	Fixed effects	χ^2	χ^2 df	p-value	
Pollen beetle abundance					
Model 1	Type	3.044	41	0.551	
	SNH	0.054	1	0.816	
	Distance	34.972	1	**< 0.001**	***
	Treatment	5.751	1	**0.016**	*
	Type * Treatment	4.556	4	0.336	
	SNH * Treatment	2.535	1	0.111	
	Distance * Treatment	0.246	1	0.620	
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	

III.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 III.1, Table III.S1, Fig. III.3A). The pesticide treatment significantly reduced larvae infestation in OSR fields next to the continuous flower fields and the calcareous grasslands by 36% and 14%. Larvae infestation on pesticide treated plants increased by 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, Fig. III.4A). The size of the flower fields and calcareous grasslands had no effect on larvae infestation (Table III.1).

(A)


*
*
*
*
*
Larvae infestation
400
300
200
100
0
Crop field
New flower field
Refreshed flower field
Continuous flower field
Calcareous grassland
Type of adjacent field
Treatment
+ Pesticide
- Pesticide

(B)

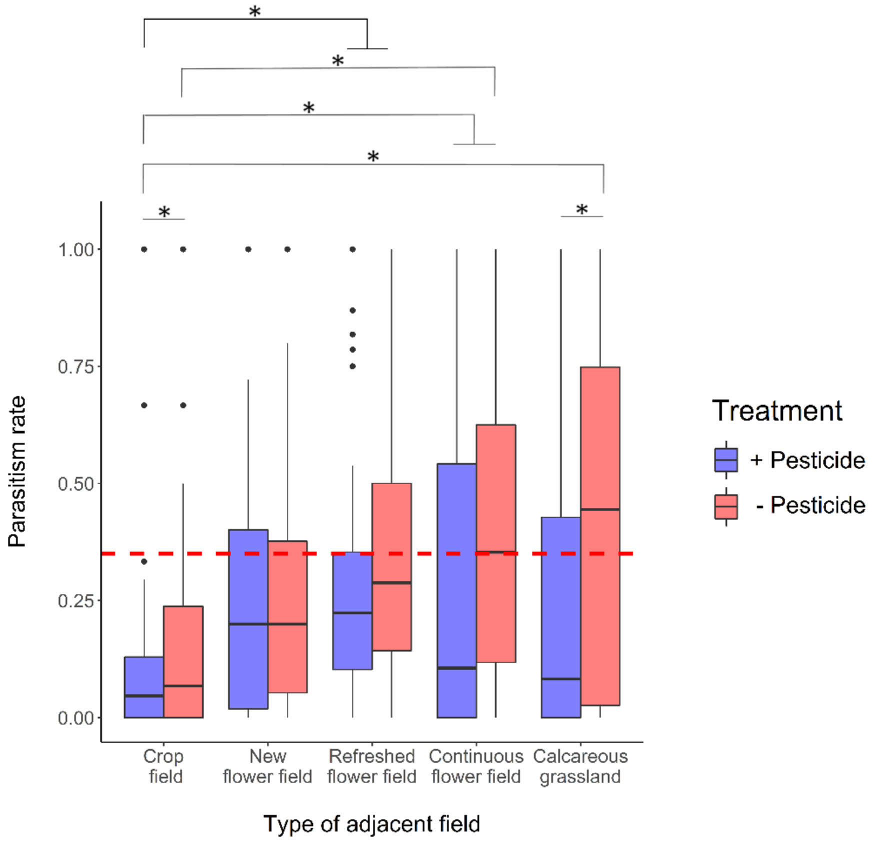
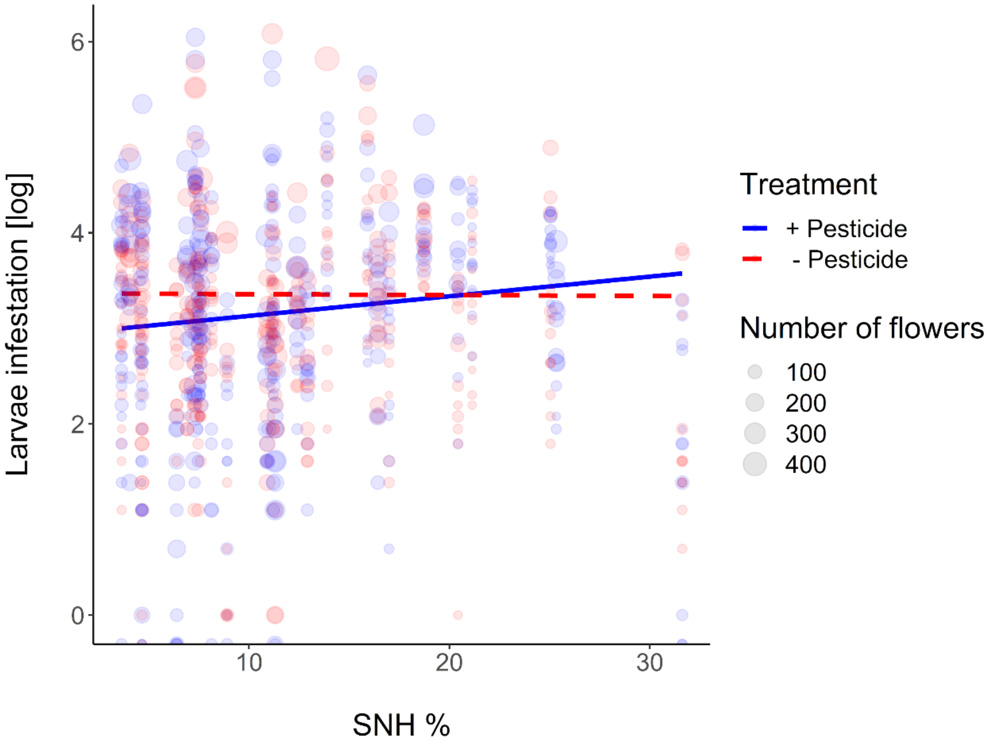

*
*
*
*
*
*
Parasitism rate
1.00
0.75
0.50
0.25
0.00
Crop field
New flower field
Refreshed flower field
Continuous flower field
Calcareous grassland
Type of adjacent field
Treatment
+ Pesticide
- Pesticide

Fig. III.3. Pollen beetle larvae (A) infestation and (B) parasitism rate in oilseed rape (OSR) plants adjacent to different types of fields and with different pesticide treatments. Boxplots show median and the 1st and 3rd quartiles, circles show outliers. Whiskers represent 1.5 interquartile range (* $P < 0.05$; Table III.S1, Table III.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 years prior to this study and left without further management, ploughed and re-sown the previous year and left without further management. Continuous flower field: established 5 years prior to this study, left without management until the previous year and since mulched yearly. Treatment: + Pesticide: pesticides applied according to regular farming scheme, - Pesticide: No pesticides applied on OSR.

III.3.3 Parasitism

Parasitism rates in OSR were higher next to refreshed and continuous flower fields as well as calcareous grasslands than next to the crop control, but only on the pesticide treated plants (Fig. III.3B, Table III.S2). The parasitism rate of on untreated plants next to crop fields instead was only higher on untreated plants next to continuous flower fields (Table III.1, Table III.S2, Fig. III.3B). The threshold parasitism rate for effective control of pollen beetles of 35% (THIES ET AL., 2008) was reached on the untreated plants of the continuous flower field and calcareous grasslands. Parasitism rates declined with increasing amount of SNH in the surrounding landscape (Fig. III.4B). 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% (Fig. III.4B). Furthermore, a 40% decline of parasitism was observed with increasing distance into the OSR fields on the pesticide treated plants, whereas the parasitism rate on untreated plants decreased less (17%) over the whole tested distance of 124.7m (Fig. III.5A). 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 III.1, Fig. III.S2A). Additionally, we examined the relationship between pollen beetle larva infestation and the parasitism rate and found that the parasitism rate increases with the infestation (χ^2=12.465, χ^2 df=1, p-value <0.001).

(A)



(B)

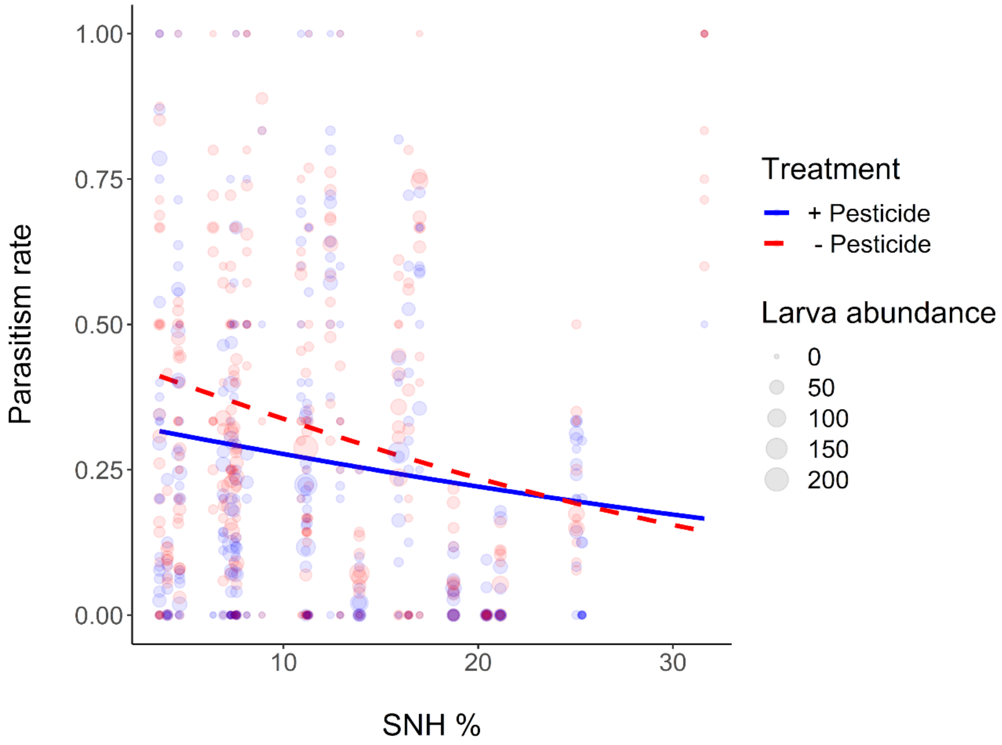
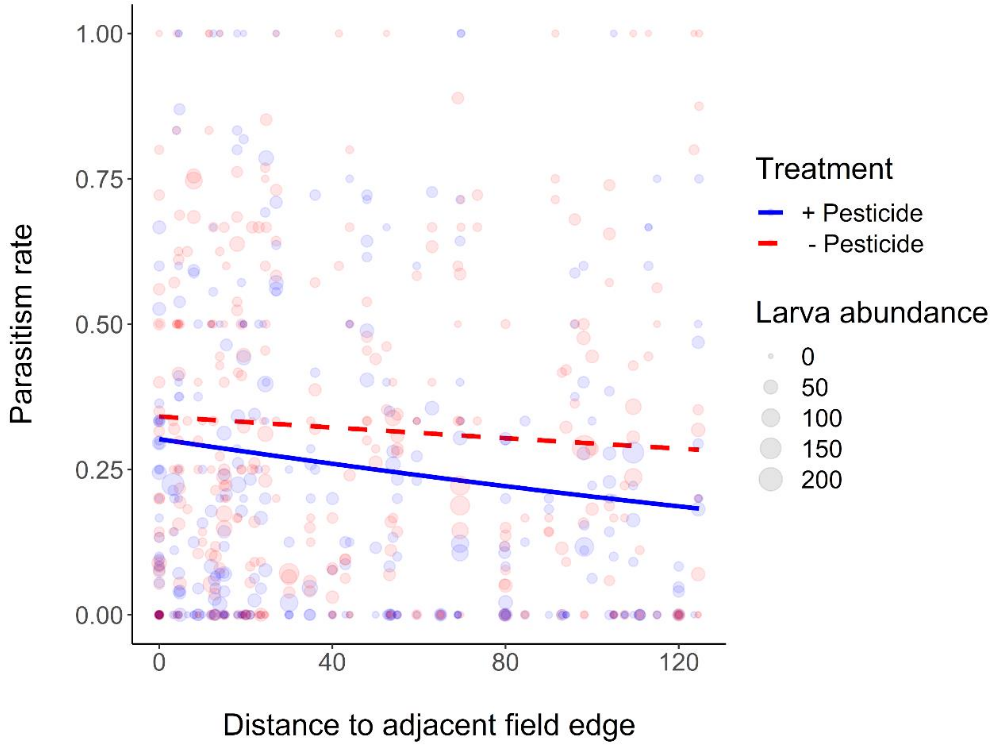


Fig. III.4. Pollen beetle larvae (A) infestation (log transformed) and (B) parasitism rate in oilseed rape (OSR) in landscapes along a semi-natural habitat (SNH) gradient in 1km radius. Fitted lines show model predictions for the two different pesticide treatments on the OSR plants, dot size reflects flower respectively larva abundance (+ Pesticide: pesticides applied according to regular farming scheme, - Pesticide: No pesticides applied).

III.3.4 Superparasitism

Similar to the parasitism rate, superparasitism declined by 47% with growing distance into the field on pesticide treated plants compared to untreated plants, where it even increased slightly (2%) over the whole tested distance (124,7m; Fig. III.5B). Additionally, the superparasitism rate was higher in OSR fields next to large flower fields compared to small flower fields (Table III.1, Fig. III.S2B).

(A)


Parasitism rate
1.00
0.75
0.50
0.25
0.00
0
40
80
120
Distance to adjacent field edge
Treatment
+ Pesticide
- Pesticide
Larva abundance
0
50
100
150
200

(B)

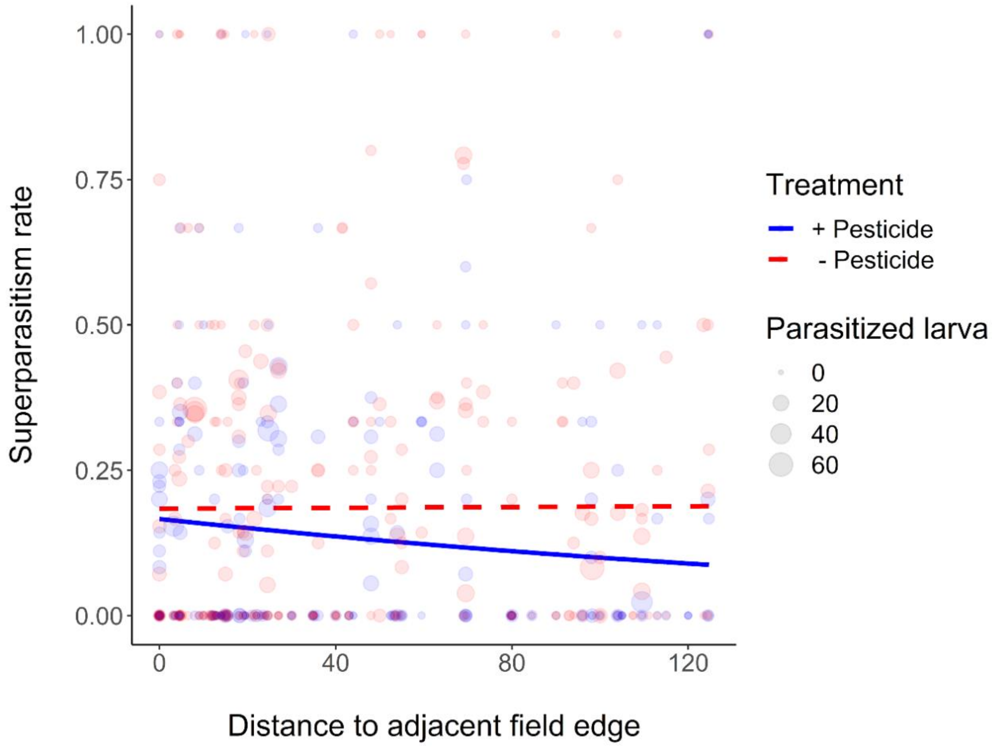

Superparasitism rate
1.00
0.75
0.50
0.25
0.00
0
40
80
120
Distance to adjacent field edge
Treatment
+ Pesticide
- Pesticide
Parasitized larva
0
20
40
60

Fig. III.5. Distance decay of pollen beetle larvae (A) parasitism rate and (B) superparasitism rate in oilseed rape (OSR) fields with different pesticide treatments on the OSR plants. Fitted lines show model predictions, dot size reflects larva respectively parasitized larva abundance (+ Pesticide: pesticides applied according to regular farming scheme, - Pesticide: No pesticides applied).

III.4 Discussion

In this study, we found that old and continuous flower fields can decrease pest infestation and increase pest control. Semi-natural habitat (SNH) does not unconditionally improve natural pest control and pest control decreases with increasing distance into the field. Most importantly, we found that pesticide use interacts negatively with positive effects of flower fields on natural pest control by keeping parasitism rates below the threshold for effective natural pest control and by displaying a stronger distance decay within oilseed rape (OSR) fields.

Adult pollen beetles showed no detectable reactions to the different flower field types. Earlier studies showed, that ground-dwelling predators are significantly enhanced close to flower fields (BOETZL ET AL., 2018). It is known that they can increase pollen beetle mortality (DAINESE ET AL., 2017) and thereby decrease pollen beetle emergence from the soil (RIGGI ET AL., 2017; ZALLER ET AL., 2008). Therefore, a lower pollen beetle abundance could have been expected adjacent to old flower fields, where pollen beetle abundance was decreased by increased predation on fields in the vicinity the previous year. However, pollen beetles are mobile and will have colonized the field from the farther surroundings (JUHEL ET AL., 2017). Furthermore, the intensive management schemes of conventional farming might possibly have diminished such effects (KRAUSS ET AL., 2011).

As expected, continuous flower fields had the lowest larval infestation numbers and the highest parasitism rates, together with calcareous grasslands. Older wildflower strips often show increased insect diversity and abundance compared to younger ones (HAALAND ET AL., 2011) and were shown to contribute more to predator species richness and abundance (FRANK ET AL., 2007). Many arthropod predators are active in the crop canopy of OSR, for example several rove beetle species (Felsmann and Büchs, 2006) or long-legged flies and dance flies (Williams, 2010). Soldier beetles, which are predatory in both their larval and adult stage (Büchs and Alford, 2003), were often observed on open OSR flowers during field work in this study. The potential of predators to suppress pollen beetle larvae already in the crop canopy is poorly studied, but higher abundances of predators next to continuous flower fields are a possible explanation for the lower numbers of larvae, but not of adult beetles. Flower fields provide natural pest control agents with several key resources (Landis et al., 2000), but the presence of floral resources does not always result in improved biological control. In our study, the pollen beetle parasitism rate was higher in OSR next to the 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 and Reichhart, 2004) and the new flower fields apparently did not yet support parasitoid populations.

We expected lower pollen beetle infestation in landscapes with high amounts of SNH due to higher levels of pest control in complex landscapes (Tscharntke et al., 2007). However, the number of pollen beetle larvae increased with the amount of SNH in plots treated with pesticides. Semi-natural habitats can benefit parasitoids and predators as well as pests (Tscharntke et al., 2016). The positive effect on pest control agents might have been diminished by excessive pesticide use while the pollen beetles themselves are partly resistant to pesticides (Slater et al., 2011; Thieme et al., 2010). Accordingly, we found lower parasitism rates with increasing SNH in our landscapes. We found an increasing parasitism rate with increasing pest infestation, so a dilution effect is not likely to have caused this pattern. Landscape configuration and local habitat characteristics affect natural enemies interactively with landscape composition (MARTIN ET AL., 2019A; RUSCH ET AL., 2012) and the quality of SNH could be more important than the quantity (HOLLAND ET AL., 2016; ZALLER ET AL., 2009). This could explain the discrepancy of our results. Calcareous grasslands, which are per definition semi-natural habitats, support parasitism while the amount of SNH in our study does not. In our study, SNH was defined as a mixture of several perennial habitat structures with varying habitat quality. The amount of the SNH was the only parameter measured and might obscure other underlying factors influencing the parasitism rate (KARP ET AL., 2018). Additionally, strong annual fluctuations of parasitism in response to landscape complexity can influence parasitism levels (MENALLED ET AL., 2003). Population dynamics interplaying with annual turnovers in landscape composition due to crop rotations might interfere with the generally positive effects of SNH on natural enemy abundance and parasitism rates.

As expected, adult pollen beetle abundance declined with growing distance into the field, since pollen beetles colonize fields from the edge (SCHNEIDER ET AL., 2015). However, the abundance of pollen beetle larvae did not decrease with increasing distance into the field. Even though pollen beetles colonize fields from the edge, larva abundance can be higher in the center 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). Parasitoids are often more abundant at field edges compared to field centers, due to their limited dispersal abilities (WITH ET AL., 1999). We found 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 AND 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 (HANSON ET AL., 2015). Stronger distance decay of parasitism and superparasitism in the presence of pesticides might therefore decrease natural pest control in OSR field centers even further.

Large flower fields supported higher parasitism and superparasitism rates than small flower fields. Natural enemy density, richness and diversity can increase with the size of the flower plantings, due to more resources and habitat (BLAAUW AND ISAACS, 2014). Therefore, the establishment of large flower fields compared to small ones or even flower strips might be more beneficial to promote natural pest control in OSR.

We found higher abundances of adult pollen beetles in the pesticide sprayed areas compare to the spray windows. The opposite would have been expected, since repellent effects and better survivability may have lead the beetles to accumulate on pesticide free plants (LONGLEY AND JEPSON, 1996A). However, it is known that pollen beetles are becoming increasingly resistant to different kind of insecticides used on OSR, due to high selection pressure (THIEME ET AL., 2010) and they might be less susceptible than beneficial insects such as natural control agents. Accordingly, we found higher parasitism numbers in the spray windows. Pesticides applied during OSR flowering have high potential to harm parasitoids searching for hosts and significantly reduced the abundance of pollen beetle parasitoids in field trials (ULBER ET AL., 2010A). Additionally, pesticides were reported to decrease parasitoid emergence in field trials (HANSON ET AL., 2015). Higher parasitism rates can therefore be explained by higher survivability, fitness and emergence of parasitoids in the spray windows. 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 AND JEPSON, 1996B). Additionally, aggregation of parasitoids on the untreated plants inside of the spray windows is likely, since pesticides can have repellent effects (LONGLEY AND JEPSON, 1996B).

The threshold parasitism rate for effective biological 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 spray windows in OSR next to the continuous flower fields and calcareous grasslands. As stated above, pesticide use can decrease the abundance of parasitoids in OSR fields (ULBER ET AL., 2010A) and could therefore potentially diminish natural pest control to a level where there is no pest reducing effect anymore. Flower fields can help to mitigate these negative effects, but in our study were not successful to push the parasitism rate above the critical threshold if treated with pesticides, indicating that natural pest control is prevented by pesticide application.

The provision of flower fields can have effects on pollen beetles in OSR fields and in our study 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 fields over 1.5ha promote more parasitism than small fields. We also found that landscape composition is not always the best parameter to explain natural pest control and that the local management on field level is very important for successful ecological intensification. Excessive pesticide use not only poses the risk of resistances, it also diminished positive effects of flower fields on natural pest control. Our study highlights the need for alternative measures to promote natural pest control in conventional farming and the negative impact of pesticides on natural pest control.

III.5 Supplementary material

Table III.S1. Post hoc analysis on pollen beetle larvae infestation in oilseed rape fields next to different types of flower fields in relation to pesticide treatment (p-values). Significance levels: *$p < 0.5$, **$p < 0.1$, ***$p < 0.01$.

p-value	New flower field - Pesticide	Refreshed flower field + Pesticide	Refreshed flower field - Pesticide	Continuous flower field + Pesticide	Continuous flower field - Pesticide	Calcareous grassland + Pesticide	Calcareous grassland - Pesticide	Crop field + Pesticide	Crop field - Pesticide
New flower field + Pesticide	0.340	0.123	0.066	0.123	0.501	0.898	0.340	0.123	0.265
New flower field - Pesticide		0.201	0.105	0.095	0.346	0.993	0.415	0.176	0.346
Refreshed flower field + Pesticide			0.123	**0.002** **	**0.032** *	0.415	0.993	0.836	0.984
Refreshed flower field - Pesticide				**0.001** **	**0.0095** **	0.309	0.862	0.993	0.751
Continuous flower field + Pesticide					**0.002** **	0.265	0.066	**0.005** **	**0.017** *
Continuous flower field - Pesticide						0.531	0.176	**0.038** *	0.105
Calcareous grassland + Pesticide							**0.0095** **	0.340	0.513
Calcareous grassland - Pesticide								0.862	0.993
Crop field + Pesticide									0.123

Table III.S2. Post hoc analysis on pollen beetle larvae parasitism in oilseed rape fields next to different types of flower fields in relation to pesticide treatment (p-values). Significance levels: *$p < 0.5$, **$p < 0.1$, ***$p < 0.01$.

p-value	New flower field - Pesticide	Refreshed flower field + Pesticide	Refreshed flower field - Pesticide	Continuous flower field + Pesticide	Continuous flower field - Pesticide	Calcareous grassland + Pesticide	Calcareous grassland - Pesticide	Crop field + Pesticide	Crop field - Pesticide
New flower field + Pesticide	0.410	0.662	0.548	0.503	0.287	0.621	0.287	0.064	0.287
New flower field - Pesticide		0.769	0.621	0.603	0.392	0.694	0.343	0.052	0.226
Refreshed flower field + Pesticide			0.140	0.769	0.603	0.821	0.467	**0.024** *	0.134
Refreshed flower field - Pesticide				0.924	0.706	0.924	0.568	**0.013** *	0.079
Continuous flower field + Pesticide					0.192	0.976	0.621	**0.013** *	0.079
Continuous flower field - Pesticide						0.866	0.752	**0.011** *	**0.048** *
Calcareous grassland + Pesticide							**0.013** *	0.058	0.192
Calcareous grassland - Pesticide								**0.013** *	0.058
Crop field + Pesticide									**0.011** *

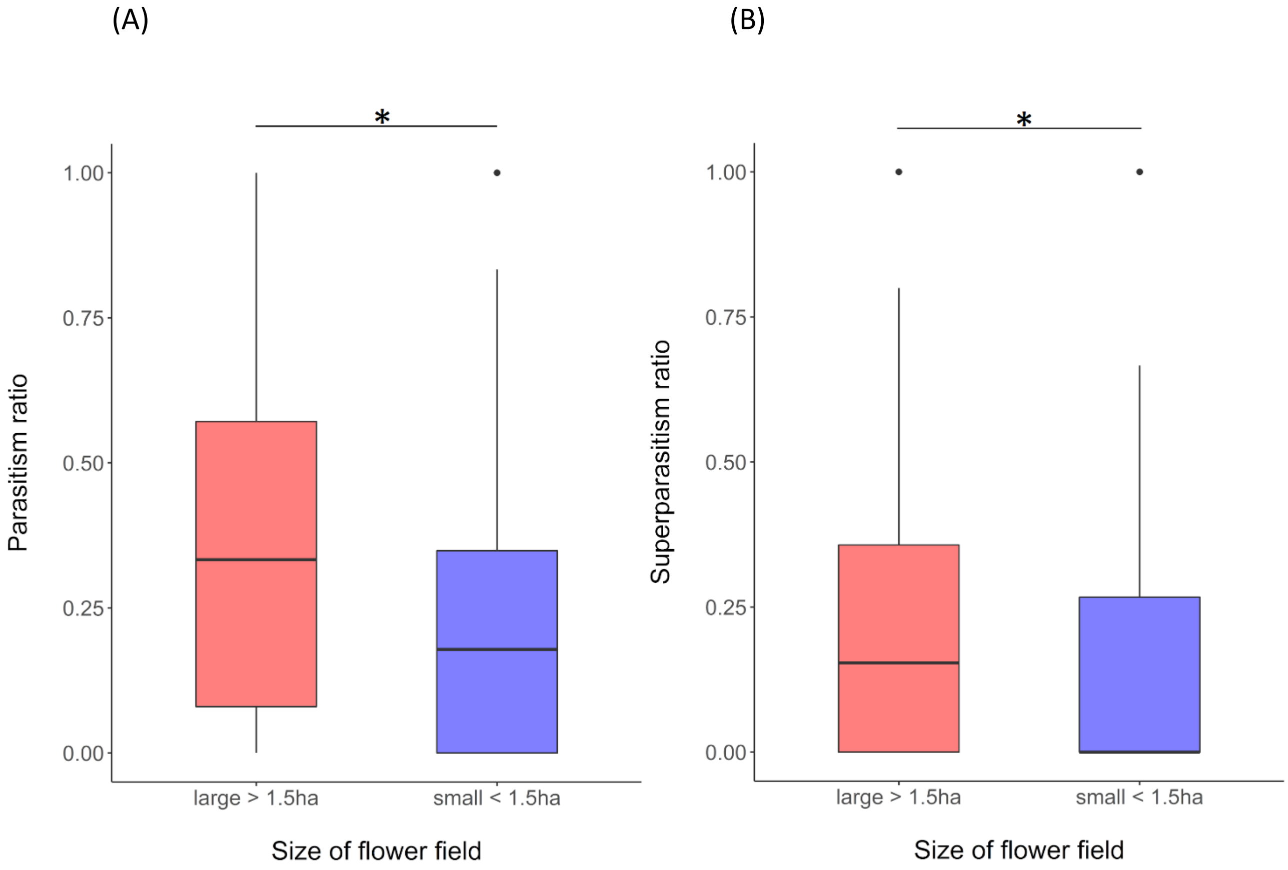


Fig. III.S1. Pollen beetle larvae (A) parasitism ratio and (B) superparasitism ratio in oilseed rape (OSR) adjacent to different types of flower fields in two different sizes (large >1.5ha, small <1.5ha). Boxplots show median and the 1st and 3rd quartiles, circles show outliers. Whiskers represent 1.5 interquartile range. Lines display significant differences in post-hoc analysis (* $P < 0.05$; Table III.S1)

Chapter IV: Oilseed rape yield

The contribution of sown flower fields to oilseed rape yield.

Conventional agriculture has reached its input limits and alternative and more sustainable ways to deliver crop yields are needed. Sown flower fields are implemented as agri-environment schemes in many European countries. They can deliver key resources to beneficial organisms like pollinators and parasitoids, thereby increasing their population and subsequently ecosystem services. However, their potential to increase yields may depend on the specific field crop and there is a lack of studies examining the effects of flower fields on yield. We conducted experiments in oilseed rape (OSR) fields adjacent to three types of sown flower fields differing in their age and continuity as well as adjacent to calcareous grasslands and crop fields. We established spray windows at various distances from the field edge to examine effects of pesticide treatment and distance decay functions. The field quality was included in the analysis as an additional factor. Structural equation models were used to disentangle indirect effects of flower fields on different OSR yield parameters, via the ecosystem services pollination and natural pest control. Old and continuous flower fields increased natural pest control of pollen beetles, which in turn increased OSR seed set and total seed weight. We found no effect of pollination on OSR yield. Pesticide treatment had negative effects on natural pest control, but positive effects

on yield. Pollination and natural pest control declined with the distance from field edges, but the fruit set slightly increased. The field quality had no effect on the OSR yield parameters we used in the model. OSR yield formation is a complex process in which many factors are involved. Perennial flower fields can promote ecological intensification by improving yield via natural pest control. Our study is an important contribution to the understanding of the role of flower fields in OSR yield formation and further research is needed to examine the potential effects of flower fields on different crop yields.

IV.1 Introduction

In past decades, land-use change and conventional agricultural intensification were the main drivers of crop yield increases (FOLEY ET AL., 2005), leading to severe biodiversity losses in agricultural landscapes (NEWBOLD ET AL., 2015) and putting biodiversity-dependent ecosystem services at risk (OLIVER ET AL., 2015). Landscape simplification contributes to the decline of pollination and natural pest control, thereby decreasing crop yields (DAINESE ET AL., 2019). As a matter of fact, yields of several important cereals are stagnating or even declining in major growing areas (RAY ET AL., 2012). At the same time, global food demands are ever growing, leading to concerns about global food security (GODFRAY ET AL., 2010) and raising demands for novel and sustainable ways of crop production with high outputs and at the same time minimised impact on the environment (PRETTY, 2018; PRETTY ET AL., 2018).

Ecological intensification is a promising concept to close existing yield gaps. It aims to promote biodiversity-dependent ecosystem services in agricultural landscapes, thereby making crop production more sustainable and lessening the need for fertilizer and pesticide use (BOMMARCO ET AL., 2013). Ecological intensification is based on the promotion of ecosystem service providing organisms by incorporating alternative and non-hazardous management practices (BOMMARCO ET AL., 2013). Agri-environment schemes (AES) put into effect by the European Union can help to promote ecological intensification by the implementation of several on-field and off-field measures, for example the conservation of semi-natural habitats (BATÁRY ET AL., 2015; KLEIJN ET AL., 2019).

A common on-field AES measure available in several European countries is the establishment of sown flower fields (HAALAND ET AL., 2011). Sown flower fields or strips can improve ecosystem services like pollination and natural pest control (WESTPHAL ET AL., 2015) by increasing the abundance of beneficial insects such as bees, hoverflies, beetles and parasitoids (BOETZL ET AL., 2018; HAALAND ET AL., 2011). Perennial flower fields offer several key resources to many ecosystem service providing insects: they are valuable sources for nectar, pollen and alternative prey in addition to providing habitat, shelter and a favourable microclimate for nesting and overwintering (LANDIS ET AL., 2000; SCHEPER ET AL., 2015). However, the quality of the flower field is decisive for its efficiency to promote ecosystem services (SCHEPER ET AL., 2013). Important factors influencing the successful improvement of ecosystem services can be the age and continuity of the flower field (HÄUSSLER ET AL., 2017). Older flower fields have been shown to increase pollination more effectively than younger fields (BLAAUW AND ISAACS, 2014). Several studies examining the effects of sown flower fields on the ecosystem services pollination and natural pest control exist, but studies examining effects on yield are scarce (GARIBALDI ET AL., 2014; SUTTER AND ALBRECHT, 2016).

Crop yields are determined by a plurality of factors: Fertilization, pesticide application and soil quality are decisive for yield formation (GAGIC ET AL., 2017; LEACH ET AL., 1994). In addition, insect pollination contributes to yield quality and quantity in crops and fruits (BOMMARCO ET AL., 2012; KLATT ET AL., 2014). Furthermore, improved natural pest control can effectively increase yields (TSCHUMI ET AL., 2016). Compelling evidence points to interactive effects of pollination and natural pest control in shaping yields (BARTOMEUS ET AL., 2015; LUNDIN ET AL., 2013). For example, synergistic effects of pollination and pest control accounted for 10% of increased yield in OSR (SUTTER AND ALBRECHT, 2016). Additionally, there could be trade-offs in the improvement of pollination versus natural pest control (Rodríguez et al., 2006). Therefore, interactions of ecosystem services need to be considered and properly managed if crop yields are to be improved (Lundin et al., 2013). In-field conditions such as the distance to habitats suitable for ecosystem service providers affect crop yields. Distance decay over short distances of less than 100m into crop fields has been shown for pollination as well as natural pest control (Morandin and Kremen, 2013; Tschumi et al., 2015). Furthermore, edge effects such as competition for nutrients and water, allelopathy as well as fungi and weed pressure are known to have negative effects on yields close to hedges (Kuemmel, 2003) and might also be possible for perennial flower fields. To date, how these factors shape the response of ecosystem services to flower field establishment is not sufficiently researched, especially considering their impact on crop yields.

In our study, we aim to disentangle the indirect effects of differently aged sown flower fields on oilseed rape (*Brassica napus* L.) yield parameters under field conditions. Oilseed rape is an important oilseed crop cultivated in many European countries and is used for consumption and industrial purposes (Wittkop et al., 2009). We expect flower fields to directly increase the ecosystem services pollination and natural pest control. We predict that pollination and natural pest control interactively shape OSR yield. We also expect that these services improve with age and continuity of the flower fields, and that within-field conditions such as pesticide use and distance from the field edge have negative effects on ecosystem services. We further predict, that OSR yield is to a certain degree explained by the soil quality, with higher quality fields supporting higher yields. Our results contribute to the understanding of oilseed rape yield formation and to a more target-oriented implementation of sown flower fields to optimize crop yields by improving ecosystem service delivery.

IV.2 Material & Methods

IV.2.1 Study sites

The field work for this study was conducted in Lower Franconia, Germany in 2016 on 31 conventionally managed oilseed rape (OSR) fields, either adjacent to different types of flower fields, calcareous grasslands or conventional crop fields. The adjacent flower fields consisted of three types of sown flower fields which differed in their age, continuity and management ('New flower fields', n=8; 'Refreshed flower fields', n=8; 'Continuous flower fields', n=7; Table IV.1, Fig. IV.1). New flower fields were established the previous year of the study out of crop fields and left without further management. Refreshed flower fields were established five years prior to this study but were re-established and re-sown the previous year and left without further management. Continuous flower fields were also established five years prior to this study, but were not newly sown and are mulched once a year since 2015. The sown flower fields were or had been part of an agri-environment scheme (AES) and were sown and managed according to state regulations (Table IV.1; see also KRIMMER ET AL 2019). In addition to the flower fields, we selected calcareous grasslands (n=4) as well as conventional crop fields (n=4; 3 cereal fields and 1 OSR field) with adjacent OSR fields as controls. Calcareous grasslands belong to the most species-rich habitats in Europe (STEFFAN-DEWENTER AND TSCHARNTKE, 2002) and were chosen as a natural comparison to the managed and sown flower fields. Data sampling was conducted only on the conventionally managed OSR fields. In total, 16 different OSR cultivars were grown on the fields of our study, all commonly used hybrid lines (Table IV.S1). Due to the maximized heterosis effect, hybrid OSR lines are assumed to be especially vital and tolerant and have come to dominate the European market (LINDSTRÖM ET AL., 2016). Due to the high number of available OSR cultivars on the market, it was not possible to select the same OSR cultivars on all the fields. The pairs consisting of the OSR fields and the respective adjacent field were at least 2.1km apart from each other.

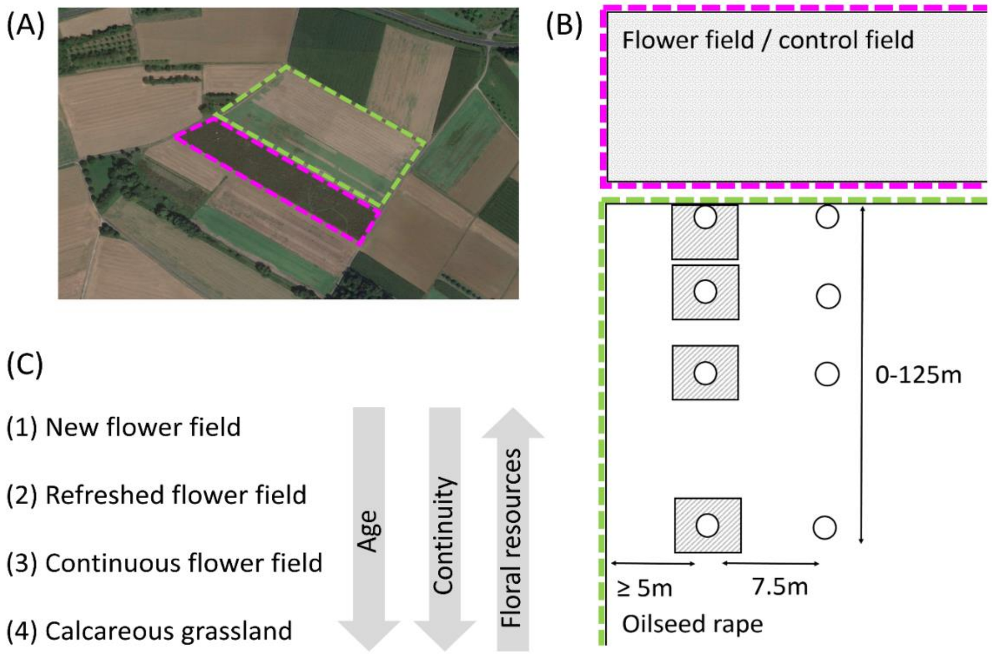


Fig. IV.1. Study design on field level. (A) Aerial photograph (Google earth) of the two adjacent fields in a typical landscape: Oilseed rape (OSR; green) and flower field or control field (pink). (B) Schematic depiction of the sampling design: Observation plots (circles) were located in the fields at increasing various distances in the Oilseed rape field and half of them were placed in spray windows of 25m² size (striped squares). (C) The three different types of sown flower fields and calcareous grasslands show opposing gradients of continuity, age and floral resources. (1) New flower field, newly established the previous year, ploughed and sown with a flower mixture and then left without further management. (2) Refreshed flower field: established 5 years prior to this study, ploughed and re-sown the previous year and left without further management. (3) Continuous flower field: established 5 years prior to this study, since the previous year mulched yearly.

Table IV.1. Age, continuity and floral resource characteristics of the three different sown flower field types, calcareous grasslands, crop control and adjacent oilseed rape fields (OSR). Flower cover, Field quality: Mean ± SE.

	New flower field (N)	**Refreshed flower field (R)**	**Continuous flower field (C)**	**Calcareous grassland (CG)**	**Crop control**
Age in years	1	≥6	≥6	Continuous	-
First established	2015	2009/2010	2009/2010	-	-
Re-established	-	2015	-	Never	-
Maintenance	None	None	Mulched since 2015	None, mowing, grazing	-
Flower cover in May/June (%)	17.88 ± 6.87	6.45 ± 2.90	1.35 ± 0.33	0.47 ± 0.26	-
OSR Field quality	47.63 ± 6.90	49.38 ± 5.84	43.57 ± 3.15	36.25 ± 3.28	44.50 ± 5.87

IV.2.2 Sampling methods

Plots of 4m² were established along two parallel transects within the OSR field with an increasing distance to the adjacent flower field, grassland or crop field edges (0-124.7m; Fig. IV.1). To obtain evenly distributed plots over the whole tested distance, we created four distance sets and applied them randomly to the different field types: (1) 0m, 8m, 30m, 80m; (2) 0m, 10m, 40m, 100m; (3) 0m, 15m, 55m, 105m; (4) 0m, 20m, 65m, 120m, with slight adjustments due to tractor lanes. Earlier studies showed that 120m is a reasonable distance to examine distance decay of pollinators (KOHLER ET AL., 2008; MORANDIN AND KREMEN, 2013) and parasitoids (TYLIANAKIS ET AL., 2004). Transects had a distance of 25m to other field edges and in six narrow fields at least a distance of 5-10m. Spray windows of 25m² size were established around the 4m² plots of one of the two transects. Within these spray windows, no pesticides were applied on the OSR plants. Plots within the spray windows and the parallel sprayed plots were 7.5m apart from each other. The field quality was assessed for every OSR field as a combined value of soil quality and climatic as well as specific site conditions (Table IV.1). This value ranges from 10 to 100 and is provided by the Bavarian state department for Digitisation, High-Speed Internet and Surveying (BAYERNATLAS PLUS 2019).

IV.2.2.1 Yield parameters

After OSR ripening (BBCH growth stage 87-89, see MEIER ET AL. 2009 for details), three plants per plot were harvested in July 2016 and stored individually under dry greenhouse conditions until further analysis. Several parameters important to OSR yield formation were used to measure OSR yield: total seed weight, fruit set, seed set and 100 seed weight (DIEPENBROCK, 2000; HUDEWENZ ET AL., 2014, SCHNEIDER ET AL. 2015). Fruit set and seed set are more direct measures of plant reproduction (GARIBALDI ET AL., 2013), while 100 seed weight is a measure for resulting yield in terms of oil production (KLATT ET AL., 2014). The total seed weight is a combination of plant health, reproductive success and oil production and therefore best reflects economic value. Hence, we set the focus of our analysis on total seed weight (GAGIC ET AL., 2016). Several plant species have high compensation capacities and are able to reallocate resources within the plant in case of deficiencies and to increase a yield component at a later stage of development to reach full yield potential (BOS ET AL., 2007). A lower number of seeds per pod could therefore be compensated by higher seed weight (HUDEWENZ ET AL., 2014; LINDSTRÖM ET AL., 2016), but this compensation capacity is limited (GARRATT ET AL., 2018). As a result, variation in plant development and seed production can be high (McGregor, 1987) and it is reasonable to examine different yield parameters that might be influenced by factors differently.

We measured fruit set by counting the number of pods per OSR plant, and calculated seed set (the number of seeds per plant) by multiplying the mean number of seeds per pod, assessed on 20 pods per plant, by the total number of pods per plant. We measured the 100 seed weight for every plant on seeds dried at 65°C for 24h. Total yield was measured as the total seed weight per plant. Total seed weight was calculated by the number of seeds per plant, divided by 100 and multiplied with the 100 seed weight. The mean production per plant is a good indicator for the yield per hectare obtained by farmers (Schneider et al., 2015).

IV.2.2.2 Pollination

We used the number of pollinator visits to OSR flowers during a certain amount of time as a proxy for pollination service. Flower visitation rate is a more accurate measure for pollination service than pollinator abundance (Vázquez et al., 2005). Pollinator visits to OSR flowers were observed on plots of 4m² at varying distances to the flower field edge (see IV.2.2) for 5 minutes each, resulting in a total of 40 minutes for every field. Half of the observation plots were located in the spray windows of 25m², and the other half of the observation plots in pesticide sprayed areas. Two observation rounds were conducted during the short period of OSR flowering in late April and May under standardized weather conditions of a minimum of 15°C, no rain, low cloud cover and wind speeds in the hours between 9am and 6pm. Flower visits that included contact to the flower stigma were recorded for three major pollinator groups (honeybees, wild bees and flies) and the visitation rate of all pollinator groups combined was used for analysis.

IV.2.2.3 Natural pest control

To assess the level of natural pest control in OSR, we measured the parasitism of pollen beetle larvae (*Brassicogethes* spec.). Three plants within each of the eight 4m² plots at varying distances to the flower field edge (see IV.2.2) were cut during blooming (BBCH growth stage 64 – 65) and frozen until further analysis, resulting in 24 plants per field. Parasitism of pollen beetle larvae in open flowers was assessed by dissecting collected second instar larvae larger than 3mm and counting eggs of pollen beetle parasitoids. We only found black eggs of *Tersilochus heterocerus* in the pollen beetle larvae in our study were. Pollen beetle larvae smaller than 3mm were discarded, since *T. heterocerus* prefers second instar larvae and other studies detected low parasitism rates in smaller larvae (THIES ET AL., 2003). We calculated the parasitism rate by dividing the number of parasitized larvae by the total number of larvae > 3mm found on the plant.

IV.2.3 Statistical analysis

To assess the effects of flower field age and continuity as well as effects of pollination and natural pest control measures on oilseed rape yield, we performed structural equation models (SEM) for each of the four yield parameters (total seed weight, seed set, fruit set, 100 seed weight; Fig. IV.2). Linear mixed models were performed in 'R' version 3.5.3 (R CORE TEAM 2019) with the package 'nlme' (PINHEIRO ET AL. 2019). The response variables were ln +1 transformed to model normality of the residuals and residual plots were used to check model assumptions. We included *Field identity* as a random effect in all models to account for pseudoreplication, and *OSR variety* in the yield parameter models to account for differences between the OSR cultivars.

The different yield parameters total seed weight, fruit set, seed set and 100 seed weight were used as response variables in different SEMs. We used the following parameters as fixed effects: (1) *Type:* different types of flower fields (new flower field, refreshed flower field, continuous flower field) calcareous grasslands and crop fields, (2) *Distance:* distance to the adjacent field edge, (3) *Treatment:* Sprayed pesticide treatment of the OSR plants (+ Pesticide: pesticides applied according to regular farming scheme, - Pesticide: No pesticides applied), (4) *Field quality*: Value for soil quality in combination with climatic and site conditions as well as (5) *Pollination*: flower visitation and (6) *Natural pest control*: pollen beetle parasitism. Pollination and natural pest control were also used as response variables (Fig. IV.2). For the flower visitation rate, the mean of both observation rounds per plot was used for the statistical analysis. For parasitism rate and all yield parameters, the mean of the three plants per plot was used for analysis. We expected pollination and pest control to have direct positive effects on OSR yield. In-field conditions like within-field distance and pesticide treatment could have direct and indirect effects on OSR yield. Likewise, flower fields could have indirect effects on OSR yield, by influencing pollination and natural pest control. To examine if the ecosystem services pollination and natural pest control had interactive effects, we included a *pollination – natural pest control* interaction to the full SEMs. Full SEMs with all possible coefficients were performed for all yield parameters (Fig. IV.2) by using the R package 'piecewiseSEM' (LEFCHECK, 2016; SHIPLEY, 2013). P-values for the full SEMs were assessed using the function ‘sem.coefs’. Coefficients with p-values larger than 0.1 were excluded from the final SEMs. Subsequently, conditional R^2 values were calculated of the final SEMs using the function ‘rsquared’ and coefficient estimates using the function ‘sem.coefs’.

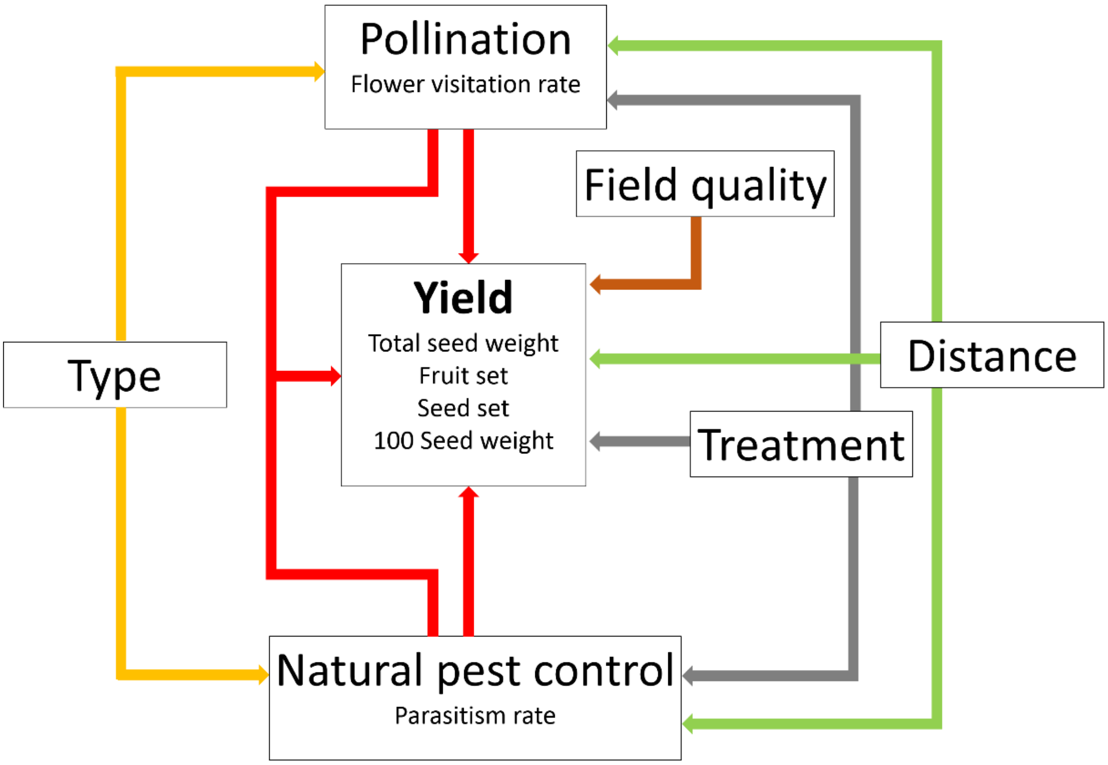


Fig. IV.2. Full structural equation model (SEM) displaying all hypothesized direct and indirect predictor variables affecting oilseed rape yield parameters (total seed weight, fruit set, seed set, 100 seed weight). Pollination (red): Flower visitation rate. Natural pest control (red): Pollen beetle parasitism rate. Type (yellow): Type of adjacent field (New flower fields; Refreshed flower fields; Continuous flower fields; Calcareous grasslands; Crop field). Distance (green): Distance to adjacent field edge; Treatment (grey): Pesticide treatment (+ pesticides; - pesticides). Field quality (brown): Value for soil quality in combination with climatic and site conditions.

IV.3 Results

In all structural equation models (SEM), the important predictors for pollination ($R^2=0.65$) were the type of adjacent field and the within-field distance (Fig. IV.3). Compared to the crop control, new flower fields had a negative effect on pollination in the oilseed rape (OSR) while more flower visits were conducted in OSR fields next to calcareous grasslands. Additionally, pollination showed distance decay with growing distance into the field. For natural pest control ($R^2=0.69$), the type of adjacent field, distance and treatment were important, thereby indirectly influencing the yield parameters total seed weight, fruit set and seed set. Refreshed and continuous flower fields had a positive effect on parasitism rate compared to the crop field, the parasitism rate decayed with the distance and pesticide application influenced it negatively (Fig. IV.3).

SEMs showed different predictor variables influencing the OSR yield parameters (total seed weight, seed set, fruit set, 100 seed weight; Fig. IV.3, Fig. IV.S1). Total seed weight ($R^2=0.18$) and seed set ($R^2=0.27$) were influenced positively by the parasitism rate (Fig. IV.4). High proportions of 75% parasitism increased total seed weight by a mean of 24.5% for both pesticide treatments. However, the intercept differs with the pesticide treatment (Fig. IV.4). All yield parameters except for 100 seed weight were positively influenced by pesticide application (+ pesticide treatment; Table IV.2; Fig. IV.3, Fig. IV.S1, Fig. IV.3). The fruit set ($R^2=0.31$) showed no connection to the parasitism rate, but instead showed to be slightly positive related to increasing distance to the field edge (Table IV.2). In fact, the 100 seed weight could not be explained by any of the tested fixed effects in our model. Remarkably, the field quality and pollination had no effect on any of the yield parameters. Additionally, the pollination and natural pest control interaction dropped out of all SEMs for the different yield parameters.

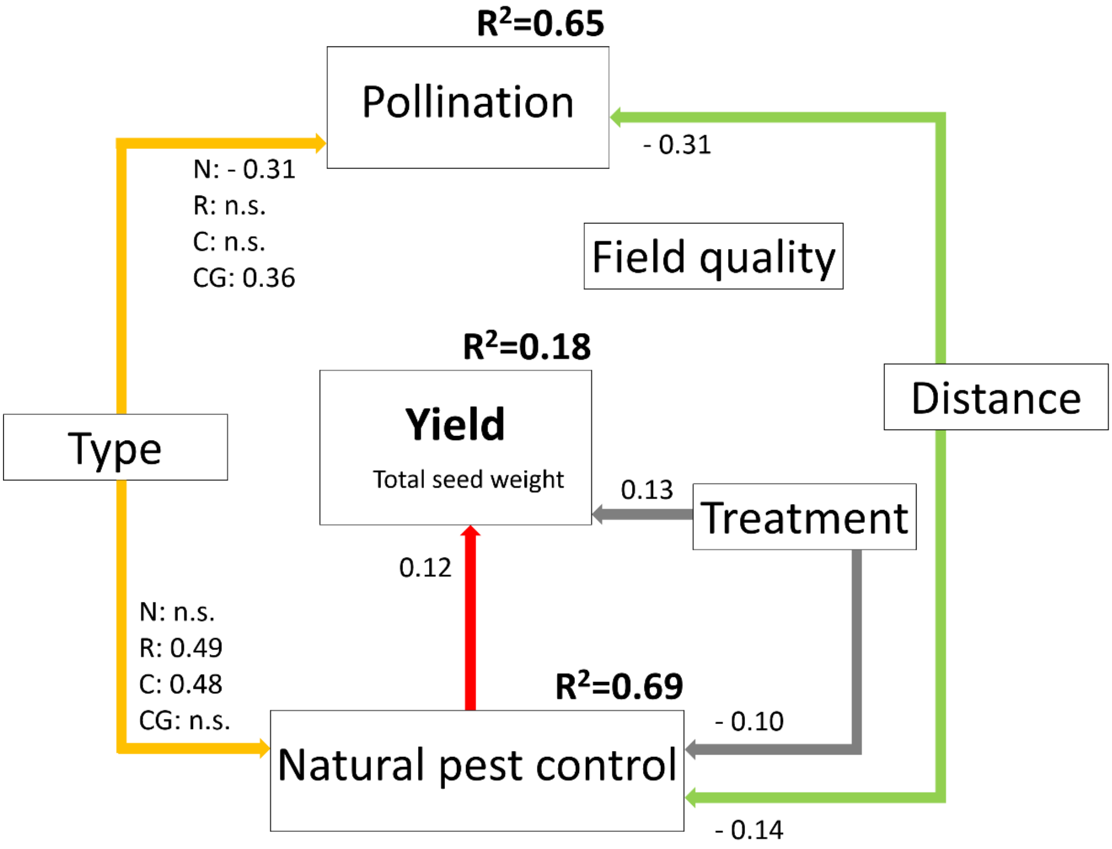


Fig. IV.3. Structural equation model (SEM) best supported by the data (coefficient p-value > 0.1, Table IV.S2) displaying direct and indirect predictor variables affecting total seed weight per plant. The relative amount of explained variance (R^2) is given for all endogenous variables. Numbers above paths represent estimates for standardized path coefficients. Pollination (red): Flower visitation rate. Natural pest control (red): Pollen beetle parasitism rate. Type (yellow): Type of adjacent field (N: New flower fields; R: Refreshed flower fields; C: Continuous flower fields; CG: Calcareous grasslands; estimates are depicted in relationship to the crop field negative control). Distance (green): Distance to adjacent field edge; Treatment (grey): Pesticide treatment (+ pesticides; estimates are depicted in relationship to the pesticide free treatment). Field quality (brown): Value for soil quality in combination with climatic and site conditions.

Table IV.2. Estimates for standardized path coefficients of the structural equation models (SEM) for the different yield parameters fruit set, seed set and 100 seed weight. Distance: Distance to adjacent field edge; Treatment: Pesticide treatment (+ pesticides; estimates are depicted in relation to the pesticide free treatment); Field quality: German value for soil quality in combination with climatic and site conditions.

	Fruit set	Seed set	100 Seed weight
Pollination	n.s.	n.s.	n.s.
Natural pest control	n.s.	**0.14**	n.s.
Distance	**0.07**	n.s.	n.s.
Treatment	**0.12**	**0.12**	n.s.
Field quality	n.s.	n.s.	n.s.

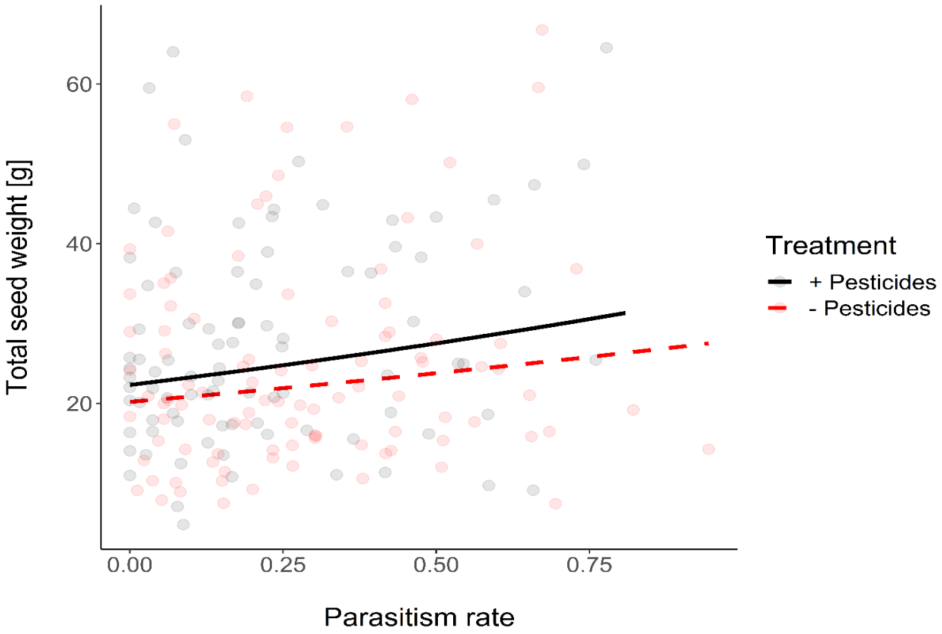


Fig. IV.4. Effects of the parasitism rate and the pesticide treatment on the total seed weight per oilseed rape plant. The fitted lines show model predictions for the parasitism rate on total seed weight in interaction with the pesticide treatment. Treatment: + Pesticide: pesticides applied according to regular farming scheme, - Pesticide: No pesticides applied on OSR.

IV.4 Discussion

In this study, we want to disentangle how differently aged flower fields might indirectly influence oilseed rape (OSR) yield via the ecosystem services pollination and natural pest control. Refreshed and continuous flower fields had positive effects on natural pest control, which in turn had a positive influence on total seed weight, fruit set and seed set. Unexpectedly pollination showed no positive effect on any of the different OSR yield parameters. Additional factors we tested were pesticide treatment, which had a negative effect on natural pest control but a positive impact on yield, within field distance, which had negative effects on the ecosystem services but a slight positive effect on fruit set and field quality, which had no effects on any of the tested yield parameters.

Yield formation is a complex process, with many factors influencing the development of the different yield parameters. Accordingly, while the R²-values for pollination (0.65) and natural pest control (0.69) were high, the R²-values for the different yield parameters were relatively low (total seed weight: 0.18; fruit set: 0.31; seed set: 0.27; 100 seed weight: 0). Overall, yield formation is heavily influenced by breeding and selection of preferable traits (DIEPENBROCK, 2000). Furthermore, fertilisation is an important factor influencing OSR yield (GAGIC ET AL., 2017). The fruit set of OSR plants, thus the number of pods per plant, is influenced by the supply of nutrients and water (ROOD AND MAJOR, 1984), while the seed weight is the last component formed during plant development and is influenced to a lesser extent by environmental conditions than other yield parameters (DIEPENBROCK, 2000). Ecosystem services contribute to yield formation: Pollination is important for the seed set and influences the number of seeds per plant, while natural pest control increases the fruit set, by reducing flower abortions (SUTTER AND ALBRECHT, 2016). Ecosystem services can interact with agronomic inputs such as fertiliser or pesticides (GARRATT ET AL., 2018). Only if fertiliser is not a limiting factor can OSR benefit from insect pollination (GARRATT ET AL., 2018). In our study, we did not interfere with the fertiliser application on our field. However, all farmers participating were experienced in OSR growing and we therefore expect no fertiliser shortcomings on our fields.

New flower fields had a negative effect on pollination compared to the conventional crop fields. They most likely act as pollinator concentrators due to their high flower cover (Table IV.1) and consequential attractiveness (KRIMMER ET AL., 2019). Calcareous grasslands on the other hand improved pollination compared to the crop fields. Calcareous grasslands are among the most species-rich habitats and support many wild pollinator species (STEFFAN-DEWENTER AND TSCHARNTKE, 2002) and many crops were shown to profit especially from pollination by wild pollinators (GARIBALDI ET AL., 2013). However, pollination showed no effect on seed set or any of the other yield parameters in our study. Oilseed rape flowers have many zoophilous adaptions that all point to pollination by insects rather than wind (CRESSWELL ET AL., 2004). However, wind and self-pollination is possible in OSR and responses of OSR yield to cross pollination differ, from no effect (WILLIAMS ET AL., 1986) to an increase of yield and market value if additionally pollinated by insects (BOMMARCO ET AL., 2012). Therefore, the benefits of cross insect pollination might be strongly depending on the OSR variety (HUDEWENZ ET AL., 2014). In field trials, increased insect pollination led to higher yields only in conventional OSR lines and not in hybrid OSR varieties (LINDSTRÖM ET AL., 2016). Due to maximized heterosis in hybrid OSR breeds, the plants could be less sensitive to pollination deficits and show higher compensation capacities (Diepenbrock, 2000). Since all OSR varieties grown in our experiment were hybrid, this could explain why pollination had no influence on yield in our experiment. However, another explanation would be that despite differences in pollination next to the different flower fields and low numbers of flower visits especially close to newly established flower fields (Krimmer et al., 2019), overall pollination was still sufficient to reach saturation levels and the threshold for full seed set formation. The same was observed in another study, where pollinators decreased with increasing distance, but yield did not (Lindström et al., 2016).

In this study, natural pest control was positively influenced by the refreshed and continuous flower fields only. However, in chapter III of this thesis we found, with a more elaborated statistical analysis not suitable for SEMs, that calcareous grasslands can also have positive effects on pollen beetle parasitism. Flower fields offer potential alternative hosts and food resources to parasitoids, thereby increasing their longevity (Lee and Heimpel, 2008; Segoli and Rosenheim, 2013). They may also aid strengthening parasitoid populations by improving their fecundity (Wratten et al., 2003). New flower fields however were only established a year prior to this study and did not have a positive effect on pollen beetle parasitism yet. We measured natural pest control in terms of parasitism rates of pollen beetles by *T. heterocerus*. Oilseed rape is attacked by several major pest species that cause massive yield losses and among them, pollen beetles are reported to have the strongest negative effect on OSR yield (Gagic et al., 2016; Schneider et al., 2015). Pollen beetles mainly affect the OSR fruit set by creating podless stalks: the pollen beetle adults and larvae feed on the pollen inside the flower buds, often causing them to drop off (Skellern and Cook, 2018). Effects of natural pest control of pollen beetles by parasitoids will mainly be visible in a reduced pollen beetle emergence of the following generation (ULBER ET AL., 2010B). However, a slight positive effect of natural pest control on the total seed weight and the seed set was visible in our experiment. Pollen beetle larvae can have negative effects on seed set and yield by excessive consumption of pollen and resulting pollen shortage, which is especially true for hybrid lines (WILLIAMS, 2010). *T. heterocerus* preferably parasitises second instar larvae in already open flowers (NILSSON, 2003). The parasitoid larva hatches inside the pollen beetle larva already before they drop to the ground to pupate (NILSSON, 2003). It can therefore be assumed, that the vitality of pollen beetle larvae suffers by being parasitized. Indeed, parasitized pollen beetle larvae were found to have smaller head capsules than unparasitized ones (NISSEN, 1997), which could point to a hindered development. Even though the reduction of the seed set could be to a degree compensated by a higher seed weight (WILLIAMS AND FREE, 1979), the OSR plants in our study directly benefitted from the natural pest control at the stage of seed set development, which then translated into an overall benefit on total seed weight per plant. Therefore, we conclude that flower fields have the potential to increase OSR yield by increasing natural pest control even in the same season.

Pesticide application had a negative effect on natural pest control, as can be expected since pesticides are known to have negative effects on non-target organisms such as beneficial parasitoids (HANSON ET AL., 2015; ULBER ET AL., 2010A). However, it had an overall positive effect on yield. First, farmers also refrained from spraying fungicides within the spray windows. Many different fungal diseases affect OSR (SÖCHTING AND VERREET, 2004), thereby possibly diminishing yield. Second, we were only able to take natural control of pollen beetles into account, whereas other pests also cause damage to OSR (Williams, 2010). Pesticide application might have reduced these additional pests, thereby increasing yield. In conventional agricultural landscapes, the potential of natural pest control can be diminished by excessive pesticide use (Krauss et al., 2011; Martin et al., 2019). Ecological intensification and the implementation of insect friendly management practices like organic farming or conservation tillage could increase natural pest control again (Krauss et al., 2011; Tamburini et al., 2016), maybe even to a level where pesticide application could be reduced. Pesticide treatment showed no effect on 100 seed weight, since pests do not directly influence this stage of yield formation.

Effects of the distance to the field edge can be ambiguous. On the one hand, pollinators and natural pest control agents can benefit from flower fields, but they can have limited mobility and show a strong distance decay to flower fields (Tylianakis et al., 2004), especially in landscape with low amounts of alternative habitats (Krimmer et al., 2019), thereby influencing yield negatively. On the other hand, flower fields can entail edge effects that have negative effects on yield, for example competition for nutrients and water (Brown and Glenn, 1999) or the facilitation of plant diseases (Wisler and Norris, 2005). In our study, pollination and natural pest control declined with growing distance into the field, while the fruit set slightly increased. As mentioned earlier, parasitism had no effect on fruit set in our study. And pest species such as pollen beetles colonize crop field from the edges (Schneider et al., 2015), which might explain the slight increase in OSR fruit set with growing distance to the field edge.

Unexpectedly, the field quality had no effect on any of the yield parameters in our study. The measure of field quality in our study is defined by a value combining soil quality and additional climatic or structural site conditions that could influence yields and should therefore be an adequate measure to at least partly explain yields (DIEPENBROCK, 2000). However, even though it differed between the individual OSR fields, the overall field quality might have been too good to detect any effects (Table IV.1).

Earlier studies showed positive effects of added flowering plants on yield, for example for winter wheat and blueberries due to improved ecosystem services (BLAAUW AND ISAACS, 2014; TSCHUMI ET AL., 2016). To our knowledge, this is the first study examining the indirect effects of sown flower fields and the direct effects of the ecosystem services pollination and natural pest control on oilseed rape yield in a combined model. We conclude, that flower fields have the potential to increase OSR yield by increasing natural pest control, except for newly established flower fields. Annual flower fields would therefore have no positive effects on OSR yield. An increase of pollination had no effect on OSR yield in our study. In general, many studies explore the effects of flower fields on ecosystem services (GARIBALDI ET AL., 2014), but more research is needed to see if these ecosystem services indeed in turn have effects on crop yield.

IV.5 Supplementary material

Table IV.S1. Oilseed rape (OSR) varieties grown on the different fields of our experimental field study and their distribution among the different adjacent fields. All grown OSR varieties are hybrids. N: New flower field, R: Refreshed flower field, C: Continuous flower fields, CG: Calcareous grassland, CF: Crop field.

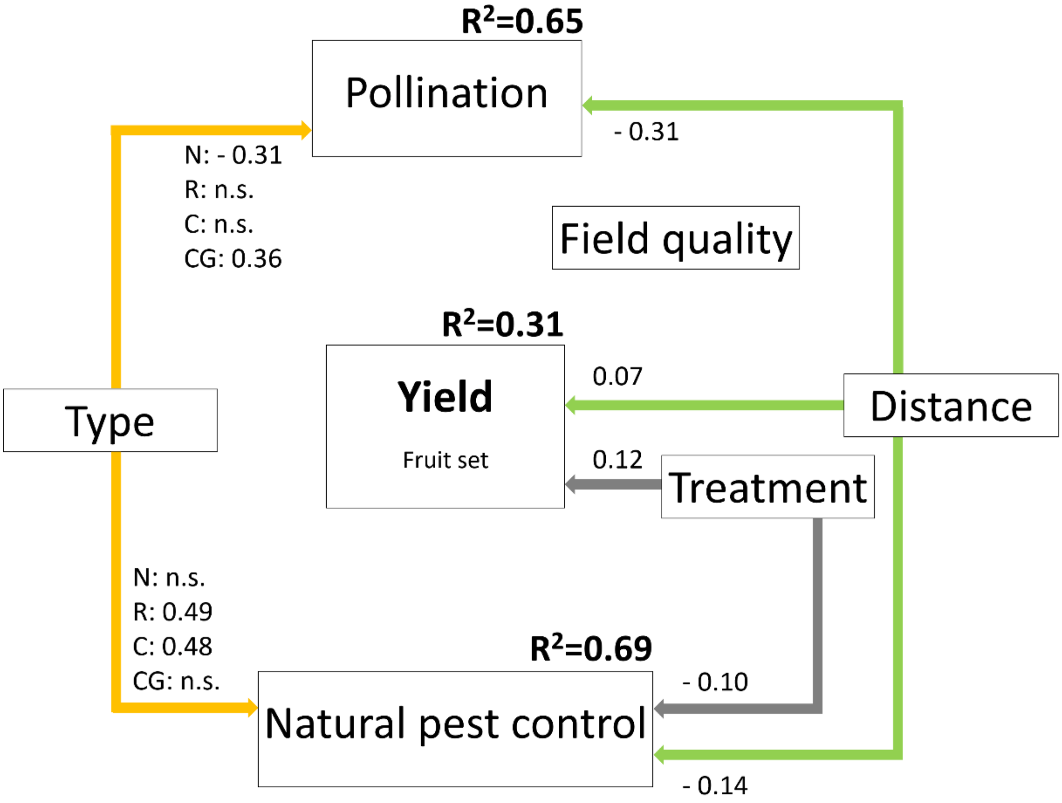
Name	Manufacturer	No. of fields	Types of adjacent fields
PR46W26	Du Pont Pioneer	4	N, N, N, R
PR46W20	Du Pont Pioneer	1	C
PT225	Du Pont Pioneer	4	N, CG, CF, CF
PT229CL	Du Pont Pioneer	2	C, C
Ivan 106 /PX 106	BayWa	1	N
Müller 24/PR46W24	BayWa	3	R, C, CG
Mercedes	Rapool	1	N
Avatar	Rapool	6	R, R, R, C, CG, CF
Visby	Rapool	1	C
Raptor	KWS	1	N
Sherlock	KWS	1	R
DK Excellium	Dekalb Monsanto	1	R
DK Eximus	Dekalb Monsanto	1	CG
Alabama	LG seeds	1	R
Flyer	Bayer	1	C
Basalti CS	Caussade	2	N, CF

Table IV.S2. P-values of the coefficients in the full structural equation models (SEM) for (A) the different yield parameters (total seed weight, fruit set, seed set, 100 seed weight) as well as (B) pollination and natural pest control. Type: Type of adjacent field (N: New flower fields; R: Refreshed flower fields; C: Continuous flower fields; CG: Calcareous grasslands; p-values are depicted in relation to the crop field negative control). Distance: Distance to adjacent field edge; Treatment: Pesticide treatment (+ pesticides; p-values are depicted in relation to the pesticide free treatment). Field quality: Value for soil quality in combination with climatic and site conditions. Significance levels: **.** *p*<0.1; **p* < 0.05, ***p* < 0.01, ****p* < 0.001.

(A)	Total seed weight	Fruit set	Seed set	100 seed weight
Pollination	0.448	0.695	0.577	0.404
Natural pest control	**0.091 .**	0.111	**0.054 .**	0.262
Pollination*Natural pest control	0.482	0.102	0.147	0.146
Distance	0.181	**0.092 .**	0.131	0.318
Treatment	**0.067 .**	**0.044 ***	**0.068 .**	0.536
Field quality	0.673	0.797	0.531	0.557

(B)	Pollination	Natural pest control
Type		
N	**0.093 .**	0.157
R	0.576	**0.059 .**
C	0.517	**0.076 .**
CG	**0.091 .**	0.153
Distance	**< 0.001 *****	**0.001 ****
Treatment	0.143	**0.024 ***

(A)


R²=0.65
Pollination
- 0.31
N: - 0.31
R: n.s.
C: n.s.
CG: 0.36
Field quality
R²=0.31
Yield
Fruit set
0.07
Distance
Type
0.12
Treatment
N: n.s.
R: 0.49
C: 0.48
CG: n.s.
R²=0.69
- 0.10
Natural pest control
- 0.14

(B)

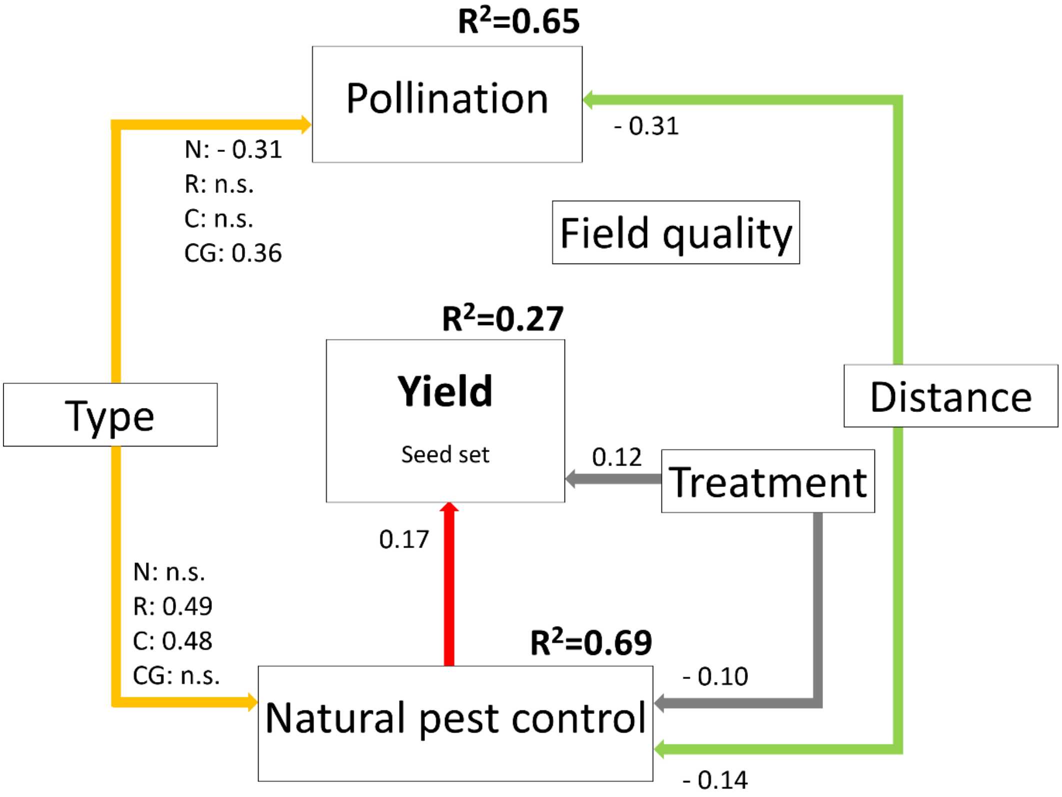

R²=0.65
Pollination
- 0.31
N: - 0.31
R: n.s.
C: n.s.
CG: 0.36
Field quality
R²=0.27
Yield
Seed set
Distance
Type
0.12
Treatment
0.17
N: n.s.
R: 0.49
C: 0.48
CG: n.s.
R²=0.69
- 0.10
Natural pest control
- 0.14

Fig. IV.S1. Structural equation models (SEM) best supported by the data (coefficient p-value > 0.1, Table IV.S2) displaying direct and indirect predictor variables affecting (A) fruit set, (B) seed set. The 100 seed weight could not be explained by the fixed effects in the model, therefore no path model is shown for 100 seed weight. The relative amount of explained variance (R^2) is given for all endogenous variables. Numbers above paths represent estimates for standardized path coefficients. Type: Type of adjacent field (N: New flower fields; R: Refreshed flower fields; C: Continuous flower fields; CG: Calcareous grasslands; estimates are depicted in relationship to the crop field negative control). Distance: Distance to adjacent field edge; Treatment: Pesticide treatment (+ pesticides; estimates are depicted in relationship to the pesticide free treatment).

Chapter V: General Discussion

Specific recommendations for the implementation of flower-rich agri-environment schemes improve their impact on certain ecosystem services.

V.1 Flower-rich agri-environment schemes

Agri-environment schemes often include measures that aim to improve natural habitat quality or quantity, such as the restoration of hedgerows or the implementation of flower fields or strips (BOMMARCO ET AL., 2013). Many European countries offer AES that include the establishment of sown flower fields, for example Austria and Germany (HAALAND ET AL., 2011). The sown flower fields examined in this study were or have been part of a German agri-environment scheme (AES) called 'Kulturlandschaftsprogramm'. According to the state department for Agriculture in Bavaria, the flower fields of the 'Kulturlandschaftsprogramm' aim to provide nectar and pollen to flower visitors as well as structure, cover and nourishment for wild animals (STMELF 2019).

Apparently, the 'Kulturlandschaftsprogramm' just generally aims to enhance biodiversity and the AES itself provides only few guidelines for flower field implementation. The farmers participating can decide the specifics themselves within a certain framework. Annual flower fields that rotate each year as well as perennial flower fields that persist five years are available within the program. Farmers can choose crop fields, longtime set-asides or former flower fields to establish their new flower fields, thereby creating flower fields with varying history. Additionally, farmers can choose the location of the flower field at will and it can be assumed that farmers are driven by economic considerations (BURTON ET AL., 2008) and would not dispense their most productive fields, even if the compensation increases with the yield potential of the respective field. Subsequently, it can be assumed that flower fields in intensively used agricultural landscapes with high quality soil will be scarce. Furthermore, the maximum flower field area per farmer funded by government is 3ha, but farmers can distribute the area variably among their fields. No recommendation is made by the AES restrictions if single big or several small fields are preferable. Without specific recommendations on how to implement flower-rich agri-environment schemes to reach a specific aim, the measures cannot be expected to unfold their full potential (SCHEPER ET AL., 2013).

V.2 Why agri-environment schemes fail

Agri-environment schemes (AES) aim to conserve rare species and enhance biodiversity-dependent ecosystem services in the agricultural landscape (EKROOS ET AL., 2014; KLEIJN ET AL., 2006). Oftentimes, the direction of a certain AES is not specifically defined (SCHEPER ET AL., 2013) and AES just aim to generally enhance biodiversity (KLEIJN AND SUTHERLAND, 2003). The problem is that AES lacking specific conservation goals are often poorly designed and prone to failure (KLEIJN ET AL., 2006; KLEIJN AND SUTHERLAND, 2003). In order to achieve its goals and to improve certain measures, the object of an AES needs to be clearly defined (SCHEPER ET AL., 2013). Otherwise, spatial or temporal mismatches can occur and the AES can have little to no effect on biodiversity (WHITTINGHAM, 2007).

For example, in the Netherlands an AES for wet meadows designed to increase the number of waders also incorporated relatively dry fields that are of little value to waders, thereby showing low effectiveness in increasing wader numbers (VERHULST ET AL., 2007). An AES in the United Kingdom for farmland bird preservation failed to provide sufficient food resources during winter time and therefore failed to enhance bird survival (SIRIWARDENA ET AL., 2008). Just as important as the temporal scale is the spatial scale, and the success of the farmland bird AES in the UK also depended on the distance between complementary food resources (SIRIWARDENA, 2010). Misguided AES can have severe negative consequences for certain species: the intense mowing regime of a grassland AES in the Czech Republic, implemented to benefit grass species richness and rare orchids, lead to the rapid extinction of the globally threatened butterfly *Colias myrmidone* (KONVICKA ET AL., 2008). Some measures that are part of an agri-environment scheme might directly oppose species living within the same habitat as the supposedly beneficial species, thereby explaining the low overall biodiversity benefits achieved by insufficiently elaborated AES (KLEIJN ET AL., 2006; KONVICKA ET AL., 2008). The impact of AES can largely depend on the specifics of their implementation, and interacting effects of the AES measure and the surrounding landscape can be crucial for their success or failure (CARVELL ET AL., 2011; SCHEPER ET AL., 2013). The goal of this study was to examine how the flower field characteristics age, size and the complexity of the surrounding landscape influence the provision of the ecosystem services pollination and natural pest control, as well as ultimately yield. The results of this study provide knowledge that can specify recommendations for flower field implementation to maximize benefits on ecosystem services.

V.3 Flower field characteristics and ecosystem services

V.3.1 Flower field age

Several sown flower field characteristics can influence their effectiveness to promote ecosystem services like pollination and natural pest control, one of them being the age of the flower field. Older flower strips generally harbour increased insect diversity compared to younger ones (HAALAND ET AL., 2011). Wildflower patches were shown to increase pollinator abundance with increasing age (BLAAUW AND ISAACS, 2014; WOODCOCK ET AL., 2014) as well as natural enemy species richness and abundance (FRANK ET AL., 2007). However, an earlier study on the same fields as the present study found no influence of the differently aged flower fields on ground-dwelling predator communities (BOETZL ET AL., 2018).

In this study, it was shown that flower field age can affect pollinator abundance within the field itself as well as the amount of flower visits an adjacent oilseed rape (OSR) field receives. Young and newly established flower fields show a wide variety of annual flowers and high flower cover already in spring, making them attractive for pollen and nectar collecting insects such as bees and flies (KOHLER ET AL., 2008). However, this also seems to lure pollinators away from adjacent crops and into the flower field itself, since there were fewer flower visits in OSR adjacent to large new flower fields than compared to older fields. It is possible, that flower fields that are very attractive act as pollinator concentrators and prevent the pollinators from distributing into the surrounding landscape (LANDER ET AL., 2011; MORANDIN AND KREMEN, 2013). It was also shown in another study, that young and newly established flower fields can have negative effects on pollinator richness and abundance in their surroundings (KOHLER ET AL., 2008). Most likely, this negative effect on close-by pollination is caused by a combination of the high attractiveness and missing pollinator populations. Since populations need time to develop, habitat restoration does not translate into immediate population increases (ILES ET AL., 2018). However, an increase in pollinator abundance can be expected over time (BLAAUW AND ISAACS, 2014) and indeed in our study, flower visits were higher in OSR fields next to older flower fields. Additionally, pollen beetle parasitism in the OSR fields in our study was increased next to older flower fields compared to conventional crop fields, but not next to new flower fields. Accordingly, in a study on ground-dwelling predators higher abundances were found next to three year old compared to one year old flower strips (FRANK AND REICHHART, 2004). It can therefore be concluded, that annually rotating flower fields are not desirable if you want to increase pollination or natural pest control to nearby crops. On the contrary, this study shows that neutral or negative effects on ecosystem services can be expected from newly established flower fields.

V.3.2 Flower field size

The single large or several small question is an ongoing debate in conservation biology (OVASKAINEN, 2002). The question is, if one single large or several small fragments of habitat are to be preferred when it comes to biodiversity conservation (TSCHARNTKE ET AL., 2012). The argument for many small fragments is, that they can be distributed over a wider landscape and therefore cover more diverse habitats and support more species (QIAN AND SHIMONO, 2012). However, large fragments often support larger populations and higher immigration rates, therefore being less prone to extinction (MACARTHUR AND WILSON, 1967). This debate can be translated partially into the question if one large flower field or several small flower fields should be preferred when it comes to the improvement of ecosystem services. If the goal is to increase pollination to crops, it was shown that small patches of high quality forage such as wildflower plantings can be sufficient to increase pollinator abundance and flower visits to crops (CARVELL ET AL., 2011; FELTHAM ET AL., 2015). Nevertheless, it was also shown that natural enemy density and richness increased with the size of the flower field, since larger fields offer more quality habitat area and resources (BLAAUW AND ISAACS, 2012).

Flower field size interactively shaped the amount of pollination nearby crops received in our study with flower field age. As stated before, new flower fields decreased flower visits to nearby crops, but only if they were larger than 1.5ha. New flower fields only acted as pollinator concentrators when they exceeded a certain size and smaller flower fields might not have negative effects on ecosystem services in their vicinity and might therefore be preferable if you want to increase pollination. However, a study in the Netherlands found that already small patches of flowers of just 0.01ha size can decrease bee abundance in adjacent fields (KOHLER ET AL., 2008), demonstrating that these effects might also depend on other factors, such as landscape context. Furthermore, larger flower fields in our study supported higher amounts of natural pest control by exhibiting higher pollen beetle parasitism and superparasitism rates. This supports the findings of Blaauw and Isaacs (2012) that larger fields are preferable if you want to promote natural pest control. Indeed, the impact of flower field size seems to depend on the ecosystem service you want to promote and large flower fields would be needed for the simultaneous promotion of pollination and natural pest control.

V.3.3 Landscape complexity

The third factor important for the effectiveness of flower fields examined in this study is the complexity of the surrounding landscape. As already mentioned in the general introduction, it is argued that agri-environment schemes such as flower fields should have the most impact in landscapes with intermediate complexity (SCHEPER ET AL., 2013; TSCHARNTKE ET AL., 2012), but often show the highest impact in simple landscapes (BATÁRY ET AL., 2011; SCHEPER ET AL., 2013). In simple landscapes, the ecological contrast created by an AES might be the highest, explaining high biodiversity gains. On the other hand, simple landscapes often show low species richness and abundance (RICKETTS ET AL., 2008) and the species pool to colonize the habitat introduced by the AES might be missing in these landscapes (SCHEPER ET AL., 2013; TSCHARNTKE ET AL., 2012). However, flower fields might have the biggest impact on ecosystem services in intensively farmed landscapes with pollination deficits, where they can actively promote mobile generalist species (DEGUINES ET AL., 2014; KLEIJN ET AL., 2015).

In this study, landscape complexity was defined as the amount of semi-natural habitats (SNH) within the 1km area we chose for our sample landscapes. Semi-natural habitats are mostly permanent, require low maintenance, are relatively undisturbed and therefore differ from crop land in several ways (DUFLOT ET AL., 2015). Earlier studies showed, that the amount of SNH in a certain landscape is a good proxy for landscape complexity (CHAPLIN-KRAMER ET AL., 2011). The landscapes in this study were selected along a SNH gradient to examine effects and interactions of the landscape complexity with the AES sown flower fields. We found that pollination increased with the amount of SNH in the surroundings, but only for small flower fields. For large flower fields, the flower visits did not increase with SNH. The amount of SNH generally increases the amount of pollinators in the landscape (ÖCKINGER AND SMITH, 2007). However, similar to the result of the age and size interaction, large flower fields might have acted as pollinator concentrators. Therefore, the OSR fields next to large flower fields could not profit from the increased number of pollinators in complex landscapes. Again, this was not visible next to small flower fields, which might not offer enough resources to exhibit this effect. A second effect of SNH on pollination found was a less distinct distance decay within the crop fields in complex landscapes. Apparently, in complex landscapes pollinators can find suffice nesting sites and venture into the crop fields from all sides, while in simple landscapes flower fields gain importance as starting points for pollinators to spillover into crops.

Many studies show higher natural pest control in landscapes with high amounts of SNH, but there are also studies showing the opposite (KARP ET AL., 2018). In this study, pollen beetle parasitism decreased with increasing amount of SNH, especially in pesticide treated fields. The landscape configuration and local habitat characteristics can actually have a larger effect on natural pest control than pure landscape composition (MARTIN ET AL., 2019). Furthermore, temporal dynamics might obscure actual effects of landscape complexity on natural pest control. Crop dynamics and annual turnovers in landscape composition might interact with population dynamics (KARP ET AL., 2018). The pattern on landscape complexity and natural pest control observed in this study might therefore be caused by underlying factors not taken into account by the study design and analysis.

V.4 Ecosystem services and yield

Many studies examine the effects of sown flower fields on the ecosystem services pollination and natural pest control, but studies looking at the effects on actual crop yield are scarce (GARIBALDI ET AL., 2014; SUTTER AND ALBRECHT, 2016). Positive effects of flower fields on yield have been shown for winter wheat, bell pepper, mango and blueberries due to improved ecosystem services (BLAAUW AND ISAACS, 2014; CARVALHEIRO ET AL., 2012; PEREIRA ET AL., 2015; TSCHUMI ET AL., 2016). Oilseed rape yield formation is a complex process with many factors involved, among them breeding, fertilisation and the compensation capacity of the plant (DIEPENBROCK, 2000; GAGIC ET AL., 2017; ROOD AND MAJOR, 1984). Therefore, to examine the role sown flower fields and the ecosystem services pollination and natural pest control might play in the process of yield formation is also complex.

As described in the earlier paragraphs, flower fields have effects on the ecosystem services pollination and natural pest control. These ecosystem services in terms might influence crop yield (BOMMARCO ET AL., 2012; TSCHUMI ET AL., 2016). In this study, pollination had no effects on OSR yield. Even though it was shown, that OSR can profit from insect pollination (BOMMARCO ET AL., 2012), this effect might be depending on the variety (LINDSTRÖM ET AL., 2016). Many OSR varieties are hybrid lines, with a maximized heterosis effect that gives them higher compensation capacities and makes them less susceptible to pollination deficits (DIEPENBROCK, 2000; LINDSTRÖM ET AL., 2016). Hybrid lines dominate the OSR market and all varieties grown in this study were hybrid lines, which could explain why we found no effect of pollination on OSR yield. However, we found a positive effect on OSR yield facilitated by natural pest control in terms of pollen beetle parasitism. Since the parasitoids hatch inside the host pollen beetle larvae before they drop to the ground to pupate, parasitoids can have negative effects on pollen beetle larva vitality (NILSSON, 2003). Natural pest control by parasitoids therefore not only has effects on pest emergence of the next generation, by killing the pupating pollen beetle larva in the soil, but also direct effects on the crop damage facilitated by pollen beetle larvae feeding in the flowers. It was shown in this study, that sown flower fields have diverse effects on the ecosystem services pollination and natural pest control, and these in terms can have effects on OSR yield. Sown flower fields can therefore help to promote ecological intensification in agricultural landscapes and lessen the need for conventional farming inputs such as fertilizer and pesticides.

V.5 Conclusion and outlook

This study highlights the importance of the way of flower field implementation. To achieve a certain goal, for example the improvement of pollination or natural pest control, different flower field characteristics could become important. It is also noteworthy, that while a flower field characteristic is positive for one ecosystem service, it might be negative for another. In this study, this was the case for the size of flower fields. Large flower fields can have negative effects on pollination to nearby crops, since fields may act as pollinator concentrators. Hence, large flower fields can be competition for crop fields. However, on the other hand large fields support higher pollen beetle parasitism in adjacent OSR. To enhance both ecosystem services pollination and natural pest control, a mixture of differently composed fields might be most beneficial. Few large flower fields should be complemented with several small flower fields. Furthermore, while some flower fields should not be management for long periods to gain continuity, others should be re-sown frequently to warrant a high amount of floral resources in the landscape. With these combined measures, sown flower fields could improve ecosystem services successfully. In turn, these ecosystem services can improve yields, as shown in chapter IV. Ecological intensification can decrease the need for external inputs in agricultural farming, it is an unharmful and sustainable way to improve crop yields (BOMMARCO ET AL., 2013). Flower fields have the capacity to support ecological intensification. However, it was also shown that flower fields have a different quality than semi-natural habitats and cannot substitute for them. For instance, flower fields enhance pollination only very locally. This highlights the importance of conserving and restoring semi-natural habitats such as field margins, roadside vegetation and calcareous grasslands in agricultural landscapes. They serve as corridors between different habitat types and as permanent undisturbed refuge habitats (HOOFTMAN AND BULLOCK, 2012).

This study examined, how sown flower fields must be composed to impact the ecosystem services pollination, natural pest control and ultimately yield. It is a contribution to a better understanding of which factors are involved in these processes, but open questions remain. One important factor not considered in this study are the seed mixtures used for the sown AES flower fields (CARVELL ET AL., 2006). Seed mixtures differ greatly in their composition and functionality and assembling a seed mixture that exhibits high amounts of floral resources over a period of many years is challenging. Seed mixtures could also specialize on different animal groups and be adapted to their specific needs. Furthermore, the quality of the different types of sown flower fields as overwintering habitats is of interest. As part of this project, but not of this thesis, cage experiments were conducted on the different flower fields (Fig. V.1). Emerging flying and ground-dwelling insects were collected in pitfall and pantraps in early spring and for the whole subsequent field season. The age, continuity and size of flower fields as well as the surrounding landscape could also prove important in this regard.

The decline of fallows, hedgerows and flower-rich field margins in the last decades resulted in habitat loss for many insect species and the increased use of potent insecticides might add to this (SEIBOLD ET AL. 2019). As a concluding remark, it can be stated that the decline of biodiversity in intensively used agricultural landscapes (SEIBOLD ET AL 2019) highlights the need for ecologically beneficial alternatives to conventional agriculture. If implemented the right way, sown flower fields can to a degree help mitigate the problems of conventional agriculture.

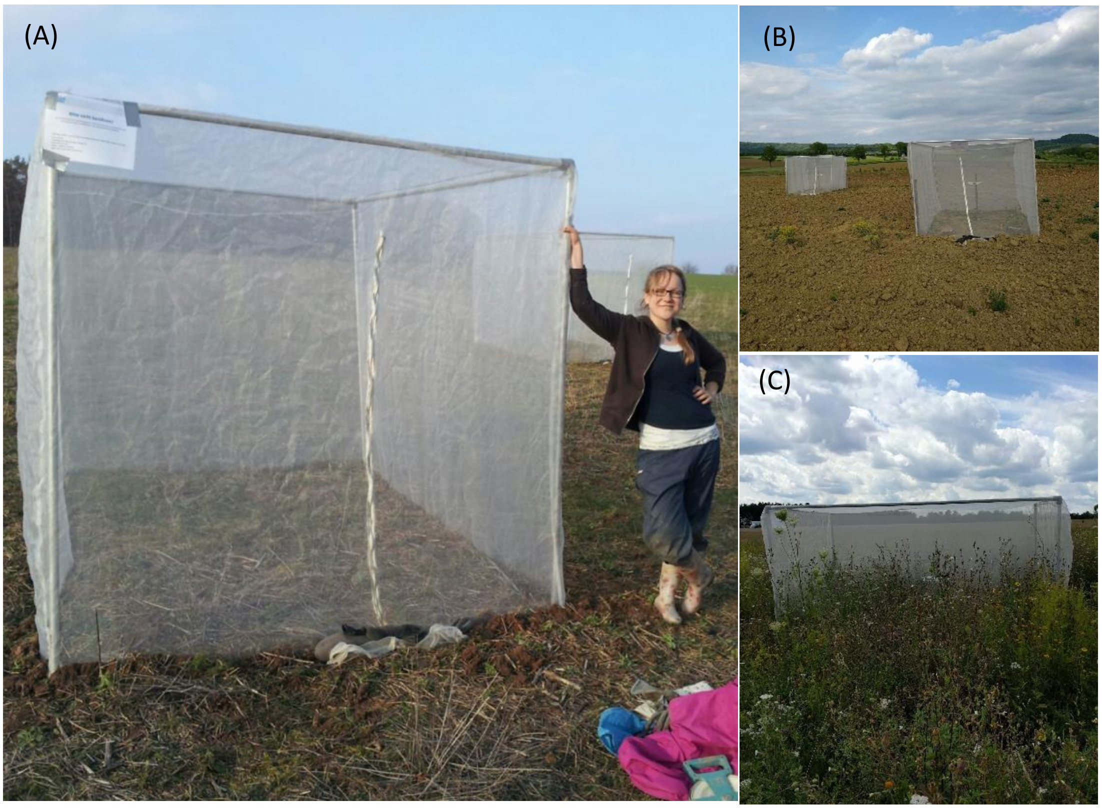


Fig. V.1 Cage experiment conducted as part of the Ecodeal project on different types of sown flower fields. (A) Continuous flower field with dense vegetation which is mulched yearly, (B) flower fields ploughed and freshly sown the same season, (C) refreshed flower field during summer.

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Author contributions

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EK, EAM, AH, JK and ISD conceived and designed the study; EK collected and analysed the data; EK, EAM and ISD interpreted the results. EK wrote the first draft of the manuscript. All authors contributed to manuscript revision and gave final approval for publication.

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* Corresponding author (contributed 80-90% of this study)

Author contributions

EK, EAM, AH, JK and ISD conceived and designed the study; EK collected and analysed the data; EK, EAM and ISD interpreted the results. EK wrote the first draft of the manuscript. All authors contributed to manuscript revision.

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Affidavit / Eidesstattliche Erklärung

I hereby declare that my thesis entitled: **„Agri-environment schemes and ecosystem services: The influence of different sown flower field characteristics on pollination, natural pest control and crop yield.”** is the result of my own work. I did not receive any help or support from commercial consultants. All sources and materials applied are listed and specified in the thesis.

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Krimmer E, Martin EA, Krauss J, Holzschuh A, Steffan-Dewenter I. (in preparation) Flower fields and pesticide use interactively shape pollen beetle infestation and parasitism in oilseed rape fields.

Krimmer E, Martin EA, Krauss J, Holzschuh A, Steffan-Dewenter I. (in preparation) The contribution of sown flower fields to oilseed rape yield.

Additional publications

König K, Zundel P, **Krimmer E**, König C, Pollmann M, Gottlieb Y, Steidle JLM. (2019) Reproductive isolation due to prezygotic isolation and postzygotic cytoplasmic incompatibility in parasitoid wasps. *Ecology and Evolution*. DOI: https://doi.org/10.1002/ece3.5588

Boetzl FA, **Krimmer E**, Krauss J, Steffan-Dewenter I. (2018) Agri-environmental schemes promote ground dwelling predators in adjacent oilseed rape fields: diversity, species traits and distance-decay functions. *Journal of Applied Ecology*. DOI: https://doi.org/10.1111/1365-2664.1316

König K, **Krimmer E**, Brose S, Gantert C, Buschlüter I, König C, Klopfstein S, Wendt I, Baur H, Krogmann L, Steidle JML. (2015) Does early learning drive ecological divergence during speciation processes in parasitoid wasps? *Proc. R. Soc. B* 282: 20141850. DOI: https://doi.org/10.1098/rspb.2014.1850

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