

Landscape-scale spillover of pollinators from oil-seed rape to crop and semi-natural habitats on different temporal scales



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„Wer glaubt, etwas zu sein, hat aufgehört, etwas zu werden“

(Sokrates)

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Ehrenwörtliche Erklärung

Hiermit erkläre ich ehrenwörtlich, dass ich die vorliegende Dissertation mit dem Titel „*Landscape-scale spillover of pollinators from oil-seed rape to crop and semi-natural habitats on different temporal scales*“ selbstständig, am Lehrstuhl für Tierökologie und Tropenbiologie (Zoologie III) der Julius-Maximilians-Universität Würzburg, unter Anleitung und Betreuung durch Frau PD Dr. Andrea Holzschuh und Herrn Prof. Dr. Ingolf Steffan-Dewenter angefertigt habe und dabei keine anderen als die von mir angegebenen Quellen und Hilfsmittel verwendet habe. Ich erkläre außerdem, dass die vorliegende Dissertation weder in gleicher, noch in ähnlicher Form bereits in einem Prüfungsverfahren vorgelegen hat. Des Weiteren habe ich außer den mit dem Zulassungsantrag urkundlich vorgelegten keine weiteren akademischen Grade erworben oder zu erwerben versucht.

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Verena Riedinger

Publication list

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Bussler, H., Bouget, C., Brustel, H., Brändle, M., **Riedinger, V.**, Brandl, R., Müller, J. (2011). Abundance and pest classification of scolytid species (Coleoptera: Curculionidae, Scolytinae) follow different patterns. *Forest Ecology and Management*, 262, 1887-1894.

Riedinger, V., Dworschak, K., Gruppe, A., Schopf, R. (2009). Induced response in spruce and performance of the spruce bark beetle (*Ips typographus*; Coleoptera: Curculionidae; Scolytinae). *Mitt. Dtsch. Ges. Allg. Angew. Ent.*, 17, 179-183.

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Summary (English)

I. Organisms use different resources in different habitat types during their life cycle. Thereby, they connect habitats and provide ecosystem services or disservices in several habitat types. In agricultural landscapes, the spillover of organisms, i.e. movement of an organism and its function from one habitat to another, especially from semi-natural to managed habitats, is one of the most important processes that influence population dynamics and community composition. Importantly, spillover connects habitats not only spatially, but also on different temporal scales, because availability of resources changes over time in agricultural landscapes, e.g. by mass-flowering events of crops, harvesting or crop rotation. Most often, semi-natural habitats are seen as beneficial source of organisms, but also managed habitats can provide valuable resources, and thereby initiate spillover to other habitats. Mass-flowering crops, like oil-seed rape, are such valuable feeding resources for pollinators, and pollinators might spillover from oil-seed rape to other habitats which provide alternative foraging resources. The focus of this dissertation was to evaluate the influence of oil-seed rape on pollinators in agricultural landscapes by studying effects (1) on different temporal scales (from effects during the flowering period of oil-seed rape, Chapter II & IV, to intermediate effects on a second mass-flowering crop, Chapter III, to spillover effects to the flowering period in the next year, Chapter IV), (2) semi-natural (Chapter II) and crop (Chapter III, IV) habitats, and (3) on various pollinator groups which differ in their life cycle (Chapter II, III, IV).

II. We studied the effects of the relative cover of oil-seed rape in the landscape in three habitat types in 16 independent landscapes around Würzburg, Germany, during and after flowering of oil-seed rape over two consecutive years. During mass-flowering, pollinators diluted with an increasing relative cover of oil-seed rape in the landscape. Thereby, local densities of bumble bees decreased on field boundaries, and densities of bumble bees and other wild bees on oil-seed rape fields. Pollinators in high quality semi-natural grasslands were only marginally negatively affected by an increasing relative cover of oil-seed rape in the landscape during the flowering period. The relative cover of semi-natural habitats in a landscape benefitted pollinator densities in crop fields. After mass-flowering, bumble bees spilled over to field boundaries, leading to increased local densities in landscapes with a high relative cover of oil-seed rape. Our results indicate that during mass-flowering a high relative

cover of oil-seed rape in the landscape might decrease pollination services per unit area on crop fields, but also the availability of pollinators for pollination of wild plants in semi-natural habitats. After mass-flowering, a high previous relative cover of oil-seed rape might support pollination services to wild plants on semi-natural habitats. Only if a semi-natural habitat is comparably attractive to oil-seed rape, it might be more independent of spillover and dilution effects of oil-seed rape.

III. On 16 sunflower fields in independent study landscapes around Würzburg, Germany, we evaluated the effects from early-flowering oil-seed rape on late-flowering sunflowers as a second managed mass-flowering crop with a non-overlapping flowering period. Highest bumble bee densities were found on sunflower fields that combined a high relative cover of oil-seed rape in spring and a high relative cover of semi-natural habitats in the surrounding landscape, while honey bees and hoverflies were not affected by the relative cover of oil-seed rape. A high relative cover of oil-seed rape in spring could even mitigate the pollinator dilution that would otherwise result in decreased local densities of bumble bees on sunflower fields with an increasing relative cover of sunflowers in the landscape. Our study suggests that management of a landscape-scale pattern of early- and late-flowering crops together with semi-natural habitats can benefit certain generalist pollinators and probably also stabilize pollination services.

IV. On 32 oil-seed rape fields (16 in two study years) in 16 independent landscapes (Chapter II) we evaluated the long-term effects of oil-seed rape on bumble bees and other wild bees by regarding not only the current relative cover of oil-seed rape but also its relative cover in the previous flowering season. By applying a mechanistic modelling approach, we could show that oil-seed rape was more attractive for foraging of both pollinator groups than the rest of the landscape. This affects the distribution of both pollinator groups in the landscape by dilution or concentration processes in the current year. The previous relative cover of oil-seed rape showed to have influence only on wild bees other than *Bombus* and increased their densities on oil-seed rape fields in the current year. Our results indicate that inter-annual spillover may be more distinct for pollinators whose sexual reproduction match the period of mass-flowering and thereby directly translate the resource supply by oil-seed rape to offspring density. In general, more studies on inter-annual effects of crops are needed to better understand dynamics and distribution of various species groups that may provide important ecosystem services in agricultural landscapes.

V. In this dissertation effects from oil-seed rape on all temporal scales – in the short term during mass-flowering and in the long term on a late-flowering crop and even in the next

year on oil-seed rape fields – were found. These effects might be important for crop and wild plant pollination, and pollinator conservation. Importantly, the effects on different temporal scales depend on the considered habitat (managed or different semi-natural habitats) and on the investigated pollinator group. The more pollinators match the flowering period of oil-seed rape in their activity period and the more dependent they are on flowering resources in their life cycle, the more pronounced are their responses. Effects were found for wild bees, but not for hoverflies and honey bees. Moreover, the availability of semi-natural habitats in the landscape is important and may modulate effects from oil-seed rape. The longevity of effects of oil-seed rape shows the importance of including several temporal scales into ecosystem-service studies, not only for pollinators, but also for other ecosystem-service providing species groups.

Zusammenfassung (German)

I. Organismen nutzen während ihres Lebens verschiedene Ressourcen in unterschiedlichen Habitaten. Dabei verbinden sie Habitate miteinander und erbringen positive oder negative Ökosystemdienstleistungen in verschiedenen Habitattypen. In Agrarlandschaften ist der „Spillover“ von Organismen, d.h. die Bewegung von Organismen und die gleichzeitige Verschiebung ihrer Funktion von einem Habitat in ein anderes, insbesondere von naturnahen Habitaten hin zu landwirtschaftlich genutzten Habitaten, einer der wichtigsten Prozesse, die die Populationsdynamik und Zusammensetzung von Gemeinschaften beeinflussen. Zu betonen ist, dass Spillover Habitate nicht nur räumlich, sondern auch auf unterschiedlichen zeitlichen Skalen verbindet, da sich die Verfügbarkeit von Ressourcen in Agrarlandschaften über die Zeit, z.B. durch die Massenblüte von Feldfrüchten, die Ernte oder die Fruchtfolge, verändert. Meist werden naturnahe Habitate als wertvolle Quelle von Organismen betrachtet, aber auch landwirtschaftlich genutzte Habitate können wertvolle Ressourcen zur Verfügung stellen und damit den Spillover von Organismen in andere Habitate initiieren. Massentrachten, wie Raps, sind solche wertvollen Ressourcen für Bestäuber. Bestäuber können von Rapsfeldern auf andere Habitate überschwappen, die ihnen alternative Futterquellen bieten. Der Schwerpunkt dieser Dissertation liegt auf der Beurteilung des Einflusses von Raps auf Bestäuber in Agrarlandschaften anhand der Betrachtung von Effekten (1) auf unterschiedlichen zeitlichen Ebenen (von Effekten während der Blühperiode des Rapses, Kapitel II & IV, über mittelfristige Effekte auf eine zweite blühende Feldfrucht, Kapitel III, bis hin zu Spillover-Effekten in die Blühperiode des nächsten Jahres, Kapitel IV), (2) in naturnahen (Kapitel II) und landwirtschaftlich genutzten (Kapitel III, IV) Habitaten und (3) für unterschiedliche Bestäubergruppen, die sich in ihrem Lebenszyklus unterscheiden (Kapitel II, III, IV).

II. Wir untersuchten die Effekte des relativen Anteils von Raps in der Landschaft in drei Habitattypen in 16 unabhängigen Landschaften rund um Würzburg, Deutschland, während und nach der Blüte von Raps in zwei aufeinanderfolgenden Jahren. Während der Rapsblüte verdünnten sich die Bestäuber mit einem zunehmenden Anteil von Raps in der Landschaft. Damit verringerten sich die lokalen Dichten von Hummeln auf Ackerrandstreifen und auch die Dichten von Hummeln und anderen Wildbienen auf Rapsfeldern. Die Bestäuber in hochqualitativen naturnahen Grasländern wurden während der Rapsblüte nur marginal

negativ durch einen steigenden Anteil an Raps in der Landschaft beeinflusst. Der Anteil von naturnahen Habitaten in einer Landschaft begünstigte dagegen die Bestäuberdichten in den Rapsfeldern. Nach der Rapsblüte schwappten die Hummeln auf die Ackerrandstreifen über, was zu erhöhten lokalen Dichten auf Ackerrandstreifen in Landschaften mit einem hohen Anteil an Raps führte. Unsere Ergebnisse legen nahe, dass ein hoher Anteil von Raps in der Landschaft die Bestäubungsleistung pro Flächeneinheit Raps, aber auch die Verfügbarkeit von Bestäubern für die Bestäubung von Wildpflanzen in naturnahen Habitaten während der Rapsblüte verringern kann. Nach der Rapsblüte kann ein vorangehender hoher Anteil von Raps die Bestäubung von Wildpflanzen in naturnahen Habitaten fördern. Nur wenn ein naturnahes Habitat eine vergleichbar hohe Attraktivität wie Raps aufweist, ist es möglicherweise unabhängiger von Spillover- und Verdünnungseffekten des Rapses.

III. Auf 16 Sonnenblumenfeldern in unabhängigen Untersuchungslandschaften rund um Würzburg, Deutschland, untersuchten wir die Effekte von frühblühendem Raps auf spätblühende Sonnenblumen, als eine zweite landwirtschaftlich genutzte Massentracht mit einem nicht-überlappenden Blühzeitpunkt. Die höchsten Dichten von Hummeln fanden wir auf Sonnenblumenfeldern, die einen hohen Anteil von Raps im Frühjahr und einen hohen Anteil von naturnahen Habitaten in der umgebenden Landschaft aufwiesen, während Honigbienen und Schwebfliegen nicht durch den Anteil von Raps in der Landschaft beeinflusst wurden. Ein hoher Anteil von Raps im Frühjahr konnte sogar die Verdünnung von Bestäubern, die ansonsten mit zunehmendem Anteil von Sonnenblumen in der Landschaft zu einer geringeren Dichte von Hummeln auf Sonnenblumenfeldern führen würde, verringern. Unsere Untersuchung legt nahe, dass ein landschaftsweites Management von früh- und spätblühenden Feldfrüchten zusammen mit naturnahen Habitaten bestimmte generalistische Bestäuber fördern und somit zur Stabilisierung von Bestäubungsleistungen beitragen kann.

IV. Auf 32 Rapsfeldern (jeweils 16 in zwei Untersuchungsjahren) in 16 unabhängigen Landschaften (Kapitel II) untersuchten wir die langfristigen Effekte von Raps auf Hummeln und andere Wildbienen, wobei wir nicht nur den momentanen Anteil von Raps in der Landschaft, sondern auch den Anteil im vorhergehenden Jahr betrachteten. Unter Verwendung eines mechanistischen Modellierungsansatzes konnten wir zeigen, dass Raps als Foragierhabitat für beide Bestäubergruppen attraktiver als der Rest der Landschaft ist. Dies beeinflusst durch Verdünnungs- oder Konzentrationsprozesse maßgeblich die Verteilung der Bestäuber in der Landschaft im aktuellen Jahr. Der Anteil von Raps im vorhergehenden Jahr beeinflusste nur die Wildbienen (ohne Hummeln) und steigerte ihre

Dichte auf Rapsfeldern im aktuellen Jahr. Unsere Ergebnisse zeigen, dass ein Spillover von einem Jahr zum nächsten ausgeprägter für Bestäuber ist, deren Reproduktion mit der Blütezeit von Raps zusammenfällt und die damit Raps als Ressource direkt in die Anzahl an Nachkommen übersetzen können. Im Allgemeinen ist eine höhere Anzahl von Studien, die interannuelle Effekte von Feldfrüchten untersuchen, nötig, um die Dynamik und Verteilung von verschiedenen Organismengruppen, die wichtige Ökosystemdienstleistungen in Agrarlandschaften erbringen können, besser zu verstehen.

V. In dieser Dissertation wurden Effekte von Raps auf allen untersuchten zeitlichen Ebenen gefunden – sowohl kurzfristig während der Rapsblüte als auch langfristig in einer spätblühenden Massentracht und sogar im nächsten Jahr während der Rapsblüte. Diese Effekte können Folgen für die Bestäubung von Kultur- und Wildpflanzen und auch für den Schutz von Bestäubern haben. Es ist wichtig, darauf hinzuweisen, dass die Effekte auf unterschiedlichen zeitlichen Ebenen abhängig von dem untersuchten Habitat (landwirtschaftlich genutzte, verschiedene naturnahe Habitate), sowie der untersuchten Bestäubergruppe sind. Je mehr die Bestäuber in ihrer Aktivitätsperiode mit der Blütezeit von Raps übereinstimmen und je mehr sie auf Blütenressourcen in ihrem Lebenszyklus angewiesen sind, umso größer scheint ihre Reaktion. Effekte wurden für Wildbienen, nicht aber für Schwebfliegen und Honigbienen gefunden. Darüber hinaus ist auch die Verfügbarkeit von naturnahen Habitaten in der Landschaft wichtig und kann die Effekte des Rapses beeinflussen. Die Langlebigkeit der Effekte von Raps zeigt die Bedeutung der Integration von unterschiedlichen zeitlichen Ebenen in die Untersuchung von Ökosystem-Dienstleistungen, nicht nur für Bestäuber, sondern auch für andere Artengruppen, die Ökosystem-Dienstleistungen erbringen.

I. General introduction

Spillover of organisms

Organisms have different requirements during their life cycle (e.g. food, shelter, nesting sites) rarely provided by only one specific habitat type. For mobile organisms, one way to meet changing requirements is to move between spatially separated habitats that provide different resources either at the same time or sequentially (Dunning et al. 1992; Benton et al. 2003; Rand et al. 2006). Thereby, ecosystem services (e.g. pollination or pest control) or disservices (e.g. herbivory or pathogen transfer), provided by moving organisms, may be shifted from one habitat to another. In this context “spillover” is defined as “movement that results in the function of an organism [...] no longer being fulfilled in the habitat where the organism comes from but in the habitat where the organism moves to” (Blitzer et al. 2012).

Spillover is one important process that influences population dynamics on a landscape scale (Polis et al. 1997; Tschardtke et al. 2012) and may be especially important in anthropogenically transformed landscapes where managed and semi-natural habitats, that may provide different resources, are intermingled and where cross-habitats fluxes and edge effects are most likely to occur (Ries et al. 2004). Here, semi-natural or natural habitats are mostly seen as source of important ecosystem services (Thies and Tschardtke 1999), but also managed habitats can provide important resources and thereby benefit organisms that spillover to the surrounding landscape (Tschardtke et al. 2005; Rand et al. 2006). Therefore, it is increasingly recognized that not only spillover from semi-natural to managed but also spillover from managed to semi-natural habitats may structure populations in agricultural landscapes (Rand et al. 2006; Blitzer et al. 2012). So far, the spillover between different managed habitats with productivity differences (Oksanen 1990) or different productivity peaks has been rarely addressed, but may also occur.

Spillover most obvious occurs on a local scale as a cross edge effect between directly adjacent habitats (Rand et al. 2006), but, depending on the organisms mobility, can also affect population densities on larger scales (Rand and Louda 2006; Ewers and Didham 2008). Importantly, spillover has a spatial, and also a temporal component. On the smallest temporal scale, various habitats are either used coevally to fulfill different resource requirements (feeding vs. nesting; Holzschuh et al. 2011; Öckinger and Smith 2007) or successively when feeding resources in semi-natural habitats become more attractive after

harvesting of crops (Rand et al. 2006) or crops gain attractiveness by mass-flowering events (Holzschuh et al. 2011). On an intermediate temporal scale, spillover between spatially separated habitats could arise when they give non-overlapping resource pulses within one year. Inter-annual changes of resources, e.g. due to crop rotation, have been shown to influence pest-enemy dynamics (Thies et al. 2008; Zhao et al. 2013). Though, spillover effects are known from a broad range of taxa, including animals, pathogens and plants (Brudvig et al. 2009; Blitzer et al. 2012) and may control single-species dynamics, but also communities (Brudvig et al. 2009), different temporal scales have rarely been addressed.

Dilution and concentration processes

Another important process that influences densities of organisms on a landscape scale are dilution and concentration/crowding processes (Tschardt et al. 2012; Vasseur et al. 2013) according to expanding or contracting resource availability in the landscape. Consequences are increased densities of organisms in small patches of their preferred habitat and decreased local densities at a large relative cover of the preferred habitat in the landscape. In agricultural landscapes the relative cover of semi-natural habitats remains either more or less stable across time or, as happened during the last decades, declines gradually with increasing intensification of agriculture (Tilman et al. 2001). This results in increased organism densities on semi-natural habitat remainders (Grez et al. 2004). But, especially when also crop habitats are attractive to organisms, immediate expansion or contraction of their relative cover in a landscape due to crop rotation or agricultural policy decisions (Tschardt et al. 2012), can affect distribution of organisms transiently – until harvesting or the end of mass-flowering periods (Holzschuh et al. 2011) – or in the long term (Thies et al. 2008). Dilution and concentration processes can also effect the provision of local ecosystem services like pest-control (Thies et al. 2008; Zhao et al. 2013) or pollination (Veddeler et al. 2006; Holzschuh et al. 2011), and therefore have to be considered, when studying population dynamics of organisms on a landscape-scale.

Pollinators and mass-flowering crops

An important group of organisms, for which spillover, but also dilution and concentration effects are observable, are pollinators. With 87% of wild plant species that are pollinated by animals (Ollerton et al. 2011) and an economic value for crop pollination of about €153 billion globally (Gallai et al. 2009), pollinators provide essential ecosystem services. Nonetheless, a global decline of pollinators attributed to a set of different drivers, e.g. land-use change, introduction of alien species, climate change (Potts et al. 2011), is commonly recognized. This dissertation was performed under the framework of the STEP project (Potts et al. 2011; STEP 2014) that tries to identify interactive effects of multiple pressures on pollinators.

Pollinators usually need to move between habitats to find required resources for nesting and foraging (Westrich 1996) and with foraging ranges between 150-3000 m (Steffan-Dewenter and Kuhn 2003; Westphal et al. 2006; Meyer et al. 2009) they are very mobile and able to react on the habitat composition on a landscape scale. Thereby, semi-natural habitats are often seen as very valuable nesting sites (Ricketts et al. 2008; Garibaldi et al. 2011; Krewenka et al. 2011). But also managed habitats, like mass-flowering crops, can provide valuable feeding resources to pollinators (Morandin and Winston 2005; Diekötter et al. 2013). Given that worldwide pollinator decline is not only driven by loss of nesting sites, e.g. through landscape fragmentation and land-use intensification, but also by loss of feeding resources (Potts et al. 2010), mass-flowering crops can potentially be used to benefit pollinators. Though, it is still questionable if the short period of mass-flowering is effectual for supporting pollinators (Corbet 2000) and previous studies on the effects from mass-flowering crops gave mixed results on this question (Westphal et al. 2009; Diekötter et al. 2010; Jauker et al. 2012; Holzschuh et al. 2013).

As there is increasing demand for biofuel production, the area cultivated with mass-flowering crops has expanded in the last decades in Europe (FAO 2014) and can therefore be associated to a major land-use change in agricultural landscapes (Koh 2007). As land-use change is one important driver of pollinator loss (Potts et al. 2011), effects of mass-flowering crops are of major concern. In the STEP project, a network of study sites in six European countries (Germany, Netherlands, Serbia, Spain, Sweden, and United Kingdom) was established to focus on the effects of different mass-flowering crops on pollinators. In Germany the most important mass-flowering crop is oil-seed rape (*Brassica napus*, Fig. I.1), which belongs to the so called first generation biofuels (Dauber et al. 2010) and of which the

cultivated area increased from 1.297 million hectares to 1.463 million hectares between 2002 and 2013 (European Commission 2013). The flowering period of oil-seed rape lasts for about four weeks and starts approximately in mid/late April in the study region. A further mass-flowering crop we included in our study, sunflower (*Helianthus annuus*, Fig. I.1, Chapter III), is of less importance in Germany with only 0.022 million hectares cultivated in 2013 (European Commission 2013). Sunflowers start to flower in July in the study region.



Fig. I.1: Important mass-flowering crops in the study region: sunflowers (*Helianthus annuus*; left) and oil-seed rape (*Brassica napus*; right).

Study design and chapter outline

In this dissertation the focus was the pollinator spillover from oil-seed rape on different temporal scales and between oil-seed rape as a managed habitat and different other habitat types. In 2011 we selected 32 independent study landscapes in the surrounding of Würzburg (49°44' N, 9°51' E; Fig. I.4). For all parts of the study, we focused on different pollinator groups. We assessed effects on central-place foraging honey bees, bumble bees and other wild bees that comprise managed and unmanaged pollinators with different sociality. Additionally, we looked at hoverflies, as another important pollinator group (Larson et al. 2001), that differ in resource requirements for adults and larvae in most species and are less spatially restricted than bees (Almohamad et al. 2009). In all parts of the study, pollinators were assessed during standardized transect walks, which is an efficient method to measure abundances and species richness in a given area (Westphal et al. 2008).

On the smallest temporal scale, on which spillover of pollinators may occur, pollinators use feeding resources on managed habitats, and simultaneously in semi-natural habitats, where they often have their nesting sites. On the one hand, mass-flowering crops may outcompete wild plants in semi-natural habitats regarding pollinator visitation, on the

other hand, mass-flowering crops can facilitate visitation of wild plants in adjacent habitats (Holzschuh et al. 2011; Hanley et al. 2011). As soon as the life cycle of pollinators exceeds the flowering of the mass-flowering crop, pollinators are forced to use resources in other habitats (Blüthgen and Klein 2011) and the effect of mass-flowering crops may change after the mass-flowering period (Jauker et al. 2012; Kovács-Hostyánszki et al. 2013; Haenke et al. 2014). 16 of the 32 study landscapes (Fig. I.4) were selected along a maximum gradient of relative cover of oil-seed rape in the surroundings of focal study sites to evaluate during and after flowering effects on different habitat types. As effects might differ for the crop habitat itself and different types of semi-natural habitats (Kovács-Hostyánszki et al. 2013), we selected one oil-seed rape field, and two semi-natural habitats with different relative attractiveness to oil-seed rape (field boundaries and semi-natural grasslands, Fig. I.2) in each landscape (Fig. I.3). All habitats types were observed in two study years (Chapter II).

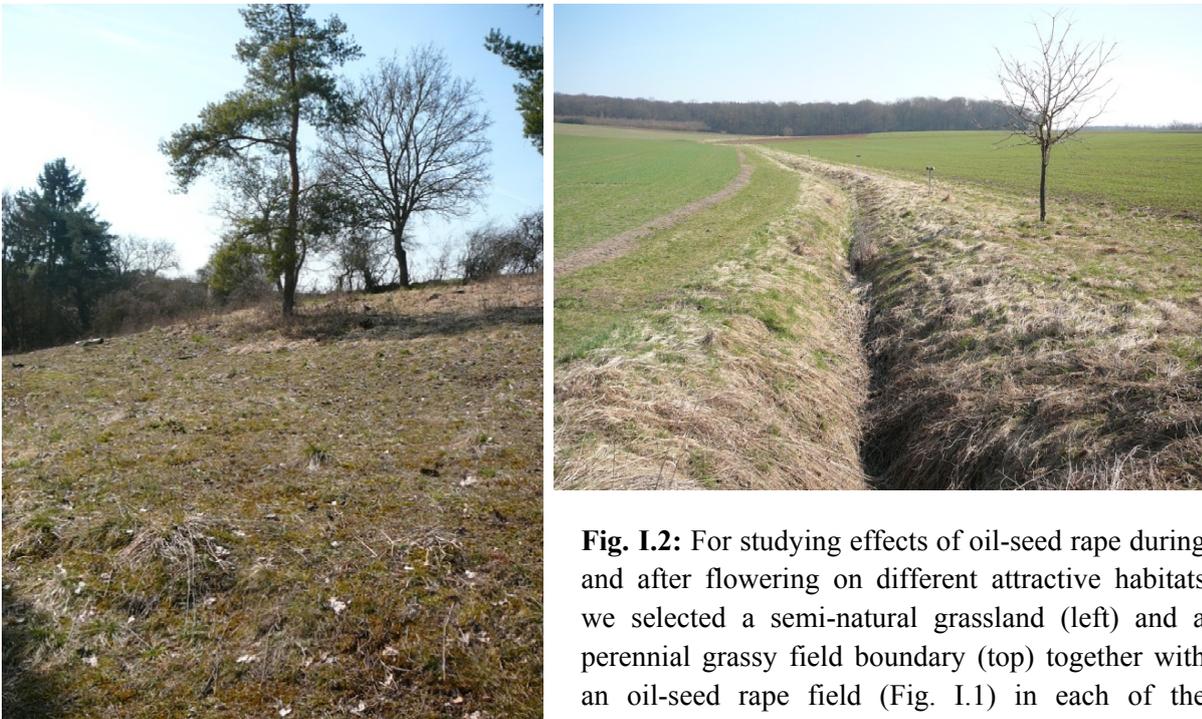


Fig. I.2: For studying effects of oil-seed rape during and after flowering on different attractive habitats we selected a semi-natural grassland (left) and a perennial grassy field boundary (top) together with an oil-seed rape field (Fig. I.1) in each of the independent study landscapes (Fig. I.3).

Previous studies showed that effects from oil-seed rape can outlast weeks after the flowering period (Westphal et al. 2003; Herrmann et al. 2007). During this time other resource pulses can occur in the agricultural landscape. In case pollinators are active for several months or have more than one generation per year, and are able to use several resource pulses, the pollinators affected by an early resource pulse may on an intermediate time scale spillover to a crop that gives a later resource pulse. The connection between several managed habitats by spillover of pollinators has been rarely addressed (but see e.g.

Rundlöf et al. 2014). By selecting additional 16 study landscapes (Fig. I.4) with a focal sunflower field as a late flowering crop along a gradient of relative cover of oil-seed rape as an early-flowering crop, we tried to address this issue (Chapter III).

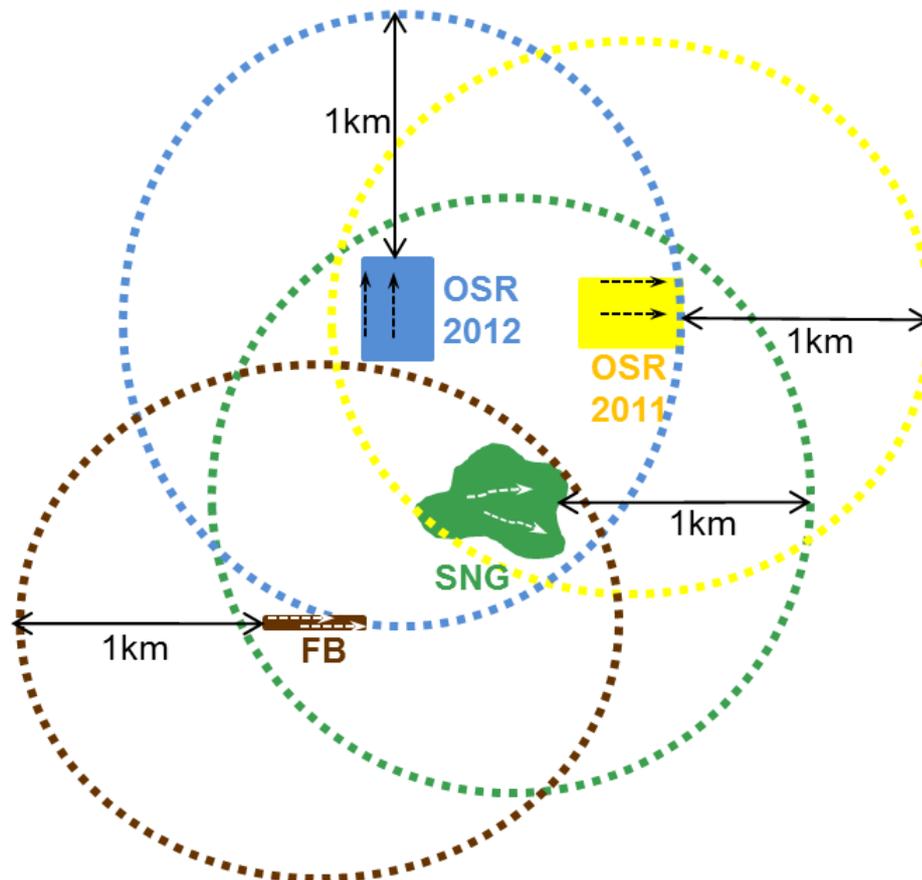


Fig. I.3: Study design (displaying one study landscape) for studying the effects of oil-seed rape on pollinators in a crop field and different semi-natural habitats during and after mass-flowering of oil-seed rape (Chapter II). In each of 16 study landscapes (Fig. I.4) we selected an oil-seed rape field (OSR) in 2011 (yellow) that switched in 2012 (blue) due to crop rotation, a perennial field boundary (FB; brown) and a semi-natural grassland (SNG; green). For each habitat type we calculated the relative cover of landscape parameters (i.e. relative cover of oil-seed rape and semi-natural habitats) in a 1-km radius around the study sites with the geographical information system ArcMap (ESRI 2008). Information for the relative cover of crops was provided by the Bavarian State Ministry of Nutrition, Agriculture and Forestry. For calculating the relative cover of semi-natural habitats this information was combined with information from aerial photographs (Bayerisches Landesamt für Digitalisierung, Breitband und Vermessung 2010) and the Bavarian biotope mapping (Bayerisches Landesamt für Umwelt 2012). Arrows within habitats mark the two transects, where we sampled pollinators two times during flowering and two times after flowering (only in semi-natural habitats). For more details see Chapter II. The data from oil-seed rape fields (yellow, blue) were also used to evaluate the inter-annual effects of oil-seed rape on bumble bees and other wild bees (Chapter IV).

As soon as mass-flowering crops influence also the reproductive output of pollinators (Westphal et al. 2009; Jauker et al. 2012; Williams et al. 2012; Holzschuh et al. 2013; Rundlöf et al. 2014), effects can potentially even spillover to the next year. By using the study landscapes from Chapter II (Fig. I.3, Fig. I.4), we tried to integrate not only effects by current landscape-scale availability of oil-seed rape, like dilution or crowding effects, but also the potential inter-annual spillover of pollinators from the previous year to the current year initiated by a high relative cover of oil-seed rape in the previous year (Chapter IV). We focused on bumble bees and other wild bees. Depending on the time of reproduction, oil-seed rape in the previous year might contribute differentially to reproductive output of these two pollinator groups and thereby affect the densities of pollinators in the current year.

Fig. I.4: Map of the study landscapes around Würzburg, Germany. Circles around focal field boundaries (brown), semi-natural grasslands (green), oil-seed rape fields in 2011 (yellow) and oil-seed rape fields in 2012 (blue) cluster together in 16 independent study landscapes to study the effects of oil-seed rape on different habitat types in different seasons (Chapter II, Fig. I.3). Orange circles represent the 16 landscapes around focal sunflower fields, where effects from early-flowering oil-seed rape to late-flowering sunflowers were studied (Chapter III). Blue and yellow circles represent landscapes with oil-seed rape fields on which we studied inter-annual effects of oil-seed rape on pollinators (Chapter IV). Background map: © Bayerisches Landesamt für Vermessung und Geoinformation 2010.

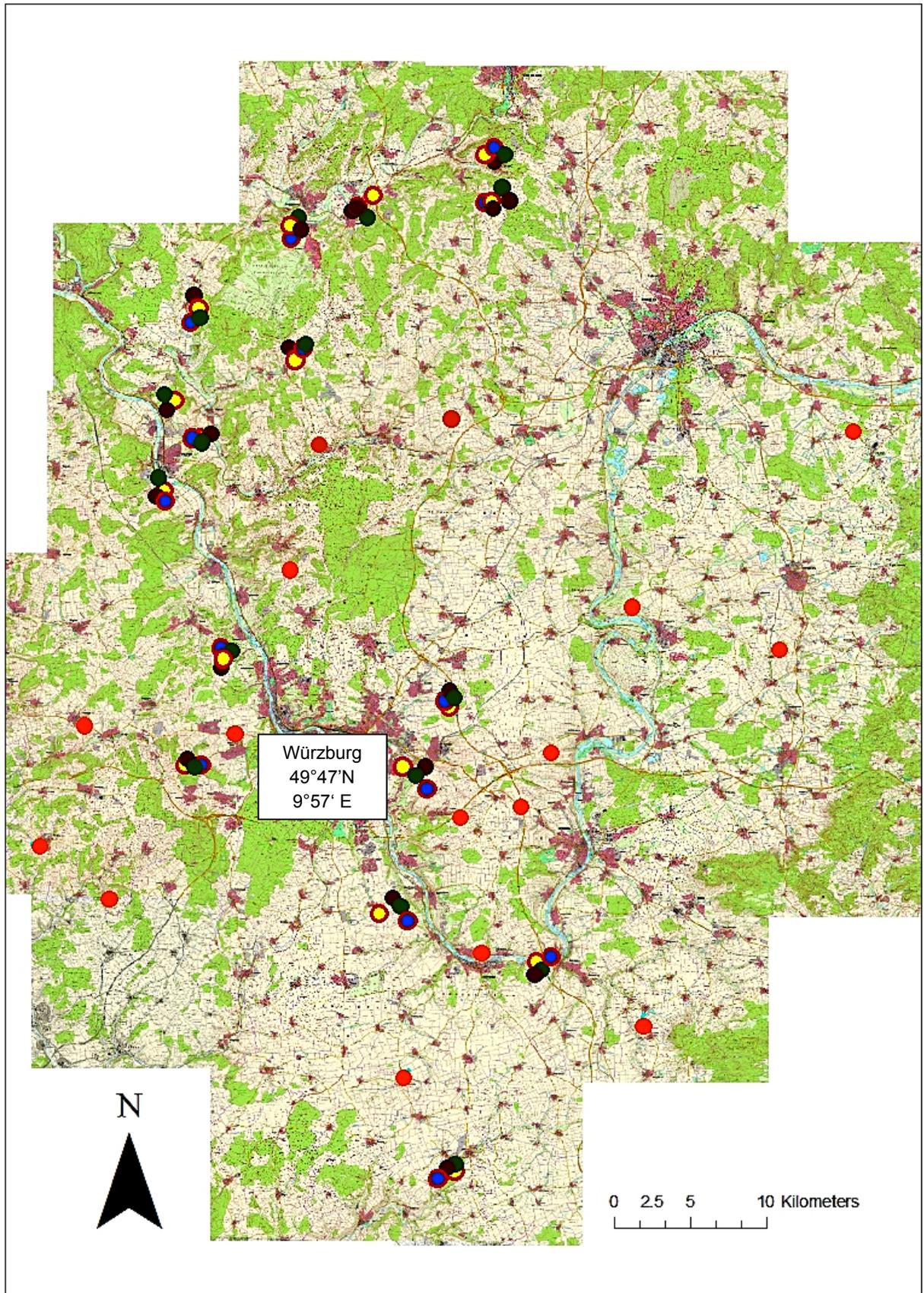


Fig. I.4

II. Effects of oil-seed rape on pollinators differ among habitat types and seasons

This chapter is prepared for submission as: Riedinger, V., Holzschuh, A., Steffan-Dewenter, I. Effects of oil-seed rape on pollinators differ among habitat types and seasons.

Running title: Effects differ between habitats and seasons

Keywords: *Apis mellifera*, annual crops, field boundaries, hoverflies, pollination services, semi-natural grasslands, spillover, wild bees

Abstract

Mass-flowering crops can affect forager distribution and population size of pollinators in agricultural landscapes with possible consequences for pollination services in crops, and pollinator diversity and biotic interactions in semi-natural habitats. Here, we tested the hypotheses that the temporally fluctuating availability of mass-flowering crops leads (1) to transient pollinator dilution during crop flowering and (2) enhanced population densities after flowering in different habitat types.

We monitored pollinators (bumble bees, other wild bees, honey bees, hoverflies) on oil-seed rape, field boundaries and semi-natural grasslands during two years in 16 non-overlapping landscapes differing in the cover of oil-seed rape and semi-natural habitats.

During the mass-flowering period, an increasing cover of oil-seed rape diluted pollinator densities in oil-seed rape fields, perennial field boundaries and marginally in semi-natural grasslands, while the cover of semi-natural habitats in a landscape benefitted pollinator densities in crop fields.

After the mass-flowering period, bumble bee densities increased on field boundaries in landscapes with an increasing cover of oil-seed rape indicating a population-level response.

Our findings suggest that a possible shortage of pollinators due to the expansion of biofuel crops such as oil-seed rape can be buffered by semi-natural habitats but also requires additional agri-environmental schemes. Competition for pollinators in semi-natural habitats during oil-seed rape flowering could negatively affect wild plant pollination. We conclude that effects of mass-flowering crops for pollinators and pollination services have to be

critically evaluated for different periods of the year and by taking into account potential negative effects in semi-natural habitats.

Introduction

Organisms often use different resources in different habitats during their life (Benton *et al.* 2003). By moving among habitats, they connect these habitats and ecosystem services (e.g. bio-control, pollination) or disservices (e.g. herbivory) provided in a habitat might depend on other surrounding habitats (Tscharntke *et al.* 2012). Habitats with highly attractive resources might distract organisms from less attractive habitats (Rand *et al.* 2006). On the other hand, attractive resources might not only enhance population densities and diversity in the attractive habitat itself but organisms might also spillover from there to other habitats (Tscharntke *et al.* 2005). So far, mostly organism spillover from natural or semi-natural habitats to managed habitats has drawn attention (Blitzer *et al.* 2012). In contrast, spillover from managed to (semi-)natural habitats has been studied rarely and might be greatly underestimated, although it might be an important determinant of population sizes, diversity and ecosystem functions in (semi-)natural habitats embedded in human-dominated landscapes (Blitzer *et al.* 2012).

Spillover effects can connect habitats on different spatial scales, e.g. habitats on a landscape scale or directly adjacent habitats (e.g. Holzschuh *et al.* 2008). Furthermore, the occurrence and direction of spillover effects can change within short time periods, because habitats often rapidly change in their attractiveness throughout the year (e.g. after mass-flowering or harvesting). If the attractiveness of managed habitats is only temporary, population densities in other habitats could be reduced transiently, but could increase later in the year when the managed habitat has lost its attractiveness and organisms spill over to alternative habitats. This temporal component of organism spillover has been rarely studied at landscape scales to date (Jauker *et al.* 2012; Kovács-Hostyánszki *et al.* 2013; Haenke *et al.* 2014), but can be expected to affect all organisms that move at landscape scales and hereby connect habitat types changing in their relative attractiveness over time.

Pollinators have to cover different resource requirements during their life cycle (i.e. nesting and foraging), resulting in usage of different habitat types (Westrich 1996), where they provide critical ecosystem services to wild plants (Ollerton *et al.* 2011) and crops (Klein *et al.* 2007). Pollinators are usually highly abundant in semi-natural habitats where they have their nesting sites, but decline in agricultural landscapes when distances from these source habitats increase (Garibaldi *et al.* 2011; Krewenka *et al.* 2011). On the other hand,

pollinators use agricultural habitats such as mass-flowering crops, which can provide attractive food resources for pollinators (Diekötter *et al.* 2013), especially when wild floral resources in the landscape are scarce (Potts *et al.* 2011). Temporal dynamics of resources in agricultural landscapes arise through crop rotation, harvesting or rather short flowering periods of crop monocultures. Since the flight period of a certain pollinator species is usually longer than the flowering period of a visited plant species (Blüthgen and Klein 2011), density shifts of pollinators between different habitat types that change in attractiveness can be expected throughout the year.

At landscape scales, the results of previous studies on effects of mass-flowering crops on pollinators in semi-natural habitats are mixed. There is evidence for positive as well as negative effects on pollinators during and after mass-flowering depending on the pollinator group, habitat type and whether the focus was on nesting or foraging pollinators (Westphal *et al.* 2003; Herrmann *et al.* 2007; Holzschuh *et al.* 2011; Jauker *et al.* 2012; Kovács-Hostyánszki *et al.* 2013; Diekötter *et al.* 2013; Haenke *et al.* 2014).

The main aim of this study was therefore to assess the relative impact of negative and positive effects of a mass-flowering crop on flower visitors within one study design (1) by taking temporal changes in the attractiveness of the mass-flowering crop compared to the attractiveness of semi-natural habitats into account, (2) by focusing on two types of semi-natural habitats that vary in their value as pollinator habitat and thereby in their attractiveness relatively to the mass-flowering crop and (3) by focusing on various pollinator groups differing in sociality and phenology. The study was conducted over two years in 32 semi-natural habitats (small perennial field boundaries and large grasslands) and 16 oil-seed rape fields. The landscapes surrounding the study sites differed in the relative cover of oil-seed rape and in the relative cover of semi-natural habitat (hereafter referred to as cover of oil-seed rape/semi-natural habitats). We included semi-natural habitats and the local flower cover as other important determinants of pollinator densities in agricultural landscapes (Kleijn and van Langevelde 2006; Öckinger and Smith 2007; Haenke *et al.* 2009) as covariates in our study.

We tested the following hypotheses:

1. During the mass-flowering period, pollinator densities per area decrease in field boundaries, grasslands and oil-seed rape fields with increasing cover of mass-flowering crops in the surrounding landscapes.

2. After mass-flowering, a high resource availability of mass-flowering crops in a landscape earlier in the season leads to spatio-temporal spillover and increased pollinator densities in semi-natural habitats.
3. Both potential negative and positive effects of oil-seed rape are more pronounced on small, low-quality field boundaries than on large, high quality grasslands.
4. Duration and extent of effects for different pollinator groups depend on the importance of mass-flowering resources within their life cycle and the phenological match between its flowering and the activity period of pollinators.

Our data suggest that during mass-flowering, pollinator densities decreased on oil-seed rape fields, field boundaries and marginally on semi-natural habitats with increasing cover of oil-seed rape in the landscape, while the cover of semi-natural habitats benefitted pollinators on crop fields. After mass-flowering, bumble bee densities increased on field boundaries in landscapes with an increasing cover of oil-seed rape.

Material and Methods

Study region and study sites

The study was conducted in 2011 and 2012 in the surroundings of Würzburg, Bavaria, Germany (49°47' N, 9°57' E). This region is intensively used for agriculture and thereby important for cultivation of mass-flowering crops, like oil-seed rape. In the study region, we selected 16 study areas in an area of 27 km x 70 km. Study areas were selected in a way that they covered a wide gradient of cover of oil-seed rape in a 1-km radius around the study sites in the first study year which was independent of the cover of semi-natural habitats in the same radius. Furthermore, study areas had to contain a semi-natural grassland, which was a limiting factor for possible study areas. In each study area we selected three different habitat types as study sites (i.e. in total 48 field boundaries, grasslands and oil-seed rape fields per year). Study sites of the same habitat type in two different study areas were at least 2 km apart.

Field boundaries

The selected field boundaries were grassy, linear and perennial elements located e.g. between a cereal field and a farm track (Holzschuh et al. 2009). Since these elements are more stable than cultivated fields, they are suggested to act as potential refuge or dispersal corridors in intensified agricultural landscapes (Holzschuh et al. 2009) and have been shown

to provide e.g. nesting sites for bumble bees (Kells and Goulson 2003) or flower resources for adult hoverflies (Ernould *et al.* 2013). On the other hand, field boundaries can be rather disturbed habitats through drift of agro-chemicals from adjacent agriculture (Marshall and Moonen 2002). Field boundaries were 1-4 m wide, at least 100 m long, had an area of at least 300 m² for pollinator observations and were not directly adjacent to oil-seed rape. In 2012, we replaced five field boundaries, which were directly adjacent to oil-seed rape due to crop rotation by new field boundaries which were at least 100 m apart from the next oil-seed rape field and as close as possible to the field boundaries from the previous year (100–675 m distance).

Semi-natural grasslands

In each study area we selected a semi-natural grassland that was usually protected for nature conservation (hereafter “grassland”). These grasslands (often calcareous) are among the most species rich habitats in central Europe (Steffan-Dewenter & Tschardtke 2002) and are, in comparison to field boundaries large and structurally complex. The grasslands were between 0.4 and 4.9 ha (mean \pm SE: 1.8 \pm 0.2 ha) and are either mown at most once per year, grazed or not managed at all. The grasslands were the same for the two study years.

Oil-seed rape fields

In each study area, we selected an oil-seed rape field in 2011. In 2012, we switched in all 16 study areas to the oil-seed rape field that was as close as possible to the study field of 2011 and contributed to a maximal gradient of cover oil-seed rape in a 1-km radius around oil-seed rape fields, because locations of oil-seed rape fields changed annually due to crop rotation. Fields had a size of 0.5–5.4 ha (mean \pm SE: 2.0 \pm 0.2 ha).

Landscape parameters

For all three habitats we measured the cover of oil-seed rape and the cover of semi-natural habitats in a 1-km buffer around the edge of the sites (including the site) in each study year. The cover of oil-seed rape covered a gradient from 0 to 19.8 percent, the cover of semi-natural habitats covered a gradient from 0.9 to 28.5 percent (for means, SE, minima and maxima for all habitat types and years see Supplement Table II.S1). The cover of oil-seed rape and the cover of semi-natural habitats were not correlated in landscape sectors of any habitat type (Pearson-correlation-coefficient: field boundaries: $r=-0.36$; grasslands: $r=-0.25$; oil-seed rape: $r=-0.29$, all $n=32$). We classified all habitats potentially valuable as nesting

and foraging sites for pollinators as semi-natural habitats: semi-natural grasslands, forest edges (the 10 m wide border strip of forests), hedgerows, shrubs, orchard meadows, gardens outside settlements, annual flower-rich fallows and sown flower strips. The land-use data were provided by the Bavarian State Ministry of Nutrition, Agriculture and Forestry. For calculating the cover of semi-natural habitats we combined these data with the Bavarian biotope mapping and information from aerial photographs. The geographical information system ArcMap (ESRI, v. 9.3.1) was used to calculate the cover of the different habitat types in each landscape sector.

Pollinator survey

Pollinators (bees and hoverflies) were recorded during and after (i.e. two “sampling periods”) the flowering of oil-seed rape on two 150 m² transects per study site. Semi-natural habitats (field boundaries and grasslands) were surveyed twice during and twice after the mass-flowering of oil-seed rape, oil-seed rape fields were surveyed twice during its mass-flowering only. On the field boundaries, the two transects were optimally parallel, each 1.5 m wide and 100 m long. On grasslands, transects were laid through the most flower rich parts of the grassland and were thus variable across sampling rounds. In oil-seed rape fields, one transect was located on the outer crop line paralleling the edge of the field, the other one was parallel to the first, located in the centre of the field with at least 20 m distance from each edge. A transect had a width of 1 m and a length of 150 m.

All transects were sampled two times during flowering of oil-seed rape in late April/early May (sampling period – “during”). The third sampling round started directly after the end of the flowering of oil-seed rape in late May/early June and the fourth sampling round approximately six weeks later in July (sampling period – “after”). Immediately after the pollinator surveys, we collected information on the local flower cover on the two semi-natural habitats. We counted the number of flower units (single flowers, flower heads, umbels) for each flowering plant species during each sampling round on each transect and estimated the size of flower units to calculate percentage cover. We calculated the mean flower cover over two transects and two sampling rounds separately for the two sampling periods. *Galium mollugo*, which was the dominant flowering plant on some field boundaries, was not included in our calculation of total flower cover. Although its flower cover was many times higher than the total cover of other flowers, flower visitors were observed there in exceptional cases only.

Pollinators were sampled under standardized weather conditions (temperatures above 15 °C, no rain, low or no cloud cover, low wind speeds) between 09.00 and 18.00 h, while slowly walking along each transect for 15 minutes and recording all flower-visiting pollinators. Honey bees and bumble bees were identified in the field to species level (except for *B. terrestris* and *B. lucorum* agg.). Other wild bees than *Bombus* and hoverflies were collected for species identification in the lab. Densities and species richness of pollinators were pooled for the two transects per site and for the two survey rounds per sampling period (during/after), respectively, i.e. they correspond to 600 m² and 60 min.

Data analysis

Densities of different pollinator groups (bumble bees, other wild bees, honey bees and hoverflies), as well as total species richness were analysed in linear mixed-effect models (lme, Pinheiro & Bates 2000) separately for each habitat type. We ln-transformed (when necessary $\ln(x+1)$) the species richness of pollinators and densities of single pollinator groups to reach homoscedasticity of variance and normality of residuals (Crawley 2007).

In models for field boundaries and grasslands we added study area and year as random effects to take the hierarchical structure of data into account (data from two sampling periods nested within a study year; data from two study years nested within study area). Fixed effects were the covers of oil-seed rape and of semi-natural habitats in the 1-km radius landscape sectors, the mean local flower cover, and the two-fold interactions between cover of oil-seed rape and sampling period, cover of semi-natural habitats and sampling period and local flower cover and sampling period. In case there was a significant interaction ($P < 0.05$) between cover of semi-natural habitats and sampling period or local flower cover and sampling period, we checked in a subsequent test if also the interaction between the covariate (local flower cover/semi-natural habitat) and cover of oil-seed rape was significant in one of the two sampling periods. Thereby, we wanted to evaluate if temporally different results from covariates are caused by the availability of oil-seed rape or simply by phenology, but avoided three-fold interactions with two continuous variables in our models. In models for oil-seed rape we added study area as random effect (data from two study years nested within study area). Fixed effects were the covers of oil-seed rape and of semi-natural habitats in the 1-km radius landscape sectors.

Model simplification was performed by manually removing non-significant terms using likelihood ratio tests (Zuur *et al.* 2009). We present P-values of the F-statistics (Type I SS). All models were calculated in R (v. 2.15.1, R Development Core Team 2012). All

graphs show raw data on a logarithmic scale. Regression lines were calculated from the model output, where all other fixed factors included in the final models were held constant at their mean.

Results

We recorded a total of 6786 pollinators belonging to 180 species. In field boundaries we recorded 429 bumble bees (6 species), 655 other wild bees (75 species), 121 honey bees and 1461 hoverflies (31 species) in eight sampling rounds in two years. In grasslands we recorded 925 bumble bees (8 species), 838 other wild bees (97 species), 383 honey bees and 744 hoverflies (29 species) in eight sampling rounds in two years. In oil-seed rape fields we recorded 153 bumble bees (6 species), 273 other wild bees (40 species), 709 honey bees and 95 hoverflies (11 species) in four sampling rounds in two years during mass-flowering. A detailed list of pollinator species is given in Supplement Table II.S2.

On field boundaries, the density of bumble bees decreased with increasing cover of oil-seed rape in the landscape during the mass-flowering of oil-seed rape, but increased with cover of oil-seed rape after the mass-flowering (Fig. II.1, Table II.1). The local flower cover of field boundaries had a positive effect on densities of all pollinator groups and species richness independently of the sampling period (Table II.1). Cover of semi-natural habitats did neither affect pollinator densities nor species richness on field boundaries.

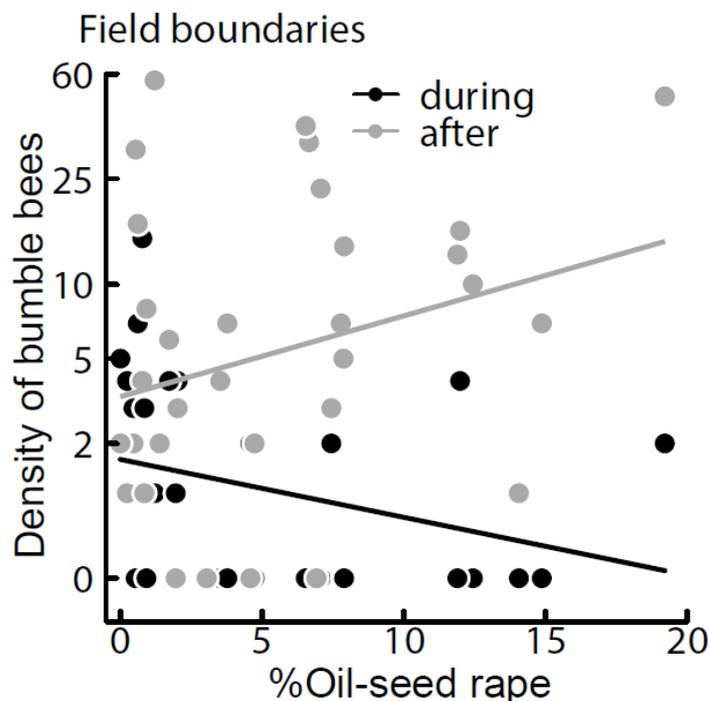


Fig. II.1 Relationship between cover of oil-seed rape (%OSR) on a 1-km scale and density of bumble bees on field boundaries. Each point represents the pooled densities for 600 m² transects. Regression lines were obtained from the original model output (during: $\ln(y+1) = -0.05 \times \%OSR + 0.75 + 1.00 \times \text{mean \%flower cover} (=0.22)$, after: $\ln(x+1) = 0.07 \times \%OSR + 1.26 + 1.00 \times \text{mean \%flower cover}$)

Table II.1. Results for pollinators on field boundaries from linear-mixed-effects models (F-statistic for Type I SS). Landscape predictors were measured in a 1-km radius around the field boundaries. Predictors are shown when $P < 0.1$ or when they are part of a significant interaction ($P < 0.05$); %OSR = cover of oil-seed rape

| | | Df | F | P |
|-----------------------------------|--------------------------------|------|-------|--------|
| <i>Species richness</i> | Flower cover ↑ | 1,30 | 83.0 | <0.001 |
| | Sampling period (after>during) | 1,30 | 64.6 | <0.001 |
| <i>Density of bumble bees</i> | %OSR | 1,15 | 0.0 | 0.881 |
| | Sampling period | 1,29 | 24.8 | <0.001 |
| | Flower cover ↑ | 1,29 | 5.3 | 0.029 |
| | %OSR x Sampling period | 1,29 | 5.2 | 0.030 |
| <i>Density of other wild bees</i> | Flower cover ↑ | 1,30 | 54.5 | <0.001 |
| | Sampling period (after>during) | 1,30 | 19.7 | <0.001 |
| <i>Density of honey bees</i> | Flower cover ↑ | 1,30 | 19.7 | <0.001 |
| | Sampling period (after>during) | 1,30 | 6.7 | 0.015 |
| <i>Density of hoverflies</i> | Flower cover ↑ | 1,30 | 33.1 | <0.001 |
| | Sampling period (after>during) | 1,30 | 144.2 | <0.001 |

On grasslands, pollinators were not affected by the cover of semi-natural habitats and only densities of wild bees other than *Bombus* showed a tendency to decrease with increasing cover of oil-seed rape (Table II.2; Fig. II.2a). Flower cover had a positive effect on honey bees and hoverflies, which was independent of the sampling period and on other wild bees than *Bombus* and on species richness during the flowering of oil-seed rape (Fig. II.2b, Table II.2). Though, a subsequent test for the interaction between local flower cover and cover of oil-seed rape in case of other wild bees than *Bombus* and species richness revealed no significant result during mass-flowering.

Fig. II.2 Density of wild bees other than *Bombus* on grasslands during and after flowering of oil-seed rape (OSR). Relationship between (a) %OSR on a 1-km scale and density of other wild bees, (b) local flower cover and density of other wild bees; note that a subsequent test for the interaction between local flower cover and %OSR during flowering revealed no significant result. Regression lines were obtained from the original model output. Each point represents the pooled densities for 600 m² transects. Continuous lines show significant interactions ($P < 0.05$) and dashed lines marginal significant relationships ($P < 0.1$) according to F-statistics in Table II.2

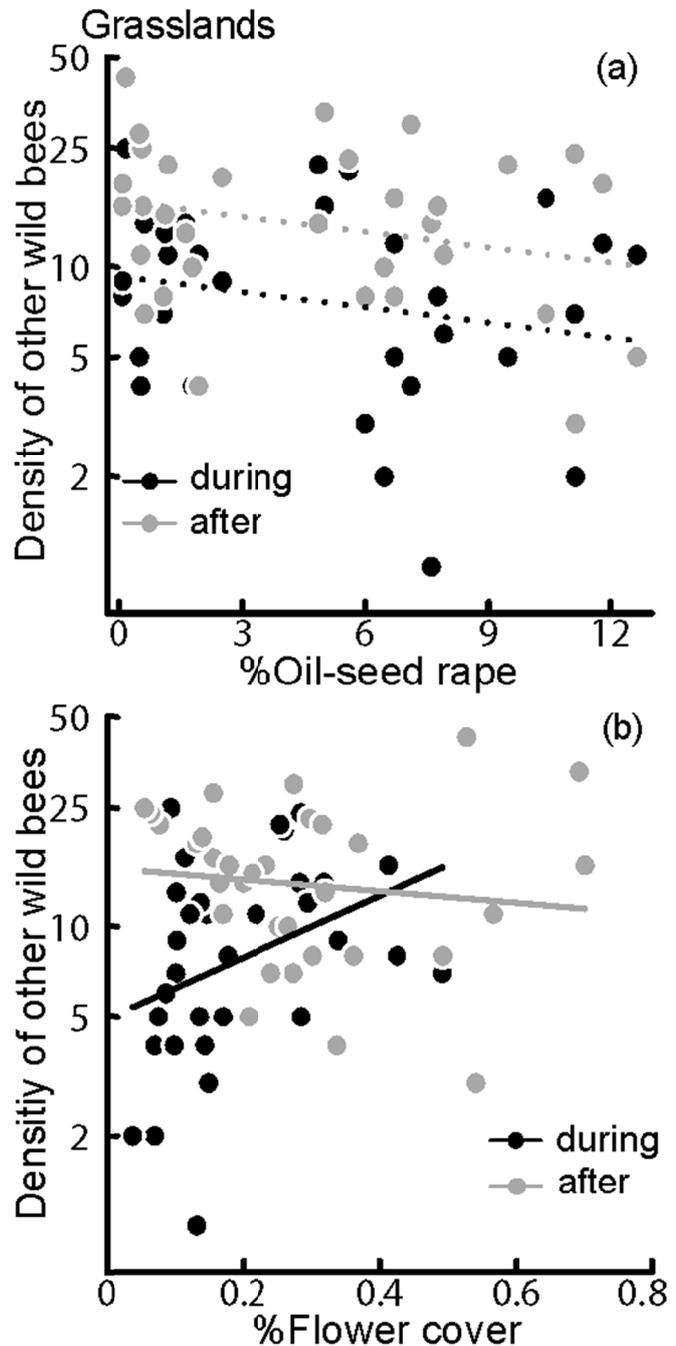


Table II.2. Results for pollinators on grasslands from linear-mixed-effects models (F-statistic for Type I SS). Landscape predictors were measured in a 1-km radius around the grasslands. Predictors are shown when $P < 0.1$ or when they are part of a significant interaction ($P < 0.05$); %OSR= cover of oil-seed rape

| | | Df | F | P |
|-----------------------------------|--------------------------------|------|-------|--------|
| <i>Species richness</i> | Flower cover | 1,29 | 27.9 | <0.001 |
| | Sampling period | 1,29 | 88.8 | <0.001 |
| | Flower cover x Sampling period | 1,29 | 10.1 | 0.004 |
| <i>Density of bumble bees</i> | Sampling period (after>during) | 1,31 | 164.0 | <0.001 |
| <i>Density of other wild bees</i> | %OSR↓ | 1,15 | 3.5 | 0.082 |
| | Flower cover | 1,29 | 3.9 | 0.058 |
| | Sampling period | 1,29 | 9.9 | 0.004 |
| | Flower cover x Sampling period | 1,29 | 5.2 | 0.030 |
| <i>Density of honey bees</i> | Flower cover↑ | 1,30 | 16.6 | <0.001 |
| | Sampling period (after>during) | 1,30 | 23.3 | <0.001 |
| <i>Density of hoverflies</i> | Flower cover↑ | 1,30 | 32.1 | <0.001 |
| | Sampling period (after>during) | 1,30 | 81.0 | <0.001 |

In oil-seed rape fields, the density of bumble bees (Fig. II.3a), other wild bees (Fig. II.3c) and total species richness (Fig. II.3e) decreased with increasing cover of oil-seed rape in the landscapes during the flowering of oil-seed rape (Table II.3). The cover of semi-natural habitats had a significant positive effect on hoverflies (Fig. II.3b) and a marginally positive effect on the density of other wild bees than *Bombus* (Fig. II.3d) and on total species richness (Fig. II.3f).

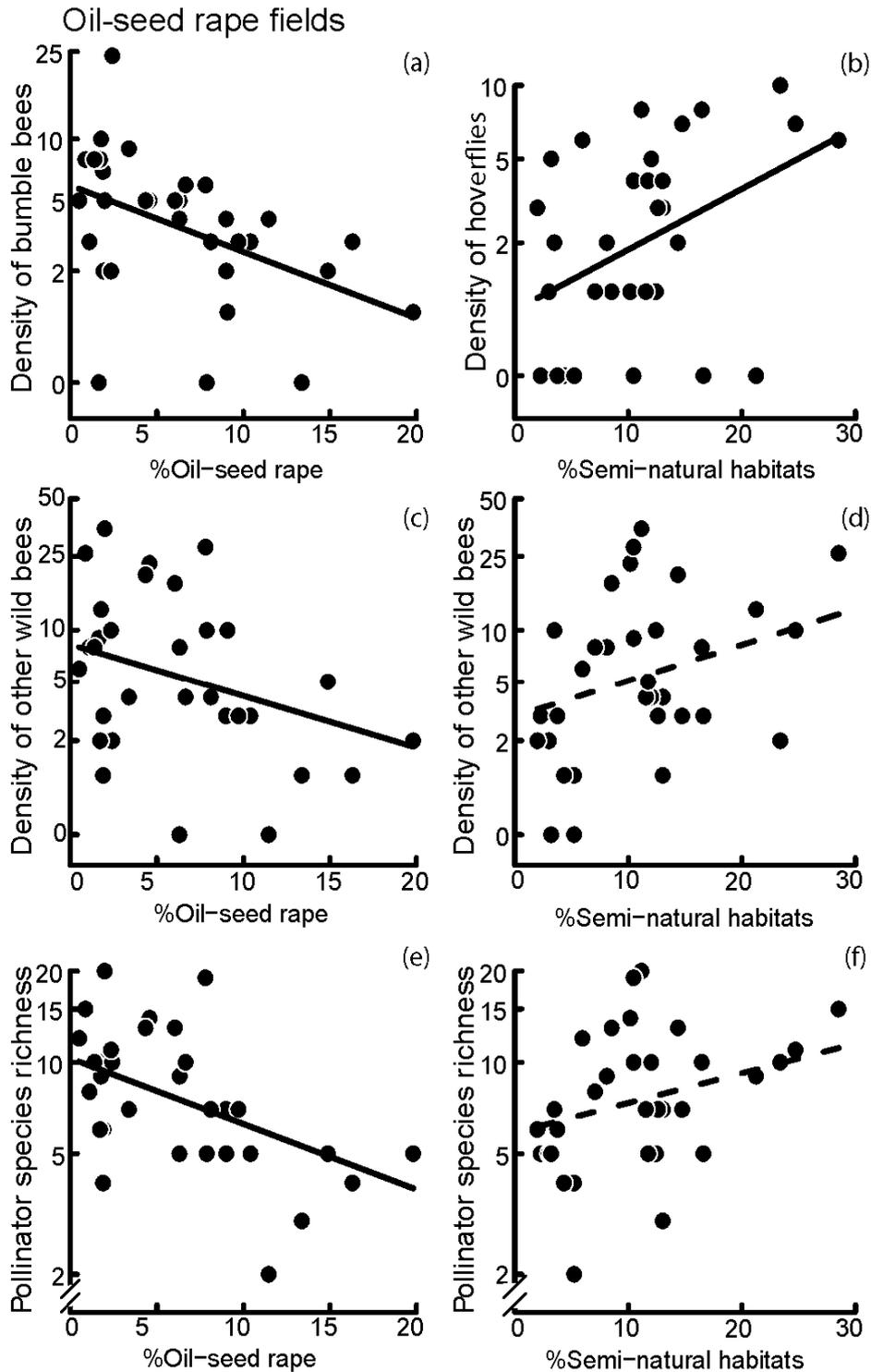


Fig. II.3 Pollinators on oil-seed rape (OSR) fields during mass-flowering. Relationship between (a) %OSR and density of bumble bees, (b) %Semi-natural habitats (SNH) and density of hoverflies, (c) %OSR and density of wild bees other than *Bombus* ($\ln(y+1) = -0.06 \times \%OSR + 0.04 \times \text{mean \%SNH} (=11.00) + 1.77$), (d) %SNH and density of wild bees other than *Bombus* ($\ln(y+1) = -0.06 \times \text{mean \%OSR} (=6.36) + 0.04 \times \%SNH + 1.77$), (e) %OSR and species richness, (f) %SNH and species richness. Each point represents the pooled densities for 600 m² transects. Regression lines were obtained from the original model output. Continuous lines show significant ($P < 0.05$) and dashed lines marginal significant relationships ($P < 0.1$) according to F-statistics in Table II.3

Table II.3. Results for pollinators on oil-seed rape fields from linear-mixed-effects models (F-statistic for Type I SS). Landscape predictors were measured in a 1-km radius around the oil-seed rape fields. Predictors are shown when $P < 0.1$; %OSR= cover of oil-seed rape, %SNH= cover of semi-natural habitats

| | | Df | F | P |
|-----------------------------------|------------|------|------|-------|
| <i>Species richness</i> | %OSR ↓ | 1,14 | 13.6 | 0.002 |
| | %SNH ↑ | 1,14 | 3.3 | 0.091 |
| <i>Density of bumble bees</i> | %OSR ↓ | 1,15 | 7.9 | 0.013 |
| <i>Density of other wild bees</i> | %OSR ↓ | 1,14 | 6.5 | 0.024 |
| | %SNH ↑ | 1,14 | 3.2 | 0.094 |
| <i>Density of honey bees</i> | Null model | | | |
| <i>Density of hoverflies</i> | %SNH ↑ | 1,15 | 6.5 | 0.023 |

Discussion

Our study evaluates the effects of a dominant mass-flowering crop concurrently in different habitat types during and after the flowering season. We find that flowering oil-seed rape can lead to the dilution of pollinators in crop fields but also in semi-natural field boundaries and (marginally) in grasslands at a landscape scale, whereas the landscape cover of semi-natural habitats benefitted pollinator densities in oil-seed rape. After the flowering period, we could show that a high landscape cover of oil-seed rape enhanced the densities of bumble bees in field boundaries, but not in semi-natural grasslands. Thus our study reveals that different seasons, habitat types and pollinator groups show specific and partly antagonistic responses to mass-flowering crops with significant potential consequences for crop pollination services and biotic interactions in semi-natural habitats. Since effects substantially differed, we will discuss results for crop and semi-natural habitat types separately, followed by a comparison of effects for various pollinator groups.

According to our results, an expansion of oil-seed rape from 5% to 10% cover would lead to a decline of bumble bees by 41% on field boundaries during mass-flowering, whereas the same expansion of oil-seed rape would lead to an increase of bumble bees by 47% after

mass-flowering. A similar pattern was found for bumble bees in hedges (Kovács-Hostyánszki *et al.* 2013), suggesting that these effects might apply for different kinds of fields margins in agricultural landscapes. Our results suggest that during mass-flowering, bumble bees were diluted by an increasing availability of oil-seed rape in the landscape, whereupon probably the competition for pollination services between flowers on field boundaries and the highly rewarding crop increased (Holzschuh *et al.* 2011). Increased densities of bumble bees after mass-flowering were previously explained by the enhanced colony establishing and growth rates enabled by the high availability of valuable feeding resources in landscapes with a high cover of oil-seed rape (Westphal *et al.* 2003). Because flowers in oil-seed rape fields are than no longer available, bumble bees have to forage increasingly in semi-natural habitats. The more bumble bee populations are enlarged in landscapes with a high cover of oil-seed rape the more pollinators are potentially available for the pollination of wild plants. However, we are not aware of any evidence for increased pollination success of wild plants induced by mass-flowering crops after the flowering period, neither on a landscape nor on a local scale (Kovács-Hostyánszki *et al.* 2013).

The results on field boundaries during mass-flowering mirrored at least partly the patterns on oil-seed rape fields. Densities of bumble bees and of other wild bees on oil-seed rape fields decreased with increasing cover of oil-seed rape in the landscape. This is the first evidence that not only bumble bees, but also other wild bees dilute over mass resources at the landscape scale. Dilution of bumble bees on a landscape scale is also known from other regions (Holzschuh *et al.* 2011) and on a field scale also for bees in other crops (Veddeler *et al.* 2006), which together with our results indicates this to be an important and widespread pattern. Consequences may be decreased pollination services for crops and thereby decreasing yields.

Our results indicate a much weaker dilution effect of oil-seed rape on pollinators in semi-natural grasslands and a possible related decrease in pollination success of wild flowers by increasing competition for pollinators during oil-seed rape flowering (Holzschuh *et al.* 2011). However, increased population growth, e.g. in bumble bee colonies, could potentially also increase visitation rates on wild flowers in grasslands after mass-flowering. While we found this effect after oil-seed rape flowering in field boundaries, such a pattern did not occur on grasslands. In semi-natural grasslands pollinators usually find everything they need to finish their life cycle – various nesting and feeding resources – which makes them similarly attractive than mass-flowering crops. Therefore the motivation for bees in grasslands to forage in mass-flowering crops might rather be low and interaction with the

surrounding landscape less pronounced than in field boundaries. Additionally, grasslands are more stable and less disturbed than field boundaries (Steffan-Dewenter and Tschardt 2002). Although, especially at the beginning of the year, feeding resources for pollinators in grasslands may be rather scarce, across the year they are attractive pollinator habitats by providing continuous resources (Rundlöf et al. 2008). Our results suggest that pollinators on high quality grasslands are compared to field boundaries more independent from the landscape context and rather buffer effects from resource pulses during and after the mass-flowering.

Not all pollinator groups in our study were affected to the same degree in the different habitats. The pattern that we found for foraging bumble bees in field boundaries did not apply to other foraging wild bees (Kovács-Hostyánszki *et al.* 2013). In contrast to bumble bees, early in the year other wild bees may preferably choose nest sites adjacent to oil-seed rape fields (Holzschuh *et al.* 2013) and forage mainly in the nearest resource (Zurbuchen *et al.* 2010). On field boundaries dilution of foraging wild bees may therefore not be observable. Against this background, the dilution of bees on crop fields with increasing cover of oil-seed rape in the landscape may have different reasons for bumble bees and other wild bees. While bumble bees, nesting somewhere in semi-natural habitats in the landscape, might dilute in the landscape during foraging, other wild bees than *Bombus* might dilute in the landscape already when they search for nesting sites, by preferring sites close to oil-seed rape. After mass-flowering, other wild bees than *Bombus* which already occurred during flowering, might have already finished their reproduction and do not have to forage in field boundaries anymore. Only 21 of 75 wild bee species other than *Bombus* occurred during and after the mass-flowering on field boundaries, indicating a huge species turnover between the two sampling periods. In contrast, bumble bee colonies still persist after mass-flowering and provision of food for larvae has to be ensured until the production of sexuals in midsummer.

In none of the habitats we found effects from oil-seed rape on honey bees, which can be explained by the fact that bee hives might be preferably positioned in landscapes with high cover of oil-seed rape indicating that managed colonies could compensate for dilution of wild pollinators. However, general honey bee densities in central Europe are far below demands for crop pollination (Breeze *et al.* 2014).

In none of the habitats we found effects from oil-seed rape on hoverflies. There is increasing evidence that the distribution of hoverflies depends more on larval requirements (Haenke et al. 2009; Jauker et al. 2009), which are rather independent from abundant floral

resources. Though, landscape effects from oil-seed rape on hoverfly densities cannot be completely disregarded depending on the habitat under consideration (Haenke *et al.* 2014). We found a positive effect of the cover of semi-natural habitats on hoverfly densities in crop fields. Although the cover of semi-natural habitats may increase hoverfly species richness (Kleijn and van Langevelde 2006), previous studies indicated decreasing densities of aphidophagous hoverflies through missing larval habitats in more heterogeneous landscapes in midsummer (Haenke *et al.* 2009; Jauker *et al.* 2009). Early in the year, during oil-seed rape flowering, the semi-natural habitats as overwintering habitats (Sarthou *et al.* 2005) possibly acted more as a source of hoverflies and larval habitats were not limiting at this time of the year.

Species richness decreased with increasing cover of oil-seed rape during flowering on oil-seed rape fields, which may not surprise given that species richness was mainly driven by densities of wild bees other than *Bombus*, but increased with increasing cover of semi-natural habitats in the landscape. Presumably accountable to the study design with at least one patch of semi-natural habitat in each landscape this effect was less pronounced than in other studies (Steffan-Dewenter *et al.* 2002). Since previous results on effects of oil-seed rape on pollinator species richness are mixed (Holzschuh *et al.* 2011; Diekötter *et al.* 2013) and mainly generalists may benefit (Diekötter *et al.* 2010), semi-natural habitats seem to be more important to maintain a diverse pollinator community.

Conclusion

During mass-flowering, farmers are most concerned about the dilution of pollinators in landscapes with an increasing cover of oil-seed rape that could potentially decrease yields. From a conservation perspective effects for pollinator diversity and possible consequences for pollination of wild plants need to be considered. Our study could not reveal changes of pollinator population dynamics, but could show that the distribution of pollinators is affected by the cover of mass-flowering crops on a landscape scale (Holzschuh *et al.* 2011; Kovács-Hostyánszki *et al.* 2013). Moreover, our study suggests that pollination services for wild plants could be decreased during mass-flowering in landscapes with a high cover of oil-seed rape, but direct evidence is still scarce (Cussans *et al.* 2010; Holzschuh *et al.* 2011; Kovács-Hostyánszki *et al.* 2013). After mass-flowering, our results suggest that oil-seed rape can benefit pollinators and potentially pollination services for wild plants and also for other crops on a landscape scale (Riedinger *et al.* 2014).

A point for future research is the relative value of mass-flowering crops compared to semi-natural habitats for benefitting pollinators. As suggested by results in the crop habitat, an increase of oil-seed rape from 5% to 10% would decrease densities of wild bees other than *Bombus* by 31%, while the same increase of semi-natural habitats would increase it by 30%. Given that expansion of mass-flowering crops is more likely than expansion of semi-natural habitats, shows the paramount importance of semi-natural habitats compared to mass-flowering crops for pollinators.

From a farmer perspective highest pollinator densities, indicating high yields, are reached by cultivating only few oil-seed rape fields (i.e. moderate cover on the landscape scale) in landscapes with a high cover of semi-natural habitats. Benefits for pollinator densities and species richness seem to be highly trait dependent (e.g. degree of specialization or phenology), with ostensive advantageous for generalists (Diekötter *et al.* 2010). Regarding effects of oil-seed rape on pollination services for wild plants, there might be losers (during flowering) and winners (after flowering). We conclude that management of landscape-scale relation between mass-flowering crops and pollinator-providing semi-natural habitats and targeted conservation schemes to improve the quality of semi-natural habitats are required to ensure crop pollination services and maintain pollinator diversity and wild plant pollination functions.

Supplement**Table II.S1.** Range and mean \pm SE for the landscape parameters cover of oil-seed rape (%OSR) and cover of semi-natural habitat (%SNH) in landscape sectors with a radius of 1 km around field boundaries, grasslands and oil-seed rape fields in the two study years 2011 and 2012

| | Field boundary | | Grassland | | Oil-seed rape field | |
|------|------------------------------|------------------------------|------------------------------|------------------------------|------------------------------|------------------------------|
| | 2011 | 2012 | 2011 | 2012 | 2011 | 2012 |
| %OSR | 0.5-19.2 (6.6 \pm 1.5) | 0.0-12.4 (4.3 \pm 1.0) | 0.5-12.6 (5.0 \pm 1.1) | 0.1-11.8 (4.6 \pm 1.0) | 0.5-19.8 (7.0 \pm 1.4) | 0.9-16.3 (5.7 \pm 1.1) |
| %SNH | 1.9-25.9 (11.5 \pm 1.6) | 0.9-25.9 (11.3 \pm 1.6) | 3.7-20.5 (11.9 \pm 1.2) | 3.7-20.5 (11.9 \pm 1.2) | 2.0-24.7 (11.4 \pm 1.7) | 2.3-28.5 (10.5 \pm 1.8) |

Table II.S2. Summed abundances of pollinators for two sampling years in 16 study areas on each type of study sites. There were two sampling rounds in oil-seed rape fields and four sampling rounds in field boundaries and grasslands in each study year. * marks species occurring during and after mass flowering in field boundaries and grasslands.

| Species | Field boundaries | Grasslands | Oil-seed rape fields |
|--|------------------|------------|----------------------|
| <i>Bombus</i> | 429 | 925 | 153 |
| <i>B. hortorum</i> | — | 36* | 1 |
| <i>B. hypnorum</i> | 2 | 8* | — |
| <i>B. lapidarius</i> | 247* | 459* | 93 |
| <i>B. pascuorum</i> | 60* | 85* | 13 |
| <i>B. pratorum</i> | 17* | 42* | 1 |
| <i>B. sylvarum</i> | 27* | 93* | 6 |
| <i>B. terrestris/lucorum</i> agg. | 73* | 169* | 37 |
| <i>B. rupestris</i> | — | 1 | — |
| <i>B. spp.</i> | 3 | 32 | 2 |
| Other wild bees than <i>Bombus</i> spp. | 655 | 838 | 273 |
| <i>Andrena</i> | | | |
| <i>A. bicolor</i> | 4* | 3 | 2 |
| <i>A. chrysoseles</i> | 6* | — | 1 |
| <i>A. cineraria</i> | 10* | 2 | 30 |
| <i>A. curvungula</i> | — | 1 | — |
| <i>A. decipiens</i> | — | 1 | — |
| <i>A. dorsata</i> | 1 | 2 | 2 |
| <i>A. falsifica</i> | 4* | 64* | — |
| <i>A. flavipes</i> | 12* | 20* | 16 |
| <i>A. florea</i> | — | 1 | — |
| <i>A. floricola</i> | 1 | — | — |
| <i>A. fulva</i> | — | — | 2 |
| <i>A. fulvata</i> | — | 2 | 2 |

Table II.S2. continued

| Species | Field boundaries | Grasslands | Oil-seed rape fields |
|-------------------------------------|------------------|------------|----------------------|
| <i>A. fulvicornis</i> | 2 | — | 1 |
| <i>A. gravida</i> | — | — | 2 |
| <i>A. haemorrhoea</i> | 6 | 2* | 16 |
| <i>A. hattorfiana</i> | — | 1 | — |
| <i>A. helvola</i> | 2* | — | 4 |
| <i>A. humilis</i> | — | 2 | — |
| <i>A. labiata</i> | — | 1 | 1 |
| <i>A. lagopus</i> | — | — | 2 |
| <i>A. lathyri</i> | 2 | — | — |
| <i>A. minutula</i> | 17 | 10* | 4 |
| <i>A. minutuloides</i> | 17* | 2 | 1 |
| <i>A. nana</i> | — | — | 2 |
| <i>A. nigroaenea</i> | 10* | — | 12 |
| <i>A. nitida</i> | — | — | 2 |
| <i>A. nitidiuscula</i> | 1 | 1 | — |
| <i>A. ovulata</i> | — | 1 | — |
| <i>A. potentillae</i> | 1 | 11 | — |
| <i>A. proxima</i> | — | 2 | — |
| <i>A. strohmella</i> | — | — | 1 |
| <i>A. subopaca</i> | 9* | 5* | 1 |
| <i>A. viridescens</i> | — | 1 | — |
| <i>A. wilkella</i> | 1 | 6* | — |
| <i>A. spp.</i> | 1 | 1 | 3 |
| <i>Anthidium</i> | | | |
| <i>A. nanum</i> | — | 2 | — |
| <i>A. punctatum</i> | — | 2* | — |
| <i>A. strigatum</i> | — | 3 | — |
| <i>Anthophora aestivalis</i> | — | 1 | 1 |

Table II.S2. continued

| Species | Field boundaries | Grasslands | Oil-seed rape fields |
|---------------------------------------|------------------|------------|----------------------|
| <i>Ceratina</i> | | | |
| <i>C. cucurbitina</i> | — | 1 | — |
| <i>C. cyanea</i> | — | 4* | — |
| <i>Chelostoma florissomnis</i> | 1 | — | — |
| <i>Colletes</i> | | | |
| <i>C. cunicularius</i> | — | 1 | — |
| <i>C. daviesanus</i> | 2 | — | — |
| <i>Eucera nigrescens</i> | 5 | 6* | 1 |
| <i>Halictus</i> | | | |
| <i>H. maculatus</i> | 6* | 5* | 1 |
| <i>H. rubicundus</i> | 1 | 1 | — |
| <i>H. scabiosae</i> | 3* | 4* | — |
| <i>H. simplex</i> | 8 | 59* | — |
| <i>H. subauratus</i> | — | 4 | — |
| <i>H. tumulorum</i> | 30* | 54* | 6 |
| <i>Heriades truncorum</i> | 11 | 9 | — |
| <i>Hylaeus</i> | | | |
| <i>H. annularis</i> | 3 | 4 | — |
| <i>H. brevicornis</i> | 1 | 3 | — |
| <i>H. communis</i> | 5 | 4 | — |
| <i>H. confusus</i> | 10 | 2 | — |
| <i>H. difformis</i> | 3 | 3 | — |
| <i>H. duckei</i> | 3 | — | — |
| <i>H. gredleri</i> | 3 | — | — |
| <i>H. hyalinatus</i> | 2 | — | — |
| <i>H. nigritus</i> | — | 1 | — |
| <i>H. paulus</i> | — | 2* | — |
| <i>H. signatus</i> | 2 | — | — |
| <i>H. sinuatus</i> | 3 | — | — |

Table II.S2. continued

| Species | Field boundaries | Grasslands | Oil-seed rape fields |
|----------------------------|------------------|------------|----------------------|
| <i>H. styriacus</i> | 3 | — | — |
| <i>H. variegatus</i> | — | 1 | — |
| <i>Lasioglossum</i> | | | |
| <i>L. albipes</i> | 1 | 6* | — |
| <i>L. calceatum</i> | 38* | 19* | 4 |
| <i>L. clypeare</i> | — | 1 | — |
| <i>L. costulatum</i> | — | 2 | — |
| <i>L. fulvicorne</i> | 5* | 13* | 7 |
| <i>L. glabriusculum</i> | 70* | 32* | 2 |
| <i>L. interruptum</i> | 6 | 19* | 3 |
| <i>L. laevigatum</i> | — | 1 | — |
| <i>L. laticeps</i> | 2 | 4* | 22 |
| <i>L. leucozonium</i> | 5 | 3* | — |
| <i>L. malachurum</i> | 53* | 8* | 9 |
| <i>L. morio</i> | 14* | 37* | 4 |
| <i>L. nitidulum</i> | — | 6 | 3 |
| <i>L. pauxillum</i> | 77* | 40* | 6 |
| <i>L. politum</i> | 1 | 4 | — |
| <i>L. punctatissimum</i> | 2 | 2* | — |
| <i>L. puncticolle</i> | 19 | — | — |
| <i>L. pygmaeum</i> | — | 1 | — |
| <i>L. quadrinotatum</i> | 2 | — | — |
| <i>L. villosulum</i> | 12 | 17* | — |
| <i>L. xanthopus</i> | 9 | 4* | 2 |
| <i>L. zonulum</i> | — | 2 | — |
| <i>Megachile</i> | | | |
| <i>M. alpicola</i> | — | 1 | — |
| <i>M. circumcincta</i> | 1 | 1 | — |
| <i>M. ericetorum</i> | 2 | 2 | — |

Table II.S2. continued

| Species | Field boundaries | Grasslands | Oil-seed rape fields |
|---------------------------------|------------------|------------|----------------------|
| <i>M. lagopoda</i> | — | 3 | — |
| <i>M. pilidens</i> | 1 | 2 | — |
| <i>M. rotundata</i> | — | 1 | — |
| <i>M. versicolor</i> | 2 | 2 | — |
| <i>M. willughbiella</i> | — | 1 | — |
| <i>Melecta albifrons</i> | — | 1 | — |
| <i>Melitta leporina</i> | 5 | 1 | — |
| <i>Nomada</i> | | | |
| <i>N. bifasciata</i> | 1 | 2 | — |
| <i>N. distinguenda</i> | 1 | — | — |
| <i>N. fabricana</i> | 1 | — | — |
| <i>N. flavoguttata</i> | 1 | 4* | — |
| <i>N. lathburiana</i> | 2 | — | — |
| <i>N. ruficornis</i> | 1 | — | — |
| <i>N. succincta</i> | — | 2 | 1 |
| <i>Osmia</i> | | | |
| <i>O. adunca</i> | 1 | 3 | — |
| <i>O. aurulenta</i> | — | 5* | 1 |
| <i>O. bicolor</i> | 7* | 42* | 12 |
| <i>O. bicornis</i> | 12* | 5* | 12 |
| <i>O. brevicornis</i> | — | — | 2 |
| <i>O. caerulea</i> | — | 1 | — |
| <i>O. campanularum</i> | — | 2 | — |
| <i>O. claviventris</i> | 1 | 1 | — |
| <i>O. gallarum</i> | — | 6* | — |
| <i>O. leucomelana</i> | 1 | 2 | — |
| <i>O. rapunculi</i> | 3 | 1 | — |
| <i>O. rufohirta</i> | 1 | 5* | — |

Table II.S2. continued

| Species | Field boundaries | Grasslands | Oil-seed rape fields |
|--------------------------------------|------------------|------------|----------------------|
| <i>O. spinulosa</i> | 1 | 11 | — |
| <i>O. submicans</i> | — | 3 | — |
| <i>O. tridentata</i> | 1 | 2* | — |
| <i>O. xanthomelana</i> | — | 3* | — |
| <i>Sphecodes</i> | | | |
| <i>S. crassus</i> | — | 1 | — |
| <i>S. ephippius</i> | 14* | — | 2 |
| <i>S. geoffrellus</i> | — | 2 | — |
| <i>Stelis punctulatissima</i> | — | 1 | — |
| <i>Trachusa byssinum</i> | — | 7 | — |
| Halictidae spp. | 4 | 16 | 11 |
| Megachilidae spp. | — | 2 | 6 |
| Apiformes spp. | 63 | 155 | 48 |
| Syrphidae | 1461 | 744 | 95 |
| <i>Cheilosia</i> | | | |
| <i>C. flavipes</i> | 1 | 1 | — |
| <i>C. lenis</i> | 1 | — | — |
| <i>C. nebulosa</i> | — | 1 | — |
| <i>C. scutellata</i> | — | 1 | — |
| <i>C. urbana</i> | — | 1 | — |
| <i>C. vernalis</i> | 1 | 1 | — |
| <i>C. spec.</i> | — | 1 | — |
| <i>Chrysotoxum</i> | | | |
| <i>C. bicinctum</i> | — | 2 | — |
| <i>C. cautum</i> | 1 | 2 | 3 |
| <i>Dasysyrphus venustus</i> | 1 | — | — |
| <i>Epistrophe melanostoma</i> | 1 | — | — |
| <i>Episyrphus balteatus</i> | 147 | 159 | 2 |

Table II.S2. continued

| Species | Field boundaries | Grasslands | Oil-seed rape fields |
|-------------------------------------|------------------|------------|----------------------|
| <i>Eristalis</i> | | | |
| <i>E. arbustorum</i> | — | 2 | 1 |
| <i>E. intricarius</i> | — | — | 1 |
| <i>E. similis</i> | — | 1 | — |
| <i>E. tenax</i> | 2 | 7 | — |
| <i>Eumerus</i> | | | |
| <i>E. strigatus</i> | 5 | 1 | — |
| <i>E. spp.</i> | 2 | — | — |
| <i>Eupeodes</i> | | | |
| <i>E. bucculatus</i> | — | 1 | — |
| <i>E. corollae</i> | 53 | 10 | — |
| <i>E. luniger</i> | 24 | 6 | — |
| <i>Helophilus pendulus</i> | 1 | — | — |
| <i>Melanostoma</i> | | | |
| <i>M. mellinum</i> | 17* | 16* | 34 |
| <i>M. scalare</i> | — | 1 | — |
| <i>Meliscaeva auricollis</i> | 1 | — | — |
| <i>Merodon spp.</i> | — | 12* | — |
| <i>Myathropa florea</i> | 4 | 10 | — |
| <i>Paragus</i> | | | |
| <i>P. bicolor</i> | 1 | — | — |
| <i>P. haemorrhous</i> | — | 3 | — |
| <i>Parasyrphus spec.</i> | — | — | 1 |
| <i>Pipizella</i> | | | |
| <i>P. viduata</i> | 1 | 14* | 2 |
| <i>P. virens</i> | 2 | — | — |
| <i>Platycheirus</i> | | | |
| <i>P. albimanus</i> | 3* | — | — |
| <i>P. clypeatus</i> | 4* | 1 | 1 |

Table II.S2. continued

| Species | Field boundaries | Grasslands | Oil-seed rape fields |
|------------------------------|------------------|------------|----------------------|
| <i>P. scutatus</i> | 1 | — | — |
| <i>P. spp.</i> | 8 | — | — |
| <i>Scaeva</i> | | | |
| <i>S. dignota</i> | 2 | — | — |
| <i>S. pyrastris</i> | 16 | 7 | — |
| <i>S. selenitica</i> | 8 | 3 | — |
| <i>Sphaerophoria</i> | | | |
| <i>S. scripta</i> | 402* | 352* | 22 |
| <i>S. taeniata</i> | 1 | — | — |
| <i>Syrirta pipiens</i> | 11 | 9* | — |
| <i>Syrphus</i> | | | |
| <i>S. ribesii</i> | 6* | — | — |
| <i>S. torvus</i> | 1 | — | — |
| <i>S. vitripennis</i> | 14 | 7* | 1 |
| <i>Tropidia scita</i> | 1 | — | — |
| <i>Volucella pellucens</i> | — | 1 | — |
| <i>Xanthogramma</i> | | | |
| <i>X. citrofasciatum</i> | — | 5 | — |
| <i>X. festivum</i> | — | — | 1 |
| <i>Syrphidae spp.</i> | 717 | 106 | 26 |

III. Early mass-flowering crops mitigate pollinator dilution in late-flowering crops

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Running title: Effects in late-flowering crops

Keywords: *Apis mellifera*, *Bombus*, Germany, oil-seed rape, spillover, sunflower, syrphids

Abstract

Previous studies focused mainly on the provision of ecosystem services by species movements between semi-natural and managed habitats, whereas data on spillover effects between two managed habitats or between habitats that provide target resources in non-overlapping time periods are lacking.

We studied densities of three pollinator groups on sunflower fields as a late mass-flowering crop in 16 landscapes that differed in the relative cover of oil-seed rape as an early mass-flowering crop, in the relative cover of sunflowers and in the relative cover of semi-natural habitats. Our aim was to evaluate dynamics between two crops with non-overlapping flowering periods.

Densities of bumble bees in late-flowering sunflower fields were enhanced by early-flowering oil-seed rape. Highest bumble bee densities in the late-flowering crop were reached in landscapes that combined high relative covers of oil-seed rape and semi-natural habitats. Further, low relative covers of oil-seed rape in spring led to decreased bumble bee densities in late-flowering sunflower fields in landscapes with high relative covers of sunflower fields (dilution effect), whereas in landscapes with high relative covers of oil-seed rape, no dilution of bumble bees was found. Thus, our results indicate that early mass-flowering crops can mitigate pollinator dilution in crops flowering later in the season. We conclude that the management of landscape-scale patterns of early and late mass-flowering crops together with semi-natural habitats could be used to ensure crop pollination services. Similar processes could also apply for other species groups and may be an important, but so far disregarded, determinant of population densities in agroecosystems.

Introduction

Pollinators provide an important ecosystem service to animal-pollinated wild plants (Ollerton et al. 2011) and crops (Klein et al. 2007; Gallai et al. 2009). The occurrence of pollinators in agroecosystems is mainly determined by the interplay between agricultural habitats and natural or semi-natural habitats. With increasing distance from natural or semi-natural habitats pollinator richness and density decline in major animal-pollinated crops (Ricketts et al. 2008; Garibaldi et al. 2011). On the other hand, mass-flowering crops providing additional food resources can increase pollinator densities in adjacent habitats (Westphal et al. 2003). Thus, to understand how landscape composition determines densities of functionally relevant species is critical for maintaining ecosystem services in anthropogenically transformed landscapes (Tscharntke et al. 2012). So called spillover effects between different habitats in agricultural landscapes on local and landscape scales recently received much interest across different species groups (Blitzer et al. 2012). These effects occur, when organisms have changing requirements during their life-cycle or move between habitats that provide different resources (Benton et al. 2003). So far most spillover research focused on the fluxes from natural to managed habitats (Blitzer et al. 2012). Here, semi-natural or natural habitats are mostly seen as beneficial sources for bio-control or pollination services (Thies and Tscharntke 1999; Kremen et al. 2002). Now, it is more and more recognized that spillover effects from managed to semi-natural habitats or between different agricultural habitats may be also important for transferring ecosystem services or disservices, although only rarely studied to date (Blitzer et al. 2012). Managed habitats can provide large amounts of resources and thereby increase species densities in adjacent natural habitats (Rand et al. 2006). Importantly, these spillover effects have not only a spatial, but also a temporal component. Few previous studies have reported on different temporal scales of spillover. On the smallest temporal scale, different habitats are either used simultaneously to fulfill different resource requirements (nesting vs. feeding; Holzschuh et al. 2011; Öckinger and Smith 2007) or consecutively when feeding resources in semi-natural habitats gain attractiveness after harvesting of crops (Rand et al. 2006). On a larger temporal scale, inter-annual shifts of resources, e.g. due to crop rotation, have been found to influence pest-enemy dynamics (Thies et al. 2008) as well as abundance and species richness of pollinators (Le Féon et al. 2013). Moreover, on an intermediate temporal scale, spillover between spatially separated habitats could arise when habitats give non-overlapping resource pulses within one year. If species are active for several months or have multiple generations within

one season and can make use of non-overlapping resource pulses, effects of a habitat with an earlier resource pulse on another habitat with a later resource pulse can be expected even though other habitat types might have been used in between. This type of spatio-temporal spillover (hereafter referred to as temporal spillover) might strongly affect species communities and associated ecosystem services in agricultural landscapes, where mass resources in crop fields appear and disappear in short time intervals.

In the case of pollinators, spillover effects can arise through the movement between nesting and foraging habitats (Westrich 1996). Moving is also necessary due to the fact that the flowering period of a certain plant species is often short compared to the activity period of pollinators (Blüthgen and Klein 2011). Since worldwide pollinator decline is caused not only by loss of nesting sites, which are mainly found in semi-natural habitats, but also by loss of food resources (Potts et al. 2010), managed habitats that provide such food resources can benefit pollinator populations. Mass-flowering crops provide a valuable food resource during a short period of time (Morandin and Winston 2006) and are increasingly available in Europe (European Commission 2013). At the local scale, densities of bumble bees and cavity-nesting bees increased in semi-natural habitats adjacent to mass-flowering crops compared to isolated semi-natural habitats (Hanley et al. 2011; Holzschuh et al. 2013). At the landscape scale, higher relative covers of mass-flowering crops were shown to enhance densities of bumble bees in more natural habitats (Westphal et al. 2003; Herrmann et al. 2007). Westphal et al. (2009, 2003) showed that these effects may be long-lasting, when measuring higher bumble bee densities and colony weights weeks after flowering of oil-seed rape had ceased in landscapes with higher relative covers of this mass-flowering crop. On the other hand, high densities of mass-flowering crops can result in the transient dilution of available pollinators during the mass-flowering period with potential negative consequences for crop pollination (Holzschuh et al. 2011). Long-lasting negative effects of mass-flowering crops were shown for densities of specialized long-tongued bumble bees, which were explained by the increasing competition with short-tongued bumble bees benefitting from the mass-flowering crop (Diekötter et al. 2010). So far no study addressed temporal spillover between crops flowering in different seasons and the question whether early mass-flowering crops can enhance pollinator populations to benefit pollination services for later flowering crops.

In this study we evaluated whether such temporal spillover occurs between two crops with non-overlapping flowering periods. We studied pollinator densities on 16 sunflower fields in 16 landscape sectors that formed independent landscape gradients in the relative cover of an early-flowering crop (oil-seed rape) and of a late-flowering crop (sunflowers).

Both crops are mainly pollinated by managed honey bees, bumble bees and hoverflies (Bommarco et al. 2012; Mudri-Stojnic et al. 2012). These pollinator groups greatly differ in their life cycles and resource requirements. Colonies of many bumble bee species persist from spring till late summer and colony growth of some species has already been shown to be enhanced by high availability of oil-seed rape (Westphal et al. 2009). Though, it is not known if also the pollination service provided by these larger bumble bee colonies is augmented. Also growth of honey bee colonies can potentially be enhanced by mass-flowering resources early in the year. Hoverflies, which often have several generations within one season, are less restricted to nesting sites than central-place foraging bumble bees and honey bees, and can disperse to other landscapes after oviposition (Jauker et al. 2009). Furthermore, only adult hoverflies depend on flowers as feeding resources and probably cannot benefit from mass-flowering crops to the same extent than bumble bees or honey bees over the year. The availability of semi-natural habitats, which can be used continuously as alternative feeding resource and at least by bumble bees also as nesting sites, may additionally modulate the effect of mass-flowering crops on these pollinator groups. Additionally, hoverflies and bumble bees may respond differently to isolation from semi-natural habitat, partly depending on ecological traits (Ekroos et al. 2013). Positive effects of semi-natural habitats have already been found for bumble bees (Öckinger and Smith 2007; Rundlöf et al. 2008). Negative effects were detected for hoverfly densities, because aphidophagous species, which prefer crop fields as larval habitats, are often most abundant in crop-dominated landscapes (Haenke et al. 2009; Jauker et al. 2009). Although apiaries are not restricted to nesting sites in semi-natural habitats, managed honey bee hives are often positioned in or close to semi-natural habitats by beekeepers, possibly leading to higher colony densities in landscapes with a high relative cover of semi-natural habitats (Steffan-Dewenter et al. 2002). We hypothesized (1) that densities of pollinators in sunflower fields are increased in landscapes where high relative covers of oil-seed rape are available in spring, and that responses to the early-flowering crop are stronger for central-place foraging bumble bees and honey bees than for less spatially restricted hoverflies, (2) that a high proportion of sunflower fields leads to pollinator dilution and reduced abundances per area sunflower during sunflower bloom and (3) that semi-natural habitats modulate the spillover from oil-seed rape to sunflowers differentially for bumble bees, honey bees and hoverflies due to their diverse reproductive requirements.

Material and Methods

Study sites and landscape parameters

The study was conducted in 2011 in the surroundings of Würzburg, Bavaria, Germany (49°47' N, 9°57' E). This region is intensively used for agriculture, mainly for the production of annual crops, and with a rather small relative cover of grassland. Additionally, the region is important for cultivation of mass-flowering crops, like oil-seed rape. Calcareous grasslands are the main semi-natural habitat found in this region.

We selected 16 sunflower fields in an area of 45 x 55 km that were at least 4 km apart from each other. The study fields were located in the center of 16 non-overlapping landscape sectors with a radius of 2 km distributed along a gradient of relative cover of oil-seed rape, as an early mass-flowering crop. Bumble bees and honey bees are supposed to be the main pollinators recorded on sunflowers (Carvalho et al. 2011). We focused on landscape sectors within 2 km of the study fields, because most of the expected pollinator species react on a 2-km scale or even on larger radii to semi-natural habitats and mass-flowering crops (Steffan-Dewenter et al. 2002; Westphal et al. 2006), also in comparison to small-sized solitary bees that have smaller foraging ranges (Greenleaf et al. 2007). The 2-km radius may also fit for hoverflies due to their strong dispersal abilities (Kleijn and van Langevelde 2006). In the study region, oil-seed rape flowers from late April until beginning of June. Oil-seed rape covered a gradient from 0.1 to 11.7 % (mean \pm SD: 5.1 \pm 4.4 %) in the landscape sectors. Additionally, the study fields covered gradients in relative cover of sunflowers (0.2–3.1 percent, mean \pm SD: 0.9 \pm 0.8 %) and of semi-natural habitats (1.5–11.3 %, 5.7 \pm 3.0 %). As semi-natural habitats we classified all habitats potentially valuable as nesting and foraging sites for pollinators namely calcareous grasslands, forest edges (the 10 m wide border strip of forests), hedgerows, fallows and orchard meadows. The three selected landscape parameters were not strongly intercorrelated (Pearson's correlation coefficient, all $r < 0.32$, $n = 16$). The three other most abundant land-use types in our study landscapes were non-flowering crops (24.1–84.3 %, mean \pm SD: 52.4 \pm 17.4 %), settlements (6.1–33.4 %, 12.6 \pm 6.8 %), forest interior (0.2–32.5 %, 12.0 \pm 10.0 %), but since these are not seen as valuable feeding or nesting habitats they are not expected to influence pollinator densities. The average field size of the study sites was 1.19 \pm 0.56 ha (mean \pm SD) and did not correlate with any of the three selected landscape parameters (Pearson's correlation coefficient, all $r < -0.12$, $n = 16$). The land-use data were provided by the Bavarian State Ministry of Nutrition, Agriculture and Forestry. For calculating relative cover of semi-

natural habitats we combined these data with the Bavarian biotope mapping. The geographical information system ArcMap (ESRI, v. 9.3.1) was used to calculate the relative covers for the different habitat types in each landscape sector.

Pollinator survey

Pollinators (bumble bees, hoverflies, honey bees, solitary bees) were observed during flowering of sunflowers on two 150 m² transects on each sunflower field. Solitary bees were not further analysed, because of their very low densities in sunflower fields (28 individuals in total). To ensure that the observation of pollinators was representative for different locations of the field, one transect was located on the outer crop line paralleling the edge of the field, the other one was parallel to the first, located in the center of the field with at least 20 m distance from each edge. A transect had a width of 1 m and a length of 150 m. Transects were sampled three times, each time for 15 minutes, between the 4th of July and 6th of August 2011 during the sunflower bloom, while slowly walking along the transect and recording only pollinators on sunflower heads. On two fields we managed to perform four sampling rounds, on three fields we had three sampling rounds on the edge transect but only two sampling rounds on the center transect. Sunflower fields were sampled under standardized weather conditions (temperatures above 16 °C, no rain, low or no cloud cover, low wind speeds) between 09.00 and 18.00 h. In each landscape sector observations were performed on different days and at different times of the day (Westphal et al. 2006). Honey bees and bumble bees were identified in the field to species level (except for *B. terrestris* and *B. lucorum* agg.). Hoverflies and wild bees other than bumble bees were collected for species identification in the lab.

Data analyses

Mean densities of different pollinator groups (bumble bees, hoverflies, honey bees) over all sampling rounds were averaged for the two 150 m² transects and analysed in linear regressions. Full models contained the relative cover of oil-seed rape, sunflowers and semi-natural habitats in the 2-km radius landscape sectors, as well as the two-fold interaction between relative cover of oil-seed rape and the two other landscape parameters. We ln-transformed the densities of pollinators to reach homoscedasticity of variance and normality of residuals (Crawley 2007). Model simplification was performed by removing non-significant terms from the full model using likelihood ratio tests in a backward selection procedure (Zuur et al. 2009). Non-significant main-effects always remained in the model,

when they were included in a (marginally) significant interaction ($p < 0.1$). All models were calculated in R (v. 2.15.1, R Development Core Team 2012). We display mean densities over all sampling rounds and two 150 m² transects in all figures based on raw data. To visualize interactions between two continuous variables in a two-dimensional figure, we split the data points at the median relative cover of oil-seed rape (low vs. high relative cover of oil-seed rape) and calculated regression lines with coefficients from the final models by fixing oil-seed rape at its median value of the low, respectively high relative cover oil-seed rape subset.

Results

We recorded 7708 bumble bees (8 species), 975 hoverflies (13 species), 12,074 honey bees, and 28 other wild bees (6 species) on the 16 sunflower fields during 97 transect walks (Supplement Table III.S1, bumble bee and hoverfly species that can be found in both crops are shown in Supplement Table III.S2).

For the density of bumble bees in sunflower fields, the interaction between the relative cover of oil-seed rape and the relative cover of sunflowers in the landscape sectors surrounding the sunflower fields was significant (Table III.1). While the bumble bee density increased with increasing relative covers of sunflowers at high relative covers of oil-seed rape (Fig. III.1a), it decreased with increasing relative covers of sunflowers at low relative covers of oil-seed rape (Fig. III.1b). At low relative cover of sunflowers, bumble bee densities did not differ between landscapes with a high or low relative cover of oil-seed rape. In landscapes with more than 1% relative cover of sunflowers, bumble bee densities were higher in landscapes with high relative covers of oil-seed rape than with low relative covers of oil-seed rape (Fig. III.1a-b). Additionally, for the density of bumble bees in sunflower fields, the interaction between the relative cover of oil-seed rape and the relative cover of semi-natural habitats was marginally significant (Table III.1). The bumble bee density increased with an increasing relative cover of semi-natural habitats at high relative covers of oil-seed rape only (Fig. III.2a), whereas in landscapes with low relative covers of oil-seed rape there was no increase (Fig. III.2b). Highest bumble bee densities in sunflower fields were found in landscapes with high relative covers of oil-seed rape and semi-natural habitats.

For the density of hoverflies the interaction between the relative cover of oil-seed rape and relative cover of semi-natural habitats was significant. The hoverfly density decreased with an increasing relative cover of semi-natural habitats both at high and low

relative covers of oil-seed rape, but this decrease was more pronounced at high than at low relative covers of oil-seed rape (Table III.1, Fig. III.2c-d).

The density of honey bees was explained by a similar interaction between the relative cover of oil-seed rape and the relative cover of semi-natural habitats (Table III.1, Fig. III.2e-f). The honey bee density was affected by the relative cover of semi-natural habitats in landscapes with high relative covers of oil-seed rape only, where it decreased with increasing relative covers of semi-natural habitats (Fig. III.2e). Neither the densities of hoverflies (Fig. III.1c-d), nor the densities of honey bees (Fig. III.1e-f) were affected by the relative cover of sunflower.

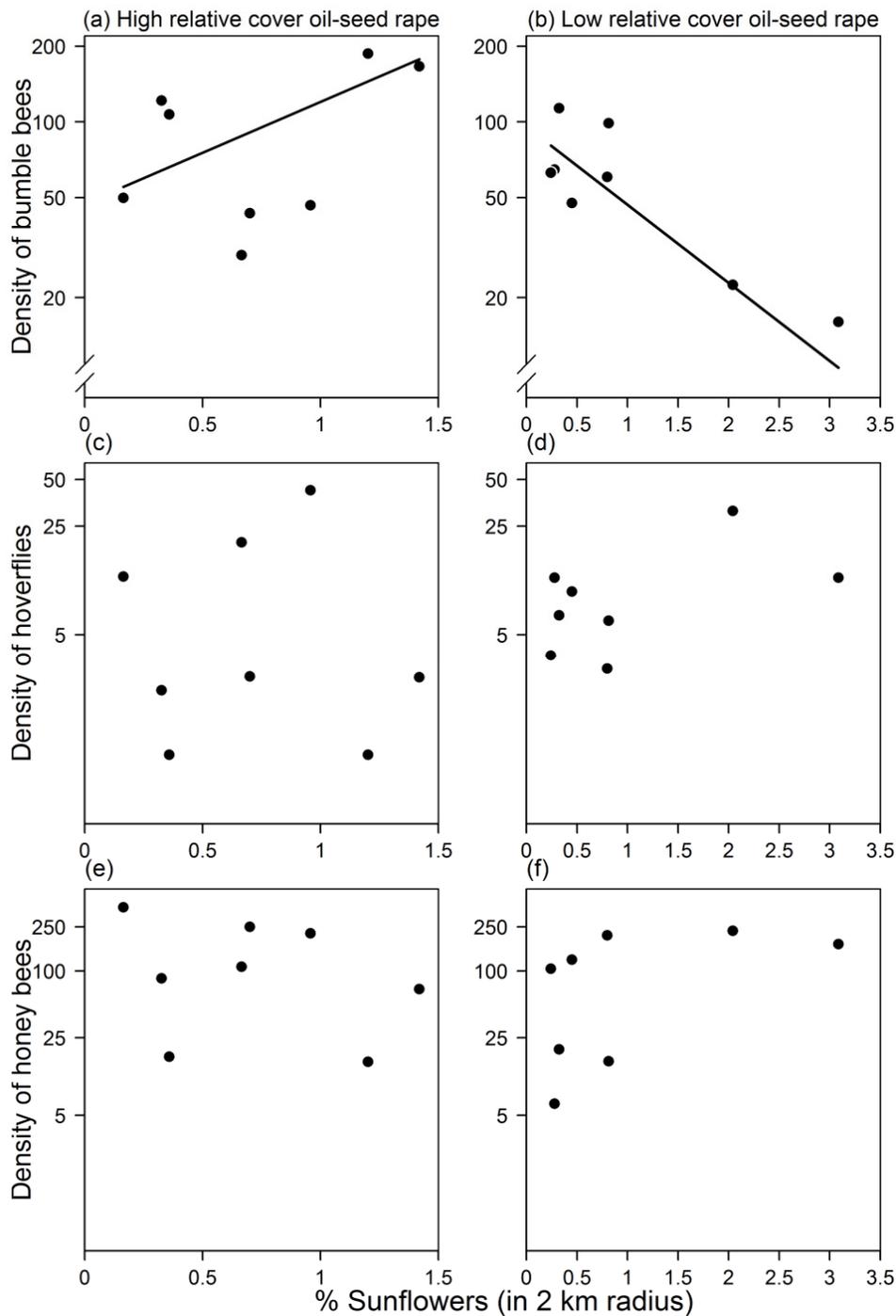


Fig. III.1 Relationship between relative covers of sunflowers on a 2–km radius and the density of bumble bees (a, b), hoverflies (c, d) and honey bees (e, f). Note that the data points were split at the median of the relative cover of oil-seed rape (high vs. low). (a, c, e) High relative cover of oil-seed rape (7.5-11.7 %, median = 9.0 %), (b, d, f) low relative cover of oil-seed rape (0.1-2.4 %, median = 0.8%). Each point represents the mean density across all sampling rounds averaged then for the two transects. For regression lines for high vs. low relative cover of oil-seed rape we fixed relative cover of oil-seed rape at its median value in each of the groups in the model equation (Table III.1). In the bumble bee model, also the predictor relative cover of semi-natural habitats was held constant at its mean value in the equation.

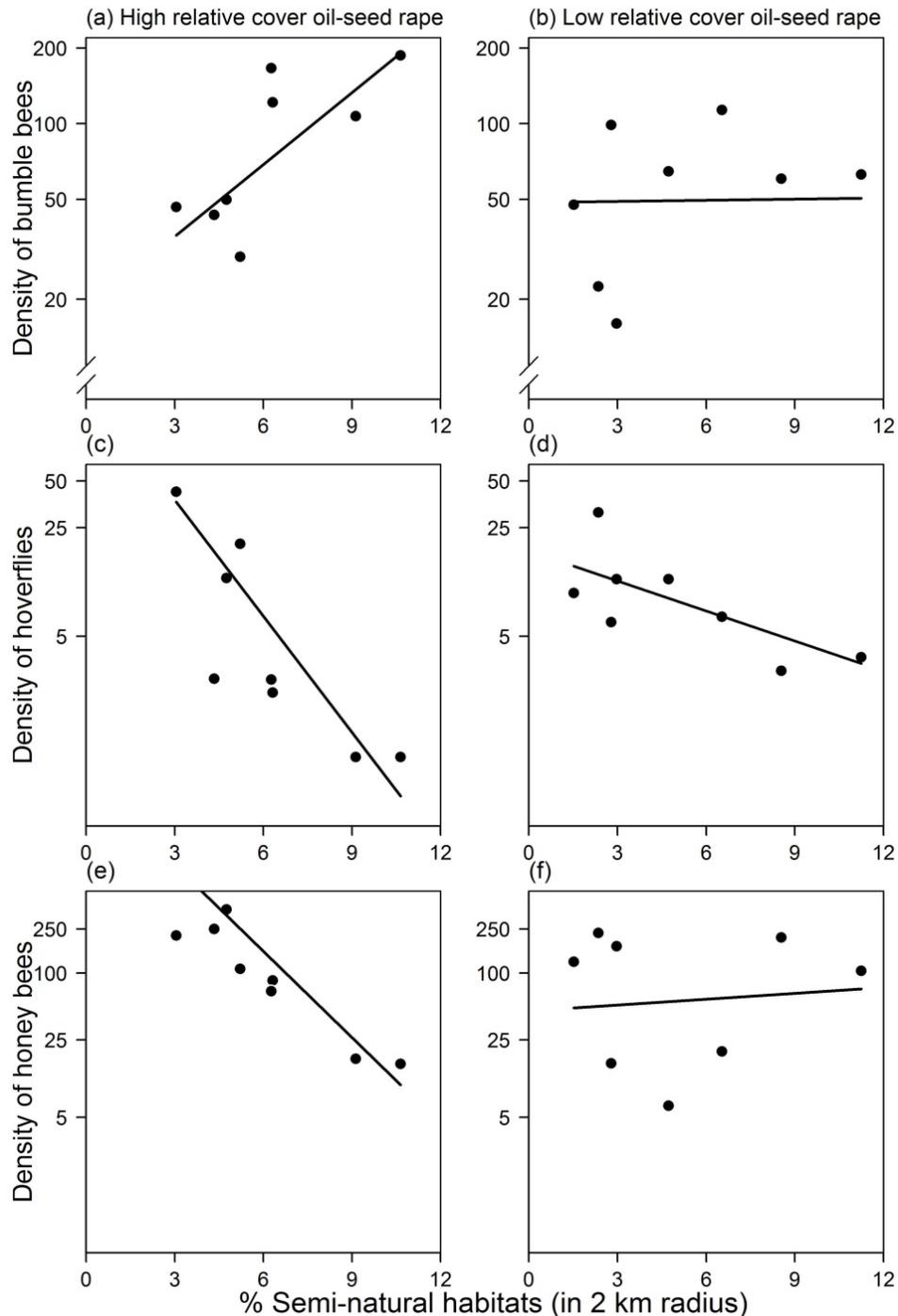


Fig. III.2 Relationship between relative covers of semi-natural habitats on a 2-km radius and the density of bumble bees (a, b), hoverflies (c, d) and honey bees (e, f). Note that the data points were split at the median of the relative cover of oil-seed rape (high vs. low). (a, c, e) High relative cover of oil-seed rape (7.5-11.7 %, median = 9.0 %), (b, d, f) low relative cover of oil-seed rape (0.1-2.4 %, median = 0.8 %). Each point represents the mean density across all sampling rounds averaged then for the two transects. For regression lines for high vs. low relative cover of oil-seed rape we fixed relative cover of oil-seed rape at its median value in each of the groups in the model equation (Table III.1). In the bumble bee model, also the predictor relative cover of sunflowers was held constant at its mean value in the equation

Table III.1. Landscape effects on bumble bee, hoverfly and honey bee densities on sunflower fields (n=16). Results are from linear regressions. Landscape predictors were measured in a 2-km radius around the sunflower fields. Predictors are shown when $p < 0.1$ or when they are part of a significant interaction.

| | Coefficient | SE | t | p |
|---|-------------|------|------|--------|
| <i>Density of bumble bees</i> | | | | |
| Intercept | 4.63 | 0.47 | 9.9 | <0.001 |
| % oil-seed rape | -0.18 | 0.08 | -2.3 | 0.046 |
| % semi-natural habitats | -0.01 | 0.06 | -0.2 | 0.837 |
| % sunflowers | -0.80 | 0.26 | -3.1 | 0.011 |
| % oil-seed rape x % semi-natural habitats | 0.02 | 0.01 | 2.0 | 0.070 |
| % oil-seed rape x % sunflowers | 0.13 | 0.06 | 2.3 | 0.044 |
| <i>Density of hoverflies</i> | | | | |
| Intercept | 2.73 | 0.53 | 5.1 | <0.001 |
| % oil-seed rape | 0.17 | 0.11 | 1.6 | 0.135 |
| % semi-natural habitats | -0.12 | 0.09 | -1.4 | 0.194 |
| % oil-seed rape x % semi-natural habitats | -0.04 | 0.02 | -2.4 | 0.034 |
| <i>Density of honey bees</i> | | | | |
| Intercept | 3.45 | 0.79 | 4.4 | <0.001 |
| % oil-seed rape | 0.45 | 0.16 | 2.8 | 0.015 |
| % semi-natural habitats | 0.09 | 0.13 | 0.7 | 0.496 |
| % oil-seed rape x % semi-natural habitats | -0.06 | 0.02 | -2.7 | 0.019 |

Discussion

Our study is the first that addresses temporal spillover of pollinating insects between different mass-flowering crops with non-overlapping flowering periods. We found that early-flowering oil-seed rape enhances densities of bumble bees in late-flowering sunflower fields, but this effect was independently modulated by the relative cover of semi-natural habitats and by the relative cover of sunflower fields in the landscape. Highest bumble bee densities in the late-flowering crop were reached in landscapes that combined high relative covers of oil-seed rape and semi-natural habitats. Further, only landscapes with high relative covers of oil-seed rape maintained high bumble bee densities in landscapes with increasing relative covers of sunflower fields indicating that early mass-flowering crops can mitigate pollinator dilution in crops flowering later in the season.

Our results are consistent with the previously described positive influence of mass-flowering crops on bumble bee densities (Westphal et al. 2003; Herrmann et al. 2007; Williams et al. 2012), but, for the first time, we showed this effect in a second later mass-flowering crop and not, as done before, on experimental floral patches or colonies placed in semi-natural habitats (Westphal et al. 2003; 2009). The interaction effect between the two different mass-flowering crops influenced bumble bee densities at the landscape scale. At low relative covers of oil-seed rape in spring we found decreasing densities of bumble bees in late-flowering sunflower fields with an increasing relative cover of sunflowers on the 2-km radius, suggesting pollinator dilution and a limited pollinator pool in the landscape (Veddeler et al. 2006; Holzschuh et al. 2011). A consequence of dilution effects might be decreased pollination services and yields, because sunflowers depend at least partly on high pollinator densities (Carvalho et al. 2011). A dilution of bumble bees may be especially disadvantageous for yields, because sunflower yields seems to be more positively influenced by bumble bee pollination than by pollination through honey bees (Aslan et al. 2010). In contrast, when the relative cover of oil-seed rape reached a certain level in spring, this dilution effect was no longer observable. Unfortunately we could not span equal gradients of relative cover of sunflowers in landscapes with a high relative cover and in landscapes with a low relative cover of oil-seed rape. We can therefore not predict, if increasing relative cover of sunflowers in landscapes with a high relative cover of oil-seed rape would further increase bumble bee densities in the sunflower fields or if densities would converge to an upper limit. Nonetheless, if we compare landscapes with a relative cover of sunflowers of more than one percent (i.e. high relative cover of sunflowers), densities of bumble bees on sunflower fields

were definitely higher in landscapes with a high relative cover of oil-seed rape (~175) than in landscapes with a low relative cover of oil-seed rape (~20). Hence, a high relative cover of oil-seed rape in spring could buffer a possible pollinator shortage for later-flowering crops like sunflower.

Additionally, we found a positive effect of semi-natural habitats on bumble bees in sunflower fields. Interestingly, this effect of semi-natural habitats only showed up at high relative covers of oil-seed rape in spring, but not at low relative covers of oil-seed rape. A positive landscape scale effect of semi-natural habitats on local bumble bee densities is in line with the findings in several studies (e.g. Ekroos et al. 2013; Rundlöf et al. 2008; Öckinger and Smith 2007), although other studies reported no correlation between the relative cover of semi-natural habitats and local bumble bee densities (Steffan-Dewenter et al. 2002; Westphal et al. 2006). Our results suggest that landscapes with high relative cover of oil-seed rape and suitable nesting sites in semi-natural habitats potentially enhance bumble bee densities by attracting nest-seeking queens, and enabling successful establishment and early growth of colonies (Westphal et al. 2009). Additionally, flower resources in semi-natural habitats might contribute to colony growth throughout the season, but only if oil-seed rape gives a first impulse for colony establishment early in the season (Williams et al. 2012). In contrast, in landscapes with a low relative cover of oil-seed rape colonisation rates might be low and queen mortality rates high because feeding resources are more limited at the beginning of the year. Thus, only the early flowering peak of oil-seed rape in combination with nesting sites and continuous floral resources in semi-natural habitats could promote pollinator densities in sunflowers fields by facilitating temporal spillover from early to late flowering crops. Previous studies with contradictory results on the importance of semi-natural habitats for bumble bees do not consider the combined effects of mass-flowering crops, semi-natural habitats and temporal spill-over between annual crops (e.g. Westphal et al. 2003).

So far, there are no other studies investigating landscape effects of mass-flowering crops on hoverflies. Though, adults of all syrphid species need pollen and nectar and were therefore proposed to profit from flowering plants (Hickman and Wratten 1996). We found lower densities of syrphid flies on sunflower fields located in landscapes with a high relative cover of semi-natural habitats. Recent studies showed relative covers of arable land to be positively correlated with the densities of hoverflies (Haenke et al. 2009; Meyer et al. 2009). Since in our study the relative cover of semi-natural habitats is negatively correlated with the relative cover of arable land ($r = -0.76$), our results indirectly support these findings. In

landscapes with high relative covers of arable land and low relative covers of semi-natural habitats, larval habitats of hoverflies might be less limited, resulting in positive effects on the larvae of many species that depend for feeding on aphid populations in arable fields (Tenhumberg and Poehling 1995). In our study, ten of the thirteen species found in the sunflower fields (89% of all identified individuals) had larvae with aphidophagous nutrition (Supplement Table III.S1). Comparable to bumble bees where semi-natural sites are the larval habitat, the positive effect of increasing larval habitats for hoverflies was highest in landscapes that provide a high relative cover of oil-seed rape and thereby abundant adult feeding resources. There are two factors that may lead to a missing temporal spillover of hoverflies from oil-seed rape to sunflower in comparison to bumble bees: (1) adults and larvae of bumble bees require flowering plants as feeding resources, whereas only adults of most hoverfly species depend on flowering plants (2) hoverflies are less restricted to nesting sites than central-place foraging bumble bees and may therefore disperse to other landscapes after flowering of oil-seed rape. Interestingly, our results indicate that, in contrast to pollination services by bumble bees, pest control by syrphid flies might be reduced in sunflower fields located in landscapes with both, high relative cover of mass-flowering crops and semi-natural habitats. Thus, optimising multiple ecosystem services at landscape scales requires a detailed knowledge of possible constraints and trade-offs (Bommarco et al. 2012; Martin et al. 2013).

Besides bumble bees and hoverflies, honey bees were the dominating flower visitors in the sunflower fields, whereas very few solitary bees or other insects visited the crop. For honey bees we found an interaction effect between semi-natural habitats and mass-flowering crops similar to the patterns for hoverflies. Thus, honey bees on sunflower fields were not most abundant in landscapes that combined a high relative cover of oil-seed rape and semi-natural habitats, but here we lack an intuitive explanation. One could speculate that landscapes with high relative cover of oil-seed rape as well as semi-natural habitats lead to faster development of colonies and a density peak earlier in the season, resulting in smaller colonies and thereby lower forager densities later in the season during sunflower bloom. Like for the hoverflies there are no studies showing any effect from mass-flowering crops on a landscape scale so far. Only Holzschuh et al. (2011) found a local spillover of honey bees from oil-seed rape fields into adjacent grasslands during the mass-flowering period of oil-seed rape. At the landscape scale, honey bee densities might depend more strongly on the distance to the next apiary (which we have no information on) than on the relative cover of semi-natural habitats or other landscape parameters (Garibaldi et al. 2011). Furthermore,

temporal spillover of honey bees between the two crops could have been masked by the practice that beekeepers place honey bee hives in landscapes with high relative covers of oil-seed rape in spring, and move them to landscapes with a high relative cover of sunflowers later in the year.

Conclusion

Our results suggest that the management of landscape-scale patterns of early and late mass-flowering crops and also semi-natural habitats could be used to enhance densities of certain pollinators to ensure crop pollination services. Farmers, growing mass-flowering crops, should consider in their management practice that providing different mass-flowering crops with early and late periods of flowering in a landscape can increase the overall amount of food for pollinators, enhance wild pollinator densities and stabilize yields. Increasing temporal landscape heterogeneity might also lead to increased biodiversity due to ‘landscape complementation’ for organisms that need more than one habitat type during their life cycle (Fahrig et al. 2011). Though, from a conservation perspective it has to be taken into account that mainly generalized pollinators can benefit from such temporal spillover effects (Diekötter et al. 2010). More specialized pollinators even may disappear from the late-flowering crop, because competition from the benefiting generalized pollinators, using both crops, could be enhanced. Further, it should be studied whether a late-seasonal food supply such as sunflowers could be translated to the production of sexuals in bumble bee colonies (Westphal et al. 2009; Williams et al. 2012). An increased number of bumble bee queens could potentially enhance bumble bee densities in early-flowering crops in the next season that can benefit again from that early-flowering crop. A synergy between several mass-flowering crops with different flowering periods might keep pollinator densities high across years. Our study is amongst the first considering the temporal component of spillover effects in case of pollinators. Moreover, different scales of temporal spillover induced by mass-flowering crops, e.g. during and after flowering effects (Jauker et al. 2012) and inter-annual variability through crop rotation (Thies et al. 2008) can be expected to affect pollinator densities in agricultural landscapes. Temporal spillover could also affect dynamics of other species groups, which use resources in different habitats during the course of the season, and connected ecosystem services, but this has not gained much attention so far.

Supplement

Table III.S1: Absolute density of pollinators on 16 sunflower fields on 97 transects walks. There were more hoverflies and wild bees recorded than identified to species level (see Results). Hoverflies with aphidophagous larvae are indicated by an asterisk (*).

| Species | No. of identified individuals |
|---|-------------------------------|
| <i>Bombus</i> | 7705 |
| <i>B. lapidarius</i> | 5594 |
| <i>B. terrestris/lucorum</i> agg. | 1893 |
| <i>B. pascuorum</i> | 135 |
| <i>B. sylvarum</i> | 80 |
| <i>B. hortorum</i> | 2 |
| <i>B. hypnorum</i> | 1 |
| <i>B. bohemicus</i> | 1 |
| <i>B. rupestris</i> | 2 |
| Syrphidae | 433 |
| <i>Sphaerophoria scripta</i> | 256* |
| <i>Eristalis tenax</i> | 55 |
| <i>Episyrphus balteatus</i> | 66* |
| <i>Syrphus vitripennis</i> | 5* |
| <i>Syrphus ribesii</i> | 6* |
| <i>Syrphus torvus</i> | 1* |
| <i>Melanostoma mellinum</i> | 2* |
| <i>Eumerus strigatus</i> | 2 |
| <i>Eupeodes luniger</i> | 7* |
| <i>Eupeodes corrolae</i> | 18* |
| <i>Meliscaeva auricollis</i> | 1* |
| <i>Scaeva pyrastris</i> | 13* |
| <i>Scaeva selenitica</i> | 1* |
| Wild bees other than <i>Bombus</i> | 10 |
| <i>Halictus tumulorum</i> | 1 |
| <i>Halictus scabiosae</i> | 2 |
| <i>Lasioglossum pauxillum</i> | 3 |
| <i>Lasioglossum malachurum</i> | 2 |
| <i>Lasioglossum calceatum</i> | 1 |
| <i>Andrena flavipes</i> | 1 |

Table III.S2. Bumble bee and hoverfly species recorded in oil-seed rape (unpublished data, recorded in the same study year and region) and sunflower fields (according to Supplement Table III.S1). Species occurring in both crops are in bold face.

| Oil-seed rape | Sunflower |
|--|--|
| <i>Bombus</i> | |
| <i>B. lapidarius</i> | <i>B. lapidarius</i> |
| <i>B. terrestris/lucorum</i> agg. | <i>B. terrestris/lucorum</i> agg. |
| <i>B. pascuorum</i> | <i>B. pascuorum</i> |
| <i>B. sylvarum</i> | <i>B. sylvarum</i> |
| <i>B. hortorum</i> | <i>B. hortorum</i> |
| <i>B. pratorum</i> | <i>B. hypnorum</i> |
| | <i>B. bohemicus</i> |
| | <i>B. rupestris</i> |
| <i>Syrphidae</i> | |
| <i>Sphaerophoria scripta</i> | <i>Sphaerophoria scripta</i> |
| <i>Episyrphus balteatus</i> | <i>Episyrphus balteatus</i> |
| <i>Syrphus vitripennis</i> | <i>Syrphus vitripennis</i> |
| <i>Melanostoma mellinum</i> | <i>Melanostoma mellinum</i> |
| <i>Chrysotoxum cautum</i> | <i>Eumerus stricatus</i> |
| <i>Eristalis intricarius</i> | <i>Eupeodes luniger</i> |
| <i>Eristalis arbustorum</i> | <i>Eupeodes corrolae</i> |
| <i>Pipizelle viduata</i> | <i>Meliscaeve auricollis</i> |
| <i>Platycheirus clypeatus</i> | <i>Scaeva pyrastris</i> |
| | <i>Scaeva selenitica</i> |
| | <i>Eristalis tenax</i> |
| | <i>Syrphus ribesii</i> |
| | <i>Syrphus torvus</i> |

IV. Wild bees: attractiveness and productivity effects of oil-seed rape

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Running title: Inter-annual effects

Keywords: *Bombus*, mass-flowering crops, solitary bees, temporal spillover, crop rotation, population dynamics, landscape modelling

Abstract

Mass-flowering crops have transient within-season effects on pollinators in agricultural landscapes. Although mass-flowering crops may affect long-term population dynamics, effects on pollinators have never been studied across several years.

We focused on inter-annual effects of the relative cover of oil-seed rape across three years and monitored wild bees in two years in 16 landscapes in Germany on oil-seed rape during its flowering. We developed a model for these data to evaluate the attractiveness and productivity of oil-seed rape in comparison to the rest of the landscape and consequences on pollinator densities in consecutive years.

Our results show that a high relative cover of oil-seed rape in the previous year increases densities of wild bees (excl. *Bombus*) on oil-seed rape in the current year, but does not increase densities of bumble bees. Moreover, we show a strong attractiveness of and dilution on oil-seed rape for bees during flowering in the current year, modulating the effect from the previous relative cover of oil-seed rape in case of wild bees (excl. *Bombus*).

Under the precondition that nesting sites are available in the landscape, our findings suggest long-term positive effects of mass-flowering crops, which possibly stabilize pollination services for crops even when crop areas will increase. Contrariwise, mass-flowering crops may enhance competition pressure on specialists by benefitting generalists disproportionately. Since little is known about the effects of changing availability of mass-

flowering crops on landscape scales, e.g. due to crop rotation or agricultural policy, long-term consequences of mass-flowering crops for pollinators have to be evaluated.

Introduction

Agricultural landscapes are often characterized by rapidly changing resource availability (Rand et al. 2006; Mandelik et al. 2012), initiated by harvesting or mass-flowering events in crops. Thereby, “resource pulses” as a transient affluence of resources in a landscape can greatly affect consumer population dynamics (Holt 2008) and, importantly, also influence the relative attractiveness of alternative, more continuous resources in less productive habitats (Oksanen 1990; Anderson et al. 2008). Effects from resource pulses may persist long-term, even if the pulse itself is of short duration (Thies et al. 2008; Yang et al. 2008; Zhao et al. 2013). However, not all consumers may be able to use resource pulses to the same extent, and to equally translate the pulse to individual fitness (Armstrong *et al.* 2010).

Mass-flowering crops can be a very valuable and attractive resource for bees, providing an ample amount of pollen and nectar (Morandin and Winston 2005) and releasing a recurrent resource pulse every season. Oil-seed rape is one of these mass-flowering crops grown worldwide, increasingly so for biofuel production (Diekötter et al. 2013; Stanley and Stout 2013). It is questionable, however, if such crops have any use for pollinators due to their short flowering period (Corbet 2000). Moreover, bees do not exclusively focus on oil-seed rape during its flowering (Holzschuh et al. 2013; Stanley and Stout 2014), and they additionally rely on other landscape types, like semi-natural habitats, which predominantly provide nesting sites, but also alternative feeding resources.

As shown by previous studies, there might be two important spatio-temporal effects of mass-flowering crops on the landscape scale: (1) During flowering of mass-flowering crops local densities of bees decrease with increasing relative cover of the mass-flowering crop on the landscape scale (dilution effect; Holzschuh *et al.* 2011; Jauker *et al.* 2012; Kovács-Hostyánszki *et al.* 2013). (2) After flowering a higher relative cover of the mass-flowering crops results in increased local densities in other habitats (Westphal et al. 2003; Kovács-Hostyánszki et al. 2013), possibly mediated by increased population growth (Herrmann et al. 2007; Westphal et al. 2009). The duration of this after-flowering effect within one year remains unclear (Westphal *et al.* 2009; Hanley *et al.* 2011; Riedinger *et al.* 2014) and also effects to the subsequent production of offspring, that would be necessary to carry over effects between years, are mixed. While bumble bees showed no effect of mass-flowering crops on sexual reproduction (Westphal *et al.* 2009), wild bees other than *Bombus*

(hereafter referred to as ‘other wild bees’) may benefit (Jauker *et al.* 2012; Holzschuh *et al.* 2013). Although, a previous study showed inter-annual effects of oil-seed rape for parasitoids of pollen beetles (Thies *et al.* 2008), we are not aware of any study investigating inter-annual effects of mass-flowering crops on bees, although this type of temporal spillover might strongly affect pollinator densities and associated ecosystem services in agricultural landscapes.

In our study we focused on two possible features of oil-seed rape that might influence pollinator density and distribution in consecutive years. (1) A higher relative attractiveness of oil-seed rape as a feeding resource compared to other available landscape resources should result in a landscape-scale dilution of pollinators (Fig. IV.1a). (2) A higher per area productivity, i.e. a higher output of bees entering the next year, of oil-seed rape compared to the rest of the landscape should result in a positive dependence of current bee densities on the relative cover of oil-seed rape in the previous year (Fig. IV.1b). A higher attractiveness of oil-seed rape should probably result in a higher productivity of oil-seed rape compared to the rest of the landscape and vice versa.

In a three year study we investigated the inter-annual effects of oil-seed rape on bees in 16 different study areas. We evaluated effects of the relative cover of oil-seed rape in the previous year, and the modulation of these effects by the current relative cover of oil-seed rape for bumble bees and other wild bees. To evaluate the combined effects of the relative cover of oil-seed rape in the previous and the current year (hereafter referred to as the year of pollinator sampling) and by additionally considering its attractiveness and productivity compared to the rest of the landscape, we developed a mechanistic model and tested the following hypotheses:

1. A higher attractiveness of oil-seed rape compared to the rest of the landscape reduces the local density of bees on oil-seed rape fields during the mass-flowering period when the relative covers of oil-seed rape in the year of pollinator sampling increases.
2. Higher relative cover of oil-seed rape in the previous year increases pollinator densities on oil-seed rape fields in the year of pollinator sampling due to a higher productivity effect of oil-seed rape compared to the rest of the landscape.
3. Productivity effects of oil-seed rape are less pronounced for bumble bees with a reproduction of sexuals after flowering of oil-seed rape than for other wild bees with reproduction simultaneously to flowering of oil-seed rape.

Material and Methods

Study region and landscape parameters

The study was conducted in 2011 and 2012 in the surroundings of Würzburg, Bavaria, Germany (49°47' N, 9°57' E). This region is intensively used for agriculture, mainly for the production of annual crops, including mass-flowering crops, like oil-seed rape. In the study region we selected 16 study areas in an area of 27 km x 70 km. Due to crop rotation we selected different oil-seed rape fields in 2011 and 2012, in each study area. In each study year, fields in two different study areas were at least 2 km apart. The fields had a size of 2.0 ± 0.2 ha (0.5-5.4 ha).

Around each study field we calculated the relative cover of oil-seed rape in a 1-km buffer around the edge of the field (including the field) in each study year. The land-use data were provided by the Bavarian State Ministry of Nutrition, Agriculture and Forestry. The geographical information system ArcMap (ESRI 2008, v. 9.3.1.) was used to calculate the relative cover of oil-seed rape. We calculated the relative cover of oil-seed rape around each study field in the two years when we sampled pollinators, and also in the previous year. The relative cover of oil-seed rape around study fields in the two years of pollinator sampling (p_t) covered a gradient from 0.5 to 19.8 percent in the landscape sectors (Mean \pm SD: $6.4 \pm 5.0\%$, 2011: 0.5-19.8%; $7.0 \pm 5.7\%$, 2012: 0.9-16.3%; $5.7 \pm 4.3\%$). The relative cover of oil-seed rape around study fields in the two years before pollinator sampling (i.e. previous year, p_o) covered a gradient from 0.3 to 18.3 percent in the landscape sectors (Mean \pm SD: $6.4 \pm 4.6\%$, 2010: 0.9-13.2%; $6.2 \pm 4.0\%$, 2011: 0.3-18.3%; $6.5 \pm 5.3\%$). The Pearson-correlation-coefficient between the relative cover of oil-seed rape in the year of pollinator sampling and the previous year was 0.54 (n=32; 2011=0.76; 2012=0.38).

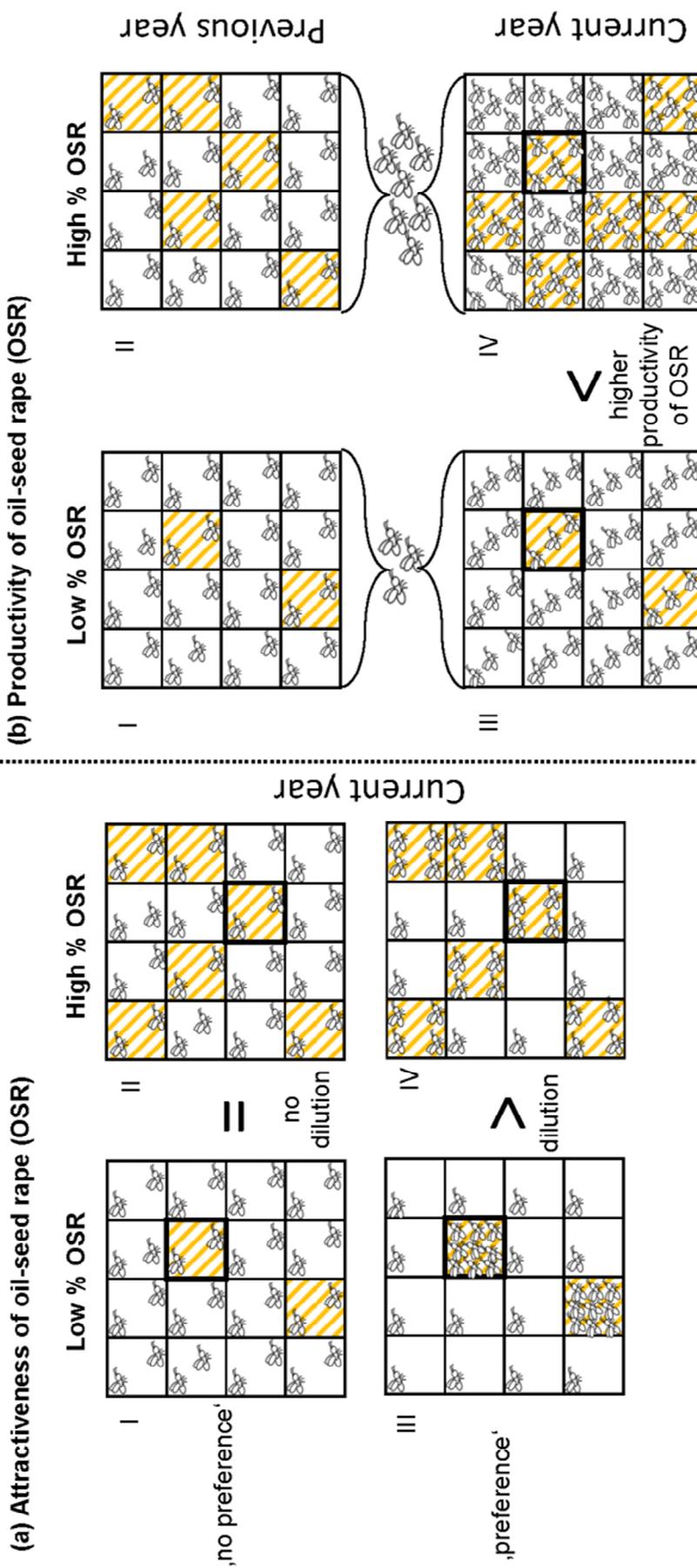


Fig. IV.1: (a) Within-season and (b) inter-annual effects of oil-seed rape (OSR) on pollinators in a landscape (large squares). Each landscape consists of 16 small squares, which either represent OSR (yellow shaded) or the rest of the landscape (white). We compare landscapes with a comparatively low relative cover of oil-seed rape (I/III) with landscapes with a comparatively high relative cover of oil-seed rape (II/IV). A thick edge marks the OSR field where pollinators are sampled. Within one season (a) pollinators show either no preference for OSR compared to the rest of the landscape (I/II) or a preference for OSR (III/IV). Note that dilution effects, which decrease local pollinator densities, only occur when there is a preference for OSR (hypothesis 1). On an inter-annual scale (b) the densities of pollinators increase in the year of pollinator sampling (III/IV) with increasing relative cover of oil-seed rape in the previous year (I/II) only when we assume a higher productivity of OSR than for the rest of the landscape (IV, hypothesis 2). Note that in this simple example the relative cover of oil-seed rape stays constant between the previous year and the year of pollinator sampling (current year) and we only show single effects of previous and current relative cover of oil-seed rape, but not combined effects.

Pollinator observation

Bumble bees and other wild bees were sampled under standardized weather conditions (temperatures above 17 °C, no rain, low or no cloud cover, low wind speeds) between 09.00 and 18.00 h, while slowly walking along transects and recording only flower visitors. Bumble bees were identified in the field to species level (except for *B. terrestris* and *B. lucorum* agg.). Other wild bees were collected for species identification in the lab.

Bees were observed during flowering of oil-seed rape on two 150 m² transects on each oil-seed rape field. One transect was located on the outer crop line paralleling the edge of the field, the other one was parallel to the first, located in the centre of the field with at least 20 m distance from each edge. A transect had a width of 1 m and a length of 150 m. Transects were sampled two times, each time for 15 minutes, in late April/early May 2011 and 2012. We present pooled densities for 600 m² (two sampling rounds x two 150 m² transect) with a total searching time of 60 minutes separately for the two sampling years.

Model description

We developed a mechanistic model to reflect the underlying causal relationships and allow for the estimation of meaningful model parameters (Hobbs and Hilborn 2006). For the focus of our study a mechanistic model should allow for the inference on the attractiveness and the per area productivity effect of oil-seed rape on bee densities in comparison to the rest of the landscape. For this reason we start with the presentation of a mechanistic model of the relevant processes potentially affecting bee densities.

Both oil-seed rape and other habitats, especially semi-natural habitats, provide valuable resources and thus will contribute to the total number of bees B produced in a landscape until the end of the previous season $t = 0$. However, there might be differences in the effect of productivities b_{OSR} and b_L of oil-seed rape and the rest of the landscape (average of all other landscape types) respectively, thus the number of bees produced in year 0 is

$$(IV.1) B = b_{OSR}p_0A + b_L(1 - p_0)A$$

with p_0 the fraction of the landscape covered with oil-seed rape in year 0 and A the size of the landscape sector. For the sake of simplicity we restrict our approach to linear effects of area size A .

Oil-seed rape will have a favourable impact on bee production if b_{OSR} is (significantly) greater than b_L . In this case a high relative cover of oil-seed rape in the landscape in the previous year leads to a comparatively high population size in the (beginning) of the year of pollinator sampling and increasing pollinator densities on oil-seed rape fields at constant relative cover of oil-seed rape in the two consecutive years (hypothesis 2, Fig. IV.1b). Negative effects of landscape types are indicated, if one of the coefficients is negative.

During mass-flowering, at the beginning of the year of pollinator sampling $t = 1$ a proportion f of all bees B will forage in oil-seed rape fields (of size p_1A) resulting in a local bee density per area unit of

$$(IV.2) \quad N_{OSR} = \frac{fB}{p_1A} = \frac{f(b_{OSR}p_0 + b_L(1-p_0))}{p_1}$$

We will refer to f as the ‘concentration factor’. If $f > p_1$, more bees than expected by chance forage within oil-seed rape fields. In contrast, $f < p_1$ would indicate avoidance of oil-seed rape fields while $f = p_1$ indicates ‘no preference’. For obvious reasons, concentration factor f is strictly bounded in its range. Specifically, it must be 0 when $p_1 = 0$ (no oil-seed rape at all) and 1 if $p_1 = 1$ (exclusively oil-seed rape). However, f will also depend on the relative ‘attractiveness’ of oil-seed rape fields for bees compared to other landscape elements. This relationship can be accounted for by a simple monotonically function for f in dependence of p_1 :

$$(IV.3) \quad f = \frac{(p_1+1)^a - 1}{2^a - 1}$$

with a as the ‘parameter of attractiveness’ (see Fig. IV.2a). If $a = 1$, the bees are indiscriminately and f increases linearly with the relative cover p_1 of oil-seed rape. Note that in this case $f = p_1$ and p_1 thus cancels out of equation (2). Oil-seed rape has then neither a higher nor a lower attractiveness to bees than the rest of the landscape. $a < 1$ (!) indicates a preference for oil-seed rape (hypothesis 1, Fig. IV.1a) and $a > 1$ indicates avoidance (Fig. IV.2b). A value of $a < 1$ is also the precondition that a higher relative cover of oil-seed rape in the landscape in the year of pollinator sampling reduces the local density of bees on oil-seed rape fields during the mass-flowering period (Fig. IV.1a-III/IV).

With equations (IV.2) and (IV.3) we thus get a model that combines the effect of oil-seed rape in the previous year and in the year of pollinator sampling on bee densities. Further note that the model distinguishes between the effect of oil-seed rape on (relative) bee productivity (parameter b_{OSR} vs. b_L) and the attractiveness of oil-seed rape fields as foraging area (parameter a).

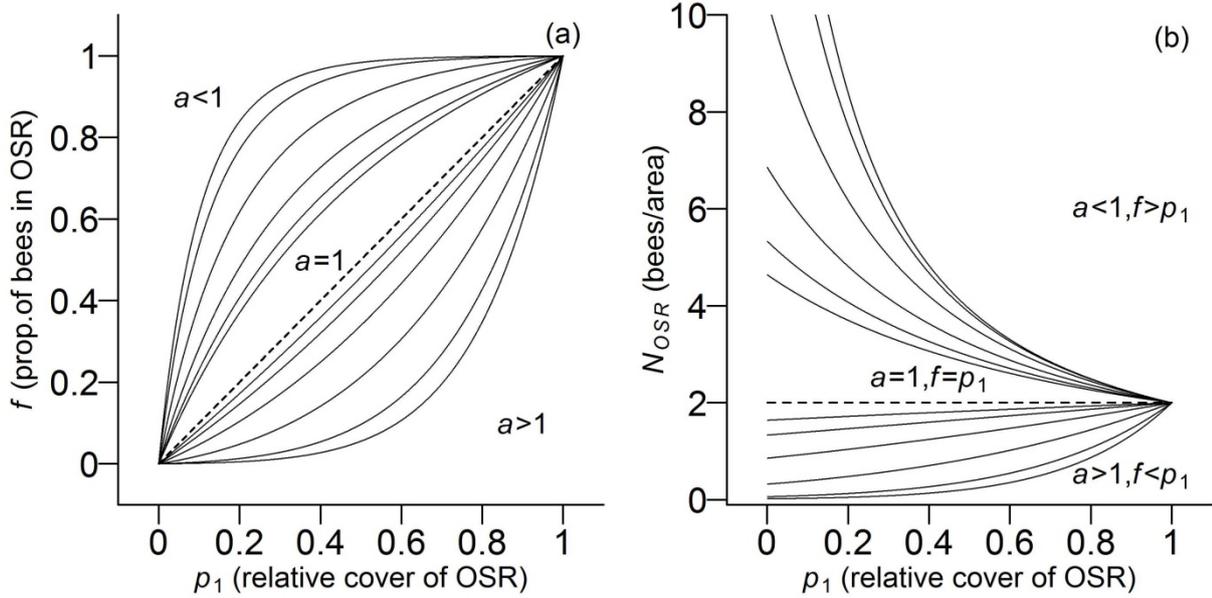


Fig. IV. 2: (a) Theoretical relationship between f (proportion of bees foraging in oil-seed rape = OSR) and p_1 (relative cover of OSR) for different values of a (parameter of attractiveness for OSR $a = \{1, \pm 1.5, \pm 2, \pm 3, \pm 5, \pm 8, \pm 10\}$) (b) Theoretical relationship between N_{OSR} (local bee density) and p_1 (relative cover of OSR) for values of a used in (a). $a < 1$ ($f > p_1$): preference of OSR, $a > 1$ ($f < p_1$): avoidance of OSR, $a = 1$ ($f = p_1$) random distribution with no observable preference or avoidance.

Estimating model parameters

The model is non-linear with respect to p_1 and we estimated b_{OSR} , b_L and a by a maximum likelihood approach (Hilborn and Mangel 1997). We assume bee densities to be Poisson distributed with N_{OSR} (equation IV.2) a predictor of mean bee density. Additionally we allow for inter-annual effects by multiplying the parameters with year-specific factors s_{OSR} , s_L and s_a , reflecting e.g. different weather conditions in the two study years, before entering the model for the second pair of years. The parameters b_{OSR} , b_L , a (and year specific factors, respectively) have to be estimated in a way that logLikelihood LL is maximized:

$$LL\{b_{OSR}, b_L, a, s_{OSR}, s_L, s_a | N_{OSR}, p_0, p_1\} = \sum_{i=1}^n \log\left(\lambda_i^{N_{OSR,i}} \frac{e^{-\lambda_i}}{N_{OSR,i}!}\right)$$

with i as the index of observations, n the total number of observation (32), and λ_i being

$$(IV.4) \quad \frac{(p_{1,i}+1)^{s_{a,i}a}-1}{2^{s_{a,i}a}-1} \times \frac{(s_{OSR,i}b_{OSR}p_{0,i}+s_{L,i}b_L(1-p_{0,i}))}{p_{1,i}}$$

or one of eight model simplifications of equation (IV.4) that we compared in our modelling approach. Observations are indexed from $i=1$ to n' for the first study year and from $i= n'+1$ to n for the second study year. In the first study year ($i \leq n'$) parameters $s_{OSR,i}$, $s_{L,i}$, $s_{a,i}$ are equal 1, in the second study year ($i > n'$) parameters $s_{OSR,i}$, $s_{L,i}$, $s_{a,i}$ take constant values estimated by the model. Simplifications included various combinations with $a = 1$ (same attractiveness for oil-seed rape and the rest of the landscape), $b_{OSR} = b_L$ (same productivity for oil-seed rape and the rest of the landscape), $s_{OSR}, s_L, s_a = 1$ (no effect from year) and $s_{OSR}=s_L$ (same effect from year for productivities of oil-seed rape and the rest of the landscape; see full model specifications in Supplement Table IV.S1).

We restrict N_{OSR} to values equal or greater than 0. Parameter values are estimated with the function *optim* () in R (v. 2.15.1, R Development Core Team 2012) by applying the default Nelder and Mead algorithm and confirmed by a screening of the entire parameter space. The relative statistical quality of a model is approximated by its AICc value (corrected for low sample size). Parameter errors are estimated via standard errors based on Hesse matrix computation during optimization (Bolker 2008).

Results

In oil-seed rape fields we recorded 153 bumble bees (6 species) and 273 other wild bees (40 species) in four sampling rounds in two years during mass-flowering.

For other wild bees the estimated parameters from the two best models (Table IV.1) indicated that oil-seed rape is in general more attractive than the surrounding landscape ($a < 1$). Inserting the value from the best model of $a = -27.21$ in equation (IV.3) for a relative cover of oil-seed rape of 10% reveals that 93% of all other wild bees in the landscape concentrate on oil-seed rape compared to only 10%, if a would equal 1. Thus, the local density of other wild bees on oil-seed rape fields was higher, when the relative cover of oil-seed rape in the year of pollinator sampling is comparatively low (5 %, Fig. IV.3) than when it is comparatively high (10%, Fig. IV.3).

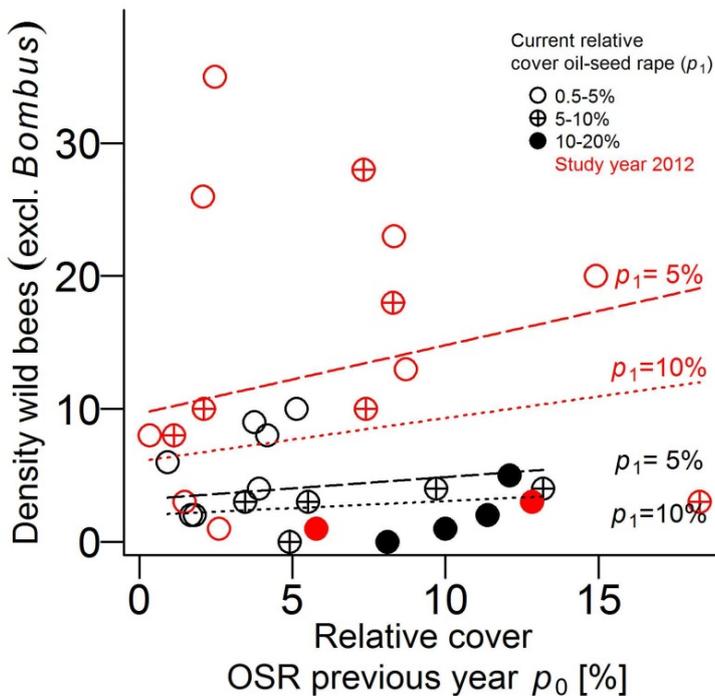


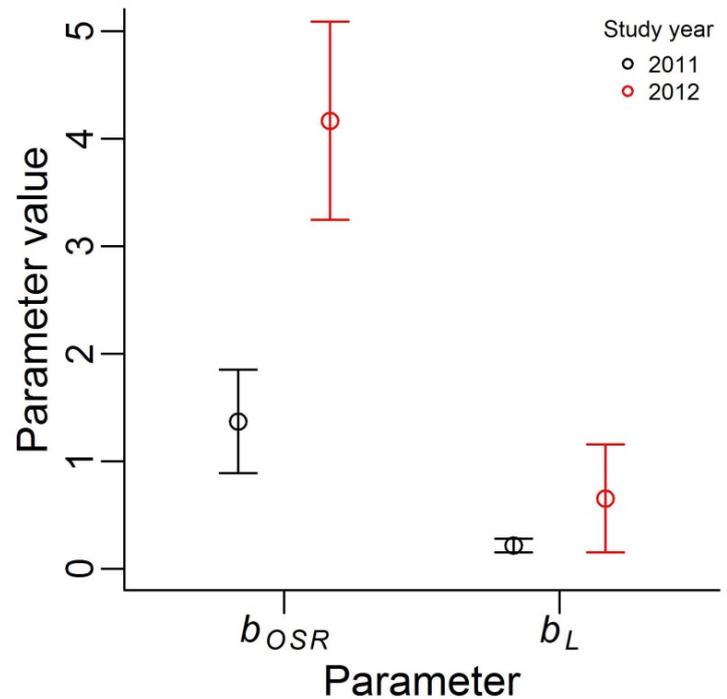
Fig. IV.3: Relationship between the relative cover of oil-seed rape (OSR) in the previous year (p_0) and the densities of wild bees (excl. *Bombus*) on 32 OSR fields in two years (16 in each year). Fitted lines are calculated with the estimated parameters of the best model (Table IV.1) and the corresponding model equation (Supplement, Table IV.S1) for specific values of relative cover of current OSR in the year of pollinator sampling (p_1 : 5%, 10% respectively). Black symbols show densities in study year 2011, red symbols show densities in study year 2012.

Different symbols represent different values of relative cover of OSR in the year of pollinator sampling (p_1).

Moreover, the two best models yield a higher productivity for oil-seed rape than for the rest of the landscape ($b_{OSR} > b_L$) (best model: Fig. IV.4; second best: Supplement, Fig. IV.S1a). For the best model the productivity from oil-seed rape ($b_{OSR} = 1.37$) is about 6.2 times higher than from the rest of the landscape ($b_L = 0.22$). Thus, local densities of other wild bees on oil-seed rape fields increased with increasing relative cover of oil-seed rape in the

previous year (best model: Fig. IV.3; second best: Supplement, Fig. IV.S1b). In 2012, the densities of other wild bees on oil-seed rape fields were in general higher than in 2011, indicated by the two best models containing the year-specific parameter s , and s_L respectively.

Fig. IV.4: Comparison of the estimated model parameters b_{OSR} (per area productivity of oil-seed rape) and b_L (per area productivity of the rest of the landscape) for the best model (Table IV.1) for densities of wild bees other than *Bombus* with confidence intervals for study years 2010/2011 (black) and study years 2011/2012 (red).



For bumble bees, the productivity of oil-seed rape equals the productivity of the rest of the landscape ($b_{OSR} = b_L$) in the two best models (Table IV.2). Nonetheless, the parameter $a < 1$ in these models indicated that oil-seed rape is in general more attractive than expected under an even distribution of bees in the landscape. Inserting the value from the best model of $a = -24.74$ in equation (IV.3) for a relative cover of oil-seed rape of 10% reveals that 91% of all bumble bees in the landscape concentrate on oil-seed rape compared to only 10%, if a would equal IV.1. Thus, the local density of bumble bees on oil-seed rape fields was higher, when the relative cover of oil-seed rape in the year of pollinator sampling is comparatively low (5 %, Fig. IV.5) than when it is comparatively high (10%, Fig. IV.5), while the relative cover of oil-seed rape in the previous year had no effect (Fig. IV.5, second best: Supplement, Fig. IV.S2). The relationships between fitted data from our models and observed data are shown in Supplement Fig. IV.S3.

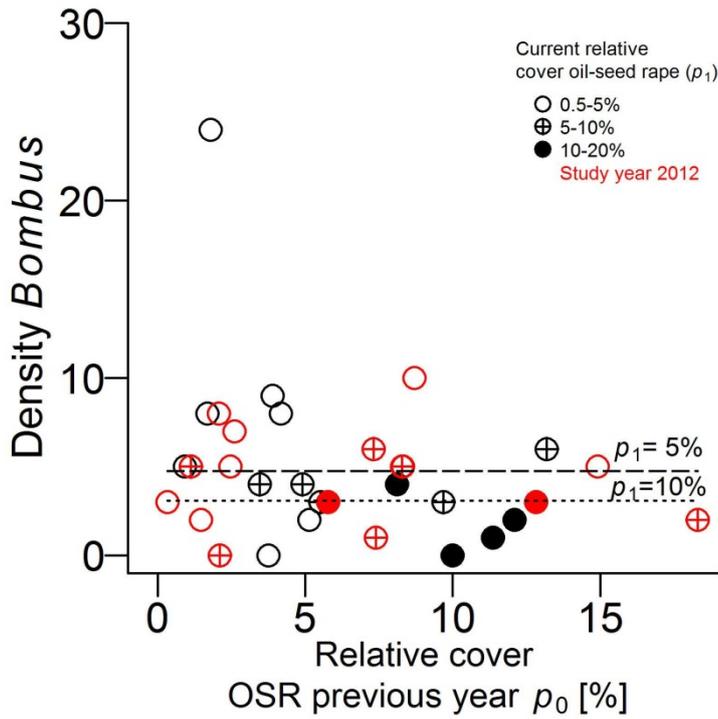


Fig. IV.5: Relationship between the relative cover of oil-seed rape (OSR) in the previous year (p_0) and the densities of bumble bees on 32 OSR fields in two years (16 in each year). Fitted lines are calculated with the estimated parameters of the best model (Table IV.2) and the corresponding model equation (Supplement, Table IV.S1) for specific values of relative cover of current OSR in the year of pollinator sampling (p_1 : 5%, 10% respectively). Black symbols show densities in study year 2011, red symbols show densities in study year 2012. Different symbols represent different values of relative cover of OSR in the year of pollinator sampling (p_1).

represent different values of relative cover of OSR in the year of pollinator sampling (p_1).

Table IV.1: Comparison of different models tested for density prediction of wild bees other than *Bombus* on oil-seed rape fields (Supplement, Table IV.S1), based on corrected Akaike-Information Criterion (AICc), shown with Δ AICc, AICc weights (wAICc) and their parameter estimates with 95% confidence intervals. Parameters not fitted in a model are marked 'n.f.'. Models are sorted by increasing AICc (best model at the top). b_{OSR} = per area productivity oil-seed rape, b_L = per area productivity rest of the landscape, s_{OSR} = multiplier for b_{OSR} in second study year, s_L = multiplier for b_L in second study year, a = parameter of attractiveness, s_a multiplier for a in second study year. Figures are shown for the two best models (grey shaded, Fig. IV.3-4, Supplement Fig. IV.S1).

| Model parameters | | | | | | | | | |
|--|-------|---------------|-------|-------------------------------------|-------------------------------------|-------------------------------------|-----------------|-------------------|-------|
| Wild bees (excl. <i>Bombus</i>) | AICc | Δ AICc | wAICc | b_{OSR} | b_L | s_{OSR} | s_L | a | s_a |
| $b_{OSR} \neq b_L, a \neq 1$, effect from year (s) (M4) | 262.2 | 0.0 | 0.412 | 1.37 ± 0.48 | 0.22 ± 0.06 | $s = s_{OSR} = s_L = 3.04 \pm 0.44$ | | -27.21 ± 7.96 | n.f. |
| $b_{OSR} \neq b_L, a \neq 1$, effect from year only for b_L (s_L) (M6) | 262.6 | 0.4 | 0.336 | 2.72 ± 0.92 | 0.15 ± 0.07 | n.f. | 4.82 ± 1.56 | -27.21 ± 7.90 | n.f. |
| $b = b_{OSR} = b_L, a \neq 1$, effect from year $s = s_{OSR} = s_L$ (M5) | 264.0 | 1.8 | 0.168 | $b = b_{OSR} = b_L = 0.35 \pm 0.08$ | $b = b_{OSR} = b_L = 0.35 \pm 0.08$ | $s = s_{OSR} = s_L = 3.15 \pm 0.45$ | | -18.17 ± 4.80 | n.f. |
| $b_{OSR} \neq b_L, a \neq 1$, independent effect from year for b_{OSR} (s_{OSR}) and b_L (s_L) (M8) | 265.5 | 3.3 | 0.078 | 1.00 ± 0.76 | 0.23 ± 0.07 | 3.75 ± 2.95 | 2.94 ± 0.72 | -27.00 ± 7.42 | n.f. |

| <i>Table IV.1 continued</i> | Model parameters | | | | | | | | | |
|---|------------------|---------------|--------|-------------------------------------|-------------|---------------|-------------|---------------|-------------|--|
| | AICc | Δ AICc | wAICc | b_{OSR} | b_I | s_{OSR} | s_I | α | s_a | |
| Wild bees (excl. <i>Bombus</i>) | | | | | | | | | | |
| $b_{OSR} \neq b_I, a \neq 1$, independent effect from year for b_{OSR} (s_{OSR}), b_I (s_I), α (s_a) (M9) | 270.4 | 8.2 | 0.007 | 0.42 ± 0.58 | 0.34 ± 0.11 | 9.35 ± 12.88 | 2.21 ± 0.75 | -19.26 ± 7.29 | 1.21 ± 0.47 | |
| $b_{OSR} \neq b_I, a \neq 1$, effect from year only for b_I (s_I) (M7) | 282.9 | 20.7 | <0.000 | 0.17 ± 0.22 | 0.30 ± 0.06 | 42.78 ± 54.65 | n.f. | -34.97 ± 8.36 | n.f. | |
| $b_{OSR} \neq b_I, a \neq 1$, no effect from year (M1) | 328.8 | 66.6 | <0.000 | 3.64 ± 0.84 | 0.34 ± 0.09 | n.f. | n.f. | -33.92 ± 8.81 | n.f. | |
| $b = b_{OSR} = b_I, a \neq 1$, no effect from year (M2) | 336.6 | 74.4 | <0.000 | $b = b_{OSR} = b_I = 0.70 \pm 0.12$ | | n.f. | n.f. | -19.66 ± 4.67 | n.f. | |
| $b_{OSR} \neq b_I, a = 1$, no effect from year (M3) | 371.1 | 108.9 | <0.000 | -2.31 ± 10.84 | 9.26 ± 0.93 | n.f. | n.f. | $\alpha = 1$ | n.f. | |

Table IV.2: Comparison of different models tested for density prediction of bumble bees on oil-seed rape fields (Supplement, Table IV.S1), based on corrected Akaike-Information Criterion (AICc), shown with Δ AICc, AICc weights (wAICc) and their parameter estimates with 95% confidence intervals. Parameters not fitted in a model are marked 'n.f.'. Models are sorted by increasing AICc (best model at the top). b_{OSR} = per area productivity oil-seed rape, b_L = per area productivity rest of the landscape, s_{OSR} =multiplier for b_{OSR} in second study year, s_L =multiplier for b_L in second study year, a = parameter of attractiveness, s_a multiplier for a in second study year. Figures are shown for the two best models (grey shaded, Fig. IV.5, Supplement Fig. IV.S2).

| Model parameters | | | | | | | | | |
|--|-------|---------------|-------|-------------------------------|-----------------|-------------------------------|-----------------|-------------------|-------|
| <i>Bombus</i> | AICc | Δ AICc | wAICc | b_{OSR} | b_L | s_{OSR} | s_L | a | s_a |
| $b=b_{OSR}=b_L$, $a \neq 1$, no effect from year (M2) | 179.0 | 0.0 | 0.343 | $b=b_{OSR}=b_L=0.34 \pm 0.07$ | | n.f. | n.f. | -24.74 ± 7.47 | n.f. |
| $b=b_{OSR}=b_L$, $a \neq 1$, effect from year (S) (M5) | 179.3 | 0.4 | 0.284 | $b=b_{OSR}=b_L=0.38 \pm 0.08$ | | $s=s_{OSR}=s_L=0.79 \pm 0.13$ | | -24.96 ± 7.41 | n.f. |
| $b_{OSR} \neq b_L$, $a \neq 1$, no effect from year (M1) | 181.4 | 2.4 | 0.102 | 0.25 ± 0.73 | 0.35 ± 0.12 | n.f. | n.f. | -24.11 ± 9.12 | n.f. |
| $b_{OSR} \neq b_L$, $a \neq 1$, effect from year only for $b_L(s_L)$ (M6) | 181.6 | 2.6 | 0.090 | 0.55 ± 0.68 | 0.36 ± 0.11 | n.f. | 0.75 ± 0.15 | -26.65 ± 9.61 | n.f. |

| <i>Table IV.2 continued</i> | | Model parameters | | | | | | | |
|---|-------|------------------|-------|-------------------|-----------------|-------------------------------------|-----------------|-------------------|-------|
| <i>Bombus</i> | AICc | Δ AICc | wAICc | b_{OSR} | b_L | s_{OSR} | s_L | a | s_a |
| $b_{OSR} \neq b_L, a \neq 1,$ effect from year (s) (M4) | 182.0 | 3.0 | 0.077 | 0.42 ± 0.81 | 0.37 ± 0.12 | $s = s_{OSR} = s_L = 0.79 \pm 0.13$ | | -25.22 ± 9.32 | n.f. |
| $b_{OSR} \neq b_L, a \neq 1,$ independent effect from year for b_{OSR} (s_{OSR}) and b_L (s_L) (M8) | 182.2 | 3.2 | 0.067 | 0.07 ± 0.20 | 0.36 ± 0.08 | 19.83 ± 59.32 | 0.59 ± 0.16 | -28.40 ± 9.00 | n.f. |
| $b_{OSR} \neq b_L, a \neq 1,$ effect from year only for b_{OSR} (s_{OSR}) (M7) | 184.1 | 5.1 | 0.027 | -0.004 ± 0.09 | 0.37 ± 0.09 | -43.57 ± 1010.53 | n.f. | -22.87 ± 7.41 | n.f. |

Table IV.2 continued

| <i>Bombus</i> | Model parameters | | | | | | | | |
|---|------------------|---------------|--------|-------------------|-----------------|-----------------|-----------------|--------------------|-----------------|
| | AICc | Δ AICc | wAICc | b_{OSR} | b_L | s_{OSR} | s_L | a | s_a |
| $b_{OSR} \neq b_L, a \neq 1$, different effect from year for $b_{OSR} (s_{OSR})$, $b_L(s_L), a(s_a)$ (M9) | 185.9 | 6.9 | 0.010 | 0.42 ± 0.33 | 0.37 ± 0.10 | 2.93 ± 2.37 | 0.44 ± 0.28 | -26.15 ± 10.52 | 1.67 ± 1.30 |
| $b_{OSR} \neq b_L, a = 1$, no effect from year (M3) | 195.6 | 16.6 | <0.000 | -16.35 ± 6.59 | 6.22 ± 0.67 | n.f. | n.f. | $a=1$ | n.f. |

Discussion

Our study provides the first evidence for long-term effects of mass-flowering crops on bee densities. Densities of other wild bees increased with increasing relative landscape-scale cover of oil-seed rape in the previous year. The per area production of bees from oil-seed rape is – according to the best model – about 6 times the production from the rest of the landscape. Especially early solitary bees, which are active during the flowering of oil-seed rape, were previously shown to benefit from the resource boost and to produce more offspring during the flowering of oil-seed rape (Holzschuh *et al.* 2013) that can result in a larger F₁-generation measured by abundances in nests (Jauker *et al.* 2012). We now could show the positive effect of oil-seed rape on forager densities in mass-flowering crops in the next season by focusing not only on one study species like in the two previous studies, but on the entire community of wild bees that is active during the flowering of oil-seed rape. The advantage in landscapes with a high relative cover of oil-seed rape, may even overcome previously shown drawbacks in landscapes with a high relative cover of oil-seed rape after flowering by higher parasitism load (Jauker *et al.* 2012), so that there is a net gain of other wild bees across the season. An effect on population fitness may not only apply to the previously studied solitary bee species *Osmia rufa*, that made up only 4% of all individuals using oil-seed rape in our study, but also for other polylectic species with an early activity peak, like several species of the genera *Andrena* and *Lasioglossum* (Stanley and Stout 2013; Le Féon *et al.* 2013). However, of the 40 species recorded on oil-seed rape in the two study years 31 species were also active after the flowering of oil-seed rape in the study region (unpublished data). Yet, effects may be most important for bee species that have a shorter activity period more or less in parallel to flowering of oil-seed rape (9 of 40 species were recorded only during oil-seed rape flowering in the two study years, unpublished data).

Importantly, the local bee densities depended not only on the availability of oil-seed rape in the previous year but also on oil-seed rape in the year of pollinator sampling, which can be explained by the high relative attractiveness ($a < 1$) of oil-seed rape in comparison to other landscape features. While bee densities increased with increasing relative cover of oil-seed rape in the previous year, bee densities decreased with increasing relative cover of oil-seed rape in the year of pollinator sampling. This decline in local bee densities can be interpreted as a transient dilution effect (Tschardt *et al.* 2012), which occurs when the bees present in the landscape (produced in the previous year) spread over an increased area of oil-seed rape currently flowering in the landscape. The dilution is highest for comparatively high relative cover of oil-seed rape and can not only result in decreased bee densities in oil-seed

rape fields (Holzschuh *et al.* 2011), but also in semi-natural habitats (Kovács-Hostyánszki *et al.* 2013). Our model explains that a higher relative attractiveness of oil-seed rape is a precondition for an observable dilution effect.

From the ecosystem-service perspective – high bee densities can increase yield in oil-seed rape (Steffan-Dewenter 2003; Mänd *et al.* 2010) – the ‘disadvantages’ of low local bee densities from a dilution effect in the year of pollinator sampling might be more pronounced than the ‘advantages’ by increased productivity of oil-seed rape in the previous year and resulting higher bee densities. For example, bee densities in 2012 were 21% higher, when the relative cover of oil-seed rape in the *previous* year was 10% instead of 5% (at constantly 10% relative cover of oil-seed rape in the year of pollinator sampling). In contrast, bee densities in 2012 were 59% higher, when the relative cover of oil-seed rape in the year of pollinator sampling was 5% instead of 10% (at constantly 10% relative cover of oil-seed rape in the previous year). Together with varying pollinator populations also pollination services may vary over time (Rader and Howlett 2012). From a management perspective it might be reasonable to keep relative cover of oil-seed rape at moderate levels across consecutive years to stabilize pollination services. Thereby, farmers could benefit from higher productivity of bees from oil-seed rape on the one hand, but mitigate dilution effects on the other hand. From the conservation perspective, one could argue that the positive effect of the previous year on landscape bee populations is more important and sustainable than transient dilution effects in the year of pollinator sampling, but this holds only if enough food and nesting sites are available for the increased population to capitalize in consecutive years. Additionally, this suggests that the effect from previous year oil-seed rape will be limited by the availability of semi-natural habitats. Moreover, the increase of species densities, which benefitted from oil-seed rape, may change bee communities during the rest of the year in various directions (Diekötter *et al.* 2010; Diekötter *et al.* 2013).

In general, population dynamics of solitary bees are little understood, since long-term studies are rare (Franzén and Nilsson 2013). The obvious effect of the study year in our best models suggests that many different factors may affect densities, like nesting sites, weather or natural enemies (Steffan-Dewenter and Schiele 2008), which makes it difficult to predict long-term influences of changing availability of mass-flowering crops on pollinator dynamics. Nonetheless, with our mechanistic model we tried to disentangle productivity and attractiveness effects, whereas previous studies on inter-annual population dynamics worked directly with the change in relative cover of the productive habitat between years (Thies *et al.* 2008; Zhao *et al.* 2013).

Positive productivity effects from oil-seed rape seem not to apply for bumble bees. Oil-seed rape was nonetheless very attractive to bumble bees, which led also to dilution effects, but there was no net gain across the season leading to increased local densities in the year of pollinator sampling with increasing relative cover of oil-seed rape in the previous year. This is in accordance with Westphal *et al.* (2009), who showed that oil-seed rape supports colony growth but not the production of sexuals, which would be necessary to carry over benefits to the next season. The production of sexuals in bumble bees might not start before midsummer, i.e. weeks after flowering of oil-seed rape had ceased, and bumble bees may store resources only for short periods (Pelletier and McNeil 2003). Although the production of a large workforce early in the year, which is supported by oil-seed rape (Westphal *et al.* 2003; Herrmann *et al.* 2007), is necessary to collect later the food for sexuals (Schmid-Hempel and Schmid-Hempel 1998), there is also the need for enough pollen and nectar at time of reproduction to supply larger larvae of males and young queens with food (Goulson 2010; Williams *et al.* 2012; Rundlöf *et al.* 2014). Consequently, a high availability of food across the season seems to be indispensable. Clearly during flowering oil-seed rape is highly attractive, also due to lack of many alternatives early in spring, yet its availability is short in relation to bumble bees' life cycle. Therefore, the effect of early-mass flowering crops for promoting bumble bees must not be overestimated. Other habitats, like semi-natural habitats, that potentially provide continuous forage resources and at the same time nesting sites may be more important (Persson and Smith 2013).

Conclusion

In our study we focused on temporal spillover effects of mass-flowering crops on pollinators in agricultural landscapes. Our results suggest that besides the spatial effects of mass-flowering crops shown in previous studies (e.g. dilution, local spillover) and short- to medium-term effects within one year, effects can even extend to the next year. Inter-annual spillover of bees as a long-term effect, that is suggested by our results, may be more distinct for pollinators, whose production of sexuals matches the period of mass-flowering (Jauker *et al.* 2012). Moreover, local bee densities during flowering of oil-seed rape seem to be less influenced by long-term effects from the oil-seed rape availability in the previous year than by transient effects, e.g. dilution, within the year of pollinator observation. Our results on inter-annual spillover give only a first clue on how mass-flowering crops in a landscape act on pollinator population dynamics in consecutive years. Nonetheless, our study together with

previous results on effects of mass-flowering crops reveals the complex interactions on different spatial and temporal scales that influence pollinators.

In general, inter-annual changes of crops in agricultural landscapes can influence dynamics of various species groups (Thies *et al.* 2008; Zhao *et al.* 2013) and also networks between different species groups (Massol and Petit 2013), but have been only rarely studied. Future research should include these long-term effects to understand and predict densities and distribution of organisms in agricultural landscapes and the ecosystem services they provide, as well as to develop new strategies for conservation management.

Supplement

Table IV.S1: Model specifications for alternative models for influence of relative cover of oil-seed rape in the previous year (p_0) and relative cover of oil-seed rape in the year of pollinator sampling (p_1) with parameters b_{OSR} =per area productivity of oil-seed rape, b_L = per area productivity of the rest of the landscape, a = preference parameter ($a=1$ no preference/avoidance of oil-seed rape compared to the rest of the landscape, Fig. IV.2) and s_{OSR} , s_L , s_a as year-specific multipliers for the second pair of study years 2011/2012; observations are indexed from $i=1$ to n' for the first study year and from $i=n'+1$ to n for the second study year; † first and † † second best models for other wild bees (Table IV.1); * first and **second best model for bumble bees (Table IV.2)

| Model | No. of parameters | Model equation |
|--|-------------------|---|
| M1: $b_{OSR} \neq b_L, a \neq 1$, no effect from year | 3 | $\frac{(p_{1,i}+1)^a - 1}{2^a - 1} \times \frac{(b_{OSR}p_{0,i} + b_L(1-p_{0,i}))}{p_{1,i}}$ |
| M2: $b = b_{OSR} = b_L, a \neq 1$, no effect from year * | 2 | $\frac{(p_{1,i}+1)^a - 1}{2^a - 1} \times \frac{b}{p_{1,i}}$ |
| M3: $b_{OSR} \neq b_L, a = 1$, no effect from year | 2 | $(b_{OSR}p_{0,i} + b_L(1 - p_{0,i}))$ |
| M4: $b_{OSR} \neq b_L, a \neq 1$, effect from year $s = s_{OSR} = s_L$ for b_{OSR} , b_L ($s_i = 1$ if $i \leq n'$; $s_i = s$ otherwise) † | 4 | $\frac{(p_{1,i}+1)^a - 1}{2^a - 1} \times \frac{s_i(b_{OSR}p_{0,i} + b_L(1-p_{0,i}))}{p_{1,i}}$ |
| M5: $b = b_{OSR} = b_L, a \neq 1$, effects from year $s = s_{OSR} = s_L$ for b_{OSR} , b_L ** | 3 | $\frac{(p_{1,i}+1)^a - 1}{2^a - 1} \times \frac{s_i b}{p_{1,i}}$ |
| M6: $b_{OSR} \neq b_L, a \neq 1$, effect from year only for $b_L(s_L)$ † † | 4 | $\frac{(p_{1,i}+1)^a - 1}{2^a - 1} \times \frac{(b_{OSR}p_{0,i} + s_{L,i}b_L(1-p_{0,i}))}{p_{1,i}}$ |
| M7: $b_{OSR} \neq b_L, a \neq 1$, effects from year only for b_{OSR} (s_{OSR}) | 4 | $\frac{(p_{1,i}+1)^a - 1}{2^a - 1} \times \frac{(s_{OSR,i}b_{OSR}p_{0,i} + b_L(1-p_{0,i}))}{p_{1,i}}$ |

Table IV.S1 continued

| | | |
|--|---|--|
| M8: $b_{OSR} \neq b_L, a \neq 1$, independent effect from year for b_{OSR} (s_{OSR}) and b_L (s_L) | 5 | $\frac{(p_{1,i}+1)^a - 1}{2^a - 1} \times \frac{(s_{OSR,i} b_{OSR} p_{0,i} + s_{L,i} b_L (1 - p_{0,i}))}{p_{1,i}}$ |
| M9: $b_{OSR} \neq b_L, a \neq 1$, independent effects from year for b_{OSR} (s_{OSR}), b_L (s_L), a (s_a) | 6 | $\frac{(p_{1,i}+1)^{s_a i^a} - 1}{2^{s_a i^a} - 1} \times \frac{(s_{OSR,i} b_{OSR} p_{0,i} + s_{L,i} b_L (1 - p_{0,i}))}{p_{1,i}}$ |

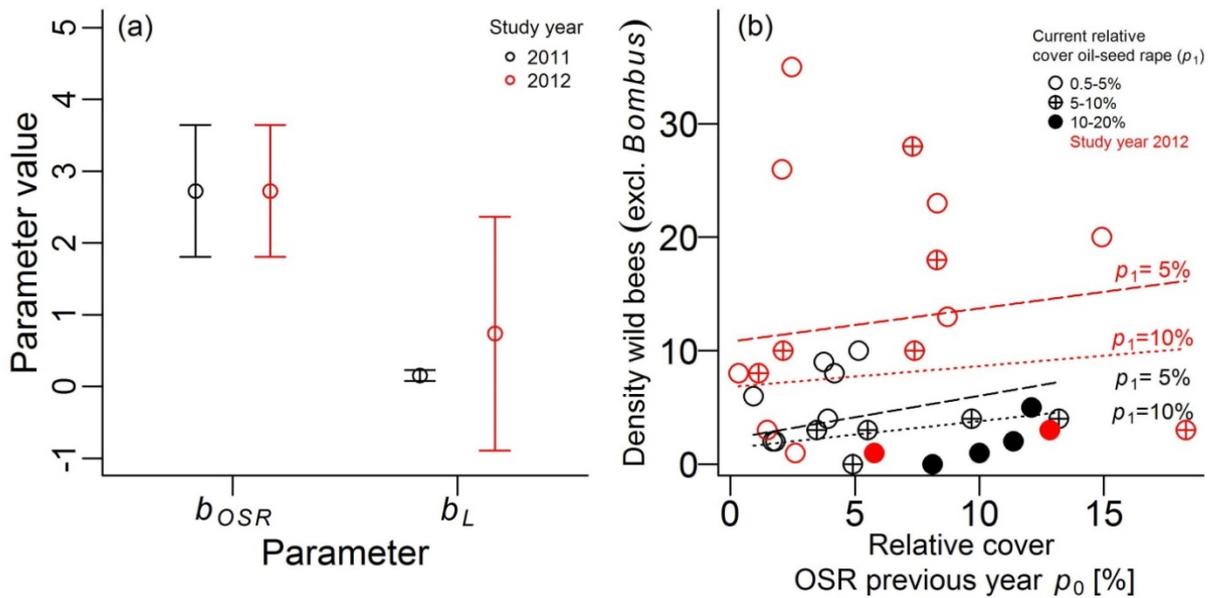


Fig. IV.S1: (a) Comparison of the estimated model parameters b_{OSR} (per area productivity of OSR) and b_L (per area productivity of remaining landscape) for the second best model (Table IV.1) for densities of wild bees other than *Bombus* with confidence intervals for study years 2010/2011 (black) and study years 2011/2012 (red); (b) Relationship between the relative cover of oil-seed rape (OSR) in the previous year and the densities of wild bees (excl. *Bombus*) on 32 OSR fields in two years. Fitted lines are calculated by the second best model (Table IV.1) and the corresponding model equation (Supplement, Table IV.S1) for specific values of relative cover of OSR in the year of pollinator sampling year (p_1 : 5%, 10% respectively). Black symbols show densities in study year 2011, red symbols show densities in study year 2012. Different symbols represent different values of relative cover of current OSR in the year of pollinator sampling (p_1).

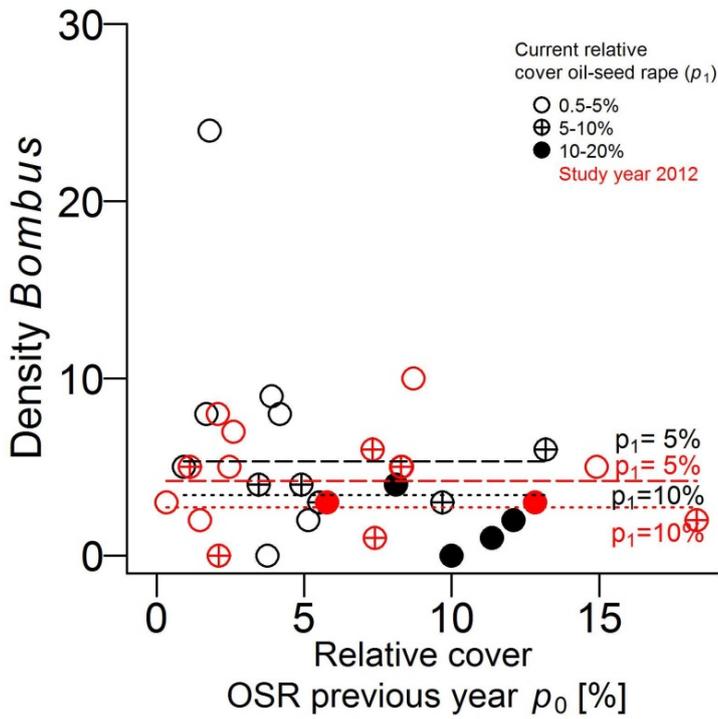


Fig. IV.S2: Relationship between the relative cover of oil-seed rape (OSR) in the previous year and the densities of bumble bees on 32 OSR fields in two years. Fitted lines are calculated by the second best model (Table IV.2) and the corresponding model equation (Supplement, Table IV.S1) for specific values of relative cover of OSR in the year of pollinator sampling (p_I : 5%, 10% respectively). Black symbols show densities in study year 2011, red symbols show densities in study year 2012. Different symbols represent different

values of relative cover of OSR in the year of pollinator sampling (p_I).

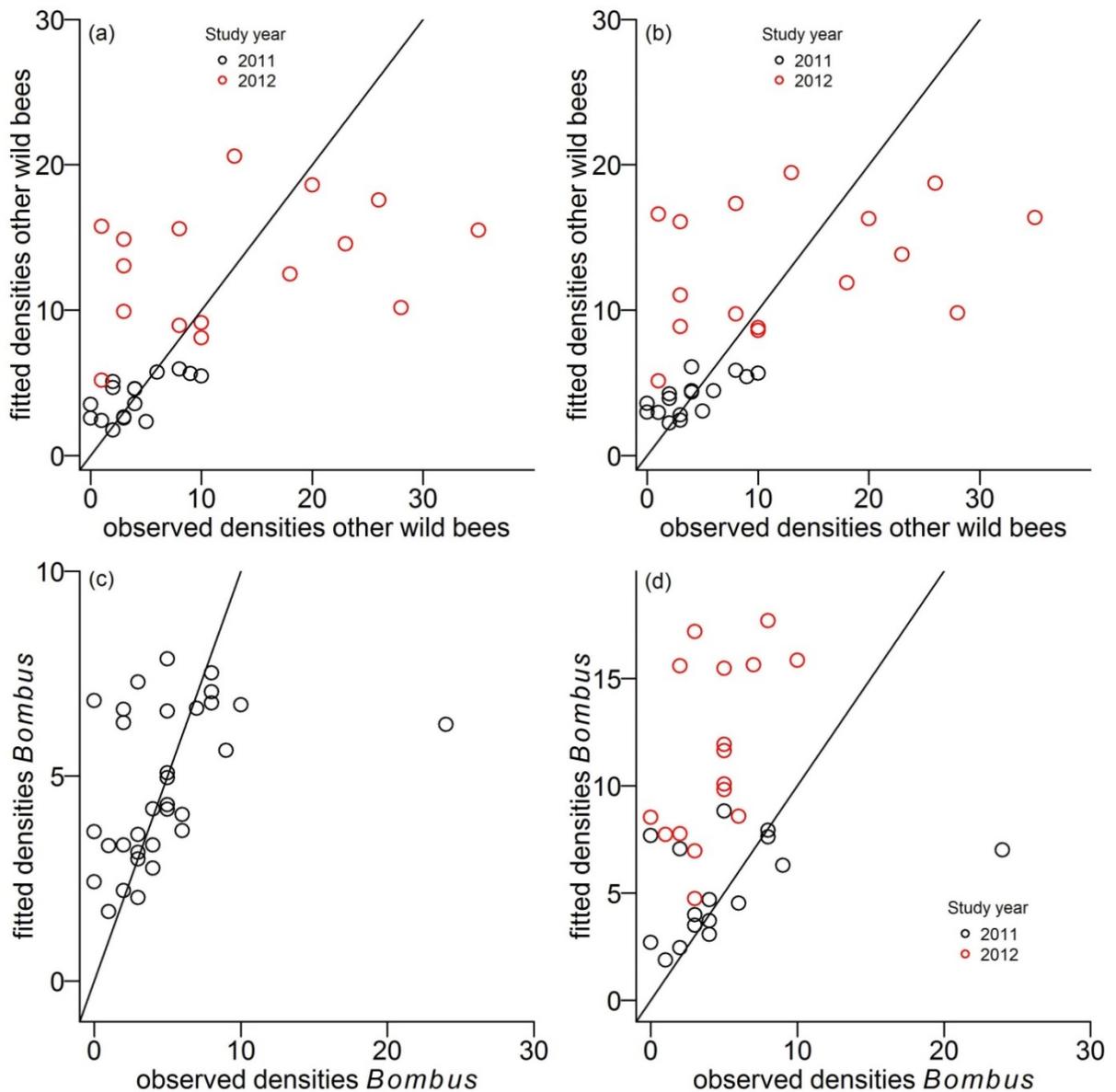


Fig. IV.S3: Relationship between fitted and observed values for (a) the best model for other wild bees (Table IV.1, Fig. IV.3) (b) the second best model for other wild bees (Table IV.1, Supplement Fig. IV.S1b) (c) the best model for bumble bees (Table IV.2, Fig. IV.5) (d) the second best model for bumble bees (Table IV.2, Supplement Fig. IV.S2). As expected with Poisson distributed data the variance is directly coupled to the mean value. This results in a funnel shaped pattern of observed bee densities.

V. General discussion

From short- to long-term effects

In my Phd-thesis I spanned a temporal gradient for the effects of oil-seed rape as a mass-flowering crop on pollinators in agricultural landscapes from short-term (Chapter II) via medium-term (Chapter III) to long-term (Chapter IV) processes. On all temporal scales we found oil-seed rape to have effects, depending on the considered habitat type and pollinator group.

Transiently during flowering, the relative cover of oil-seed rape in a landscape may – due to its high attractiveness – on the one hand greatly affect the distribution of pollinators on the crop itself (Chapter II, IV) leading to a decreased density per unit area crop in landscapes with a high relative cover of oil-seed rape. On the other hand, oil-seed rape may also outcompete other habitat types and reduce visitation rate of pollinators on wild plants in these habitats (Chapter II). In the period after flowering of the crop, semi-natural habitats might benefit from a previous high availability of oil-seed rape that supported for example high population growth in the landscape (Westphal et al. 2003). We found that bumble bee densities increased on semi-natural field boundaries after flowering in landscapes with a high relative cover of oil-seed rape, indicating a landscape-scale spatio-temporal spillover (Chapter II). This spillover could potentially enhance the ecosystem service the pollinators provide to wild plants, although we did not measure effects on plant fitness, like seed or fruit set.

In the medium term, even if other feeding resources in continuously available semi-natural habitats are used after the flowering of oil-seed rape, pollinator densities in another mass-flowering crop with a non-overlapping flowering period, e.g. sunflowers, might still be influenced by the landscape availability of oil-seed rape (Chapter III). Our results suggest that bumble bees, which are active during several months, might spillover from oil-seed rape to sunflowers and thereby increase local densities of bumble bees on sunflower fields in landscapes where oil-seed rape was highly available in spring. This link between managed habitats by the spillover of ecosystem-service providing species was so far disregarded compared to spillover between semi-natural habitats and managed habitats and vice versa (Blitzer et al. 2012), but may be of special interest for management of agricultural landscapes, e.g. to stabilize yields or pest control.

We evaluated long-term effects of oil-seed rape by trying to disentangle effects from oil-seed rape availability in the year of pollinator sampling from effects that arise by the availability of oil-seed rape in the previous year that probably led to higher population growth (Chapter IV). Effects of landscape parameters for pollinator species that finish their life cycle within one year can only be expected when they have influence on the reproductive output of species. Our study suggests that effects from oil-seed rape may carry over to the next season, but only if benefits directly act in the reproductive period, which applies especially to early active solitary bees (e.g. *Osmia spp.* or *Andrena spp.*) and less so for bumble bees that produce males and young queens not before midsummer.

In general, short-term effects of oil-seed rape might be more pronounced than long-term effects. This is suggested by the fact that during flowering oil-seed rape did influence distribution of all wild bees but long-term effects might depend heavily on the life cycle and phenology. Moreover, we found for wild bees other than *Bombus* that in one of the study years an increase of the relative cover of oil-seed rape in the previous year from 5% to 10% at constant relative cover of 10% in the current year increased local bee densities by only 21%. In contrast, a decrease of relative cover of oil-seed rape in the current year from 10% to 5% at constant relative cover of oil-seed rape of 10% in the previous year increased local bee densities by 59%. Especially, in agricultural landscapes where resources appear and disappear in short time intervals it might be important to evaluate species dynamics on different temporal scales.

Landscape-scale impact of mass-flowering crops

In this dissertation I focused on the landscape scale and effects of oil-seed rape on the local scale may be quite different (Holzschuh et al. 2011; Kovács-Hostyánszki et al. 2013). At small spatial scales, mass-flowering crops have been found to enhance pollinators (Holzschuh et al. 2011; Hanley et al. 2011) and pollination services (Kovács-Hostyánszki et al. 2013) in directly adjacent semi-natural habitats during the mass-flowering period. In contrast to the effects we found on the landscape scale after the mass-flowering period (Chapter II), no pollinator spillover from the crop to directly adjacent habitats have been detected so far (Hanley et al. 2011; Kovács-Hostyánszki et al. 2013).

On the landscape-scale mass-flowering crops, like oil-seed rape, give an important resource pulse every year that definitely influences the distribution of pollinators during its flowering in agricultural landscapes (Chapter II, III, IV). Furthermore, we found indirect evidence that mass-flowering crops also increase population size of certain pollinator species

on the landscape scale transiently or long term (Chapter III, IV). Although there seems to be a bias towards studies that focus on oil-seed rape as a mass-flowering crop, there are other systems of mass-flowering crops that might have similar landscape-scale effects on pollinators. Studies of red clover in Sweden (Rundlöf et al. 2014), coffee in Ecuador (Veddeler et al. 2006) or field beans in the UK (Knight et al. 2009) suggest that mass-flowering crops seem to be an important determinant of pollinator distribution and abundance in agricultural landscapes.

Importantly, the landscape-scale effects from oil-seed rape greatly depend on the considered habitat and may be different for managed (Chapter III) and various semi-natural habitats (Chapter II, but see also Kovács-Hostyánszki et al. 2013; Haenke et al. 2014). At least for habitats that are available simultaneously to oil-seed rape the influence on pollinators may greatly depend on the quality of the considered habitat and its relative attractiveness (given by the summed availability of nesting and foraging resources) compared to oil-seed rape.

An important prerequisite for the landscape-scale effects of oil-seed rape, especially for their longevity, is the availability of semi-natural habitats in the landscape. On the one hand, they provide important nesting and overwintering sites from which crop fields are colonized in spring. On the other hand, they provide continuous foraging resources across the season that may mediate e.g. the spillover between mass-flowering crops with non-overlapping flowering periods (Chapter III). Moreover, semi-natural habitats can buffer a possible shortage of pollinators on crop fields due to the expansion of relative cover of oil-seed rape in the landscape (Chapter II).

Influence on different pollinator groups

This dissertation is also an example that landscape variables can have very different effects on different pollinator groups and landscape management of certain habitat types may support some pollinators, but have disadvantageous or neutral effects to others. Most effects of oil-seed rape were found for wild bees (Chapter II, III, IV). Within this group the sociality and phenology modulates the effects from oil-seed rape. Especially for early solitary bees oil-seed rape seems to be a highly valuable feeding resource that can be directly translated into increased reproductive output and also selection of nesting sites might be driven by the vicinity to oil-seed rape (Chapter IV; Jauker et al. 2012; Holzschuh et al. 2013). In comparison, the life cycle of bumble bees is longer and the reproductive period coincides not with the flowering period of oil-seed rape. Bumble bees seem to depend more on continuous

food supply that can consist of feeding resources in semi-natural habitats and also resource pulses from different managed crops (Chapter III, Rundlöf et al. 2014). Though, for both groups oil-seed rape was shown in previous studies to influence community composition. While the species richness of solitary wild bees may even increase by the benefits given to some species during flowering (Diekötter et al. 2013), specialized bumble bees may be discriminated by increased competitive pressure from benefitted generalized bumble bee species (Diekötter et al. 2010).

We did not find evidence that managed honey bee abundance or distribution is affected by oil-seed rape (Chapter II, III). At the landscape scale, honey bee densities might depend more strongly on the distance to the next apiary (which we had no information on) than on the relative cover of any landscape parameter (Garibaldi et al. 2011). Temporal effects from oil-seed rape on honey bees could have been masked by the practice that beekeepers move honey bee hives between landscapes according to temporally changing resource pulses. Though, managed colonies could compensate for dilution of wild pollinators. However, honey bee colony densities are anyway far below demands for crop pollination services in central Europe (Breeze *et al.* 2014).

We did also find no short- or medium term effects from oil-seed rape on hoverflies (Chapter II, III). Hoverflies are effective pollinators of oil-seed rape (Jauker and Wolters 2008). Yet, still they were not attracted in a way that their distribution in the landscape is influenced by oil-seed rape in our study. This shows their opportunistic foraging behavior and also their lower spatial restriction in comparison to central-place foraging bees. Moreover, larval and adult requirements differ very much in comparison to the similar requirements across the life cycle for bees. Hence, the distribution of hoverflies seems to be more heavily influenced by the combination of foraging and oviposition sites (e.g. larval foraging sites). Therefore, hoverflies might be especially difficult to manage for stabilizing crop pollination services.

Conclusion

The effects of oil-seed rape on pollinators on different temporal scales have different components. First, there are effects for crop pollination – the effects farmers are most interested in. Oil-seed rape was previously shown to benefit from insect pollination by increasing yields of about 18% (Bommarco et al. 2012), but increases might be higher or lower depending on the variety (Hudewenz et al. 2013) and also sunflower yields are influenced by pollinators (Greenleaf and Kremen 2006; Aslan et al. 2010). Although, we did

not focus on yield of crops, the patterns shown for the abundance of pollinators, gives the possibility for conclusions on yield effects. During the flowering period of oil-seed rape, it has already been shown that pollination services on the crop may decline with increasing relative cover of oil-seed rape on the landscape scale (Holzschuh et al. 2011) and we could confirm this pattern in this study not only for bumble bees but also for other wild bees (Chapter II, IV). What has been mostly disregarded so far is considering larger temporal scales. Oil-seed rape can by landscape scale management of different flowering crops contribute to stabilize yields of other crops in the same year (Chapter III), and on the inter-annual scale its own yield by spillover of pollinators in consecutive years (Chapter IV). Future research should try to directly link landscape availability of oil-seed rape, pollinator abundance and yield to give resilient arguments for landscape-scale management of mass-flowering crops.

Second, oil-seed rape might have effects on conservation of pollinators and pollination services to wild plants. Parts of this dissertation show distribution patterns of pollinators during and after flowering of oil-seed rape as a consequence of its relative cover in the landscape (Chapter II), though the results also suggest that oil-seed rape may increase population growth (Westphal et al. 2003). Importantly, we could show this effect in another mass-flowering crop (Chapter III) and also for the population size in consecutive years (Chapter IV). We did not investigate the changes in community composition during and after mass-flowering or in the next year in landscapes with different relative covers of oil-seed rape. Previous studies suggest that oil-seed rape is not appropriate or even counterproductive to counteract an ongoing pollinator diversity decline in agricultural landscapes (Diekötter et al. 2010), but this may highly depend on the traits present in a pollinator community (Jauker et al. 2012). Future research should focus on the long-term changes in community composition that are induced by changes in the relative cover of oil-seed rape, and identify traits that make advantages or disadvantages for specific species more predictable.

We did not directly focus on fitness parameters of wild plants in relation to relative cover of oil-seed rape in the landscape, but our results suggest pollination service for wild plants to be decreased during mass-flowering in landscapes with a high relative cover of oil-seed rape (Chapter II). After mass-flowering, pollinators may spillover from oil-seed rape to wild plants in semi-natural habitats and increase pollination services. If we assume that benefits of oil-seed rape can be extended to the next year (Chapter IV) and less oil-seed rape would be available then – decreasing the competition with wild plants – even inter-annual positive effects on pollination services for wild plants might be conceivable. So far, direct

evidence on the effect from oil-seed rape on fruit set is available only for a handful of wild plant species (Cussans et al. 2010; Holzschuh et al. 2011; Kovács-Hostyánszki et al. 2013). Future research should identify traits of wild plant species, which make them especially prone to competition by oil-seed rape and features (e.g. comparable high attractiveness in terms of feeding resources) of plant species habitats that might buffer competition by oil-seed rape (Chapter II). Additionally, proof has to be produced, whether or not there are advantageous effects of oil-seed rape on wild plant pollination after the mass-flowering period by spillover of pollinators.

Considering the complex and varying effects of oil-seed rape in this dissertation shows the importance of integrating multiple spatial and temporal scales in studying and managing ecosystem services and ecosystem-service providing species. Here, I used pollinators and pollination services as an example, but different temporal scales may influence a broad range of species in agricultural landscapes.

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Author contributions

Chapter II

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VR, AH and ISD designed the study; VR collected data; VR, OM and TH analyzed data; VR, AH, OM, TH and ISD interpreted results; VR wrote the first draft of the manuscript and all authors contributed to revisions.

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