

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

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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.

Keywords *Apis mellifera* · *Bombus* · Germany · Oil-seed rape · Spillover · Sunflower · Syrphids

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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; Öckinger and Smith 2007; Holzschuh et al. 2011) 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 1 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 2011). 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. 2012). 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. (2003, 2009) 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 benefiting 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.

Materials and methods

Study sites and landscape parameters

The study was conducted in 2011 in the surroundings of Würzburg, Bavaria, Germany (49°44′53″N, 9°51′34″O). 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 45×55 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 ± 4.4 %) in the landscape sectors. Additionally, the study fields covered gradients in relative cover of sunflowers (0.2–3.1 %, mean \pm SD 0.9 ± 0.8 %) and

of semi-natural habitats (1.5–11.3 %, 5.7 ± 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 ± 17.4 %), settlements (6.1–33.4 %, 12.6 ± 6.8 %), forest interior (0.2–32.5 %, 12.0 ± 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 ± 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 min, 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 dataset at the median relative cover of oil-seed rape (low vs. high relative cover of oil-seed rape) and calculated regression lines using the coefficients from the final models by fixing oil-seed rape at its median value for both the low and the high relative cover oil-seed rape subsets, respectively.

Results

We recorded 7708 bumble bees (eight species), 975 hoverflies (13 species), 12,074 honey bees, and 28 other wild bees (six species) on the 16 sunflower fields

Table 1 Landscape effects on bumble bee, hoverfly and honey bee densities on sunflower fields ($n = 16$)

	Coefficient	SE	t	p
Density of bumble bees				
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 × % semi-natural habitats	0.02	0.01	2.0	0.070
% oil-seed rape × % sunflowers	0.13	0.06	2.3	0.044
Density of hoverflies				
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 × % semi-natural habitats	−0.04	0.02	−2.4	0.034
Density of honey bees				
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 × % semi-natural habitats	−0.06	0.02	−2.7	0.019

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

during 97 transect walks (Online Appendix 1, bumble bee and hoverfly species that can be found in both crops are shown in Online Appendix 2).

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 1). While the bumble bee density increased with increasing relative covers of sunflowers at high relative covers of oil-seed rape (Fig. 1a), it decreased with increasing relative covers of sunflowers at low relative covers of oil-seed rape (Fig. 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. 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 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. 2a), whereas in landscapes with low relative covers of oil-seed rape there was no increase (Fig. 2b). Highest bumble bee densities in sunflower fields were found in landscapes with high relative covers of oil-seed rape and semi-natural habitats.

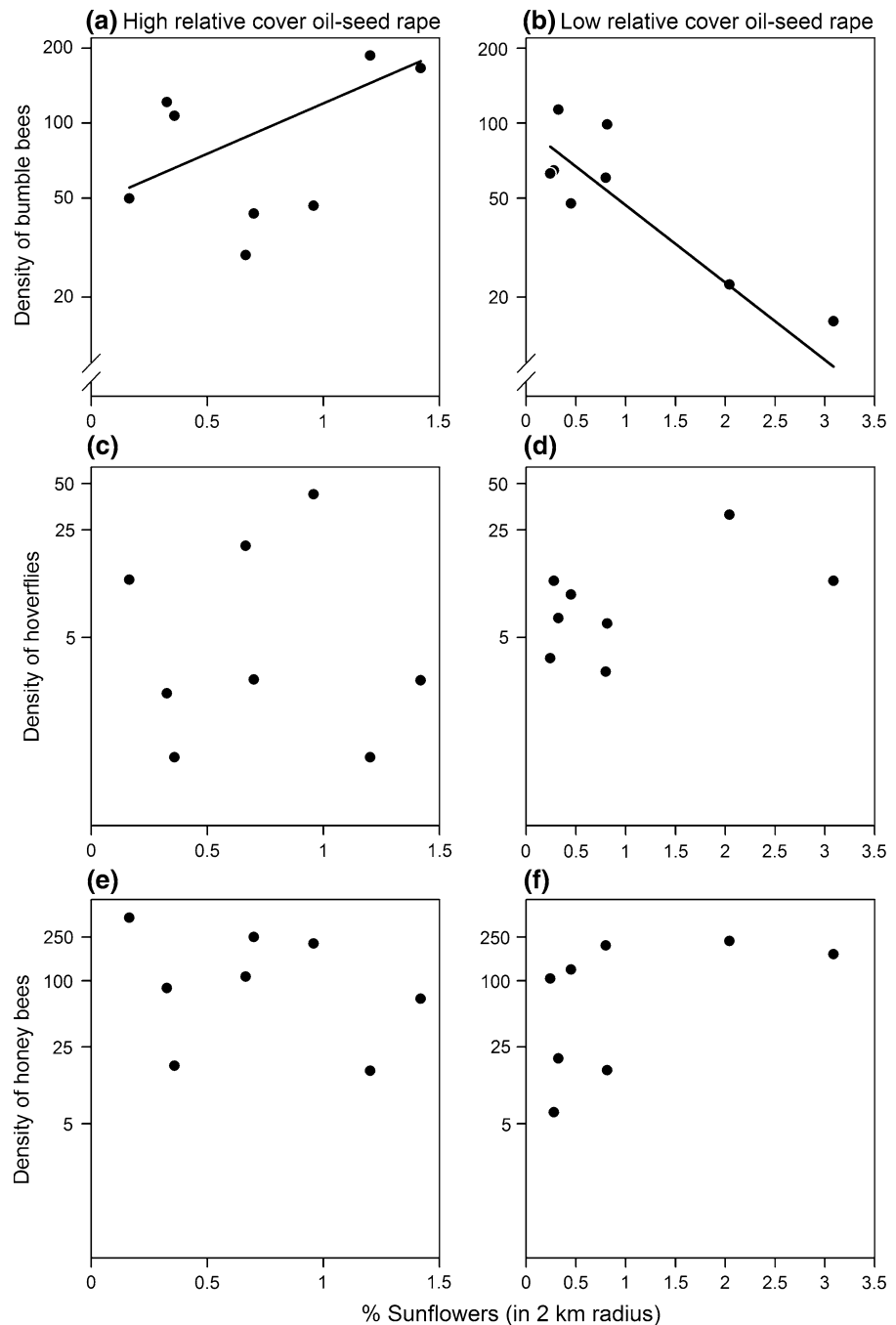
For the density of hoverflies the interaction between the relative cover of oil-seed rape and relative cover of semi-natural habitats was significant. The hoverfly density decreased with an increasing relative cover of semi-natural habitats both at high and low relative covers of oil-seed rape, but this decrease was more pronounced at high than at low relative covers of oil-seed rape (Table 1; Fig. 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 1; Fig. 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. 2e). Neither the densities of hoverflies (Fig. 1c, d), nor the densities of honey bees (Fig. 1e, f) were affected by the relative cover of sunflower.

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

Fig. 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 versus 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 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

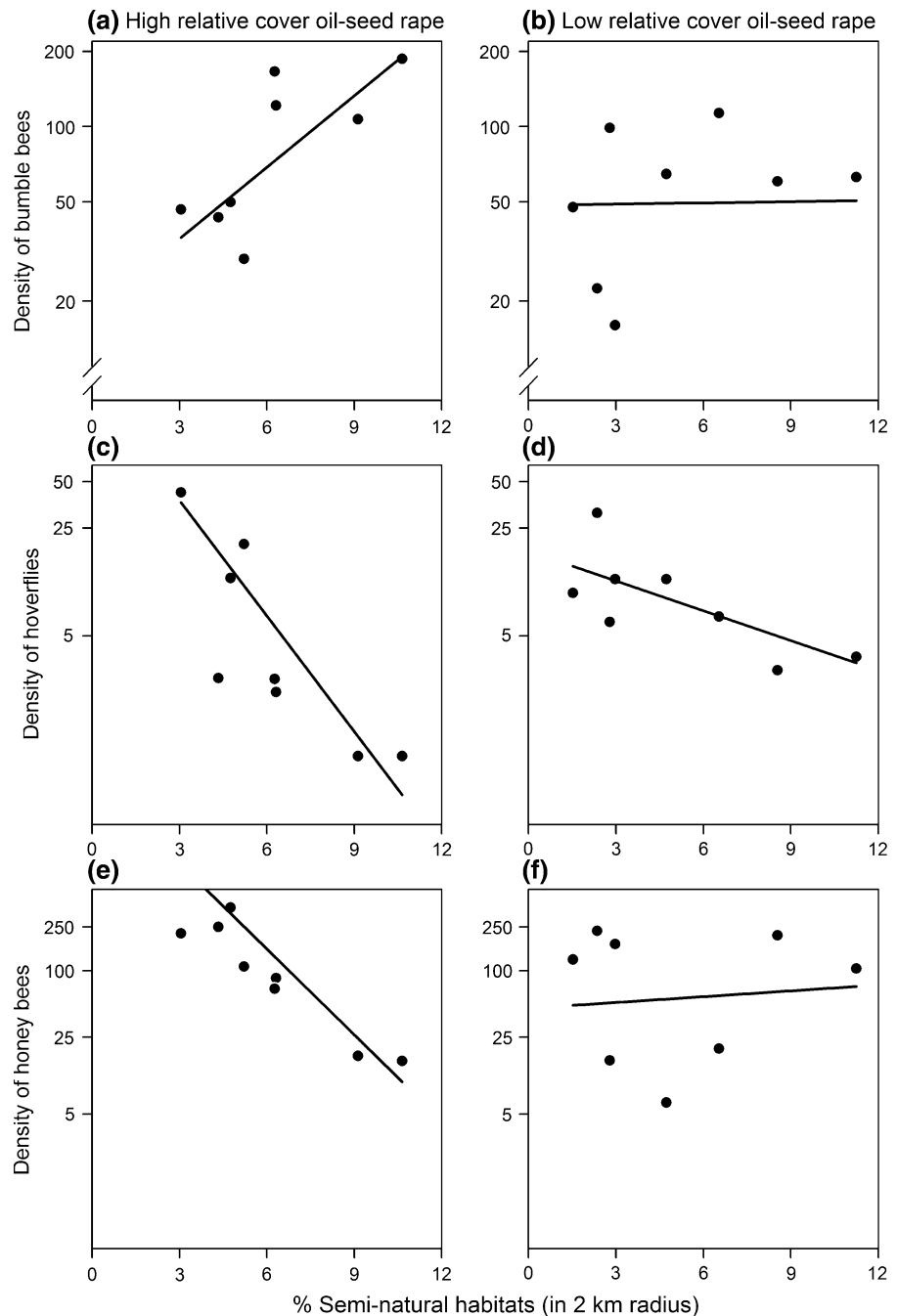


that early mass-flowering crops can mitigate pollinator dilution in crops flowering later in the season.

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

Fig. 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 versus 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 1). In the bumble bee model, also the predictor relative cover of sunflowers was held constant at its mean value in the equation



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 and Yavuksuz 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. Öckinger and Smith 2007; Rundlöf et al. 2008; Ekroos et al. 2013), 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 sunflower 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 (Online Appendix 1). 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, honeybees 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.

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