Contrasting effects of mass-flowering crops on bee pollination of hedge plants at different spatial and temporal scales

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Abstract. Landscape-wide mass-flowering of oilseed rape (canola *Brassica napus*) can considerably affect wild bee communities and pollination success of wild plants. We aimed to assess the impact of oilseed rape on the pollination of wild plants and bee abundance during and after oilseed-rape bloom, including effects on crop–noncrop spillover at landscape and adjacent-field scales. We focused on two shrub species (hawthorn *Crataegus* spp., dog rose *Rosa canina*) and adjacent herb flowering in forest edges, connected hedges, and isolated hedges in Lower Saxony, Germany. We selected 35 landscape circles of 1 km radius, differing in the amount of oilseed rape; 18 were adjacent to oilseed rape and 17 to cereal fields, and we quantified bee density via pan traps at all sites. Adjacent oilseed rape positively affected fruit mass and seed number per fruit of simultaneously flowering hawthorn (no effect on dog rose, which flowers after the oilseed rape bloom). At the landscape scale, oilseed rape had a negative effect on bumble bee density in the hedges during flowering due to dilution of pollinators per unit area and the consequently intensified competition between oilseed rape and wild shrubs, but a positive effect after flowering when bees moved to the hedges, which still provided resources. In contrast, positive landscape-scale effects of oilseed rape were found throughout the season in forest edges, suggesting that edges support nesting activity and enhanced food resources. Our results show that oilseed rape effects on bee abundances and pollination success in seminatural habitats depend on the spatial and temporal scale considered and on the habitat type, the wild plant species, and the time of crop flowering. These scale-dependent positive and negative effects should be considered in evaluations of landscape-scale configuration and composition of crops. Food resources provided by mass-flowering crops should be most beneficial for landscape-wide enhancement of wild bee populations if seminatural habitats are available, providing (1) nesting resources and (2) continuous flowering resources during the season.

Key words: bumble bee, Bombus *spp.; canola; dog rose,* Rosa canina; *ecosystem services; fruit set; Göttingen, Germany; hawthorn,* Crataegus *spp.; isolation; oilseed rape,* Brassica napus; *scale dependency.*

INTRODUCTION

Pollinating insects, in particular wild bees (Hymenoptera: Apoidea), have dramatically declined in the last few decades worldwide (Biesmeijer et al. 2006, Goulson et al. 2008, Potts et al. 2010, Cameron et al. 2011). However, pollination of crops and wild plants is one of the most important ecosystem services (Ashman et al. 2004, Klein et al. 2007, Calderone 2012). Recent estimates suggest that animal-mediated pollination is required for 88% of angiosperm species and influences yield of 70% of the major agricultural crop species, accounting for 35% of global food production (Klein et al. 2007). Causal links between extinctions of wild plant and wild pollinator

species have been suggested (Spira 2001, Biesmeijer et al. 2006), whereas managed honeybees (*Apis mellifera*) cannot replace the functional role of wild bees (Holzschuh et al. 2012, Garibaldi et al. 2013).

The effects of landscape configuration, annual crop rotation, and within-year changes in nectar/pollen availability on pollinators and pollination are still relatively unknown (Hadley and Betts 2012). As a major consequence of increasing demand for biofuel, the area of oilseed rape (*Brassica napus*) in agricultural landscapes is expanding (Rowe et al. 2009). Mass-flowering oilseed rape is mainly self-pollinated, yet pollen transport by invertebrate vectors has been shown to result in higher seed set and yield (Jauker et al. 2012). It attracts many insect groups (Bommarco et al. 2012, Jauker et al. 2012), which might spill over to the adjacent habitats (Hanley et al. 2011). However, its benefit for pollinators is questioned due to a synchronized and short flowering period (Westphal et al. 2009). The dilution of pollinators

per area and the consequent competition for pollinators may threaten the pollination of concurrently flowering wild plants (Holzschuh et al. 2011). However, flowering crops may also facilitate wild plant pollination, depending on species and season (Cussans et al. 2010).

Here we present the first study to quantify the changing importance of mass-flowering crops for wild bees and the pollination of wild plants due to possible crop–noncrop spillover at both landscape and adjacent-field scales, and the importance of hedge plants (herb and shrub flowers) at local habitat scale. We focused on two wild hedge shrubs, hawthorn (*Crataegus* spp.) and dog rose (*Rosa* spp.), which typically grow in three habitat types with similar vegetation structure but differ in how they are affected by surrounding crops. Forest edges are exposed with only one side to oilseed rape, connected hedges are exposed with two sides to crops but they are bordered from one end by forest margins, while isolated hedges are fully surrounded by crops. These landscape elements often remain the only refuges for pollinators in intensively managed agricultural landscapes, providing valuable pollen and nectar resources for foraging bees during the year as well as suitable nesting habitats (Hopwood 2008, Hannon and Sisk 2009).

We analyzed the landscape- and adjacent-field-scale effects of oilseed rape and effects of local flower resources within the hedges and forest edges on the species richness and abundance of bees sampled by pan traps and on the reproductive success of the two shrubs. The fruit set, fruit mass, and seed number of shrubs were quantified to assess possible pollination facilitation or competition by oilseed rape for pollinators. Bumble bees and other wild bee species were analyzed separately because bumble bees are usually more influenced by landscape-wide effects due to their larger body size and consequent larger foraging distance (Greenleaf et al. 2007, Osborne et al. 2008). Other mostly solitary wild bees are smaller and not able to fly larger distances; therefore they forage in the vicinity of their nesting sites, which makes them more dependent on local conditions and less sensitive to landscape-scale crop structure (Gathmann and Tscharntke 2002, Holzschuh et al. 2011). Furthermore, oilseed rape might have a strong influence on bumble bees as an important food resource (Westphal et al. 2003, 2009, Holzschuh et al. 2011).

We tested the following main hypotheses: (1) Landscape-wide increase of oilseed rape causes reduced flower visitation and reproductive output of simultaneously flowering wild plants (shrub species in hedges and forest edges). (2) Pollinator visits and reproductive success of adjacent hedge flowers increase after landscape-wide oilseed rape flowering. (3) Pollinators spill over from directly neighboring oilseed rape fields into hedges and forest edges, resulting in enhanced numbers of pollinators and pollination success of shrubs compared to hedges and forest edges adjacent to wheat fields. (4) Increasing species richness and abundance of

herb and shrub flower resources along the hedges and forest edges enhances the number of flower visitors and the pollination success of shrub species.

MATERIAL AND METHODS
Study area and design

The study took place in the vicinity of the city of Göttingen (51.5° N, 9.9° E) in southern Lower Saxony, Germany, in 2009 (Appendix A). The area is dominated by arable fields (2–5 ha in size on average), intermingled with grasslands and remnants of deciduous forests. The most widely sown crops are winter wheat and winter oilseed rape. The forests are dominated by common beech (*Fagus sylvatica*), used for timber production. The agricultural matrix is characterized by hedges, which are often close to or connected to forests, but can also be situated alongside arable fields isolated from forests. Most of the hedges and forest edges are managed regularly by pruning (every 8–15 years). The most characteristic woody plants in hedges are blackthorn (*Prunus spinosa*), hawthorn, and dog rose; however, one can also find dogwood (*Cornus sanguinea*), European ash (*Fraxinus excelsior*), common hazel (*Corylus avellana*), silver birch (*Betula pendula*), elderberry (*Sambucus nigra*), European mountain ash (*Sorbus aucuparia*), and so forth.

To study the effects of habitat isolation of the seminatural habitats (i.e., hedges) on pollinators and pollination success, three different habitat types were selected, representing different levels of how strongly they are embedded in the open-crop landscape: forests edges (n = 12), hedges connected to forests (n = 11), and isolated hedges (n = 12) (Fig. 1). Connected hedges were directly adjoined to forests. Isolated hedges were separated from forest patches, with a minimum distance of 300 m representing an adequate isolation for wild bees (Steffan-Dewenter and Tscharntke 1999, Gathmann and Tscharntke 2002). To consider the effects of the adjacent crop fields, half of the forest edges and hedges were selected next to winter cereal fields, the other half next to winter oilseed rape fields on at least one side. The length of connected and isolated hedges ranged from 100 to 300 m. None of the hedges was part of a longer hedge network or of green lanes with two hedges bordering dirt roads. The selected study sites had a minimum distance of 300 m to each other. Hedges and forest edges had a similar species composition of shrubs and trees and were surrounded by similar landscape matrices, characterized by arable fields, grasslands, and forest patches. Limitations in the availability of the suitable habitats precluded choosing equally oriented habitats. However, there was a random mix of hedge orientation across treatments, and the great majority of the samplings and observations were done on the south- or southwest-oriented sides of the hedges and forest edges getting the highest amount of sunshine during the day.
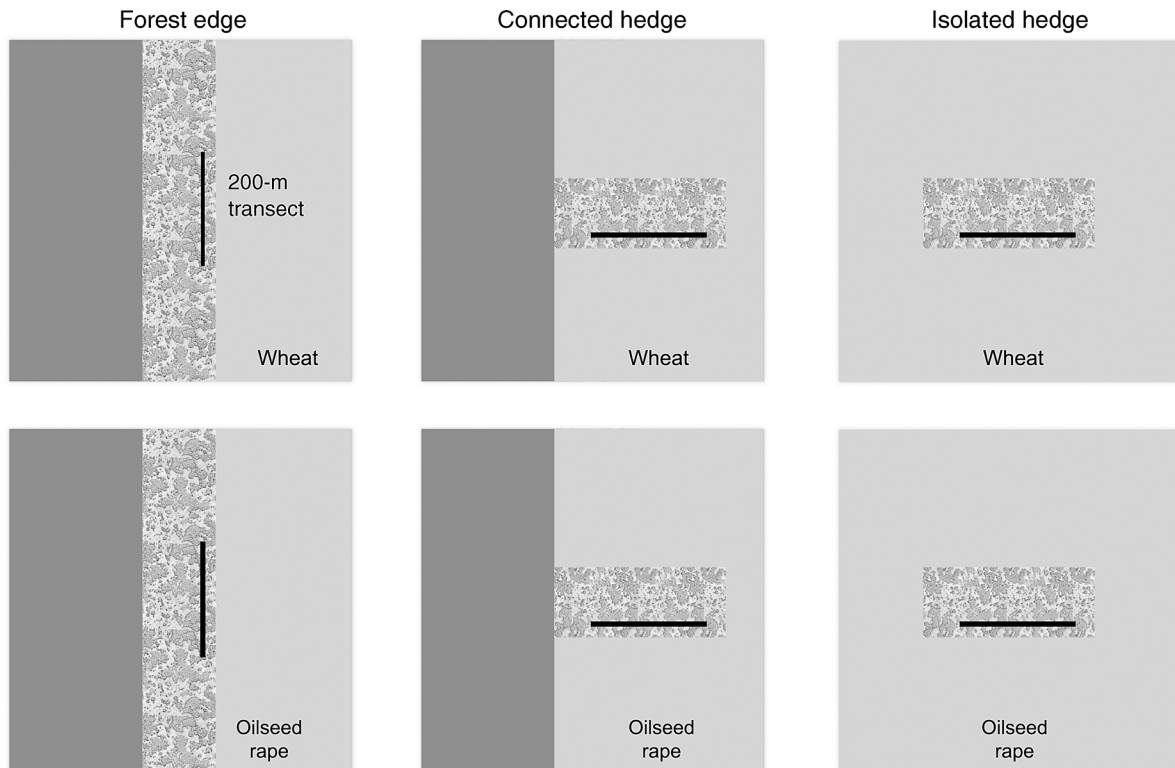
FIG. 1. The study design shows the spatial arrangement of the forest edges (left), connected hedges (middle), and isolated hedges (right) in the vicinity of Göttingen, Germany. Dark gray represents the forest, stippled gray the study site, and light gray the landscape matrix, with wheat at the top and oilseed rape at the bottom. Flowering plants were assessed along a 200-m transect (heavy line) in each study site.

Bees in pan traps

Bees were sampled by colored pan traps of 15 cm diameter and 10 cm depth during two one-week long periods in the first part of May, and also during two one-week long periods in the middle of June. Two painted white, yellow, and blue pan traps, respectively, were exposed on three woody posts (two traps of the same color on one post) along forest edges and along connected and isolated hedges, ~100 cm above ground level and ~10 m apart from each other. The traps were filled with an ethylene glycol–water mixture (1:4, volume : volume) and a small amount of detergent to reduce surface tension and enhance the effectiveness of sampling. Collected bees were taken to the laboratory and identified to species level. Data from the two sampling periods within a month and from pan traps of different colors were pooled. May data represent the period of oilseed rape flowering, and June data were those collected after oilseed rape flowering. Wild bees were divided into two groups: bumble bees (i.e., *Bombus* spp.) and other wild bees (all the remaining species except honey bees).

Pollination success

The effectiveness of pollination was measured by determining fruit set of flowers and the seed number per fruit on one individual of hawthorn and dog rose in each

site. Hawthorn was flowering in the first half of May simultaneously with oilseed rape bloom, and dog rose in the first half of June after oilseed rape bloom. Two branches per plant and ~50 flowers per branch were marked and exposed to open pollination. To test whether insect pollination adds to self-pollination, two branches per plant with similar numbers of marked flowers were bagged with a mesh bag before the beginning of the flowering period to exclude pollinators. The bags were removed after the flowering period, and all mature fruits of the two bagged and the two open branches were harvested in early autumn. Due to hedge cutting in the autumn, three bagged and three open dog rose branches were lost. The fruits were dried at 35°C for two weeks and then weighed. Afterward, seeds were extracted and counted. The pollination success was compared between the bagged and open branches using the following parameters: fruit set (number of fruits divided by the number of flowers of the two branches per treatment), fruit mass (average mass of dried fruits), seed number (average number of seeds per fruit), and aborted seed number (average number of immature seeds, only important in the case of dog rose).

Vegetation and landscape parameters

Transects of 200 m length (if possible) were assigned in all habitat types along the hedges and forest edges

(Fig. 1). The overall number of herb flowers along the transects was assessed once per pan trap sampling period, four times in total). Flower density was assessed along the transects by estimating the number of flower heads at species level in the hedges and forest edges and the adjacent grassy herbaceous margin of maximum 0.5 m width on that side of the hedge where traps were exposed. Data from the two consecutive sampling periods within a month were pooled, taking the average number of flowers. During the flowering of hawthorn and dog rose shrubs we assessed the abundance of conspecific flowers in the observed 2 × 2 m patch and the pooled number of herb flowers. Flower species richness and the number per cover of blossoms are suitable proxies of foraging resources of bees (e.g., Ebeling et al. 2008).

Landscape parameters were measured within a 1000 m radius around each site based on official digital thematic maps (Amtliches Topographisch—Kartographisches Informationssystem Digitale Topographische Karte [ATKIS DTK 50]; *available online*)[7] and mapping of the arable fields (based on Steffan-Dewenter et al. [2002]). We calculated the percent cover of oilseed rape fields (OSR%) and the percent cover of noncrop habitats excluding forest interiors (i.e., grasslands and 10 m wide forest boundaries). The percent cover of noncrop habitats was significantly related to habitat type (ANOVA, $F_{2,32} = 3.91$, $P = 0.03$), with lower values around the connected hedges (Tukey post hoc, $t = -2.15$, $P = 0.095$) and higher around the isolated hedges (Tukey post hoc, $t = 2.61$, $P = 0.035$) than around forest edges. Therefore we decided not to include this landscape parameter in the models. OSR% was not significantly related to the adjacent crop type (ANOVA, $F_{2,33} = 2.48$, $P = 0.125$).

Statistics

First, we used ANCOVAs to test which predictors affected the pollinators recorded in the pan trap samples. In the models of the pan trap analyses, response variables were species richness and the abundance of bumble bees and other wild bees. Predictors in all full models were adjacent crop type (oilseed rape vs. cereal) and habitat type (forest edge vs. connected hedge vs. isolated hedge), along with the proportion of oilseed rape in 1000 m radius and total flower abundance (number of herb flowers along the 200-m transect) included as covariates. Pan trap data were tested separately for May and June. Abundance data were square-root transformed to reach normal residual distribution.

Second, we assessed the reproductive success of hawthorn and dog rose. Reproductive success was measured as fruit set, fruit mass, seed number, or number of aborted seeds (only in the case of dog rose), which were

used as response variables in the following analyses. We used t tests for paired samples to assess the effect of open pollination vs. self-pollination of bagged flowers on reproductive success. ANCOVAs were used to test the effect of the predictors OSR%, adjacent crop, habitat type, total flower abundance, and conspecific flower abundance in the patch on the reproductive success of open-pollinated flowers. Fruit set values of hawthorn were arcsine-transformed to reach normal residual distribution.

In all of these analyses, two-way interactions were tested between habitat type and adjacent crop type and between habitat type and OSR%, respectively. Nonsignificant variables ($P > 0.05$ from F test) were excluded in backward stepwise selection, except being part of a significant interaction. Multivariate comparisons by means of Tukey contrasts were performed between habitat types. Analyses were performed using the nlme (Pinheiro et al. 2010), stats (R Development Core Team 2009), multcomp (Hothorn et al. 2008), and mvtnorm (Genz et al. 2010) packages of R 2.10.1 software. An overview on all the described ANCOVA models is provided in Appendix B.

RESULTS

Bees in pan traps

Pan traps sampled 235 individuals of 11 bumble bee species and 1315 individuals of 51 other wild bee species in May 2009, and 421 individuals of 11 bumble bee species and 1117 individuals of 45 other wild bee species in June 2009 (Appendix C). The most abundant bumble bee species were *Bombus lapidarius*, *B. pascuorum*, *B. pratorum*, and *B. terrestris* agg. in both May and June. The oilseed rape fields in the landscape (OSR%) had contrasting effects on bumble bees in May (during rape flowering) compared to June (after rape flowering). There was a significant interaction between the effects of OSR% and habitat type on bumble bee abundance in May and a marginally significant interaction for bumble bee species richness in May (Table 1). Bumble bee abundance and species richness increased with increasing OSR% in the forest edges and decreased with increasing OSR% in connected and isolated hedges (Fig. 2). Both species richness and abundance of bumble bees were higher in forest edges than in connected and isolated hedges in May, with differences being small for low OSR% and large for high OSR%. In June, species richness of bumble bees was also higher in forest edges than in the connected hedges ($t = 2.784$, $P = 0.024$), while the isolated hedges did not differ from the other two habitat types (Fig. 2). In June, OSR% had a positive effect on species richness and abundance of bumble bees in all habitat types. We found no significant difference in the abundance of bumble bees between the habitats in June.

Species richness and abundance of other wild bees were not found to be influenced by any of the tested variables. The adjacent crop had no effect on the bees sampled by pan traps.

TABLE 1. Local- and landscape-scale effects on species richness and abundance of bumble bees and other wild bees in forest edges and in connected and isolated hedges, in the vicinity of Göttingen, Germany, in May and June 2009, according to the final ANCOVA models after backward selection.

Variable	df	F	P
May			
Species richness			
Bumble bees			
OSR%	1, 29	5.21	0.029
Habitat	2, 29	10.98	<0.001
OSR% × habitat	2, 29	2.53	0.097
Other wild bees			NS
Abundance			
Bumble bees			
OSR%	1, 29	3.05	0.090
Habitat	2, 29	19.00	<0.001
OSR% × habitat	2, 29	4.87	0.015
Other wild bees			NS
June			
Species richness			
Bumble bees			
OSR%	1, 31	5.43	0.026
Habitat	2, 31	4.14	0.025
Other wild bees			NS
Abundance			
Bumble bees			
OSR%	1, 33	5.23	0.029
Other wild bees			NS

Notes: Explanatory variables of the full model are OSR% (percent cover of oilseed rape fields in 1000 m radius), adjacent crop (oilseed rape vs. cereal), habitat type (forest edge vs. connected hedge vs. isolated hedge), and total flower abundance (number of herb flowers along the 200-m transect). NS means not significant.

Pollination success

The fruit set, fruit mass, and seed number per fruit of hawthorn were significantly higher for open than for bagged branches (Appendices D, E). There was no difference in fruit set of dog rose between the two treatments; however, higher fruit mass, more seeds; and fewer aborted seeds were found in fruits from open than from bagged branches (Appendices D, E).

The fruit mass and seed number per fruit of hawthorn were higher next to oilseed rape fields than next to cereal fields (Table 2, Fig. 3a, b). The seed number per fruit of dog rose was slightly higher in connected than in isolated hedges (Tukey $t = -2.37$, $P = 0.061$); the forest edges did not differ from the other two habitat types (Tukey, forest edge–connected hedge $t = -2.05$, $P = 0.119$; forest edge–isolated hedge $t = -0.27$, $P = 0.959$). Fruit set of dog rose was positively related to the number of dog rose flowers in the observed patch.

DISCUSSION

In this study we focused on the effects of flower resources on overall species richness and abundance of bees in hedges and forest edges and pollination success

of three shrub species at three spatial scales: effects of oilseed rape at the landscape and adjacent crop field scale, and the local scale effects of hedge plants. At the landscape scale, effects on bumble bees in hedges and forest edges depended on whether oilseed rape was flowering at the time or had ceased flowering and on the habitat types of forest edges and hedges. At the adjacent-field scale, oilseed rape had positive effects on fruit mass and seed number per fruit in hawthorn growing in forest edges and hedges. The abundance of local wildflowers among hedge plants enhanced the fruit set of dog rose, particularly of conspecific flowers in the direct surroundings of the focal shrubs.

Landscape-scale effects of oilseed rape

Our study showed strong and mixed landscape-scale effects of percent cover of oilseed rape fields on bumble bees recorded in pan traps. During oilseed rape flowering in May, a higher percent cover of oilseed rape had a negative effect on bumble bee species richness and abundance in hedges, but a positive effect in forest edges. In June, when oilseed rape had ceased flowering, percent cover of oilseed rape had a positive effect on bumble bee species and individuals in all three habitat types (hedges and forest edges).

We suppose that the negative landscape-scale effect of oilseed rape on bumble bees in our hedges during oilseed rape flowering is due to the dramatically enhanced resources supplied by mass-flowering oilseed rape. Our results suggest that the distribution of pollinators depends on the amount of oilseed rape in bloom; in landscapes with high amounts of oilseed rape, pollinator abundances per area hedge decline because pollinators are attracted to the oilseed rape fields. Thus our results suggest that competition between oilseed rape and wild shrubs is higher in landscapes with high amounts of oilseed rape. Bumble bee abundance declined in oilseed rape fields when the percent cover of oilseed rape was high at the landscape scale during oilseed rape flowering (Holzschuh et al. 2011). Here we show that when oilseed rape is flowering, competition for bumble bee pollinators results in a transient decline in visitation to flowers or captures in pan traps in seminatural habitats like hedges.

In contrast to hedges, bumble bee abundance in forest edges increased with increasing percent cover of oilseed rape in the landscape and was generally higher in forest edges than in hedges. Forest edges might provide more extended nesting and foraging habitat compared to hedges. An increased abundance of bumble bees in forest edges surrounded by high percent cover of oilseed rape suggests increased nesting activity and enhanced growth of new colonies due to the increased availability of nectar and pollen resources in the landscape (West-phal et al. 2009).

After oilseed rape flowering, species richness and abundance of bumble bees in both the hedges and forest edges were positively affected by percent cover of oilseed rape in the landscape. Seminatural habitats represent
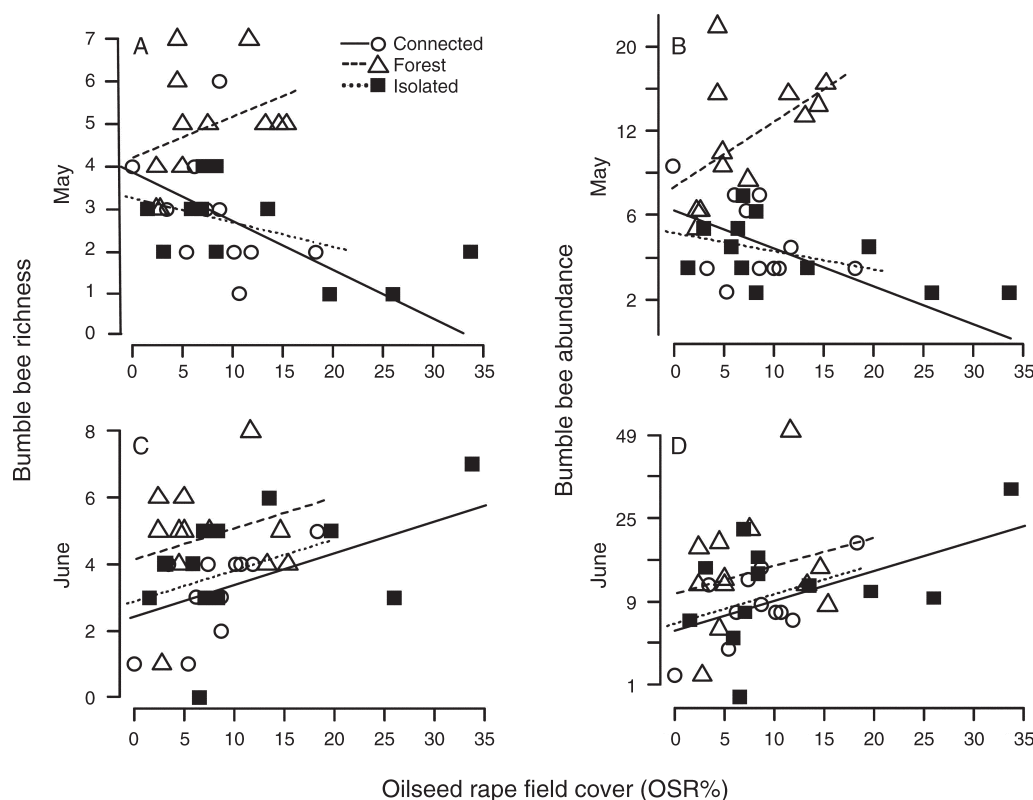
FIG. 2. Results from ANCOVA models for (A) species richness and (B) abundance of bumble bees in forest edges and in connected and isolated hedges in May 2009, and for (C) species richness and (D) abundance of bumble bees in June 2009 in relation to percentage of the area in a 1000-m radius that is oilseed rape fields.

continuous foraging resources for bumble bees when flowering crops are not available (Corbet 2000), resulting in spillover and concentration of bumble bees in the seminatural habitat patches. Our result corresponds with former studies, which showed great benefits of mass-flowering crops, especially oilseed rape, in terms of subsequent bumble bee densities in seminatural habitats (Westphal et al. 2003, Herrmann et al. 2007, Diekötter et al. 2010, Goulson et al. 2010), deviating from the general assumption that social wild bees do not profit from annual crops because of the short flowering time (Corbet 2000).

In contrast to bumble bees, we did not find a landscape-wide oilseed rape effect on the species richness and abundance of other wild bees. Other wild bee species, most of them of smaller body size, forage in the vicinity of their nesting sites, being more dependent on local conditions and less sensitive to landscape-scale crop structure (Gathmann and Tscharntke 2002). Therefore, solitary bees are more likely to be influenced by intermediate-scale oilseed rape effects, showing increased diversity and abundance in seminatural grasslands adjacent to oilseed rape fields (Holzschuh et al. 2011).

Effects of oilseed rape at the adjacent-field scale

The fruit mass and the seed number per fruit of hawthorn were higher adjacent to oilseed rape fields

than next to cereal fields. Hawthorn flowered simultaneously with oilseed rape, and therefore the adjacent flowering oilseed rape fields might have had a facilitation effect on the reproductive success of hawthorn.

TABLE 2. Final ANCOVA models on the different parameters of pollination success of hawthorn and dog rose flowers available to pollinators in forest edges and in connected and isolated hedges.

Variable	df	F	P
Hawthorn			
Fruit set			NS
Fruit mass			
Adjacent crop type (OSR > cereal)	1, 33	5.41	0.026
Seed number/fruit			
Adjacent crop type (OSR > cereal)	1, 33	4.26	0.047
Dog rose			
Fruit set			
Conspecific flower abundance (patch)	1, 30	8.35	0.007
Fruit mass			NS
Seed number/fruit			
Habitat	2, 29	3.34	0.049
Aborted seed number/fruit			NS

Notes: Explanatory variables of the full model are as for Table 1. Conspecific flower abundance (patch) is the abundance of conspecific flowers in the observation patch.
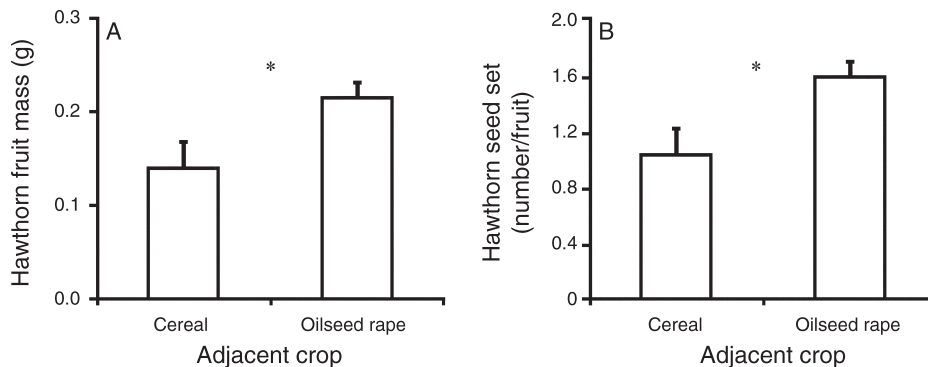
Fig. 3. (A) Fruit mass and (B) seed number per fruit of hawthorn in relation to crop type (oilseed rape vs. wheat); values are means + SE. Asterisks indicate significant differences at $P < 0.05$.

Hanley et al. (2011) described a higher bumble bee visitation rate to wildflowers in field margins next to mass-flowering bean fields than adjacent to wheat, suggesting that mass-flowering crops facilitate pollinator spillover into adjacent seminatural habitats during their flowering. However, Hanley et al. (2011) did not study the effects of pollinators on plant reproduction. Our study supports Cussans et al. (2010) in finding positive local effects of oilseed rape during its flowering on the reproductive success of a simultaneously flowering wild plant species. Adjacent oilseed rape in flower might have served as a highly attractive magnet plant as is known from abundantly flowering invasive plants, which can also facilitate the visitation and pollination of neighboring native plants by attracting high numbers of pollinators (Bartomeus et al. 2008).

Considering the functionally adequate spatial scale and further differences between pollinator guilds, however, is important to assess the effects of oilseed rape on the reproductive success of co-flowering plants. In contrast to the positive field-scale effects of oilseed rape on directly adjacent hawthorn, Holzschuh et al. (2011) found a negative landscape-scale effect of oilseed rape on cowslip (Primula veris). During mass flowering, oilseed rape might have a positive (magnet) effect on pollinator abundance and pollination success at the adjacent-field scale, but a negative (competitive) effect at the landscape scale. Whether pollinators and pollinator-dependent plants are influenced on the adjacent-field or the landscape scales might depend on the mobility of the pollinators. Therefore, wild plant species like cowslip, which are mainly pollinated by large, mobile bumble bees, might be affected at landscape scales, while plant species like hawthorn, which are also frequently visited by small solitary bees, are rather affected at smaller scales.

We found higher fruit mass, more seeds, and fewer aborted seeds in fruits from open than from bagged branches; however, the higher abundance of pollinators in hedges and forest edges adjacent to oilseed rape fields did not translate to increased fruit and/or seed production of dog rose. Spillover of arthropods subsidized by a managed agricultural land to the adjacent seminatural habitats has already been described in the case of insect natural enemies (Rand et al. 2006) and pollinators (Hanley et al. 2011). However, a positive effect on pollinators of a wild plant flowering after the mass-flowering crop has not been described yet. Hanley et al. (2011) compared bumble bee activity along hedgerow transects adjacent to mass-flowering field bean and wheat fields, but they found no difference two weeks after bean flowering.

Local effects of hedge plant flowers

The conspecific flower abundance had a positive effect on the fruit set of dog rose, which might be attributed to increased flower visitation by the higher abundance of flower-visiting insects. The higher number of flowers and the amount of available pollen might increase fruit set, showing a facilitation effect (Bjerknes et al. 2007). However, differences in pollinator generalization levels and the prevalence of main pollinators result in species-specific response of the focal shrub species to the co-flowering neighborhood (Lazaro et al. 2009). The self-compatible flowers of dog rose set fruits even without pollinators, while the self-incompatible flowers of hawthorn set no fruits without insect pollination.

CONCLUSION

We conclude that considering the right scale is important when effects of mass-flowering crops on pollinators and pollination success of wild plants are evaluated. At the landscape scale, flowering of oilseed rape resulted in a lower number of bumble bees in the hedges. However, at the adjacent-field scale, pollinators show crop–noncrop spillover. Our results on hawthorn suggest that the consequent higher number of bees might increase the pollination success of wild plants in the neighborhood hedges and forest edges. However, this has to be tested for other plant species. After the flowering of oilseed rape, the value of wildflower resources in hedges and forest edges for foraging bees increases, as demonstrated by their general spillover

from the oilseed rape fields and increase in these still flower-rich, seminatural habitats.

The total area planted in oilseed rape has considerably increased due to the increased demand for bioenergy. Understanding the effects of this mass-flowering crop on biodiversity is therefore critical. Given the potential impacts of oilseed rape on co-flowering wild plants, high amounts of mass-flowering fields in the landscape around nature reserves are critical for the conservation of wild species. Future agri-environmental management should consider the pros and cons in evaluations of landscape-scale configuration and composition of crops. Food resources provided by mass-flowering crops should be most beneficial for landscape-wide enhancement of wild bee populations, if seminatural habitats are available, providing (1) nesting resources and (2) continuously flowering resources during the season. The enhancement of the diversity of flowering plants is recommended due to reasonable hedge management in the form of diverse shrub communities and wide grassy margins along the hedges and forest edges.

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SUPPLEMENTAL MATERIAL

Appendix A

Location of the sample sites around the city of Göttingen, Germany, using Google Earth (*Ecological Archives* A023-094-A1).

Appendix B

Dependent and explanatory variables of the ANCOVAs in the analyses of the two distinct data sets (*Ecological Archives* A023-094-A2).

Appendix C

The abundance of bumble bees and other wild bees sampled by pan traps in May and June 2009 in the studied forest edges and in connected and isolated hedges (*Ecological Archives* A023-094-A3).

Appendix D

Results of the paired *t* tests on the effects of treatment (bagged vs. open branches) on the different parameters of pollination success of hawthorn (*Crataegus* spp.) and dog rose (*Rosa canina*) flowers in forest edges and in connected and isolated hedges (*Ecological Archives* A023-094-A4).

Appendix E

Different parameters of pollination success on the bagged branches and flowers open for pollinator insects on hawthorn (*Crataegus* spp.) and dog rose (*Rosa canina*) shrubs (*Ecological Archives* A023-094-A5).