Annual dynamics of wild bee densities: attractiveness and productivity effects of oilseed rape

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Abstract. Mass-flowering crops may affect long-term population dynamics, but effects on pollinators have never been studied across several years. We monitored wild bees in oilseed rape fields in 16 landscapes in Germany in two consecutive years. Effects on bee densities of landscape oilseed rape cover in the years of monitoring and in the previous years were evaluated with landscape data from three consecutive years. We fit empirical data to a mechanistic model to provide estimates for oilseed rape attractiveness and its effect on bee productivity in comparison to the rest of the landscape, and we evaluated consequences for pollinator densities in consecutive years. Our results show that high oilseed rape cover in the previous year enhances current densities of wild bees (except for bumble bees). Moreover, we show a strong attractiveness and dilution on (i.e., decreasing bee densities with increasing landscape oilseed rape cover) oilseed rape for bees during flowering in the current year, modifying the effect of the previous year’s oilseed rape cover in the case of wild bees (excluding Bombus). As long as other factors such as nesting sites or natural enemies do not limit bee reproduction, our findings suggest long-term positive effects of mass-flowering crops on bee populations, at least for non-Bombus generalists, which possibly help to maintain crop pollination services even when crop area increases. Similar effects are conceivable for other organisms providing ecosystem services in annual crops and should be considered in future studies.

Key words: agricultural landscapes; bee productivity; crop pollination services; landscape modeling; mass-flowering crops; oilseed rape; population dynamics; temporal spillover; Würzburg, Germany.

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. Thus, “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 of resource pulses may be 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 such pulses into individual or colony 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. Oilseed rape is one of these mass-flowering crops cultivated worldwide, increasingly so for biofuel production (Diekötter et al. 2013, Stanley and Stout 2013). It is questionable, however, whether such crops have any use for pollinators due to their short flowering period (Corbet 2000). Moreover, bees do not exclusively feed on oilseed rape during its flowering (Holzschuh et al. 2013, Stanley and Stout 2014); they additionally rely on other landscape types, such as seminatural habitats, which predominantly provide nesting sites, but also alternative feeding resources. Two important spatiotemporal effects of mass-flowering crops might affect bee densities at the landscape scale. (1) During the flowering of mass-flowering crops, local densities of bees decrease with increasing cover of the mass-flowering crop on the landscape scale (“dilution effect”; Holzschuh et al. 2011, Kovács-Hostyánszki et al. 2013). (2) After the flowering period, a high cover of the mass-flowering crop results in elevated 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 (West-
phal et al. 2009, Hanley et al. 2011, Riedinger et al. 2014) and previous results on the production of offspring in the same year, that would be necessary to carry over effects between years, are mixed. Although sexual reproduction of bumble bees was not enhanced by early mass-flowering crops (Westphal et al. 2009), wild bees other than Bombus (hereafter referred to as “other wild bees”) benefitted (Jauker et al. 2012, Holzschuh et al. 2013).

A previous study showed interannual effects of oilseed rape on the density of pollen beetle parasitoids (Thies et al. 2008), indicating the importance of temporal crop dynamics for ecosystem services such as biocontrol. However, we are not aware of any study investigating interannual effects of mass-flowering crops on bees, although this type of temporal spillover might strongly affect pollinator densities and associated crop pollination services in agricultural landscapes. In our study, we focused on two possible features of oilseed rape that might influence pollinator density and distribution in consecutive years. (1) A higher relative attractiveness of oilseed rape as a feeding resource compared to other available landscape resources should result in a landscape-scale dilution of pollinators (Fig. 1A). (2) A higher per-area effect of oilseed rape on bee productivity (hereafter referred to as “productivity effect of oilseed rape”) compared to the rest of the landscape should result in a positive dependence of current bee densities on the cover of oilseed rape in the previous year (Fig. 1B). More specifically, we consider here the relative area cultivated with oilseed rape in a landscape with a given radius around study sites (“cover of oilseed rape”). In a three-year study, we investigated the interannual effects of oilseed rape on bees in 16 different study areas. We evaluated effects of the cover of oilseed rape in the previous year, and the change of these effects on bumble bee and other wild bee densities by the current cover of oilseed rape. To account for the combined effects of the cover of oilseed rape in the previous year and the current year (hereafter referred to as “year of pollinator sampling”) and by additionally considering oilseed rape attractiveness and productivity effects compared to the rest of the landscape, we developed a simple mechanistic model that allows tests of the following hypotheses. (1) A higher attractiveness of oilseed rape compared to the rest of the landscape reduces the local density of bees on oilseed rape fields during the mass-flowering period when the cover of oilseed rape in the year of pollinator sampling increases. (2) A higher cover of oilseed rape in the previous year increases pollinator densities on oilseed rape fields in the year of pollinator sampling due to a higher productivity effect of oilseed rape compared to the rest of the landscape. (3) Productivity effects of oilseed rape are less pronounced for bumble bees, for which reproduction of sexuals occurs mainly after flowering of oilseed rape (von Hagen and Aichhorn 2003), than for other wild bees that reproduce during the flowering period of oilseed rape.

![Fig. 1.](image-url)
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 such as oilseed rape. Within the study region of 27 × 70 km, we selected 16 study areas. Due to crop rotation, we selected different oilseed rape fields in 2011 and 2012, within each study area. In any study year, fields investigated were at least 2 km apart. All fields were situated in intensively used agricultural landscapes dominated by cereal fields intermingled with small remnants of seminatural habitats, SNH. Overall for the study period, cover was 11.0% ± 6.7% SNH (mean ± SD; range 2.0–28.5% SNH) in a 1-km buffer around the field edges; in 2011, cover was 11.4% ± 6.6% SNH (2.0–24.7%); in 2012, cover was 10.5% ± 7.1% SNH (range 2.3–28.5%). Field size averaged 2.0 ± 0.2 ha (mean ± SD; range 0.5–5.4 ha). Fields were fertilized usually with mineral fertilizers and regularly treated with insecticides. Around each study field we calculated the cover of oilseed rape in a 1-km buffer around the edge of the field (including the field) for the year of pollinator sampling and the previous year in each study year, i.e., the calculated cover always refers to the field where we sampled pollinators in the study year. 1-km landscape buffers were chosen based on previous studies showing responses of bumble bees and other wild bees on oilseed rape cover at this special scale (Holzschuh et al. 2011, Jauker et al. 2012). The land-use data were provided by the Bavarian State Ministry of Nutrition, Agriculture and Forestry for 2010, 2011, and 2012 and the geographical information system ArcMap version 9.3.1 (ESRI 2008) was used to calculate the cover of oilseed rape. Oilseed rape cover around study fields in the two years of pollinator sampling (\(p_i\)) ranged from 0.5% to 19.8% (6.4% ± 5.0%, mean ± SD; for 2011, 0.5–19.8%; 7.0% ± 5.7%; for 2012, 0.9–16.3%; 5.7% ± 4.3%) and in the two years previous to pollinator sampling (\(p_0\)) from 0.3% to 18.3% in the landscape sectors (6.4% ± 4.6%; for 2010, 0.9–13.2%; 6.2% ± 4.0%; for 2011, 0.3–18.3%; 6.5% ± 5.3%). The Pearson correlation coefficient (\(r\)) between the cover of oilseed rape in the year of pollinator sampling and the previous year was 0.54 (n = 32; variance inflation factor VIF = 1.4; for 2011, \(r = 0.76,\) VIF = 2.4; for 2012, \(r = 0.38,\) VIF = 1.2). VIF < 3 is used as a cutoff value for noncritical collinearity (Zuur et al. 2009).

Pollinator observation

Bumble bees (no managed colonies present) and other wild bees were sampled under standardized weather conditions (temperatures above 17°C, no rain, few or no clouds, low wind speeds) between 09:00 and 18:00 hours, while slowly walking along transects and recording flower visitors only. Bumble bees were identified in the field to species level (except for B. terrestris/B. lucorum agg.). Other wild bees were collected for species identification in the lab. Additionally, we recorded honey bees (all from managed colonies) on the fields, but due to their dependence on bee-keeping practices, they were not further analyzed.

Bees were observed during flowering of oilseed rape on two 150-m² transects on each oilseed rape field. One

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**FIG. 2.** (A) Theoretical relationship between \(f\), the proportion of bees foraging in OSR (oilseed rape), and \(p_i\), the current cover of OSR, for different values of \(a\) (parameter of attractiveness for OSR, where \(a = \{1, \pm 1.5, \pm 2, \pm 3, \pm 5, \pm 8, \pm 10\}\)). (B) Theoretical relationship between \(N_{osr}\) (local bee density) and \(p_i\) (current cover of OSR) for values of \(a\) used in (A). Where \(a < 1\) and \(f > p_i\), there is a preference for OSR; for \(a > 1\) and \(f < p_i\), there is avoidance of OSR; for \(a = 1\) and \(f = p_i\), there is a random distribution of foraging bees with no observable preference or avoidance.
transect was located on the outer crop line parallelising the edge of the field, the other one was parallel to the first, located in the center of the field with a distance of ~20 m to the first, and at least 20 m distance to the other edges. A transect had a width of 1 m and a length of 150 m. Transects were sampled two times on different days and at different times of the day, each time for 15 minutes, in late April/early May 2011 and 2012 when fields were in full bloom. We present pooled densities (i.e., pollinator abundances) for 600 m² (two sampling rounds × two 150 m² transects) 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 between the cover of oilseed rape and bee densities and to allow for estimating meaningful model parameters (Hobbs and Hilborn 2006). For the focus of our study, a mechanistic model should reflect two critical (potential) effects of oilseed rape on bees: (1) the attractiveness of oilseed rape for foraging bees and (2) the per-area effect of oilseed rape on bee productivity (“productivity effect”) in comparison to the rest of the landscape. For this reason, we start with the presentation of a simple mechanistic model of the potentially relevant processes affecting bee densities. Both oilseed rape and other habitats, especially seminatural 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 on bee productivities \( b_{\text{OSR}} \) and \( b_{L} \) (reproduction rates) of oilseed rape and the rest of the landscape (average of all other landscape types), respectively, such that the number of bees produced in year 0 is

\[
B = b_{\text{OSR}}p_{0}A + b_{L}(1-p_{0})A
\]

with \( p_{0} \) being the fraction of the landscape covered with oilseed rape in year 0 and \( A \) being the size of the landscape sector. For the sake of simplicity, we restrict our approach to linear effects of area \( A \).

Oilseed rape will have a favorable impact on bee production if \( b_{\text{OSR}} \) is (significantly) greater than \( b_{L} \). In this case, a comparatively high cover of oilseed rape in the landscape in the previous year should lead to a comparatively high population size of bees in the (beginning) of the year of pollinator sampling and thereby comparatively high pollinator densities on oilseed rape fields (for constant cover of oilseed rape in the two consecutive years, hypothesis 2; Fig. 1B). Negative effects of landscape types are indicated if one of the coefficients is negative.

During mass-flowering of oilseed rape (year \( t = 1 \)) a proportion, \( f \), of the total number of bees, \( B \), will forage in oilseed rape fields (of size \( p_{1}A \)), resulting in a local bee density per area unit of

\[
N_{\text{OSR}} = \frac{fB}{p_{1}A} = \frac{f(b_{\text{OSR}}p_{0} + b_{L}(1-p_{0}))}{p_{1}}.
\]

We will refer to \( f \) as the “concentration factor.” If \( f \geq p_{1} \), more bees than expected by chance forage within oilseed rape fields. In contrast, \( f < p_{1} \) would indicate avoidance of oilseed rape fields and \( f = p_{1} \) would indicate no preference. For obvious reasons, concentration factor \( f \) is strictly bounded in its range. Specifically, it must be 0 when \( p_{1} = 0 \) (no oilseed rape at all) and 1 if \( p_{1} = 1 \) (exclusively oilseed rape). However, \( f \) will also depend on the relative “attractiveness” of oilseed rape fields for bees compared to other landscape elements. This relationship can be accounted for by a simple monotonic function for \( f \) in dependence of \( p_{1} \):

\[
f = \frac{(p_{1} + 1)^{2} - 1}{2^{2} - 1}
\]

with \( a \) as the parameter of attractiveness (see Fig. 2A). If \( a = 1 \), the bees are indiscriminate and \( f \) increases linearly with the cover \( p_{1} \) of oilseed rape. Note that in this case, \( f = p_{1} \) and

<table>
<thead>
<tr>
<th>Wild bee model</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>wAICc</th>
</tr>
</thead>
<tbody>
<tr>
<td>M4: ( b_{\text{OSR}} \neq b_{L}, a \neq 1 ) year effect (( s = s_{\text{OSR}} = s_{L} ))</td>
<td>262.2</td>
<td>0.0</td>
<td>0.412</td>
</tr>
<tr>
<td>M6: ( b_{\text{OSR}} \neq b_{L}, a \neq 1 ) year effect for ( b_{L} ) only (( s = s_{\text{OSR}} = s_{L} ))</td>
<td>262.6</td>
<td>0.4</td>
<td>0.336</td>
</tr>
<tr>
<td>M5: ( b = b_{\text{OSR}} = b_{L}, a \neq 1 ) year effect (( s = s_{\text{OSR}} = s_{L} ))</td>
<td>264.0</td>
<td>1.8</td>
<td>0.168</td>
</tr>
<tr>
<td>M8: ( b_{\text{OSR}} \neq b_{L}, a \neq 1 ) independent effect of year for ( b_{\text{OSR}} ) only (( s_{\text{OSR}}, b_{L}(s_{L}) ))</td>
<td>265.5</td>
<td>3.3</td>
<td>0.078</td>
</tr>
<tr>
<td>M9: ( b_{\text{OSR}} \neq b_{L}, a \neq 1 ) independent effect of year for ( b_{\text{OSR}} ) only (( s_{\text{OSR}}, b_{L}(s_{L}) ))</td>
<td>270.4</td>
<td>8.2</td>
<td>0.007</td>
</tr>
<tr>
<td>M7: ( b_{\text{OSR}} \neq b_{L}, a \neq 1 ) year effect for ( b_{\text{OSR}} ) only (( s_{\text{OSR}} ))</td>
<td>282.9</td>
<td>20.7</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>M1: ( b_{\text{OSR}} = b_{L}, a \neq 1 ), no year effect</td>
<td>328.8</td>
<td>66.6</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>M2: ( b = b_{\text{OSR}} = b_{L}, a \neq 1 ), no year effect</td>
<td>336.6</td>
<td>74.4</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>M3: ( b_{\text{OSR}} \neq b_{L}, a = 1 ), no year effect</td>
<td>371.1</td>
<td>108.9</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

Notes: Model rank is based on corrected Akaike information criterion (AICc) shown with ΔAICc, AICc weights (wAICc), and their parameter estimates ± 95% confidence intervals. Parameters not fitted in a model are marked “nf.” Models are sorted by confidence intervals. Parameters not fitted in a model are marked “nf.” Models are sorted by

TABLE 1. Comparison of different models tested for density prediction of wild bees (excluding Bombus) on oilseed rape fields.
p1 thus cancels out from Eq. 2. Oilseed rape is then neither more nor less attractive to bees than the rest of the landscape. In contrast, a < 1 (!) indicates a preference for oilseed rape (hypothesis 1; Figs. 1A, Fig. 2B) and a > 1 indicates avoidance (Fig. 2B). A value of a < 1 is also the precondition that a higher cover of oilseed rape in the landscape in the year of pollinator sampling reduces the local density of bees on oilseed rape fields during the mass-flowering period (Fig. 1A, III and IV). Note that a response in bee numbers to the availability of oilseed rape flowering period (Fig. 1A, III and IV). Note that a would only be attracted to forage (and not nest-found) a “migration” effect should not inasmuch bees would only be attracted to forage (and not nest-founding) could also modify the response in bee numbers to the current cover of oilseed rape (p1). Such an effect would, however, mitigate the “dilution effect” incorporated in the model and our estimates of this effect would tend to be conservative.

With Eqs. 2 and 3, we thus provide a model that combines the effect on bee densities of oilseed rape in the previous year and in the year of pollinator sampling and that distinguishes between the effect of oilseed rape on (relative) bee productivity (parameter bOSR vs. bL) and the attractiveness of oilseed rape fields as foraging area (parameter a).

Estimating model parameters

The model is nonlinear with respect to p1 and we estimated bOSR, bL, and a by a maximum likelihood approach (Hilborn and Mangel 1997). We assume bee densities to be Poisson distributed with NOSR (Eq. 2) being a predictor of mean bee density (density of bumble bees and of other wild bees, respectively). Additionally, we allow for annual effects by multiplying the parameters with year-specific factors sOSR, sL, and s0, reflecting, for example, different weather conditions in the two study years, before entering the model for the second pair of years. The parameters bOSR, bL, a (and year-specific factors, respectively) must be estimated in a way that log-likelihood (LL) is maximized:

\[
\text{LL} = \sum_{i=1}^{n} \log \left( \frac{\lambda_{i}^{N_{OSR,i}}}{N_{OSR,i}^{N_{OSR,i}}} \right)
\]

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

\[
\lambda_{i} = \frac{(p_{1,i} + 1)^{s_{0,i}a} - 1}{2^{s_{0,i}a}} - \frac{(s_{OSR,i}b_{OSR,i}p_{0,i} + s_{L,i}b_{L}(1 - p_{0,i}))}{p_{1,i}}
\]

or one of eight model simplifications of Eq. 4 that we test in our modeling optimization. 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 ≤ n'), parameters sOSR, bOSR, s0, and sL are equal to 1. In the second study year (i > n'), parameters sOSR, bOSR, sL, and s0 take constant values estimated by the model. Model simplifications included various combinations with a = 1 (same attractiveness for oilseed rape and the rest of the landscape), bOSR = bL (same productivity effect of oilseed rape and the rest of the landscape), sOSR = sL = s0 = 1 (no effect from year), and sOSR = sL (same year-specific productivity effect of oilseed rape and the rest of the landscape; see full model specifications in Appendix A: Table A1).

We restrict NOSR to values equal or greater than 0. Parameter values are estimated with the function optim() in R version 2.15.1 (R Development Core Team 2012) by applying the default Nelder and Mead algorithm; these values are 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 oilseed rape fields, we recorded 153 bumble bees (six species) and 273 other wild bees (40 species) in four sampling rounds undertaken in two years during the mass-flowering period (13.3 ± 10.2 bees per site and
year, mean ± SD; minimum 1 bee, maximum 40 bees per site and year). A complete list of pollinator species is given in Appendix B: Table B1.

For other wild bees, the estimated parameters from the two best models (Table 1) indicated that oilseed rape is considerably more attractive than the surrounding landscape (a < 1). Inserting the value from the best model of a = −27.21 in Eq. 3 for a cover of oilseed rape of 10% reveals that 93% of all other wild bees in the landscape concentrate on oilseed rape, compared to only 10% if a = 1. Thus, the local density of other wild bees on oilseed rape fields is higher when the cover of oilseed rape in the year of pollinator sampling is comparatively low (5%; Fig. 3A) than when it is comparatively high (10%; Fig. 3A). Moreover, the two best models yield a higher effect on bee productivity of oilseed rape

FIG. 3. (A) Relationship between percent cover of oilseed rape (OSR) in the previous year (p0) and density of wild bees (excluding 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 1) and the corresponding model equation (Appendix A: Table A1) for specific values (p1 = 5% or 10%) of the cover of current OSR in the year of pollinator sampling (p1). (B) Comparison of the estimated model parameters b_{OSR} (per-area bee productivity of oilseed rape) and b_L (per-area bee productivity of the rest of the landscape) for the best model (Table 1) for densities of wild bees other than Bombus; error bars are 95% confidence intervals. (C) Relationship between percent cover of OSR in the previous year (p0) and bumble bee (Bombus) density on 32 OSR fields in two years (16 in each year). Fitted lines are calculated with the estimated parameters of the best model (Table 2) and the corresponding model equation (Appendix A: Table A1) for specific values (p1 = 5% or 10%) of the cover of current OSR in the year of pollinator sampling. Symbols are as in (A). In all panels, study year 2011 is shown in black and study year 2012 in gray.
Thus, local densities of other wild bees on oilseed rape fields increased with increasing cover of oilseed rape in the previous year (best model, Fig. 3A; second best, Appendix C: Fig. C1B). In 2012, the densities of other wild bees on oilseed rape fields were in general higher than in 2011, as indicated by the two best models containing the year-specific parameters $s$, and $s_L$, respectively.

For bumble bees, the productivity effect of oilseed rape equals that of the rest of the landscape ($h_{OSR} = h_L$) in the two best models (Table 2). Nonetheless, the parameter $a < 1$ in these models indicated that oilseed rape is also more attractive for bumble bees as a foraging area than the rest of the landscape. Inserting the value from the best model of $a = -24.74$ in Eq. 3 for a cover of oilseed rape of 10% reveals that 91% of all bumble bees in the landscape concentrate on oilseed rape, compared to only 10% if $a = 1$. Similar to the results for other wild bees, the local density of bumble bees on oilseed rape fields was consequently higher, when the cover of oilseed rape in the year of pollinator sampling was comparatively low (5%; Fig. 3C) than when it was comparatively high (10%; Fig. 3C). However, the cover of oilseed rape in the previous year had no effect on current bumble bee densities, indicating that oilseed rape had little effect on bumble bee productivity and therefore on forager densities in the next year (Fig. 3C; second-best in Appendix C: Fig. C2).

The relationships between fitted data from our models and observed data are shown in Appendix C: Fig. C3.

**DISCUSSION**

Our study provides the first evidence for interannual long-term effects of mass-flowering crops on bee densities. Densities of other wild bees (excluding *Bombus*) that increased with increasing relative landscape-scale cover of oilseed rape in the previous year. The per-area effect of oilseed rape on bee productivity is, according to the best model, about six times larger than that of the rest of the landscape. In particular, solitary bees that are primarily active during the flowering of oilseed rape were previously shown to benefit from the resource boost and to produce more offspring during the flowering of oilseed rape measured by abundances in nests (Jauker et al. 2012, Holzschuh et al. 2013). We now show the positive effect of oilseed rape on forager densities in mass-flowering crops in the next season. Moreover, we focused not on one study species only, as in the two previous studies, but on the entire community of wild bees that is active during the flowering of oilseed rape. The benefit of oilseed rape for bee productivity may even overcome previously shown drawbacks, e.g., related to an increased parasite load near oilseed rape fields after the mass-flowering period (Jauker et al. 2012), so that there is a net gain of other wild bees across the season. Such effects on population density may apply not only to the previously studied solitary bee species *Osmia bicornis*, which made up only 4% of all individuals using oilseed rape in our study, but also to other polylectic species with an early activity peak, such as several species of the genera *Andrena* and *Lasigosphaera* (Le Fèon et al. 2013, Stanley and Stout 2013). However, of the 40 species recorded on oilseed rape in the two study years, 31 species remained active after the flowering of oilseed rape and effects may be more important for bee species that have a shorter activity period more or less in parallel to the flowering of oilseed rape (nine of 40 species were recorded only during oilseed rape flowering; V. Riedinger, A. Holzschuh, and I. Steffan-Derwenter, unpublished data).

Importantly, the local bee densities depended not only on the availability of oilseed rape in the previous year but also on oilseed rape in the year of pollinator sampling, which can be explained by the high relative attractiveness ($a < 1$) of oilseed rape in comparison to other landscape features. Although bee densities increased with increasing cover of oilseed rape in the previous year, bee densities decreased with increasing cover of oilseed rape in the year of pollinator sampling. This decline in local bee densities can be interpreted as a transient dilution effect (Tscharntke et al. 2012), which occurs when the bees present in the landscape (produced in the previous year) spread over an increased area of oilseed rape flowering in the landscape in the current year. The dilution is highest for comparatively high covers of oilseed rape and can result in decreased bee densities in oilseed rape fields (Holzschuh et al. 2011) and also in seminatural habitats (Kovács-Hostýnszki et al. 2013). Our model explains that a higher relative attractiveness of oilseed rape is a precondition for an observable dilution effect.

High bee densities can increase the yield in oilseed rape (Steffan-Dewenter 2003, Mänd et al. 2010). Increasing oilseed rape cover has a positive effect on bee abundances and thus ecosystem services in the future. However, more distinctively, increasing oilseed rape cover creates a dilution effect in the current year that may reduce pollination. For example, wild bee densities (excluding *Bombus*) in 2012 were 21% higher when the cover of oilseed rape in the previous year was 10% instead of 5% (at constantly 10% cover of oilseed rape in the year of pollinator sampling). In contrast, wild bee densities (excluding *Bombus*) in 2012 were 59% higher when the cover of oilseed rape in the year of pollinator sampling was 5% instead of 10% (at constantly 10% cover of oilseed rape in the previous year). Together with varying pollinator populations, pollination services also may vary over time (Rader and Howlett 2012). From a management perspective, it might be reasonable to keep the cover of oilseed rape rather constant at moderate levels across consecutive
years to stabilize pollination services. Thereby, farmers could benefit from higher productivity of bees induced by oilseed rape on the one hand, but mitigate dilution effects on the other hand. From the conservation perspective, one should be more interested in the positive effect on landscape-level bee populations induced by oilseed rape in previous years. Yet, this holds only if enough food and especially nesting sites are available for the increased population to capitalize on in consecutive years: The positive effect from previous-year oilseed rape could, in fact, be nonlinear (and weak) if bee population growth were to become limited by, e.g., the availability of nest sites (primarily in seminatural habitats), population regulation by natural enemies, or limited egg supply. This reasoning may become especially important when oilseed rape cover goes beyond our relatively “low” maximum cover of 20%. In fact, the model could easily be modified to incorporate such nonlinear effects. However, as our (limited) data show no evidence of a nonlinear effect, we here prefer the simpler version. Moreover, the increased densities of species that benefitted from oilseed rape may change bee communities during the rest of the year in various directions (Diekötter et al. 2010, 2013). Additionally, the use of oilseed rape for promoting pollinators has to be viewed under the light of heavy pesticide application on this crop, e.g., of neonicotinoids (Goulson 2013).

In general, population dynamics of solitary bees are little understood because long-term studies are rare (Steffan-Dewenter and Schiele 2008, Franzén and Nilsson 2013). The obvious effect of the study year on parameter estimates in our best models suggests that various factors such as nesting sites, weather, or natural enemies (Steffan-Dewenter and Schiele 2008) may affect densities, which makes it difficult to predict long-term influences of changing availability of mass-flowering crops on pollinator dynamics. Previous studies on interannual population dynamics directly considered the change in the cover of the productive habitat between years in addition to its absolute fractions, $p_0$ and $p_1$ (Thies et al. 2008, Zhao et al. 2013). Our approach is based on productivity/attractiveness effects (each only depending on $p_0$ or $p_1$, respectively). However, because productivity and attractiveness affect bee densities in a multiplicative way, our full model also includes the interaction of the independent variables.

Positive effects of oilseed rape on bee productivity seem not to emerge for bumble bees; there was no gain in bumble bee densities with increasing cover of oilseed rape in the previous year. Oilseed rape was nonetheless very attractive to bumble bees, which led also to dilution effects. This is in accordance with Westphal et al. (2009), who showed that oilseed rape supports colony growth but not the production of sexuals, which would be necessary to carry over productivity benefits into the next season. Because bumble bees react on a colony level, a precondition of our model is that a high forager density in the year of sampling is the consequence of more hibernating young queens and resulting higher colony densities that send more foragers to the observed oilseed rape fields. The production of sexuals in bumble bees typically does not start before midsummer, i.e., weeks after flowering of oilseed rape has 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 oilseed rape (Westphal et al. 2003, Herrmann et al. 2007), is necessary to collect the food for sexuals later (Schmid-Hempel and Schmid-Hempel 1998), there is also a need for enough pollen and nectar supply at the time of production of larger male and young queen larvae (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, oilseed rape is highly attractive, also due to lack of many alternatives early in spring, yet its availability is brief 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 seminatural habitats, that potentially provide continuous forage resources and nesting sites

### Table 2. Comparison of different models tested for density prediction of bumble bees (*Bombus*) on oilseed rape fields.

<table>
<thead>
<tr>
<th>Model</th>
<th>$b_{OSR} = h_L, a \ne 1$, no year effect</th>
<th>$b_{OSR} = h_L, a \ne 1$, year effect</th>
<th>$b_{OSR} = h_L, a \ne 1$, independent year effect for $b_{OSR}$</th>
<th>$b_{OSR} = h_L, a \ne 1$, independent year effect for $b_{OSR}$, $b_L$</th>
<th>$b_{OSR} = h_L, a \ne 1$, independent year effect for $b_{OSR} (s_{OSR})$, $b_L (s_L)$</th>
<th>$b_{OSR} = h_L, a \ne 1$, independent year effect for $b_{OSR} (s_{OSR})$, $b_L (s_L)$, $a (s_a)$</th>
<th>$b_{OSR} = h_L$, $a = 1$, no year effect</th>
<th>AICc</th>
<th>$\Delta$AICc</th>
<th>$w$AICc</th>
</tr>
</thead>
<tbody>
<tr>
<td>M2</td>
<td>$b_{OSR} = h_L, a \ne 1$, no year effect</td>
<td>179.0</td>
<td>0.0</td>
<td>0.343</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>M5</td>
<td>$b_{OSR} = h_L, a \ne 1$, year effect</td>
<td>179.3</td>
<td>0.4</td>
<td>0.284</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>M1</td>
<td>$b_{OSR} = h_L, a \ne 1$, no year effect</td>
<td>184.1</td>
<td>2.4</td>
<td>0.102</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>M6</td>
<td>$b_{OSR} = h_L, a \ne 1$, year effect</td>
<td>181.6</td>
<td>2.6</td>
<td>0.090</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>M4</td>
<td>$b_{OSR} = h_L, a \ne 1$, year effect</td>
<td>182.0</td>
<td>3.0</td>
<td>0.077</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>M8</td>
<td>$b_{OSR} = h_L, a \ne 1$, independent year effect for $b_{OSR}$</td>
<td>182.2</td>
<td>3.2</td>
<td>0.067</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>M7</td>
<td>$b_{OSR} = h_L, a \ne 1$, year effect</td>
<td>184.1</td>
<td>5.1</td>
<td>0.027</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>M9</td>
<td>$b_{OSR} = h_L, a \ne 1$, independent year effect for $b_{OSR} (s_{OSR})$, $b_L (s_L)$</td>
<td>185.9</td>
<td>6.9</td>
<td>0.010</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>M3</td>
<td>$b_{OSR} = h_L, a = 1$, no year effect</td>
<td>195.6</td>
<td>16.6</td>
<td>&lt;0.001</td>
<td></td>
<td></td>
<td></td>
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</tr>
</tbody>
</table>

**Notes:** Model rank is based on corrected Akaike information criterion (AICc), shown with $\Delta$AICc, AICc weights, and their parameter estimates $\pm 95\%$ confidence intervals. Parameters not fitted in a model are marked “nl.” Models are sorted by increasing AICc (best model at the top). Parameters are as identified in Table 1. The two models at the top of the table (M2 and M5) are the best and second-best, respectively, and are depicted in Fig. 3C and Appendix C: Fig. C2. Equations for models M1–M9 are in Appendix A: Table A1.
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at the same time, 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 following year. Interannual spillover of bees as a long-term effect that is suggested by our results may be more relevant for pollinators that produce sexuals during the period of mass-flowering (Jauker et al. 2012). Moreover, local bee densities during the flowering of oilseed rape seem to be less influenced by long-term effects from the oilseed rape availability in the previous year than by transient effects, e.g., dilution, within the year of pollinator sampling. Our results on interannual spillover give only a first clue as to 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 on pollinators, reveals the complex interactions on different spatial and temporal scales that influence pollinators.

In general, interannual 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. Together with our results, these studies show that interannual crop dynamics can influence a broad range of ecosystem services, e.g., pollination or biocontrol, or disservices like herbivory. Future research should include these long-term effects to understand and predict densities and distribution of organisms in agricultural landscapes and the ecosystem services that they provide, as well as to develop new strategies for conservation management.

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Table 2. Extended.

Model parameters

<table>
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<tr>
<th>b_OS</th>
<th>b_L</th>
<th>s_OS</th>
<th>s_L</th>
<th>a</th>
<th>s_a</th>
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<tr>
<td>0.34 ± 0.07</td>
<td>0.34 ± 0.07</td>
<td>nf</td>
<td>0.79 ± 0.13</td>
<td>0.79 ± 0.13</td>
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<tr>
<td>0.38 ± 0.08</td>
<td>0.38 ± 0.08</td>
<td>0.79 ± 0.13</td>
<td>0.79 ± 0.13</td>
<td>0.79 ± 0.13</td>
<td>nf</td>
</tr>
<tr>
<td>0.25 ± 0.73</td>
<td>0.35 ± 0.12</td>
<td>nf</td>
<td>0.75 ± 0.15</td>
<td>0.75 ± 0.15</td>
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<td>0.55 ± 0.68</td>
<td>0.36 ± 0.11</td>
<td>nf</td>
<td>20.37 ± 1.67</td>
<td>20.37 ± 1.67</td>
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<tr>
<td>0.42 ± 0.81</td>
<td>0.37 ± 0.12</td>
<td>19.83 ± 59.32</td>
<td>19.83 ± 59.32</td>
<td>19.83 ± 59.32</td>
<td>nf</td>
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<tr>
<td>0.07 ± 0.20</td>
<td>0.36 ± 0.08</td>
<td>0.79 ± 0.13</td>
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<td>0.79 ± 0.13</td>
<td>nf</td>
</tr>
<tr>
<td>−0.004 ± 0.09</td>
<td>0.37 ± 0.09</td>
<td>20.37 ± 10.52</td>
<td>20.37 ± 10.52</td>
<td>20.37 ± 10.52</td>
<td>nf</td>
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<tr>
<td>0.42 ± 0.33</td>
<td>0.37 ± 0.10</td>
<td>2.93 ± 2.37</td>
<td>2.93 ± 2.37</td>
<td>2.93 ± 2.37</td>
<td>nf</td>
</tr>
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<td>−16.35 ± 6.59</td>
<td>6.22 ± 0.67</td>
<td>nf</td>
<td>a = 1</td>
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</table>
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SUPPLEMENTAL MATERIAL

Ecological Archives
Appendices A–C are available online: http://dx.doi.org/10.1890/14-1124.1.sm