

# Crop pollination services: Complementary resource use by social vs solitary bees facing crops with contrasting flower supply

Svenja Bänsch<sup>1,2</sup>  | Teja Tschardtke<sup>1</sup>  | Doreen Gabriel<sup>3</sup>  | Catrin Westphal<sup>2</sup> 

<sup>1</sup>Agroecology, Department Crop Sciences, University of Göttingen, Göttingen, Germany

<sup>2</sup>Functional Agrobiodiversity, Department Crop Sciences, University of Göttingen, Göttingen, Germany

<sup>3</sup>Institute of Crop and Soil Science, Julius Kühn-Institut (JKI), Federal Research Centre for Cultivated Plants, Braunschweig, Germany

## Correspondence

Svenja Bänsch  
Email: svenja.baensch@agr.uni-goettingen.de

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## Abstract

1. Many farmers are facing high economic risks if pollinator declines continue or temporal and spatial variation in wild bee communities cause reduced pollination services. Co-flowering crops might compete for pollinators, while they also might facilitate the delivery of pollination services. This rarely studied topic is of particular interest with respect to the foraging decisions of bees from different functional groups and when more sparsely and mass-flowering crops are in bloom at the same time.
2. The abundance of honey bees, bumble bees and solitary bees in strawberry fields was quantified with transect walks along a gradient of oilseed rape (OSR) availability (product of OSR land cover and temporally changing OSR flower cover). We established a pollination experiment with pollination treatments (open-, wind- and self-pollination) to study the effects of insect pollination on strawberry fruit weight and quality.
3. Changes in OSR availability exhibited contrasting effects on social versus solitary bees in strawberry fields. Bumble bees and honey bees were less abundant in strawberry fields when OSR availability was high, whereas solitary bees were facilitated. With more strawberry flowers, we found more bees in general.
4. When flowers were open-pollinated, they resulted in heavier fruits with better commercial grades compared to wind- and self-pollinated flowers. A higher bee abundance enhanced the strawberry fruit weight and quality but depended on flower order and variety.
5. *Synthesis and applications.* Sparsely flowering crops may compete with mass-flowering crops for social bee pollinators, while solitary pollinators in the field might be evenly facilitated. To ensure best fruit weight and quality, it can be beneficial to support bee abundance in the field. While some social and solitary bee species can be managed for pollination services, wild bees, in particular solitary species, should be conserved and promoted for stable crop pollination services in dynamic agricultural landscapes.

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## KEYWORDS

competition, facilitation, flowering phenology, foraging behaviour, fruit quality, mass-flowering crops, oilseed rape, strawberry

## 1 | INTRODUCTION

The increasing global production of pollinator-dependent crops is causing a great demand for pollination services (Aizen & Harder, 2009). Many farmers are prone to high economic risks if pollinator numbers decline (Potts et al., 2016) or temporal and spatial variation in pollinator communities result in reduced pollination services and consequent yield losses (Garibaldi et al., 2011).

The effectiveness of a pollinator community is determined by multiple environmental factors, including competition or facilitation for pollinators among co-flowering plants (Willcox et al., 2017). The temporal and spatial co-occurrence of flowering plants affect the bees' foraging behaviour, their visitation rates and finally crop yields, especially if more sparsely and inconspicuously flowering plants compete with mass-flowering resources (Danner et al., 2017; Grab et al., 2017). To date, the effects of spatiotemporal variation in floral resources on the foraging behaviour of bees from different functional groups, and consequences for crop pollination services have rarely been studied (Danner et al., 2017; Grab et al., 2017).

Highly rewarding mass-flowering resources in the landscape can draw pollinators away from co-flowering plants leading to interactions between those plant species (Magrach et al., 2017). Important mass-flowering crops are, for instance, oilseed rape (OSR; Holzschuh et al., 2016; Westphal et al., 2003) or apple (Grab et al., 2017). Recently, Grab et al. (2017) demonstrated that the overall pollinator abundance in strawberry fields was reduced particularly in landscapes with a high land cover of mass-flowering apple orchards. Similar, large proportions of mass-flowering OSR fields can result in increased competition for pollinators with negative effects on the pollination of wild plants (Holzschuh et al., 2016; Stanley & Stout, 2014). In contrast, facilitative interactions may occur if pollinators are attracted by high densities of mass-flowering resources and they visit adjacent flower resources in the same location as well (Hegland, 2014).

Social bees, in particular honey bees *Apis mellifera* (L.) and bumble bees (*Bombus* spp.), prefer mass-flowering resources to a great extent (Rollin et al., 2013; Westphal et al., 2006). Because of their large foraging distances up to several kilometres they are able to exploit most rewarding resource patches at larger spatial scales than solitary bees (Bänsch, Tschardtke, Ratnieks, et al., 2020; Westphal et al., 2003), which mostly forage within a few hundred meters around their nests (Gathmann & Tschardtke, 2002; Zurbuchen et al., 2010). Within their relatively small foraging ranges, solitary bees exploit both scattered floral resources (Rollin et al., 2013) and mass-flowering crops (Holzschuh et al., 2013).

After mass-flowering, honey bees and bumble bee species spillover (or return) to semi-natural habitats or to more sparsely

flowering crops (Blitzer et al., 2012) where high densities of honey bees may alter the solitary bee communities and their abundance (Lindstrom et al., 2016; Magrach et al., 2017) by spatial displacement of solitary bees (Goulson, 2003; Hudewenz & Klein, 2015). Thus, the phenological sequence of crop flowering can play a major role in explaining indirect competition between different functional groups of pollinators (Kovacs-Hostyanszki et al., 2013; Magrach et al., 2017). However, during peak bloom of mass-flowering crops, solitary bees might benefit from reduced indirect competition for floral resources when social bees are rare in minor rewarding resource patches, for example, by competitive release (González-Varo & Vilà, 2017; Magrach et al., 2017).

Oilseed rape *Brassica napus* (L.) and strawberry (*Fragaria x ananassa* Duch.) are both economically important crops that can benefit from insect pollination and are flowering at the same time in our study regions (central Germany). Insect-pollinated strawberry fruits are usually heavier, have a better commercial grade and a longer shelf life than self- or wind-pollinated fruits (Castle et al., 2019; Klatt et al., 2014). In OSR, seed yield, seed weight and oil content increase when the flowers are pollinated by insects (Bommarco et al., 2012; Stanley et al., 2013).

The aim of our study was to investigate competitive and facilitative interactions among mass-flowering OSR and more sparsely flowering strawberries (see Appendix Figure S1a in Supporting Information) on the foraging behaviour of social versus solitary bees in strawberry fields. Various social and solitary bees are using strawberries and OSR as foraging resources (Wietzke et al., 2018; Appendix Figures S1b–d). Changes in bee foraging behaviour of different functional groups may have significant consequences for the provisioning of pollination services and the strawberry fruit weight and quality. To our knowledge, these indirect interactions and their implications for fruit production have not been studied so far. We focused on OSR availability which takes the phenological and spatial occurrence of OSR into account (product of OSR flower cover and OSR land cover). To develop effective pollinator management schemes for wild but also manageable pollinators, a better understanding of crop pollination is necessary. Especially with regard to the temporal shifts in the foraging behaviour of bees from different functional groups and in co-flowering crops. For this reason, we tested the following hypotheses:

1. Oilseed rape availability affects bees in the strawberry fields differently, as social bees will be withdrawn away from strawberry fields, whereas solitary bees on strawberries increase due to decreasing resource competition and their local orientation in foraging behaviour.
2. Pollination and bee abundances in strawberry fields benefit the strawberry fruit yield and quality.

## 2 | MATERIALS AND METHODS

### 2.1 | Study regions and study sites

The study was conducted on strawberry fields from May to July in 2015. Study sites were chosen in central Germany around the cities Göttingen in Southern Lower Saxony and Kassel in Northern Hesse (map and coordinates in Appendix Figures S2a–c). Eight experimental fields were located in the centre of circular landscapes (radius 1,000 m) along a gradient of OSR land cover and separated by at least 6 km. Experimental strawberry field size was on average 2.5 ha ( $\pm 0.4$  SE [=standard error]) while the size of oilseed rape fields was on average 2.1 ha ( $\pm 0.2$  SE). We chose only strawberry fields on which, among other varieties, Sonata or Honeoye was grown, because these varieties flower simultaneously with OSR and are commonly grown by our cooperating farmers. Although it is known that semi-natural habitats affect bee densities in agricultural landscapes (Ricketts et al., 2008), we did not include them in our analyses since the land cover gradient within 1,000 m was only small (mean  $2.1 \pm 1.4\%$  SE, range from 0.6% to 5.1%).

Oilseed rape availability is the product of OSR land cover at landscape scale and OSR flower cover within the next field to our study fields. We used digital land cover maps (InVeKoS: database of agricultural cropping; <https://www.zi-daten.de/>) that were provided by the agricultural departments of the German states Lower Saxony (Landwirtschaftskammer Niedersachsen, 2015) and Hesse (Landesbetrieb Landwirtschaft Hessen, 2015) to calculate the OSR land cover; that is, the percentage of OSR fields that covered the defined area of a landscape circle within a 1,000 m radius around our experimental fields. We decided upon 1,000 m as it covers the foraging distances of most relevant bee species (Bänsch, Tschardtke, Ratnieks, et al., 2020; Gathmann & Tschardtke, 2002; Zurbuchen et al., 2010). Although honey bees and bumble bees can fly larger distances (Bänsch, Tschardtke, Ratnieks, et al., 2020; Osborne et al., 2008), distances are often below <1,000 m, which has been shown in particular for honey bees in spring (Bänsch, Tschardtke, Ratnieks, et al., 2020). Additionally, we mapped our landscapes to validate the InVeKoS data using ESRI ArcGIS 10.3.1. OSR land cover in our study landscapes ranged from 4.1% to 17.6% (mean  $9.8 \pm 0.8\%$  SE).

Oilseed rape flower cover within the nearest field was visually estimated at each survey as percentage of ground that was covered by flowers within a 2 m<sup>2</sup> square at a scale ranging from 0% to 100% using increments of 5% for different levels of flower cover and 1% for flower cover below 5%. Flower cover of OSR ranged from 1% to 70% (mean  $28.8 \pm 3.0\%$  SE). The flower cover in the square was representative for the field. Due to similar management regimes of the farmers in our regions, OSR flowering was largely synchronized within the landscapes, that is, main bloom was at the same time. Data collection started with the beginning of strawberry bloom, which can differ between the landscapes mainly due to their elevation and microclimatic differences (details on temporal variation in the flower phenology of OSR and strawberry are given in Appendix Figure S3).

### 2.2 | Pollinator abundance

We used standardized transect walks to sample flower-visiting bees in our study fields. Other pollinators such as syrphid fly were observed only in a few isolated cases which is in line with (1.6% non-bee pollinator in strawberry fields; Klatt et al., 2014). Therefore, we focused on bee pollinators and we had four observation periods during the strawberry flowering period in May and June. Flowering of both crops started around the end of April and co-flowering continued for 4–5 weeks depending on the location and weather conditions. Two transects (each 50 × 4 m strawberry rows) were established within the strawberry fields: one at the edge and one inside the field (15 m from edge) to account for edge effects. Each transect lasted 15 min and was conducted between 9 a.m. and 6 p.m. while we visited each field in morning and afternoon hours. Hence, eight transects have been conducted in each strawberry field during the study period. For the observations we chose good weather conditions, that is, days with a minimum temperature of 12°C, no rain, low wind speed and low cloud cover (Westphal et al., 2008). Flower-visiting bees within the transect area were counted and identified to species level in the field or caught with an insect net for later identification in the laboratory. Solitary bees were identified by SB and Frank Creutzburg (JenInsect, Jena, Germany; see species list in Appendix Table S1). Bee individuals that escaped from the insect net were not identified to species level, but their abundance was counted if they could be assigned to one functional group. Bee abundance is quantified as number of individuals per transect.

We assigned the bees to functional groups according to their sociality and level of domestication (i.e. honey bees, bumble bees and solitary bees, Appendix Table S1). However, we found one individual of *Halictus tumulorum* which is thought to be primitively eusocial. Due to its morphological similarity with other solitary bees, we included it in the group of solitary bees for our analyses.

We quantified strawberry flower cover by counting the number of open flowers along two meters of a strawberry row within each transect area (edge and inside of the field separately).

### 2.3 | Pollination experiment

#### 2.3.1 | Fruit weight and commercial grades

To investigate the importance of insect pollination for strawberry fruit quantity and quality, we established a pollination experiment with three treatments (open-, wind- and self-pollination). Open-pollinated flowers were left open to allow access for all flower-visitors as well as for airborne pollen. To exclude only insects, but allow airborne pollen flow, we bagged individual flowers in bags with mesh sizes of 1 mm in the wind-pollination treatment. We used Osmolux bags (Pantek, France), which are permeable for water vapour (<http://www.pantek-france.fr/agriculture.html>), for the self-pollination treatment (exclude insects and airborne pollen; Klatt et al., 2014). All bags were removed after blooming to standardize the fruit ripening.

In total, we had 40 plants per field, 20 plants at the edge and 20 plants in the inside of the strawberry field according to transect location. Five plants per transect location were assigned to the self- and wind-pollinated treatment and 10 plants to the open-pollination treatment. Strawberry flowers can be assigned to different orders according to their temporal occurrence and position on the stalk. One primary flower (first order) usually occur first on the main stalk, followed by two secondary flowers which branch off the main first stalk, and followed by up to four third-order flowers which branch off the second stalks. Generally, higher flower orders produce berries with a reduced size and weight (Free, 1993). For this reason, we included only fruits from 1st to 2nd flower orders. Every strawberry fruit was weighted directly after harvest and categorized into commercial grades with respect to size, shape and colour according to the European Commission (2011). Commercial grades were categorized as G1/E, where we pooled Grade Extra and one, G2 as Grade two and NM for non-marketable fruits.

To investigate the direct effects of bee abundance, pollination treatment, variety and order on strawberry fruit weights and commercial grades, we marked the strawberry flowers that were open during the transect walks which correspond to our measurements of bee abundance at that point in time (see Appendix Table S2). While we have four observation periods for bees in the strawberry fields, we used a subset of three observation periods since the combined data of bee abundance and subsequent fruit yield and quality is only available for three points in time.

## 2.4 | Data analysis

### 2.4.1 | Pollinator abundance

Statistical analyses were done with the software R version 3.3.2 (R Development Core Team, 2016). We analysed the effects of OSR availability on bee abundance with generalized linear mixed effect models using the `GLMMTMB` package (Brooks et al., 2017). Bee abundance (i.e. number of individuals) was included as response variable. Bee functional group (i.e. honey bee, bumble bee, solitary bee), OSR availability, strawberry flower cover and interactions between bee functional group and OSR availability and bee functional group and strawberry flower cover were the explanatory variables. Observation period nested within location of the transect (edge/inside) nested within the study landscape was included as random effect. The effects of transect location on the number of bee individuals per transect of functional bee groups in the strawberry field were tested beforehand and we found no relevant differences in bee abundances between edge and inside. Continuous explanatory variables (i.e. strawberry flower cover and OSR availability) were scaled to a mean of zero and a standard deviation of 1 to improve convergence of the models. We found no significant correlations between fixed effects (all  $p > 0.1$ ,  $r$  Pearson  $< 0.1$ ). We fitted

the global model with negative binomial distribution because of overdispersion in the Poisson model. Furthermore, we compared the fit of global models with OSR availability at different spatial scales (i.e. 500 and 1,000 m radius). These global models showed the same patterns and did not differ in their fit ( $\Delta AICc < 2$ ). We conducted subsequent analyses at the 1,000 m scale as this scale comprises most likely the foraging ranges of both solitary and social bees in our study (Bänsch, Tschardtke, Ratnieks, et al., 2020; Gathmann & Tschardtke, 2002; Zurbuchen et al., 2010). We selected the best fitting models based on the multimodel inference approach (Burnham & Anderson, 2002) by fitting candidate models that contained all possible combinations of explanatory variables from the global model (function 'dredge', package `MuMIn`; Barton, 2018). Additionally, appropriateness of model assumptions was assessed by plotting residuals versus fitted values and versus explanatory variables, respectively. We ranked the models by the  $AICc$  and used the Akaike weight ( $w_i$ ) to estimate the probability of the individual models to have the best fit across models (Burnham & Anderson, 2002). All models within  $\Delta AICc$  ( $dAICc$ )  $< 2$  in comparison to the best fitting model were considered to have substantial empirical support and are reported together with the null and the global model. We considered only the best fitting model ( $dAICc = 0$ ) for our pollinator abundance analysis since the  $dAICc$  of all models was above 2 in comparison to the best fitting model. The best fitting model was refitted with restricted maximum likelihood for model interpretation. The relative importance of each explanatory variable was assessed using the sum of Akaike weights ( $\Sigma w_i$ ) over all candidate models that included the respective variables (function 'importance', package `MuMIn`; Barton, 2018). We report effects of variables with  $\Sigma w_i > 0.2$ .

### 2.4.2 | Pollination experiment: Fruit weight and commercial grades

#### *Fruit weight*

The effects of bee abundance and pollination treatment on strawberry fruit weight were analysed using linear mixed effect models (function 'glmmTMB', package `GLMMTMB`; Brooks et al., 2017). We log-transformed strawberry fruit weight to homogenize variances after inspecting residual versus fitted values. The global model was fitted with the fixed effects bee abundance (i.e. number of bee individuals), pollination treatment (open, wind, self), variety (Sonata, Honeoye) and strawberry flower order (1st, 2nd) and following interactions: bee abundance and order, bee abundance and variety, and bee abundance and pollination treatment. The random effects included plant ID nested in observation period nested in location of the transect nested within landscape. We used multimodel inference to select best fitting candidate models. Models were fitted with maximum likelihood for comparison using  $AICc$ . The best models ( $dAICc < 2$  in comparison to the best fitting model) were then refitted with restricted maximum likelihood for

model interpretation. Post-hoc test and 95% confidence intervals were obtained for interpretation (function 'emmeans', package EMMEANS; Lenth, 2017).

#### Commercial grades

We tested the effects of bee abundance, pollination treatment, variety and strawberry flower order, and interactions between bee abundance and order, bee abundance and variety and bee abundance and pollination treatment on fruit quality using cumulative linked mixed models (function 'clmm', package ORDINAL; Christensen, 2018). Commercial grade was used as response variable and the random term was included as described above in the fruit weight section. Again, we used the multimodel inference to select best fitting models.

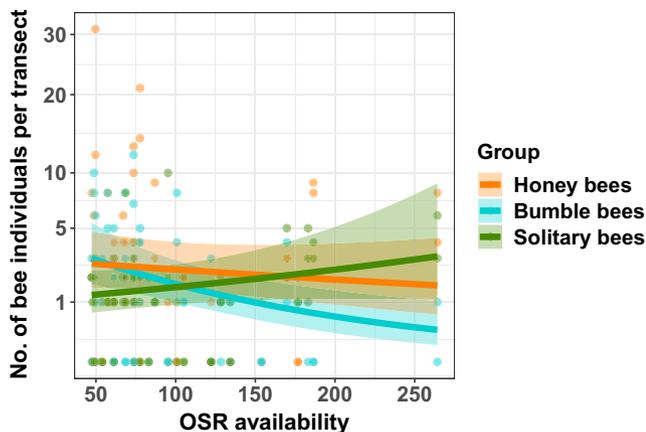
### 3 | RESULTS

In total, we recorded 527 bees visiting strawberry flowers in our experimental field sites. From these, 471 were identified to species level or at least on genus level (except 11 individuals which were only recorded as solitary bees). *Apis mellifera* represented 46.5% of the bee community, followed by bumble bees with 29.9% and solitary

bees with 23.6%. Bumble bees were dominated by *Bombus terrestris* (83.7%) and solitary bee community consisted mainly of *Andrena* species (11 species, 81.1%) with only a few individuals of *Osmia bicornis* and only one individual of *Lasioglossum parvulum* and *H. tumulorum*, respectively (see Appendix Table S1).

#### 3.1 | Effects of OSR on pollinator abundance in strawberry fields

The multimodel inference approach resulted in one best fitting model (Appendix Table S3a; see Table S4a for CIs and model estimates). The interaction between OSR availability and bee functional group was the most important predictor variable as indicated by the high  $\Sigma w_i$  of 0.95 (for all values, see Appendix Table S5). The abundance of honey bees and bumble bees in strawberry fields decreased with increasing OSR availability, while solitary bee abundance increased (Figure 1). The decrease in social bees was 3.7 times higher in bumble bee compared to honey bees. Bumble bees dominated the bee community in strawberry fields at low OSR availability, whereas solitary bees were most prevalent at high OSR availability. Increasing strawberry flower cover resulted in higher bee abundances of all functional groups ( $\Sigma w_i = 0.79$ , Appendix Figure S4).



**FIGURE 1** Effects of oilseed rape (OSR) availability (product of OSR flower cover and OSR land cover) on bee abundance (no. of individuals per transect, shown on a square root scale) in strawberry fields for each functional group. Honey bee and bumble bee abundances decrease with increasing OSR availability while solitary bee abundance increases. We show regression lines and 95% confidence intervals obtained from mixed model estimates [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.com)]

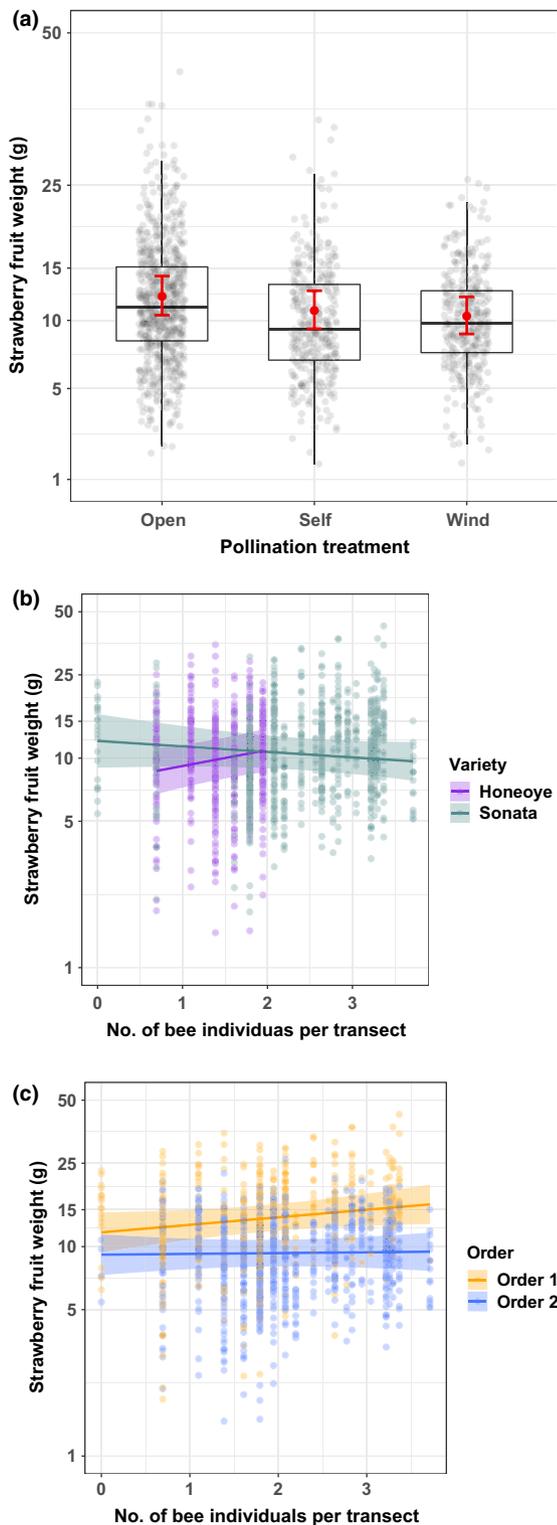
#### 3.2 | Pollination experiment: Fruit weight and commercial grades

##### 3.2.1 | Fruit weight

Two models within a range of  $dAICc < 2$  explained the strawberry fruit weight (Appendix Table S3b, CIs and model estimates are shown in Table S4b). Greatest Akaike weights were found for the main effects of pollination treatment and order ( $\Sigma w_i = 1$  respectively), followed by bee abundance ( $\Sigma w_i = 0.94$ ) and last variety ( $\Sigma w_i = 0.64$ ); however, the direct comparability of the sum of Akaike weight is limited due to the slightly different number of models in which the variable occur (Table 1a). We found high sums of Akaike weight for the two-way interactions between bee abundance and order ( $\Sigma w_i = 0.87$ ) and between bee abundance and variety ( $\Sigma w_i = 0.51$ ). Open-pollinated flowers had 6.9% higher fruit weight than wind-pollinated fruits and 4.8% higher fruit weight than fruits from self-pollinated flowers (Figure 2a). Increasing bee

**TABLE 1** The relative importance of explanatory variables expressed by the sum of Akaike weights ( $\Sigma w_i$ ) for models to explain the effects of the number of bee individuals per transect (bees), pollination treatment (PT), flower order and variety on strawberry fruit weight (a) and commercial grades (b). Number of models in which the variable occur is shown in brackets

Response variable	Bees	PT	Variety	Order	Bees: variety	Bees: order	Bees: PT
(a) Fruit weight (g)	0.95 (27)	1.00 (22)	0.64 (22)	1.00 (22)	0.51 (9)	0.88 (9)	0.22 (9)
(b) Commercial grade	0.68 (27)	1.00 (22)	0.80 (22)	1.00 (22)	0.38 (9)	0.25 (9)	0.25 (9)



**FIGURE 2** (a) Effect of pollination treatment (a) and the number of bee individuals per transect (b, c) on strawberry fruit weight (g; shown on log scale in all figures). Open-pollinated flowers resulted in heavier fruits than self- and wind-pollinated flowers (a). Increasing bee abundance increased strawberry fruit weight from the variety Honeoye but not from Sonata (b). Higher bee abundance promotes strawberry fruit weight from first-order flowers, whereas second-order flowers are less affected (c). We show regression lines and 95% confidence intervals obtained from mixed model estimates. Datapoints are jittered in (a) [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

abundance showed a positive effect on the fruit weight of the variety Honeoye, while this was not observed for the variety Sonata (Figure 2b). A higher bee abundance did particularly benefit the fruit weight of fruits from first-order flowers while second-order flowers were less affected (Figure 2c). In general fruits from second-order flowers had a 10.9% lower fruit weight than fruits from first-order flowers.

### 3.2.2 | Commercial grades

We found five models with substantial empirical support (Appendix Table S3b). The best fitting model ( $dAICc = 0$ ) included the main effects variety, order and pollination treatment with  $\Sigma w_i$  ranging from 0.68 to 1 (see Table 1b for all  $\Sigma w_i$ ). The interactions between bee abundance and variety ( $\Sigma w_i = 0.38$ ), between bee abundance and order ( $\Sigma w_i = 0.25$ ), and bee abundance and pollination treatment ( $\Sigma w_i = 0.25$ ) were included in candidate models within the range of  $dAICc < 2$  (Appendix Table S3b). Fruits of open-pollinated flowers had a high probability of being placed in the best grade (G1/E), while self-pollinated and wind-pollinated flowers were less likely to reach the best grade. The probability of a fruit being assigned to the second grade (G2) was similar for all treatments, while the probability of fruits being assigned to the non-marketable grade (NM) was highest for self-pollinated flowers and lowest for open-pollinated flowers in general (Appendix Figure S5a). Furthermore, we found that bee abundance increased the probability of achieving the best commercial grade in the open-pollinated treatment. Similar patterns were observed for fruits from the self- and wind-pollinated treatments but the effect was lower (Figure S6c). Fruits of the variety Sonata had a higher probability of occurrence of G1/E compared to fruits of the variety Honeoye (Appendix Figure S5b). However, higher bee abundances increased the probability that fruits from the variety Honeoye, but not from Sonata, were assigned to the best commercial grade. As a result, fruits were less likely to be classified in the third commercial grade when bee abundance was high for the variety Honeoye (Appendix Figure S6a). In general, second-order fruits were more likely to receive G1/E compared to first-order flowers (Appendix Figure S5c). The interaction of variety and order with bee abundance showed that a high bee abundance was particularly beneficial for the quality of first-order fruits and the variety Honeoye (Appendix Figure S6b).

## 4 | DISCUSSION

We could demonstrate that bees of different functional groups exhibit trait-based responses to temporal changes in local and landscape-wide resource availability. In contrast to other studies that analysed only landscape effects in terms of OSR land cover (Holzschuh et al., 2013; Westphal et al., 2003), we additionally identified temporal shifts in the flower cover within OSR fields. By multiplying OSR flower and land cover, we calculated an index which represents the temporal OSR flower availability in the surrounding

landscape. We demonstrate that social bees are attracted by mass-flowering resources while solitary wild bees do not react to increased mass-flowering resource availability and keep foraging in more sparsely flowering crops where they provide essential pollination services. Particularly, bumble bees showed a strong decrease in abundance in sparsely flowering strawberry fields when OSR was in full bloom. The bumble bee community consisted mainly of *B. terrestris* (>80%) which is a generalist species and known to prefer mass-flowering resources such as OSR (Walther-Hellwig & Frankl, 2003). Honey bees showed a less steep decrease but their overall density in the landscape depend on beekeeping activities. While large and old forest areas may contain wild honey bee colonies (Requier et al., 2019), only small, disturbed and fragmented forest patches occur in our agricultural landscapes. Thus, honey bees in our study belong to managed colonies. Beekeepers may favour landscapes with many and large OSR fields to increase the honey harvest. Therefore, the density of managed honey bees is likely to be linked to OSR availability (in which measurement OSR land cover is included).

In contrast to honey bees and bumble bees, solitary bees were facilitated in strawberry fields by increasing mass-flowering OSR availability. Lower densities of honey bees and bumble bees may reduce resource competition for solitary bees, thereby promoting their abundances in the fields (Lindstrom et al., 2016). Solitary bees might have spilled over from mass-flowering OSR to sparsely flowering strawberry fields. Similar spillover processes have been observed from mango (Simba et al., 2018) or OSR (Kovacs-Hostyanszki et al., 2013) to natural vegetation. Both crops, OSR and strawberry, can provide pollen and nectar as a reward (Bänsch, Tschartke, Ratnieks, et al., 2020; Knopper et al., 2016; Leidenfrost et al., 2020). It has been shown that the attractiveness of OSR to honey bees and some solitary bee species is higher than the attractiveness of strawberry while the attractiveness of both crops to bumble bees is similar (Knopper et al., 2016). Nevertheless, the amount of pollen and nectar resources provided by OSR at landscape scale is much higher than strawberry (based on the cover).

In general, pollinator facilitation and competition have been rarely studied with respect to interactions between crops including their flowering phenology. Phenological shifts in bees foraging have been shown by Grab et al. (2017) who found that mass-flowering apple blossom in their early and main flowering can decrease bee abundance in strawberry, while bee abundance can be facilitated after peak flowering.

Honey bees made up to almost half of the bee community in our study but relying completely on social bees could cause pollination shortage in crops or other plants which are in bloom at the same time but offer smaller flower resources than mass-flowering crops. Obtaining or promoting greater species diversity, in particular of solitary bees, is likely to ensure (Wietzke et al., 2018) and increase pollination (Hoehn et al., 2008). In other regions and crop types, not only bees but also other pollinators should be considered as they can play a major role in crop pollination as well (Rader et al., 2016). In correspondence with Klatt et al. (2014), who found just 1.6%

non-bee pollinators in strawberry field, we rarely observed non-bee flower-visitors in our study field.

Strawberry flowering showed, in general, positive effects on the bee abundance in strawberry fields. Through targeted variety selection, farmers could provide high flower coverages over a longer period of time to promote bee abundance in the fields. In addition, the energy supply by nectar can be variety dependent and influences the choice of flowers by bees (Abrol, 1992).

In line with Klatt et al. (2014), we found that open-pollination can benefit strawberry fruit weight and quality. As we observed only few non-bee pollinators in our study fields (like Klatt et al. (2014): 1.6% non-bee pollinator), bees are most likely the most important pollinators for strawberries in our regions. As also shown by other studies, higher pollinator abundance can enhance the fruit weight of strawberries (Castle et al., 2019) and many other crops (Garibaldi et al., 2013; Grab et al., 2017). Additionally, we demonstrate that increasing numbers of bees in the field enhanced the probability of fruits being classified in the highest quality grade in the open-pollination treatment. Unexpectedly, we found a similar pattern for self- and wind-pollinated fruits that could be related to random confounding factors we could not control for in our field experiment. However, the effect size was low and hence from minor importance. The advantages of open-pollination can be variety dependent as shown by our results and also by Klatt et al. (2014). In particular, the quality of fruits from the variety Honeoye benefited from a high bee abundance compared to Sonata, which showed weaker responses. Generally, the share of non-marketable fruits was higher in the self- than in the open-pollination treatment. As social versus solitary bees showed contrasting foraging behaviour in strawberry fields due to OSR availability, strawberry flower-visiting bees were abundant during the whole strawberry flowering season. Together, social and solitary bees can provide potential pollination services to strawberry flower throughout the season. Complementarity among pollinators has been mainly described for seasonal changes (Ellis et al., 2016; Pisanty et al., 2014), but not for changes in response to flower phenology of co-flowering crops.

Flower order effects can be explained by the flower biology. Flowers of low order (e.g. first flower order) are larger and have a greater amount of achenes which have to be pollinated to induce fruit growth (Roussos et al., 2009). Hence, fruits from low flower orders have a greater potential to gain higher weights and benefits from pollination.

## 5 | CONCLUSIONS

Pollination services for crops with rather inconspicuous flowering are strongly influenced by the temporal changes in availability of simultaneously mass-flowering crops. Solitary bees in strawberry are promoted with increasing OSR availability while honey bees and bumble bees are pulled away. Continuous pollination services during the flowering of crops with inconspicuous flowering are likely provided

by complementary abundance of social and solitary bees. It has been shown that not only bee pollination in general but also an increasing number of bees in the strawberry fields benefits strawberry fruit weight and quality. While farmers could manage different bee species for pollination services (e.g. *A. mellifera*, *Bombus* species and *Osmia* species; Garibaldi et al., 2017), focus should be the promotion of pollinator-friendly landscapes. This can increase the natural occurrence and diversity of pollinators of different functional groups.

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## AUTHORS' CONTRIBUTIONS

S.B., T.T. and C.W. conceived the study and designed the experiments; S.B. performed the experiments, analysed the data with help from C.W. and D.G. and wrote the first draft of the manuscript; T.T., C.W. and D.G. contributed substantially to revisions of the manuscript and gave final approval for publication.

## DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.q2bvq83h7> (Bänsch, Tschardtke, Gabriel, et al., 2020).

## ORCID

Svenja Bänsch  <https://orcid.org/0000-0001-7332-7213>  
Teja Tschardtke  <https://orcid.org/0000-0002-4482-3178>  
Doreen Gabriel  <https://orcid.org/0000-0003-2504-1987>  
Catrin Westphal  <https://orcid.org/0000-0002-2615-1339>

## REFERENCES

- Abrol, D. P. (1992). Energetics of nectar production in some strawberry cultivars as predictor of floral choice by honeybees. *Journal of Biosciences*, 17, 41–44.
- Aizen, M. A., & Harder, L. D. (2009). The global stock of domesticated honey bees is growing slower than agricultural demand for pollination. *Current Biology*, 19, 915–918. <https://doi.org/10.1016/j.cub.2009.03.071>
- Bänsch, S., Tschardtke, T., Gabriel, D., & Westphal, C. (2020). Data from: Crop pollination services: Complementary resource use by social vs solitary bees facing crops with contrasting flower supply. *Dryad Digital Repository*, <https://doi.org/10.5061/dryad.q2bvq83h7>
- Bänsch, S., Tschardtke, T., Ratnieks, F. L. W., Härtel, S., & Westphal, C. (2020). Foraging of honey bees in agricultural landscapes with changing patterns of flower resources. *Agriculture, Ecosystems and Environment*, 291, 106792. <https://doi.org/10.1016/j.agee.2019.106792>
- Barton, K. (2018). MuMIn: Multi-model inference. R package version 1.40.4. <https://CRAN.R-project.org/package=MuMIn>.
- Blitzer, E. J., Dormann, C. F., Holzschuh, A., Klein, A. M., Rand, T. A., & Tschardtke, T. (2012). Spillover of functionally important organisms between managed and natural habitats. *Agriculture, Ecosystems and Environment*, 146, 34–43. <https://doi.org/10.1016/j.agee.2011.09.005>
- Bommarco, R., Marini, L., & Vaissière, B. E. (2012). Insect pollination enhances seed yield, quality, and market value in oilseed rape. *Oecologia*, 169, 1025–1032. <https://doi.org/10.1007/s00442-012-2271-6>
- Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Mächler, M., & Bolker, B. M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R Journal*, 9(2), 378–400. <https://doi.org/10.3929/ethz-b-000240890>
- Burnham, K., & Anderson, D. (2002). *Model selection and multimodel inference* (2nd ed.). Springer.
- Castle, D., Grass, I., & Westphal, C. (2019). Fruit quantity and quality of strawberries benefit from enhanced pollinator abundance at hedgerows in agricultural landscapes. *Agriculture Ecosystems & Environment*, 275, 14–22. <https://doi.org/10.1016/j.agee.2019.01.003>
- Christensen, R. (2018). *ordinal – Regression models for ordinal data*. R package version 2018.0-25. Retrieved from <https://CRAN.R-project.org/package=ordinal>
- Danner, N., Keller, A., Härtel, S., & Steffan-Dewenter, I. (2017). Honey bee foraging ecology: Season but not landscape diversity shapes the amount and diversity of collected pollen. *PLoS ONE*, 12(8), e0183716. <https://doi.org/10.1371/journal.pone.0183716>
- Ellis, C. R., Feltham, H., Park, K., Hanley, N., & Goulson, D. (2016). Seasonal complementary in pollinators of soft-fruit crops. *Basic and Applied Ecology*, 19, 45–55. <https://doi.org/10.1016/j.baae.2016.11.007>
- European Commission. (2011). *Commission implementing regulations (EU) No. 543/2011*.
- Free, J. B. (1993). *Insect pollination of crops* (2nd ed.). Academic Press London.
- Garibaldi, L. A., Aizen, M. A., Klein, A. M., Cunningham, S. A., & Harder, L. D. (2011). Global growth and stability of agricultural yield decrease with pollinator dependence. *Proceedings of the National Academy of Sciences of the United States of America*, 108(14), 5909–5914. <https://doi.org/10.1073/pnas.1012431108>
- Garibaldi, L. A., Requier, F., Rollin, O., & Andersson, G. K. S. (2017). Towards an integrated species and habitat management of crop pollination. *Current Opinion in Insect Science*, 21, 105–114. <https://doi.org/10.1016/j.cois.2017.05.016>
- Garibaldi, L. A., Steffan-Dewenter, I., Winfree, R., Aizen, M. A., Bommarco, R., Cunningham, S. A., Kremen, C., Carvalheiro, L. G., Harder, L. D., Afik, O., Bartomeus, I., Benjamin, F., Boreux, V., Cariveau, D., Chacoff, N. P., Dudenhöffer, J. H., Freitas, B. M., Ghazoul, J., Greenleaf, S., ... Klein, A. M. (2013). Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *Science*, 339(6127), 1608–1611. <https://doi.org/10.1126/science.1230200>
- Gathmann, A., & Tschardtke, T. (2002). Foraging ranges of solitary bees. *Journal of Animal Ecology*, 71, 757–764. <https://doi.org/10.1046/j.1365-2656.2002.00641.x>
- González-Varo, J. P., & Vilà, M. (2017). Spillover of managed honeybees from mass-flowering crops into natural habitats. *Biological Conservation*, 212, 376–382. <https://doi.org/10.1016/j.biocon.2017.06.018>

- Goulson, D. (2003). Effects of introduced bees on native ecosystems. *Annual Review of Ecology, Evolution, and Systematics*, 34, 1–26. <https://doi.org/10.1146/annurev.ecolsys.34.011802.132355>
- Grab, H., Blitzer, E. J., Danforth, B., Loeb, G., & Poveda, K. (2017). Temporally dependent pollinator competition and facilitation with mass flowering crops affects yield in co-blooming crops. *Scientific Reports*, 7, 45296. <https://doi.org/10.1038/srep45296>
- Hegland, S. J. (2014). Floral neighbourhood effects on pollination success in red clover are scale-dependent. *Functional Ecology*, 28, 561–568. <https://doi.org/10.1111/1365-2435.12223>
- Hoehn, P., Tschartnke, T., Tylanakis, J. M., & Steffan-Dewenter, I. (2008). Functional group diversity of bee pollinators increases crop yield. *Proceedings of the Royal Society B: Biological Sciences*, 275(1648), 2283–2291. <https://doi.org/10.1098/rspb.2008.0405>
- Holzschuh, A., Dainese, M., González-Varo, J. P., Mudri-Stojnić, S., Riedinger, V., Rundlöf, M., Scheper, J., Wickens, J. B., Wickens, V. J., Bommarco, R., Kleijn, D., Potts, S. G., Roberts, S. P. M., Smith, H. G., Vilà, M., Vujić, A., & Steffan-Dewenter, I. (2016). Mass-flowering crops dilute pollinator abundance in agricultural landscapes across Europe. *Ecology Letters*, 19, 1228–1236. <https://doi.org/10.1111/ele.12657>
- Holzschuh, A., Dormann, C. F., Tschartnke, T., & Steffan-Dewenter, I. (2013). Mass-flowering crops enhance wild bee abundance. *Oecologia*, 172, 477–484. <https://doi.org/10.1007/s00442-012-2515-5>
- Hudewenz, A., & Klein, A. (2015). Red mason bees cannot compete with honey bees for floral resources in a cage experiment. *Ecology and Evolution*, 5(21), 5049–5056. <https://doi.org/10.1002/ece3.1762>
- Klatt, B. K., Holzschuh, A., Westphal, C., Clough, Y., Smit, I., Pawelzik, E., & Tschartnke, T. (2014). Bee pollination improves crop quality, shelf life and commercial value. *Proceedings of the Royal Society B: Biological Sciences*, 281(1775), 20132440. <https://doi.org/10.1098/rspb.2013.2440>
- Knopper, L. D., Dan, T., Reisig, D. D., Johnson, J. D., & Bowers, L. M. (2016). Sugar concentration in nectar: A quantitative metric of crop attractiveness for refined pollinator risk assessments. *Pest Management Science*, 72, 1807–1812. <https://doi.org/10.1002/ps.4321>
- Kovacs-Hostyanszki, A., Haenke, S., Batary, P., Jauker, B., Baldi, A., Tschartnke, T., & Holzschuh, A. (2013). Contrasting effects of mass-flowering crops on bee pollination of hedge plants at different spatial and temporal scales. *Ecological Applications*, 23, 1938–1946. <https://doi.org/10.1890/12-2012.1>
- Leidenfrost, R. M., Bänsch, S., Prudnikow, L., Brenig, B., Westphal, C., & Wüschiers, R. (2020). Analyzing the dietary diary of bumble bee. *Frontiers in Plant Science*, 11, 287. <https://doi.org/10.3389/fpls.2020.00287>
- Lenth, R. (2017). emmeans: Estimated marginal means, aka least-squares means. R package version 1.4.8. Retrieved from <https://CRAN.R-project.org/package=emmeans>
- Lindstrom, S. A. M., Herbertsson, L., Rundlof, M., Bommarco, R., & Smith, H. G. (2016). Experimental evidence that honeybees depress wild insect densities in a flowering crop. *Proceedings of the Royal Society B: Biological Sciences*, 283, 20161641. <https://doi.org/10.1098/rspb.2016.1641>
- Magrath, A., González-Varo, J. P., Boiffier, M., Vilà, M., & Bartomeus, I. (2017). Honeybee spillover reshuffles pollinator diets and affects plant reproductive success. *Nature Ecology and Evolution*, 1, 1299–1307. <https://doi.org/10.1038/s41559-017-0249-9>
- Osborne, J. L., Martin, A. P., Carreck, N. L., Swain, J. L., Knight, M. E., Goulson, D., Hale, R. J., & Sanderson, R. A. (2008). Bumblebee flight distance in relation to the forage landscape. *Journal of Animal Ecology*, 77, 406–415. <https://doi.org/10.1111/j.1365-2656.2007.01333.x>
- Pisanty, G., Klein, A. M., & Mandelik, Y. (2014). Do wild bees complement honeybee pollination of confection sunflowers in Israel? *Apidologie*, 45, 235–247. <https://doi.org/10.1007/s13592-013-0242-5>
- Potts, S. G., Imperatriz-Fonseca, V., Ngo, H. T., Aizen, M. A., Biesmeijer, J. C., Breeze, T. D., Dicks, L. V., Garibaldi, L. A., Hill, R., Settele, J., & Vanbergen, A. J. (2016). Safeguarding pollinators and their values to human well-being. *Nature*, 540, 220–229. <https://doi.org/10.1038/nature20588>
- R Development Core Team. (2016). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.
- Rader, R., Bartomeus, I., Garibaldi, L. A., Garratt, M. P. D., Howlett, B. G., Winfree, R., Cunningham, S. A., Mayfield, M. M., Arthur, A. D., Andersson, G. K. S., Bommarco, R., Brittain, C., Carvalheiro, L. G., Chacoff, N. P., Entling, M. H., Foully, B., Freitas, B. M., Gemmill-Herren, B., Ghazoul, J., ... Woyciechowski, M. (2016). Non-bee insects are important contributors to global crop pollination. *PNAS*, 113(1), 146–151. <https://doi.org/10.1073/pnas.1517092112>
- Requier, F., Paillet, Y., Laroche, F., Rutschmann, B., Zhang, J., Lombardi, F., Svoboda, M., & Steffan-Dewenter, I. (2019). Contribution of European forests to safeguard wild honeybee population. *Conservation Letters*, 13, e12693. <https://doi.org/10.1111/conl.12693>
- Ricketts, T. H., Regetz, J., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C., Bogdanski, A., Gemmill-Herren, B., Greenleaf, S. S., Klein, A. M., Mayfield, M. M., Morandin, L. A., Ochieng', A., & Viana, B. F. (2008). Landscape effects on crop pollination services: Are there general patterns? *Ecology Letters*, 11(5), 499–515. <https://doi.org/10.1111/j.1461-0248.2008.01157.x>
- Rollin, O., Bretagnolle, V., Decourtye, A., Aptel, J., Michel, N., Vaissière, B. E., & Henry, M. (2013). Differences of floral resource use between honey bees and wild bees in an intensive farming system. *Agriculture, Ecosystems and Environment*, 179, 78–86. <https://doi.org/10.1016/j.agee.2013.07.007>
- Roussos, P. A., Denaxa, N. K., & Damvakaris, T. (2009). Strawberry fruit quality attributes after application of plant growth stimulating compounds. *Scientia Horticulturae*, 119, 138–146. <https://doi.org/10.1016/j.scienta.2008.07.021>
- Simba, L. D., Foord, S. H., Thébault, E., van Veen, F. J. F., Joseph, G. S., & Seymour, C. L. (2018). Indirect interactions between crops and natural vegetation through flower visitors: The importance of temporal as well as spatial spillover. *Agriculture, Ecosystems & Environment*, 253, 148–156. <https://doi.org/10.1016/j.agee.2017.11.002>
- Stanley, D. A., Gunning, D., & Stout, J. C. (2013). Pollinators and pollination of oilseed rape crops (*Brassica napus* L.) in Ireland: Ecological and economic incentives for pollinator conservation. *Journal of Insect Conservation*, 17, 1181–1189. <https://doi.org/10.1007/s10841-013-9599-z>
- Stanley, D. A., & Stout, J. C. (2014). Pollinator sharing between mass-flowering oilseed rape and co-flowering wild plants: Implications for wild plant pollination. *Plant Ecology*, 215, 315–325. <https://doi.org/10.1007/s11258-014-0301-7>
- Walther-Hellwig, K., & Frankl, R. (2003). Foraging habitats and foraging distances of bumble bees, *Bombus* ssp. (Hym., Apidae), in an agricultural landscape. *Journal of Applied Entomology*, 124, 299–306. <https://doi.org/10.1046/j.1439-0418.2000.00484.x>
- Westphal, C., Bommarco, R., Carré, G., Lamborn, E., Morison, N., Petanidou, T., Potts, S. G., Roberts, S. P. M., Szentgyörgyi, H., Tscheulin, T., Vaissière, B. E., Woyciechowski, M., Biesmeuer, J. C., Kunin, W. E., Settele, J., & Steffan-Dewenter, I. (2008). Measuring bee diversity in different European habitats and biogeographical regions. *Ecological Monographs*, 78, 653–671. <https://doi.org/10.1890/07-1292.1>
- Westphal, C., Steffan-Dewenter, I., & Tschartnke, T. (2003). Mass-flowering crops enhance pollinator densities at a landscape scale. *Ecology Letters*, 6, 961–965. <https://doi.org/10.1046/j.1461-0248.2003.00523.x>
- Westphal, C., Steffan-Dewenter, I., & Tschartnke, T. (2006). Bumblebees experience landscapes at different spatial scales: Possible implications for coexistence. *Oecologia*, 149, 289–300. <https://doi.org/10.1007/s00442-006-0448-6>

- Wietzke, A., Westphal, C., Gras, P., Kraft, M., Pfohl, K., Karlovsky, P., Pawelzik, E., Tschardtke, T., & Smit, I. (2018). Insect pollination as a key factor for strawberry physiology and marketable fruit quality. *Agriculture, Ecosystems and Environment*, 258, 197–204. <https://doi.org/10.1016/j.agee.2018.01.036>
- Willcox, B. K., Aizen, M. A., Cunningham, S. A., Mayfield, M. M., & Rader, R. (2017). Deconstructing pollinator community effectiveness. *Current Opinion in Insect Science*, 21, 98–104. <https://doi.org/10.1016/j.cois.2017.05.012>
- Zurbuchen, A., Landert, L., Klaiber, J., Müller, A., Hein, S., & Dorn, S. (2010). Maximum foraging ranges in solitary bees: Only few individuals have the capability to cover long foraging distances. *Biological Conservation*, 143, 669–676. <https://doi.org/10.1016/j.biocon.2009.12.003>

## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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