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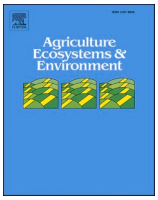

Apple pollination is ensured by wild bees when honey bees are drawn away from orchards by a mass co-flowering crop, oilseed rape

Julia Osterman [a,b,*], Panagiotis Theodorou [a], Rita Radzevičiūtė [a,b,c], Pascal Schnitker [a], Robert J. Paxton [a,d]

[a] Martin-Luther-University of Halle-Wittenberg, General Zoology, Institute for Biology, Hoher Weg 8, 06120, Halle (Saale), Germany
[b] Helmholtz Centre for Environmental Research-UFZ Leipzig, ESCALATE, Department of Computational Landscape Ecology, Permoserstrasse 15, 04318, Leipzig, Germany
[c] Life Sciences Center, Vilnius University, Saulėtekio Al. 7, LT-10223, Vilnius, Lithuania
[d] German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, D-04103, Leipzig, Germany

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ABSTRACT

Over the past two decades, the cultivated area of oilseed rape (*Brassica napus* L. or OSR), a mass-flowering crop, has markedly increased in Europe in response to bioenergy demands. As well as representing a major shift in floral composition across the landscape, mass-flowering OSR may alter pollination services to other simultaneously blooming crops, either decreasing pollination via competition for pollinators or facilitating it via pollinator spill-over. Apple (*Malus domestica* Borkh.) is an economically important, obligately insect-pollinated fruit crop that co-flowers with OSR. Using twelve independent apple orchards varying in the percentage of OSR in the surrounding landscape, we investigated the effect of OSR on pollinators and pollination of co-blooming apple. We collected bees with pan traps and quantified flower visitors during transect walks in both crops and we experimentally measured pollination service provision to apple as fruit and seed set. We confirm that apples are highly dependent on animal pollination and report pollination limitation in our apple orchards. Honey bees were the numerically dominant visitors of apple flowers observed during transect walks. Though their numbers dropped with an increasing percentage of OSR in the landscape, the number of bumble bees visiting apple flowers remained stable and those of other wild bees rose. The pan trapped Shannon diversity of bees remained constant. We could not detect an effect of OSR in the landscape on apple fruit set or seed set, both of which remained stable. Local wild bee populations might compensate for the loss of honey bees in the provision of pollination services in apple, providing especially effective pollination. Our results underscore not only the dominant role of bees in apple pollination but also the importance of wild bee conservation for providing pollination insurance and stability of apple crop yields under changing agricultural policies and cropping practices.

1. Introduction

Insect pollinators, particularly bees, are a critical component of terrestrial ecosystems by pollinating many wild plants (Ollerton et al., 2011) whilst the pollination service provided by insects to crops contributes significantly to global food production and nutritional security (Klein et al., 2007; Potts et al., 2016). However, over the last two decades pollinators have been considered under threat due to reports of both wild and managed pollinator declines (Biesmeijer et al., 2006; Potts et al., 2010; Cameron et al., 2011; Powney et al., 2019; Zattara and Aizen, 2021). Agricultural intensification is thought to be one of the main global change drivers causing shifts in insect pollinator community composition, including a decrease in insect pollinator species richness and abundance (Brown and Paxton, 2009; Potts et al., 2010, 2016; González-Varo et al., 2013; Vanbergen et al., 2013) as well as functional diversity (Woodcock et al., 2014). The perceived decline in insect pollinators threatens the stability of the ecosystem service of pollination and consequently crop production in agro-ecosystems (Potts et al., 2016).

Globally, the total area of cropped land has increased by 23 % from

* Corresponding author at: Martin-Luther-University of Halle-Wittenberg, General Zoology, Institute for Biology, Hoher Weg 8, 06120, Halle (Saale), Germany.
E-mail address: jul.osterman@gmail.com (J. Osterman).

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1961 to 2006 (Aizen et al., 2008) and, over this time, agriculture has become more pollinator-dependent (Aizen et al., 2019). In addition to food crops, there has been an expansion in biofuel production (Banse et al., 2011). In the European Union, oilseed rape (*Brassica napus* L. or OSR) is now the most common oil crop grown for biofuel (Destatis, 2018). For instance, approximately 11 % of total arable land in Germany was used for OSR production in 2016 (Destatis, 2018), a percentage that might fluctuate greatly in the future due to changes in political and agricultural policy e.g. restrictions on the use of plant protection products (e.g. neonicotinoid insecticides; Scott and Bilsborrow, 2018), climate change (e.g. droughts in spring; Pullens et al., 2019) or market forces. OSR is a mass flowering crop with bright yellow flowers that creates a large pulse of flowering resources attractive to insects for its ca. four-week-long blooming period. It can facilitate the pollination of later flowering wild plants (Herbertsson et al., 2017) and crops (Grab et al., 2017), likely by attracting many pollinators to areas with OSR grown in the vicinity. Wild plants co-flowering with OSR can also experience facilitated pollination through pollinator spillover (Kovács-Hostyánszki et al., 2013). Yet there is also the risk that they may suffer reduced pollination through competition for pollinators (Holzschuh et al., 2011; Grab et al., 2017).

While the effects of OSR on bee abundance and pollination services have been shown to vary across spatial and temporal scales (Holzschuh et al., 2011; Kovács-Hostyánszki et al., 2013; Grab et al., 2017; Herbertsson et al., 2017), OSR's impact on bees may also differ across bee taxa (Diekötter et al., 2010; Herbertsson et al., 2017; Bänsch et al., 2020a). For example, the abundance of long-tongued bumble bee species (e.g. *Bombus pascuorum* and *Bombus hortorum*) was found to decrease with increasing OSR in the landscape, while more generalist *Bombus* species increased (Diekötter et al., 2010). Moreover, it has recently been demonstrated that blooming OSR competes with nearby strawberry fields for pollinators in a taxon-specific manner, reducing honey bees and bumble bees at strawberry flowers whilst boosting numbers of other wild bees (Bänsch et al., 2020a). In the USA, strawberry yields are reduced through competition for pollinators when surrounded by co-flowering apple (Grab et al., 2017).

Apple (*Malus domestica* Borkh.) is an important fruit crop, both globally and in Europe (global production in 2014: 84.6 million tonnes; European production in 2014: 17.4 million tonnes; FAOSTAT, 2017). The predominant pollinators of apple flowers are considered to be bees and hoverflies (Delaplane and Mayer, 2000; Klein et al., 2007; Pardo and Borges, 2020). Most apple varieties are highly pollinator-dependent (Free, 1993) and need to receive pollen from a cross-compatible pollinizer cultivar for successful pollination and fruit set (Delaplane and Mayer, 2000). Seed and fruit set in apple orchards have been found to be positively correlated with an increase in wild bee species richness (Mallinger and Gratton, 2015; Blitzer et al., 2016), pollinator functional diversity (Martins et al., 2015), phylogenetic diversity (Grab et al., 2019) and abundance (Martínez-Sastre et al., 2020; Radzevičiūtė et al., 2021), suggesting that wild bees contribute considerably to apple pollination.

OSR and apple flower synchronously in many temperate localities, including Germany, and therefore OSR may impact pollinator communities in apple orchards as well as the pollination of apple. Apple flowers produce less nectar per day (e.g. 0.4−0.6 µl nectar with a sugar concentration between 28.3 % and 36.4 % (Quinet et al., 2016)) than oilseed rape flowers (e.g. 0.9 µl nectar with a sugar concentration of 32.4 % (Carruthers et al., 2017)), which might attract pollinators away from apple orchards if oilseed rape fields are present in the vicinity of an apple orchard. Yet despite the relative abundance and importance of both crops, the extent to which co-flowering OSR facilitates apple pollination or competes with apple for pollinators remains unknown (Pardo and Borges, 2020).

Here we investigated insect pollinator communities in apple orchards and nearby OSR fields as well as quantified apple pollination to understand if OSR competes with apple for flower visitors and affects the provision of pollination services to apple crops. To do so, we used 12 commercial apple orchards with a varying percentage of OSR in the landscape (from 0 % to 30 %) in addressing the following questions: (i) does OSR in the landscape affect the pollinator community in apple orchards and, as a consequence, (ii) does co-blooming OSR impact apple pollination? We hypothesized that OSR is more attractive than apple due to its higher nectar content per flower and therefore that OSR would decrease pollination in adjacent apple orchards.

2. Methods

2.1. Study sites

In spring 2017, we selected 12 independent apple orchards in the south of the federal state of Saxony-Anhalt in Germany, a state dominated by agricultural land (60 %) (locations are highlighted in Fig. 1, coordinates are listed in Table A.1). Orchards differed in the percentage of OSR within the surrounding 1 km from the orchard border, ranging from 0% to 30 % (Table A.1, Fig. 1). Furthermore, we identified the closest OSR field to each apple orchard (mean distance between an OSR field and an apple orchard at sites was 1.1 ± 0.8 km S.D.). The closest distance between apple-OSR sites (i.e. from the closest orchard-field margin of one apple-OSR site to the next apple-OSR site) averaged 31.5 km (± 17.5 km S.D., range: 2.08–69.94 km; see Fig. 1), adequate to ensure their independence (Greenleaf et al., 2007).

We used Mantel tests in the R package *ade4* (Dray et al., 2017) to check for spatial autocorrelation in our data set. There was no significant spatial autocorrelation for bee biodiversity or pollination (as *PSP*, see definition below) across apple orchards ($P > 0.05$). Distances between crops and sites were measured in ArcMap v. 10.5 and within crops using the R statistical software (R Core Team, 2016) with the function *as.dist*.

2.2. Sampling of flying insects and flower visitors

We performed a transect walk of 500 m over 30 min in apple orchards and OSR fields between 10:00 and 15:00 during the full bloom of each crop to quantify flower visitors. In apple orchards, transects ran alongside apple trees used in the pollination experiment (see below) and, in OSR fields, they ran alongside crop plants growing adjacent to pan traps (see below). During transect walks, we recorded all observed flower visitors that made contact with reproductive parts of a flower within 2 m on each side of the transect. Flower visitors observed on transect walks were identified to morpho-group: honey bees (*Apis mellifera*), bumble bees (*Bombus* spp.), other wild bees, Diptera and 'others', which included Lepidoptera and Coleoptera. In downstream analyses, we focused only on the three bee morpho-groups as they represented >95 % of all apple flower visitors (1728 of 1818 total visits, see Table A.2).

In addition, we sampled flying insects in both crops using coloured pan traps (blue, white and yellow) during full apple and OSR bloom (for sampling dates see Table A.1). Pan traps and transect walks differ in the efficiency with which they record flower-visiting insects (O'Connor et al., 2019), hence we used both methods to sample insect communities. For each site and crop, we used nine pan trap sets (three of each colour, diameter 24 cm) mounted on sticks at 70 cm in order to trap insects visiting crop flowers (Tuell and Isaacs, 2009). The pan traps were placed within a crop and at a minimum of 50 m from the orchard or field edge, with a distance of 50 m between a triplet of blue, white and yellow pan traps. In the apple orchards, a pan trap triplet was placed in a triangle with a minimum of 3 m between traps of a triplet; in OSR fields, pan traps were placed directly next to tractor tracks in a row, also with a minimum of 3 m distance between traps in a triplet. Pan traps were 2/3 filled with odour-free soapy water and exposed from 09:00 to 17:00 on the same day of full apple and OSR bloom with warm and calm spring weather. Temperature (°C) and wind speed (m/s) data were collected from the closest weather station to each site (Table A.1). Collected

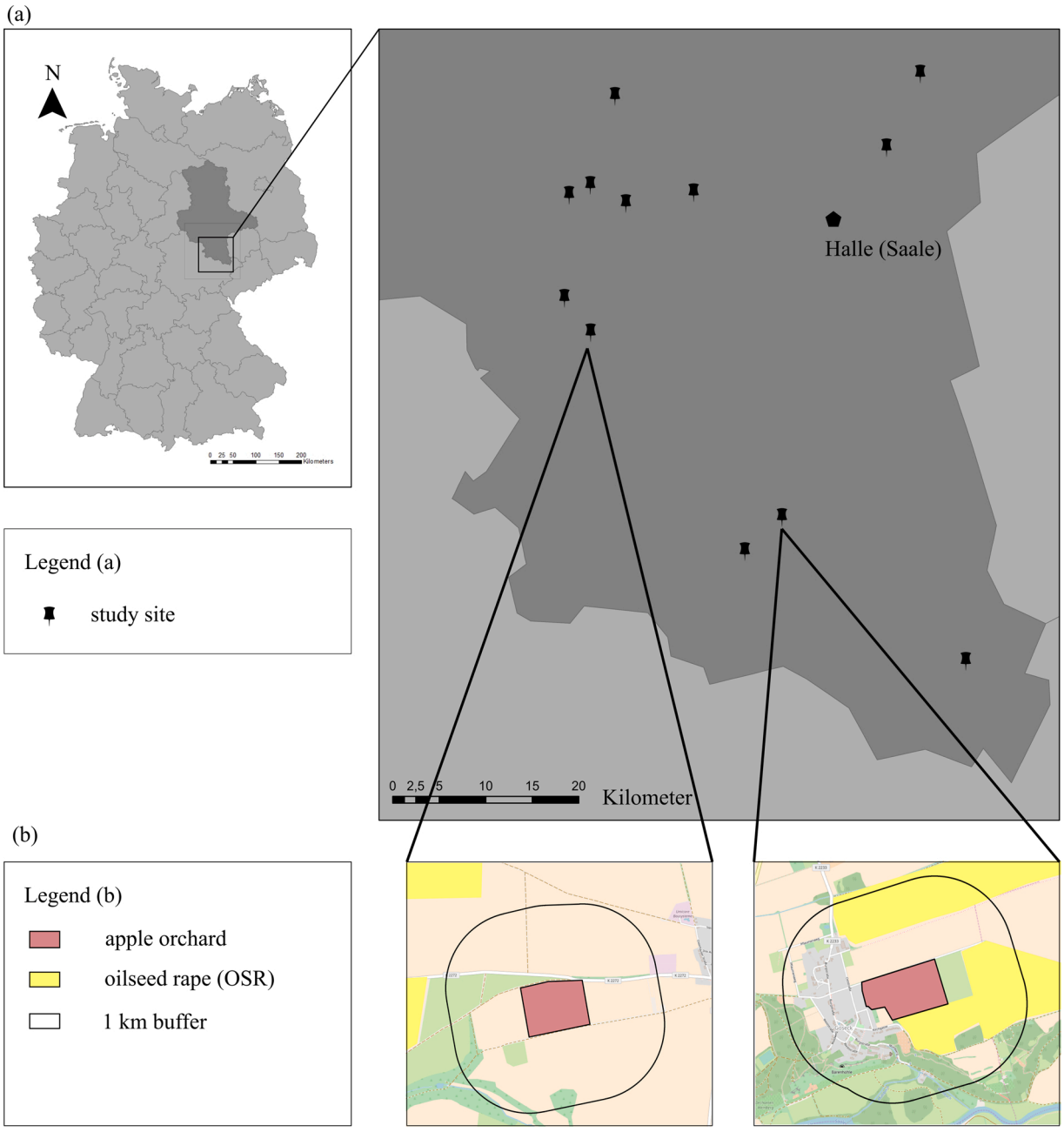

Fig. 1. (a) The twelve study sites in the federal state of Saxony-Anhalt, Germany, in the vicinity of Halle (Saale); (b) examples of two study sites, showing their percentage of oilseed rape (yellow) within a 1000 m radius buffer around each apple orchard (dark red) in 2017.

insects were stored in 70 % ethanol and later identified under a stereomicroscope (Olympus SZX7) using the key of Fauna Helvetica (Amiet, 1996). We identified bees down to genus (members of Halictidae to family; see Table A.2). We did not use finer taxonomic resolution as observed bee richness as well as Shannon bee diversity calculated from genus-level data correlated highly with the same matrics calculated with species-level data in an independent set of apple orchards (see Fig. A.1 and Supplementary Methodology).

2.3. Quantifying pollination service provision in apple orchards

To quantify provision of the ecosystem service of pollination in apple orchards, we performed a pollination experiment at all 12 sites. At 11 sites, we used the apple variety 'Pinova', one of the most common cultivars grown in Saxony-Anhalt. Pinova is self-sterile (S-alleles: S_2S_9) and requires cross-cultivar compatible pollen for successful seed and fruit development (Matsumoto, 2013). At one site (Eisleben Aue) the variety Pinova was absent and therefore we chose 'Elstar', another self-sterile cultivar (S_3S_5) also requiring cross-pollen to set fruit and seed (Matsumoto, 2013). Due to frost damage during Pinova flowering, we excluded two sites (Plößnitz and Spören) from the analysis of pollination service provision, measured as fruit set and seed set.

At each site, we selected one row of trees, centrally located within the orchard. In this row, we chose 45 trees, 15 for each flower treatment, using one flower per tree (bagged, open or hand pollinated), and at least 50 m from the orchard edge adjacent to the nearest OSR field. Inflorescences at a site were on the same side of the tree row to avoid variation in shade and microclimate. At one site, the number of replicates per treatment was higher (Gatterstädt: 20 flowers per treatment). We always used the 'king bud' (i.e. the bud producing the largest, central

flower of an inflorescence, which typically opens first) on a total of 465 inflorescences.

In the insect exclusion treatment (treatment 'bagged': B), we bagged in fine netting (1 mm PVC mesh) the king bud at the closed red-bud stage to prevent pollen deposition by insects, a treatment designed to represent fruit/seed set by wind pollination. King bud flowers assigned to the hand pollination treatment (treatment 'hand': H), designed to represent maximal pollination at an orchard, were manually pollinated with pollen from the freshly dehisced anthers of a flower of a compatible pollinizer from the same orchard. To do so, fresh pollen from a local compatible apple variety was collected and applied to the king bud flower at its most receptive stage (day 2–3 of anthesis) until fully covered with pollen. For pollination of the variety Pinova, we used the variety Elstar as pollinizer, and for the variety Elstar we used 'Idared' (Matsumoto, 2013). Treatment H was undertaken during peak apple bloom at the end of April/early May 2017. After manual pollen application, hand-pollinated flowers were left open for additional insect visitation. The third treatment, reflecting the actual pollination supply to apple flowers at each orchard, received unhindered pollination by insect flower visitors (treatment 'open': O). Flowers used for the three treatments were marked with coloured cable ties and cord so they could be located later to measure the fruit set and to harvest the apples so as to measure the seed set.

Pollination service provision (*PSP*) was calculated at each site using an index which we adapted from Spears' (1983) index of single-visit pollination efficiency (Spears, 1983). We define *PSP* as:

$$PSP = (O - B)/(H - B),$$

where O, B, and H are measured as either fruit set or seed set obtained from each treatment: open, bagged or hand, respectively. Theoretically, *PSP* varies between 0 (zero pollination service provision) and 1 (maximal service provision) to the crop. Note that when a flower did not set fruit, then seed set was also recorded as zero i.e. all flowers of all treatments were included in *PSP* fruit set and *PSP* seed set.

2.4. Measurement of fruit set and seed set

At the beginning of June 2017, we visited each site to record early apple fruit set, prior to commercial thinning. As only the flower arising from the king bud of each inflorescence was used for our experiment, the other apples on the same flower-bearing spur were removed. At the end of August, before commercial harvest (mid to end September for both Pinova and Elstar), all apples from the experiment were collected. Seed set, as a surrogate for fruit quality (Wu et al., 2021), was counted within 5 days of harvest.

2.5. Landscape variables

The percentage of OSR in the surrounding landscape of apple orchards was ground-truthed by determining the crop grown in each field during experiments in 2017 at six radii (250 m, 500 m, 750 m, 1000 m, 1500 m and 2000 m). The percentage of OSR within each of the six radii was then used to identify the scale at which OSR had the most power to explain insect occurrence and pollination service provision. To do so, we correlated the percentage of OSR with a range of measurements of bee biodiversity from the pan trap material and transect walks and of experimental pollination data (*PSP*) at each of our study sites at all five scales. Spearman rank correlation coefficients reached their greatest absolute value at a median radius of 1000 m (Table A.3), which was then chosen as the spatial scale for subsequent analyses. Though honey bees and bumble bees can fly further than this distance, their main foraging ranges are less than 1000 m (Bänsch et al., 2020b).

As land use surrounding a crop is known to impact pollinator biodiversity within the crop (Kennedy et al., 2013; Martin et al., 2019), we accounted for it by quantifying the percentages of semi-natural land (nature reserve, heathland, scrub and flower-rich grassland), farmland (arable land, vineyards, orchards and intensively grazed meadows), urban cover (residential, industrial, commercial and retail) and urban green areas (park, cemetery, allotment and recreation grounds) in the landscape surrounding each apple orchard and each OSR field. Land-use data were extracted from land cover maps (Geofabrik GmbH, Germany) in ArcMap v. 10.5 at the 1000 m radius from the OSR field or orchard border. From these data, we calculated landscape diversity (H_s) for each site and crop type as:

$$H_s = -\sum p_i \times \ln p_i$$

where pi is the proportion of each land cover type i (Krebs, 1989).

2.6. Apple orchard layout and focal field size

Within-field agronomic practices affect pollination service provision (Lundin et al., 2013; Klein et al., 2015; Marini et al., 2015). Apart from the number of insect pollinators visiting flowers (pollinator 'quantity'), suitable pollen from a compatible variety might also limit the successful pollination of an apple flower. Therefore, we additionally mapped, in each orchard, the distance of our experimental array of trees to the nearest suitable pollinizer.

To control for the effect of field size on bee biodiversity in apple orchards and in OSR fields, we additionally estimated focal field sizes of apple orchards and OSR fields with ArcMap v. 10.5.

2.7. Statistical analysis

To investigate the effect of the percentage of OSR in the landscape on the abundance of honey bees, bumble bees and other wild bees measured by transect walks in apple orchards, we used generalised linear models (GLMs) with a negative binomial error structure implemented in the R package *MASS* (Venables and Ripley, 2002). We undertook this analysis for each pollinator group separately. As the presence of honey bee hives in an orchard might influence the number of honey bee flower visitors (Bartholomée et al., 2020) as well as negatively affect the number of wild bees (Herbertsson et al., 2016; Lindström et al., 2016), the presence of honey bee hives was included in all statistical models as a fixed factor (Table A.4). Landscape heterogeneity and apple orchard size were included as explanatory variables. The same statistical approach was used to investigate the effects of apple orchards on insect abundance in OSR fields, measured by transect walks within OSR fields (Table A.5).

While transect walks are well suited to study plant-pollinator associations (Westphal et al., 2008), pan traps are an efficient, cost-effective method for sampling bee diversity excepting honey bees, which they rarely trap (O'Connor et al., 2019). From the 499 and 529 bees caught by pan traps in apple orchards and OSR fields, respectively (see Table A.2), we calculated the Shannon diversity of bees and observed bee richness per site and crop. We then used linear models (LMs) to investigate the effect of the percentage of OSR in the landscape (1000 m radius) and the percentage of apple orchard around OSR fields on observed bee richness and diversity in each crop, with the percentage of OSR/apple orchards in the landscape and the presence of honey bee hives included as fixed factors. Landscape heterogeneity as well as field size were further included as explanatory variables.

We tested the effects of pollination treatment (pollination exclusion (B) *vs.* insect pollination (O) *vs.* pollen supplementation (H)) on fruit set using a generalised linear mixed model (GLMM) with Binomial error stucture. Orchard identity was included as a random factor. A Tukey *post-hoc* comparison was used to test for differences between treatment groups using the R package *multcomp* (Hothorn et al., 2008).

To test the effect of co-flowering OSR in the surrounding 1000 m radius on apple pollination service provision (*PSP*, calculated from both fruit set and seed set), we used LMs. To do so, the percentage of OSR in

the landscape was used as a fixed factor and other potentially important environmental variables i.e. landscape heterogeneity, distance to the next pollinizer tree, the number of honey bees, bumble bees and other wild bees, as well as Shannon diversity of bees were used as further explanatory variables.

R.3.3.1 (R Core Team, 2016) was used for all statistical analyses. For the analyses of transect data, pan trap material and pollination service provision, we used an all-subset automated model selection approach based on the Akaike Information Criterion corrected for small sample size (AICc), with the *dredge* function (R package *MuMIn*; Bartón, 2018) and with a maximum of three predictors to avoid model overfitting. We used a cut-off of ΔAICc of 2 (Burnham and Anderson, 2002) to evaluate model fit (as no more than one model was retained in each analysis, we did not need to employ model averaging). We performed all mixed models using the package *lme4* (Bates et al., 2015). All models were checked for collinearity using variance inflation factors (VIFs) with a cut off value of 5. VIFs were lower than 5 for all predictors, indicating no major effects of collinearity. The residuals of all models were checked for spatial autocorrelation using Moran's I (Paradis et al., 2004). Residuals were not found to be autocorrelated ($P > 0.05$). All model assumptions (residuals normally distributed, homogeneity of variance, linearity, non-overdispersion) were checked visually using the package *LMERConvenienceFunctions* (Tremblay and Ransijn, 2015).

3. Results

3.1. Effects of OSR on bees in apple orchards

During spring 2017, we recorded a total of 1,818 insects during transect walks in apple orchards, of which the majority was bees (1,728, see Table A.2). In pan traps placed in apple orchards, we collected 11,235 insects in total, of which the majority was flies (10,511) and 499 were bees. While species were categorized into morphological groups during the transect walk (e.g. honey bees, bumble bees, other wild bees), bees caught by pan traps were identified to genus level. The bee genus richness ranged from 2 to 5 in the apple orchards. For a summmary for insects collected in apple orchards and OSR fields, see Table A.2.

Honey bees were the dominant flower visitors we observed on transect walks in apple orchards, with a mean of 123 (± 90 S.D.) honey bees out of 152 (± 90 S.D.) total flower visits per transect. Seven out of 12 orchards in our study employed managed honey bees to increase pollination service provision and, as expected, we recorded higher numbers of honey bees on apple flowers during transect walks in orchards with hives (mean 165 ± 93 S.D.) versus in orchards without hives (mean 63 ± 36 S.D.; difference between means; GLM, $t_9 = 3.361$, $P < 0.001$, $R^2_{adj} = 0.25$).

The automated model selection approach to explore the effects of OSR on the abundance of honey bees, bumble bees and other wild bees estimated by transect walks in apple orchards resulted in one best model for each bee taxon (ΔAICc < 2). Our best models included both the percentage of OSR and the presence of honey bee hives as predictors (Supplementary Table A.4). We found a negative effect of the percentage of OSR on the number of honey bees recorded on apple flowers during transect walks (GLM; $Z_9 = -3.071$, $P = 0.002$, $R^2_{adj} = 0.25$, Fig. 2a); honey bee numbers approximately halved across apple orchards with increasing OSR in the vicinity (Fig. 2a). The number of bumble bees recorded on apple flowers was not affected by the percentage of OSR in the landscape (GLM; $Z_9 = 0.897$, $P = 0.370$, $R^2_{adj} = -0.10$, Fig. 2b). The number of wild bees (excluding bumble bees) observed during transect walks in apple orchards increased with the percentage of oilseed rape in the landscape (GLM; $Z_9 = 2.123$, $P = 0.034$, $R^2_{adj} = 0.26$, Fig. 2c), approximately doubling across apple orchards with increasing OSR in the vicinity (Fig. 2c). Both the number of bumble bees and the number of other wild bees in orchards were independent of the presence of honey bee colonies (GLM; bumble bees: $Z_9 = 1.058$, $P = 0.290$, $R^2_{adj} = -0.10$; GLM; other wild bees: $Z_9 = -0.165$, $P = 0.870$, $R^2_{adj} = 0.26$).

The automated model selection approach to explore the effects of OSR on the Shannon diversity and observed bee richness of bees estimated using pan traps in apple orchards resulted in one best model for each dependent variable (ΔAICc < 2). Again, our best models included the percentage of OSR and the presence of honey bee hives (Supplementary Table A.4). Although the percentage of OSR at 1000 m radius was included as predictor in the best model, its effect on the Shannon diversity of bees was non-significant (LM; $t_9 = 0.423$, $P = 0.682$, $R^2_{adj} = -0.11$). We found a marginally negative effect of OSR on observed bee richness in apple orchards (LM; $t_9 = -1.968$, $P = 0.081$, $R^2_{adj} = 0.15$). The presence of honey bee hives did not affect the Shannon diversity or observed richness of bees (LM; Shannon diversity: $t_9 = 0.933$, $P = 0.375$, $R^2_{adj} = -0.11$; observed richness: $t_9 = -0.326$, $P = 0.752$, $R^2_{adj} = 0.15$).

Landscape heterogenity, the proportional cover of apple orchards or the size of apple orchards were not included as predictors in any of the best models for the abundance of bee taxa estimated using transect walks and for the and Shannon diversity and observed richness of bees estimated from pan trap material in apple orchards.

The results of the effects of apple orchards on bee abundances and bee diversity in OSR fields are presented in the Supplementary Results and Supplementary Table A.5.

3.2. Pollination in apple orchards

Bagged apple flowers (treatment B) set only 0.63 ± 0.63 S.E.M. % fruits across all sites, confirming that the studied apple varieties Pinovar and Elstar were obligately insect pollinated. Fruit set was higher for manually cross-pollinated flowers (treatment H; mean = 48.32 ± 4.11 S.E.M. %) compared to open flowers (treatment O; mean = 18.92 ± 6.88 S.E.M. %), suggesting that fruit set was pollen-limited. The three pollination treatments differed significantly from each other (GLMM; $P < 0.05$; Table A.6, Fig. 3).

Pollination service provision (*PSP*), calculated as the final fruit set, varied between –0.18 and 0.92 across sites and, calculated as seed set, it varied between 0.00 and 0.95. These values reflect considerable variation in pollination service provision across apple orchards. Values lower

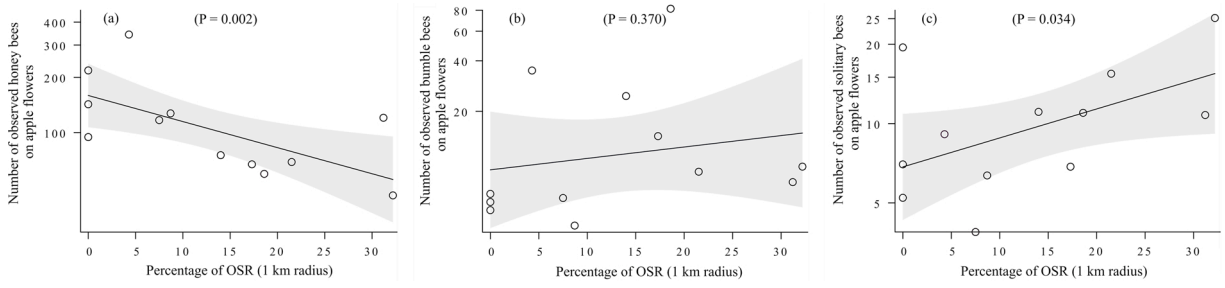

Fig. 2. Relationships between the numbers of a) honey bees, b) bumble bees and c) other wild bees as visitors of apple flowers with the % of oilseed rape within a 1000 m radius of 12 apple orchards. Plotted lines show the predicted relationships, open circles indicate negative binomial generalised linear model estimated means, shaded areas indicate the 95 % confidence intervals, and significance is shown in parentheses (negative binomial GLM).

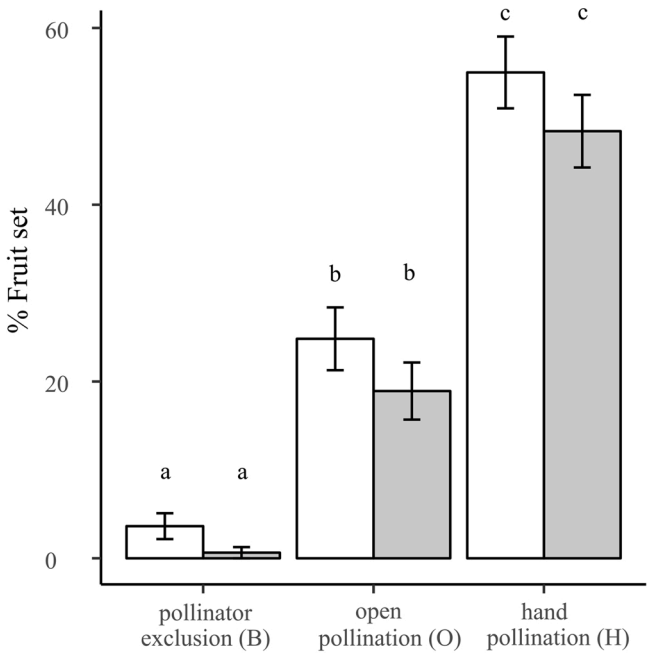

Fig. 3. Effect of pollination treatment on the initial (white) and final (grey) fruit set of apples (mean ± S.E.); means differ significantly across but not within treatments for initial (white) and final (grey) fruit set (GLMM; means with different lower case letters: $P < 0.05$; see Supplementary Table A.6).

than zero likely arose through biological variability at orchards with extremely low pollination service provision (Open < Bagged). *PSP* (fruit set) and *PSP* (seed set, a measure of fruit quality, see Wu et al., 2021) were highly correlated (Pearson correlation: $r = 0.939$, $P < 0.001$, Fig. A.2).

3.3. Effects of oilseed rape on pollination in apple orchards

The automated model selection approach to explore the effects of OSR, landscape heterogeneity, orchard size and bee taxon abundance (i.e. honey bees, bumble bees, other wild bees each treated as separate taxa) on *PSP* resulted in one best model for each of *PSP* (fruit set) and *PSP* (seed set) (ΔAICc < 2). The percentage of OSR was the only predictor included in both best models, yet neither *PSP* (fruit set) nor *PSP* (seed set) was affected by the percentage of oilseed rape in the surrounding 1 km (LM; *PSP* (fruit set): $t_8 = -0.161$, $P = 0.876$, $R^2_{adj} = -0.12$, Fig. 4a; *PSP* (seed set): $t_8 = 0.156$, $P = 0.880$, $R^2_{adj} = -0.12$, Fig. 4b). All other predictors explaining *PSP* (fruit set) and *PSP* (seed set), including abundances of honey bees, bumble bees and wild bees during transect walks, were excluded by our model selection process.

4. Discussion

We found that OSR, a mass flowering crop, attracted honey bees away from apple orchards such that there were fewer honey bees visiting apple flowers in orchards surrounded by OSR fields. Bumble bee densities in apple orchards were not affected and other wild bees even increased in number with increasing cultivation of OSR in the vicinity of apple orchards. Pollination of apple, measured as fruit or seed set, was not affected by the percentage of OSR in the landscape, even though the studied apple orchards were seemingly pollen limited due to lack of pollinators. We conclude that OSR, a mass flowering crop, competes with co-blooming apple for flower-visiting honey bees, but that wild bees may compensate for the loss of honey bees and ensure stability in apple yield. The observed higher wild bee densities in apple orchards surrounded by oilseed rape could be due to their release of competition with honey bees, as observed in other studies (Magrach et al., 2017).

In our study, we demonstrate again the fundamental importance of insect pollination in apple fruit set, as shown by Free (1993) and many others (reviewed in Pardo and Borges, 2020). The increase in fruit set of apple following hand pollination with compatible pollen collected from a pollinizer located in the same orchard suggests that there was a deficit in pollination service provision – as opposed to a deficit in the availability of viable, compatible pollen – in our study apple orchards, as also seen in many other studies in commercial apple orchards (Garratt et al., 2014; Blitzer et al., 2016; Samnegård et al., 2019). Our treatment H remained unbagged after experimental hand pollination and was therefore exposed to the same regime of flower visitation as treatment O (open) flowers. That treatment H consistently set more fruits and seeds than treatment O suggests that O flowers did not suffer from over-pollination (e.g. due to stigmatic clogging) following an excess of flower visits (Rollin and Garibaldi, 2019). Pollination service provision was therefore likely pollinator visitation limited in our orchards.

We documented a trend for decreasing honey bee abundance observed during transect walks in apple orchards with an increasing percentage of OSR in the landscape. Pollinator management by apple orchardists often includes renting honey bee hives to enhance pollination services (Park et al., 2018). This practice might be ineffective if a competing crop like oilseed rape attracts honey bees away from apple flowers. Nevertheless, we still detected an influence of the presence of hives on the number of apple flower visits by honey bees; similarly as in

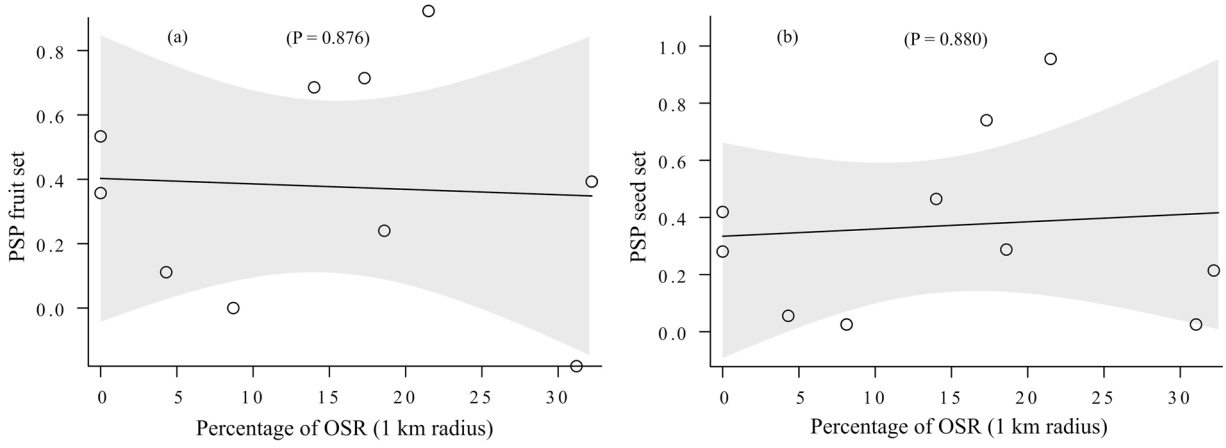

Fig. 4. Relationship between the index of pollination service provision (*PSP*) in apple orchards calculated as a) fruit set or b) seed set versus the percentage of OSR within a 1000 m radius of 10 apple orchards. Plotted lines show the predicted relationships, open circles indicate linear mixed model estimated means, shaded areas indicate the 95 % confidence intervals, and significance is shown in parentheses (LM).

France, where the presence of hives has also been found to be a good predictor of the number of honey bee flower visitors in fruit orchards (e.g. apple, pear, peach, cherry, peach; Bartholomée et al., 2020). Thus, adding honey bee hives to apple orchards still seems to have the effect of increasing honey bee visitation to apple flowers, even if OSR blooms in the vicinity and attracts honey bees from those same apple orchards.

We found that OSR co-flowering in the vicinity of commercial apple orchards seems to compete with apple for honey bee flower visitors. Previous studies have also shown that mass-flowering crops can dilute pollinator abundance in agricultural landscapes (Riedinger et al., 2015; Holzschuh et al., 2016) and co-blooming crops can compete for pollinators (Grab et al., 2017; Bänsch et al., 2020a). Yet these effects can differ between pollinator functional groups, possibly due to taxon-specific differences in pollinator flight ranges (Bänsch et al., 2020a). While we found that OSR reduced the number of flower-visiting honey bees in apple orchards, the number of bumble bees in apple orchards remained constant whilst other wild bees even increased in abundance with more OSR in the landscape, similar to findings by Bänsch et al. (2020a) in strawberry crops co-flowering in the vicinity of OSR. The significant rise in the number of non-*Bombus* wild bees we observed in apple orchards surrounded by OSR fields might be due to reduced competition for floral resources with honey bees (Herbertsson et al., 2016; Lindström et al., 2016).

That the abundance of wild bees observed during transect walks and the Shannon diversity of bees caught by pan traps were not negatively affected by OSR in the landscape might be also a consequence of the short foraging ranges of many wild bee species (Greenleaf et al., 2007); pollinators may exhibit taxon-specific responses to the increase of OSR or other mass flowering crops in the landscape (Stanley and Stout, 2013; Bänsch et al., 2020a). The maximum foraging distances between nesting site and food patch for several solitary bee species has been estimated to be below 150 m (Hofmann et al., 2020), suggesting that local habitat structures and floral resources are more important than large-scale landscape configuration in determining their abundance and, by inference, pollination services they provide (Gathmann and Tscharntke, 2002).

We then sought to test whether the observed competition by co-blooming crops for pollinators thereby hindered pollination service provision to apple. Despite OSR fields apparently drawing honey bees from apple orchards, we could not detect a negative effect of mass flowering OSR on apple yield and apple quality; *PSP* (fruit set) and *PSP* (seed set) in apple orchards remained stable. We hypothesise that, as the percentage of OSR increases in the vicinity of an apple orchard, honey bees are drawn away from apple bloom to OSR flowers, but pollination of apple is compensated by an increase in the number of wild bee visits to apple, thus guaranteeing fruit and seed set in apple orchards. Interestingly, honey bee numbers approximately halved with a rise in OSR across the experiment whereas wild bee numbers doubled, though were always less numerous than honey bees on flowers, suggesting that wild bees might be more effective pollinators or indirectly enhance honey bee pollination services (Brittain et al., 2013). Mallinger and Gratton (2015) found that apple fruit set was not affected by the number of flower-visiting honey bees but significantly increased with the richness of wild bees. In Argentina, apple fruit set was reduced by half in orchards where bumble bees were absent, even when honey bees were present at high densities (Pérez-Méndez et al., 2020). These studies underpin the importance of wild bees in apple pollination. A recent meta-analysis has suggested a non-monotonic relationship between honey bee visitation rate and fruit or seed set, with an optimum of ca. eight-ten honey bee visits per flower (Rollin and Garibaldi, 2019). By attracting honey bees away from apple orchards and reducing the number of apple flower visits by honey bees, the effect on fruit or seed set might not be consequently negative, especially if the number of visits per flower are sufficient for fertilisation of all of an apple flower's 10 ovules (Vicens and Bosch, 2000). Data on the absolute number of flower visitors would be required to test this idea, though two of our datasets: (i) our hand pollination results demonstrating good pollination by cross-compatible pollen acquired in the same orchard and lack of support for over-pollination (e.g. through stigmatic pollen clogging) and (ii) the marked decrease in honey bee visitation of apple flowers with increasing OSR in the vicinity, suggest that our orchards were limited by insufficient pollinator visits. We, therefore, conclude that in our study system the maintenance of pollination in apple orchards surrounded by co-blooming OSR is due to wild bees that compensate for the loss of honey bees to OSR.

Our study underscores the importance of wild bee conservation not only in semi-natural areas (Campbell et al., 2017) but also in agricultural landscapes that increase in pollinator dependency (Aizen et al., 2008, 2019) so as to guarantee crop pollination (Garibaldi et al., 2013). Agri-environmental measures, which have been shown to promote populations of widespread and common wild bee species (Powney et al., 2019), might compensate for the negative consequences of agricultural intensification. Further effort in wild bee conservation should be promoted to ensure stability of apple crop yields. As Nicholson et al. (2019) advocate, to promote a stable pollinator community and meet an increase in pollination demand, future agri-environmental schemes should aim to balance pollination demands in agriculture to avoid competition for pollinators among co-flowering crops and promote wild bee pollinators.

Author Contributions

J.O. participated in the design of the study, the selection of field sites, collected field data, undertook data analysis and drafted the manuscript; P.T. conceived the idea, assisted in the design of the study, analysis of the data and interpretation; R.R. conceived the idea and participated in the design of the study; P.S. was involved in selecting field sites, collecting field data and analysing the data; R.J.P. participated in study design and data interpretation. All authors contributed to revising the manuscript and gave final approval for publication.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.agee.2021.107383.

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