RESEARCH ARTICLE

Early-season mass-flowering crop cover dilutes wild bee abundance and species richness in temperate regions: A quantitative synthesis

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Abstract

1. Pollinators benefit from increasing floral resources in agricultural landscapes, which could be an underexplored co-benefit of mass-flowering crop cultivation. However, the impacts of mass-flowering crops on pollinator communities are complex and appear to be context-dependent, mediated by factors such as crop flowering time and the availability of other flower resources in the landscape. A synthesis of research is needed to develop management recommendations for effective pollinator conservation in agroecosystems.

2. By combining 22 datasets from 13 publications conducted in nine temperate countries (20 European, 2 North American), we investigated if mass-flowering crop flowering time (early or late season), bloom state (during or after crop flowering) and extent of non-crop habitat cover in the landscape moderated the effect of mass-flowering crop cover on wild pollinator abundance and species richness in mass-flowering crop and non-crop habitats.

3. During bloom, wild bee abundance and richness are negatively related to mass-flowering crop cover. Dilution effects were predominant in crop habitats and early in the season, except for bumblebees, which declined with mass-flowering crop cover irrespective of habitat or season. Late in the season and in non-crop

habitats, several of these negative relationships were either absent or reversed. Late-season mass-flowering crop cover is positively related to honeybee abundance in crop habitats and to other bee abundance in non-crop habitats. These results indicate that crop-adapted species, like honeybees, move to forage and concentrate on late-season mass-flowering crops at a time when flower availability in the landscape is limited, potentially alleviating competition for flower resources in non-crop habitats. We found no evidence of pollinators moving from mass-flowering crop to non-crop habitats after crop bloom.

4. *Synthesis and applications*: Our results confirm that increasing early-season mass-flowering crop cover dilutes wild pollinators in crop habitats during bloom. We find that dilution effects were absent late in the season. While mass-flowering crop cultivation alone is unlikely to be sufficient for maintaining pollinators, as part of carefully designed diverse crop rotations or mixtures combined with the preservation of permanent non-crop habitats, it might provide valuable supplementary food resources for pollinators in temperate agroecosystems, particularly later in the season when alternative flower resources are scarce.

KEYWORDS

dilution effects, floral resource, landscape composition, mass-flowering crops, pollinator abundance, pollinator richness, seasonal effects

1 | INTRODUCTION

Global declines in wild insect pollinator species in agroecosystems have sparked major concerns for the restoration of diverse pollinator communities and the conservation of plant diversity (IPBES, 2016). To reverse pollinator declines, international conservation initiatives and policies have been adopted (EU, 2018; IPBES, 2016). While the drivers of pollinator declines are complex, the loss of semi-natural habitats due to agricultural intensification has been identified as a major cause of pollinator decline (Potts et al., 2010). Many pollinators benefit from diverse and/or continuous pollen and nectar resources and nesting or shelter sites in the landscape (Timberlake et al., 2019). In Europe and North America, agri-environmental measures supplementing floral resources are encouraged to sustain pollinator populations in agricultural landscapes (EU, 2018; USDA, 2020). Increasing the availability of floral resources in agricultural landscapes can be achieved by sowing flowering plants or by growing mass-flowering crops. Planted flowers have been shown to benefit the abundance, diversity and reproduction of pollinators (Lowe et al., 2021; Rundlöf et al., 2022), and their implementation is now a common pollinator conservation strategy (EU, 2018; USDA, 2020). By contrast, while the impact of mass-flowering crop cover (i.e. proportion of habitat in a landscape) on pollinator abundance and richness has been investigated within the crop and in the surrounding landscape, the effect of increasing mass-flowering crop cultivation is far from clear and appears context-dependent (Holzschuh et al., 2016; Westphal et al., 2003).

Mass-flowering crops are characterised by seasonal resource pulses of floral abundance (i.e. contracted periods of high flower availability followed by periods of low availability), rather than continuous and diverse resources typical of semi-natural habitats and planted flowers. Together with the increasing cultivation of mass-flowering crops in the early 21st century, such as oilseed rape in Europe and soybeans in North America (FAOSTAT, 2022), there has been a growing interest in assessing the impact of mass-flowering crop cultivation on pollinator communities in the landscape (Supplementary Material, Figure A1). It has been hypothesised that mass-flowering crops support larger and more diverse pollinator communities in the landscape by increasing reproduction or colony growth (Holzschuh et al., 2013; Westphal et al., 2009), attracting flower visitors (*concentration effect*) to the crop and facilitating their movement into nearby habitats (*spillover effect*) (Holzschuh et al., 2016). However, mass-flowering crops can also negatively affect pollinator abundance by exposing individuals to pesticides applied to the crops (Knapp et al., 2022) or via pathogens (Tuerlings et al., 2022), and by resource competition with managed honeybee hives placed nearby crops to boost crop pollination (Page & Williams, 2022). Increasing mass-flowering crop cover in the landscape can lead to pollinator dilution in crops during bloom and potentially alleviate competitive pressure from crop-adapted species in non-crop habitats as these species move away from non-crop habitats to forage in mass-flowering crops (Fijen et al., 2019; Page & Williams, 2022). Concentration and dilution effects will depend on the pollinator taxa preference for mass-flowering crop resources as well as crop flowering time due to phenological variation in the availability and diversity of alternative flower resources in the landscape, constraining pollinators to different extent at different seasons. Pollinator groups show dissimilar responses to mass-flowering crop

cover due to variation in life-history traits and requirements for food and nesting resources (Beyer et al., 2021). As the relative importance and potential interactions between all factors described above remain unclear, the overall effect of mass-flowering crop cover on pollinators has so far been difficult to determine.

The complex and context-dependent effect of mass-flowering crop cover on pollinator abundance and species richness have hampered the understanding of their general impacts and, therefore, it has not been possible to provide clear management recommendations. However, the dilution effects of increasing mass-flowering crop cover on wild pollinator densities were demonstrated across functional groups during crop bloom in a pan-European field study (Holzschuh et al., 2016). In this study, we include three novel aspects in a quantitative synthesis of existing datasets. First, we incorporate a broad range of early (e.g. oilseed rape, apple) and late (e.g. faba bean, red clover) mass-flowering crops to investigate the impact of crop flowering time on wild pollinators. Second, we investigate pollinator species richness to more comprehensively characterise the impact of mass-flowering crop cover on wild pollinator communities. Finally, we explore the effects of mass-flowering crop cover after crop bloom in addition to during bloom to inform the pattern of transitory effects of mass-flowering crop resource pulses.

Specifically, by combining existing datasets, we assessed the impact of mass-flowering crop and non-crop habitat cover in 1-km landscapes on wild pollinator abundance and species richness in crop and non-crop (i.e. grasslands, forests, fallows and uncultivated field borders) habitats and further investigated whether mass-flowering crop seasonality (early flowering in spring vs. late-flowering in summer) and bloom state (during vs. post-crop bloom) affected these relationships. Mass-flowering crops can affect pollinator reproduction and/or survival (i.e. *population-level effects*) and their distribution across landscapes (i.e. *concentration* and *spillover effects*). We focused on within-year dynamics and therefore expected concentration and spillover effects to dominate over population-level effects. However, population-level effects might occur for social bees

such as bumblebees, whose colonies grow within a year. During crop bloom, we expected declines in wild pollinator abundance and richness with increasing mass-flowering crop cover, irrespective of sampling habitat, due to dilution effects (Figure 1a). We expected that increasing mass-flowering crop cover would be positively related to pollinator abundance and richness in non-crop habitats after crop bloom due to spillover from crop to non-crop habitats, as pollinators foraging in mass-flowering crops will change foraging habitat after bloom (Figure 1a; Beyer et al., 2020; Riggi et al., 2021). This effect is expected to be more pronounced for social bees and non-central-place foragers, such as bumblebees and non-bees, respectively, that can reproduce within the season and use flower resources over the season and across the landscape. As flower resource availability in the landscape is often lower later in the season in temperate regions (Scheper et al., 2014; Timberlake et al., 2019), we hypothesised that dilution of pollinator abundance and richness with mass-flowering crop cover would be weaker or absent later in the season (Figure 1b). We expect this outcome because pollinators, particularly mobile social bees and non-central-place foragers, might concentrate in landscapes with late-season mass-flowering crops and spillover from early-season mass-flowering crops. In addition, bumblebee colony sizes might benefit from late-season mass-flowering crops (Beyer et al., 2020; Riggi et al., 2021). Finally, we predicted that increasing non-crop habitat cover would enhance pollinator abundance and richness because it would increase nesting and non-crop floral resource availability (Figure 1c).

2 | MATERIALS AND METHODS

2.1 | Selection of publications

We searched for quantifications of the impact of mass-flowering crop cover in the landscape on pollinators sampled in crop (mass-flowering crops irrespective of field size) and/or non-crop habitats
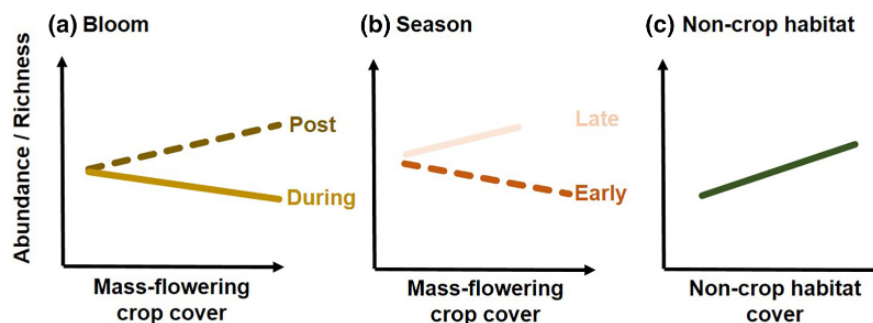
FIGURE 1 Illustration of the research hypotheses for temperate regions. First, we expect that: (a) during crop bloom, pollinator abundance and richness will decrease with mass-flowering crop cover (*dilution effect*), independent of sampling habitat. After crop bloom ('Post'), we expect pollinator abundance and richness to be higher in non-crop habitats and to positively relate to mass-flowering crop cover. Second, we hypothesise that (b) late in the season, flowering mass-flowering crop cover will increase pollinator abundance and richness inside and nearby crops (*concentration effect*) because flowering resource availability in the landscape is often lower in late than early season. Finally, we expect (c) pollinator abundance and richness to increase with non-crop habitat cover (including grasslands, forests, fallows and uncultivated field borders, Table A1).

(including grasslands, forests, fallows and uncultivated field borders, Table A1) in Web of Science in August 2021 using the topic search string: "flower* crop*" AND "pollin*" AND "landscape*". This yielded 157 publications that were scanned for inclusion in the analyses. We excluded studies from tropical regions because some of the hypotheses we tested relate to temperate seasonality. In addition, to be included, publications had to provide data on: (1) *mass-flowering crop* and *non-crop habitat* (as defined in each study, including forests, grasslands and pastures) *cover* (i.e. *area* or *proportion*) within a 1-km radius landscape around the surveyed site. Mass-flowering crop area included dominant crops flowering during pollinator surveys; and (2) *Abundance* and/or *species richness* of wild pollinators in crop and/or non-crop habitats, either bumblebees, other bees (e.g. solitary bees and social *Lasioglossum* and *Halictus* species) or non-bees (mostly hoverflies), surveyed either using transects or pan-traps (Table 1, Figure A2). Data from observational plots and trap-nests were excluded as too few studies were found. While the focus was to investigate effects on wild pollinators, honeybee abundance was included when data was available (it was not feasible to distinguish between managed and feral honeybees). We focused on 1-km radius landscapes, as it was the most commonly reported and relevant scale for the taxonomic groups of interest (Holzschuh et al., 2016; Kendall et al., 2022).

The literature search resulted in nine publications where the raw data were extractable. An additional 12 publications were identified as relevant, but raw data were not available. The authors for these 12 publications were asked to share their raw data, and we received data for seven (Table 1). This led to a final selection of 13 publications that included 22 studies, defined as a dataset of pollinator surveys performed in a given region in a given year and 498 landscapes from nine countries (Table 1, Table A1, Figure A2). For each sampling site (i.e. landscape with a 1-km radius), we compiled data on pollinators, landscape composition and study-specific information, which is summarised in Table 1 and Table A1. To investigate post-crop bloom effects, we ascertained that there were no other major crop flowering in the 1-km radius landscape after focal crop bloom by contacting authors and examining the raw data.

2.2 | Statistical analyses

Pollinator abundance (number of individuals recorded per 100 m^2 transect or pan-trap day to account for different sampling efforts within the study) and species richness (mean number of species recorded per transect or pan-trap) data were averaged within sampling habitat (crop and non-crop), crop flowering season (early and late) and bloom state (during and post-crop flowering) for each pollinator group (bumblebees, honeybees, other bees and non-bees) and each landscape site (Table 1). All response variables were log-transformed to improve model fit and then scaled and centred within study (i.e. we calculated *z*-scores for each study) and mass-flowering crop and non-crop habitat cover predictors

were centred within the study to investigate general within-study patterns. Since pollinators after crop bloom were only sampled in non-crop habitats, we divided the data based on habitat type and ran separate analyses for crop and non-crop habitats. Bumblebees and honeybees are poorly represented in pan-traps (Boyer et al., 2020); therefore, these groups were only analysed using transect data. For other bees and non-bees, to avoid issues with the low number of studies in the pan-trap data, we analysed the pan-trap and transect data together. Pan-trap efficiency declines with flower availability (Westerberg et al., 2021), potentially leading to biased results when investigating gradients in mass-flowering crop cover. Therefore, the transect data was also analysed separately for other bees and non-bees. Results from the analyses with pan-trap data removed are only reported in the main text when they differed qualitatively from results using the combined data. We used linear mixed-effects models with normal distributions for mean (scaled and centred) abundance and richness. Model assumptions were checked using diagnostic residual plots.

To explore the effects of mass-flowering crop cover on pollinator abundance of each group (bumblebees, honeybees, other bees and non-bees) and species richness (bumblebees, other bees and non-bees) in crop and non-crop habitats, the models included proportion of mass-flowering crop and non-crop habitat cover in the landscape (covariation between these variables was low across studies, Table B1), flowering season (early or late) and sampling method (pan-trap or transect, only applies to non-bee and other bee) as fixed factors. For models in non-crop habitats, crop bloom state (during and post-crop flowering) was also included as a fixed factor. In addition, two-way interactions with mass-flowering crop cover were included to test the hypotheses that mass-flowering crop cover effects were contingent on crop flowering season, non-crop habitat cover in the landscape and crop bloom state (the latter only for non-crop habitat models; Table 2). Including honeybee abundance (scaled and centred within the dataset) as a covariate in models for bumblebee, other bee and non-bee abundance and richness did not qualitatively change the results (Table C1). Study identity (Table 1) and landscape identity nested within study identity were included as random factors in the crop and non-crop models, respectively, to account for spatial dependence within studies and landscapes (for the non-crop models that had habitats sampled before and after crop bloom in the same landscape). Models including random slopes for mass-flowering crop and non-crop habitat cover were assessed and included if they improved model fit as determined by AIC (Table 2).

Multicollinearity was not an issue for any models (VIF < 2; Zuur et al., 2009). We simplified models using backward model simplification based on likelihood ratio tests (Zuur et al., 2009). Post-hoc tests using the '*emmeans*' package (Lenth et al., 2021) were carried out. We estimated the marginal R^2 of the models using '*r.squaredG-LMM*' (Nakagawa & Schielzeth, 2013). All analyses were done in R (R Core Team, 2020, version 3.6.2) using the '*glmmTMB*' package (Magnusson et al., 2021). Mean pollinator abundance and species richness per study are presented in the Supplementary Material (Tables B2 and B3).

TABLE 1 Summary of the studies used in the synthesis.

Publication	Study	Year	Country	Bloom state	Flowering season	Focal crop	Sampling habitat[a]
A	A.1	2014	UK	During	Early	Oilseed rape	Crop
A	A.2	2015	UK	During	Early	Oilseed rape	Crop
B	B	2017	Sweden	During	Late	Faba bean	Crop
C	C	2012	Canada	During	Early	Apple/Blueberry/Raspberry	Crop
D	D	2008	Germany	During	Early	Oilseed rape	Crop/Non-crop
E	E	2017	Germany	During/Post	Late	Faba bean	Non-crop
F	F	2014	Germany	During	Early	Apple	Crop
G	G	2015	Germany	During	Early	Strawberry	Crop
H	H	2019	Sweden	During/Post	Late	Red clover	Crop/Non-crop
I	I	2014	France	During/Post	Early/Late	Oilseed rape/Sunflower	Non-crop
J	J	2015	France	During/Post	Early/Late	Oilseed rape/Sunflower	Crop/Non-crop
K	K	2013	USA	During	Early	Apple/Strawberry	Crop/Non-crop
L	L	2016	Italy	During	Late	Leek	Crop/Non-crop
M	Mg.1	2011	Germany	During	Early	Oilseed rape	Crop/Non-crop
M	Mg.2	2012	Germany	During	Early	Oilseed rape	Crop/Non-crop
M	Mnl.1	2011	Netherlands	During/Post	Early	Oilseed rape	Crop/Non-crop
M	Mnl.2	2012	Netherlands	During/Post	Early	Oilseed rape	Crop/Non-crop
M	Msp.1	2011	Spain	During	Early	Orange	Crop/Non-crop
M	Msp.2	2012	Spain	During	Early	Orange	Crop/Non-crop
M	Msw.1	2011	Sweden	During	Early	Oilseed rape	Crop/Non-crop
M	Msw.2	2012	Sweden	During	Early	Oilseed rape	Crop/Non-crop
M	Muk	2012	UK	During	Early	Oilseed rape	Crop/Non-crop

Note: Publication and Study: publication and study (defined as a dataset in a given region in a given year) identifier (Table A1). Year: year the sampling was done. Country: the country where the sampling was done. Bloom state: time when sampling was done relative to the focal crop bloom, during and/or post (after) bloom. Flowering season: survey season based on focal crop flowering period, early (during flowering of early-season crops: oilseed rape, orchards and berries) and late (during flowering of late-season crops: faba bean, sunflower, clover and leek). Focal crop: mass-flowering crop the study focused on. Sampling habitat: crop and/or non-crop (including grasslands, forests, fallows and uncultivated field borders, Table A1) habitats. N° Landscapes: number of 1-km radius landscapes per study. Pollinator group: surveyed, BB (bumblebees), OB (other bees), NB (non-bees, mainly hoverflies) and HB (honeybees). MFC % and SNH %: mean, min. and max habitat cover of mass-flowering crops (MFC) and non-crop habitats (SNH, semi-natural habitats, as defined in each study, Table A1). Data: data extracted from an OD (online dataset) or RD (requested data).

[a]Post-bloom data only from non-crop habitats.

[b]Partially published/unpublished data.

3 | RESULTS

3.1 | Abundance

During crop bloom, bumblebee abundance declined with increasing mass-flowering crop cover, irrespective of sampling habitat or season (Figure 2a), and increased in crop habitats with increasing non-crop habitat cover (Figure C1a). Other wild bee abundance declined in crop habitats with increasing mass-flowering crop cover early in the season and increased in non-crop habitats with increasing mass-flowering crop cover late in the season (Figure 2b). The latter effect became weaker when excluding pan-trap data ($p = 0.088$; Table C2, Figure C2a). Non-bee abundance was not related to non-crop habitat or mass-flowering crop cover when pan-trap and transect data were combined (Figure 2c), but when pan-trap data was removed, non-bee abundance in crop habitats

increased with non-crop habitat cover and decreased with mass-flowering crop cover early in the season but increased late in the season (Table C2, Figure C2b). Honeybee abundance in non-crop habitats marginally increased ($p = 0.057$) with mass-flowering crop cover, while in crop habitats, honeybee abundance increased with mass-flowering crop cover late in the season (Figure 2d, Table 2). There were no interactive effects of mass-flowering crop cover and bloom on pollinator abundance.

3.2 | Species richness

Bumblebee richness in crop habitats decreased with mass-flowering crop cover, but only during the early season (Figure 3a), and richness in non-crop habitats increased with non-crop habitat cover (Figure C1b). Other bee richness in crop habitats declined with

Survey method	N° landscapes	Pollinator group	Response variable	MFC %		SNH%		Data
				Mean	Min-max	Mean	Min-max	
Transect/Pan-trap	12	BB/OB/NB/HB	AB/RICH	25.9	5.9-33.6	34.3	10.8-55.5	OD
Transect/Pan-trap	12	BB/OB/NB/HB	AB/RICH	27.1	2.8-35.7	32	10.9-65.7	OD
Transect	16	BB/HB	AB/RICH	7.89	2.6-20.6	8.8	0-55.6	RD[b]
Transect	58	BB/OB/HB	AB/RICH	14.3	0-50	34.2	0-70.7	OD
Transect	66	BB/OB/HB	AB/RICH	10.7	0-32.9	4.3	0.5-12.8	RD
Transect	30	BB/OB	AB	13.6	4.3-35.8	8.1	3.6-15.3	OD
Pan-trap	10	OB	AB	7.1	0-42	14.5	0-40.0	OD
Transect	8	BB/OB/HB	AB	9.8	4.1-17.6	2.1	0.6-5.1	RD[b]
Transect	20	BB/NB/HB	AB/RICH	12.2	0-26.7	15.5	3.8-63.7	RD[b]
Pan-trap	66	OB/NB	AB/RICH	19.7	0-47.7	14.5	0.2-43.	RD[b]
Transect	25	BB/OB/NB/HB	AB/RICH	14.8	4.8-32.7	5.9	1.6-14.8	RD[b]
Pan-trap	13	OB	AB/RICH	4.8	0-37.4	42.5	17.1-70.5	RD
Transect	18	BB/OB/NB/HB	AB/RICH	8	0.2-15.6	20.3	0.4-55.3	RD
Transect	16	BB/OB/NB/HB	AB	6.2	0.5-19.8	11.6	1.9-25.9	RD
Transect	16	BB/OB/NB/HB	AB	4.9	0-16.3	11.3	1.0-28.5	RD
Transect	16	BB/OB/NB/HB	AB/RICH	1.4	0-4.5	7.1	1.0-16.1	RD[b]
Transect	16	BB/OB/NB/HB	AB/RICH	0.9	0-3.8	7.1	1.0-16.1	RD[b]
Transect	16	BB/OB/NB/HB	AB	27	0-68.6	43.5	18.9-79.6	RD
Transect	16	BB/OB/NB/HB	AB	27.7	0-66.2	44.7	21.9-79.6	RD
Transect	16	BB/OB/NB/HB	AB	10.2	0.7-42	8.9	2.2-20.5	RD
Transect	16	BB/OB/NB/HB	AB	8.5	0-35.1	8.7	2.2-20.2	RD
Transect	16	BB/OB/NB/HB	AB	12	0-28.9	16	1.8-44.9	RD

mass-flowering crop cover (Figure 3b). When pan-trap data was re-moved, other bee richness in crop habitats increased with non-crop habitat cover (Table C2). Other bee richness in non-crop habitats was not related to mass-flowering crop or non-crop habitat cover (Table 2). Non-bee richness was not related to mass-flowering crop cover (Figure 3c), while richness in crop habitats increased with non-crop habitat cover (Figure C1c). There were no interactive effects of mass-flowering crop cover and bloom on pollinator richness.

4 | DISCUSSION

While our results confirm that increasing early-season mass-flowering crop cultivation dilutes wild bees in crop habitats during bloom (Holzschuh et al., 2016), we find that, later in the season, dilution effects were either absent or even reversed for honeybee abundance in crop habitats and other bee abundance in non-crop habitats. This is possibly because later in the season, mass-flowering crops provide resources at a time of nectar and pollen shortages. This can lead to concentration effects, where mobile crop-adapted species concentrate in crop habitats in landscapes with high mass-flowering crop cover. This might result in lower competition for floral resources in non-crop habitats as crop-adapted species move to forage in mass-flowering crops. Contrary to our hypothesis, crop bloom did not mediate any effect of mass-flowering crop cover on pollinator abundance or richness in non-crop habitats. Discrepancies between sampling methods were most evident for non-bee abundance and other bee richness in crop habitats, likely because pan-traps are less suited to assess the effects of gradients in floral resource availability (Westerberg et al., 2021) and sample pollinator communities, which are compositionally distinct from transects (O'Connor et al., 2019).

Increasing mass-flowering crop cover was negatively related to bumblebee abundance in both crop and non-crop habitats and to other bee abundance in crop habitats early in the season. For non-bees, a negative relationship between abundance in crop habitats early in the season and mass-flowering crop cover was present when excluding pan-trap data. This was caused by a single pan-trap publication (Shaw et al., 2020), where non-bee abundance was not related to the oilseed rape area, possibly due to the limitations of pan-traps to examine concentration and dilution effects on pollinator abundance. Negative relationships between mass-flowering crop cover and wild pollinator abundance during bloom in crop habitats are probably caused by dilution (Holzschuh et al., 2016). Dilution of pollinators in crop habitats suggests that increased mass-flowering crop cultivation in the landscape can compromise crop pollination services by wild pollinators. Declines in bumblebee abundance in non-crop habitats with mass-flowering crop cover might, in the long-term, negatively impact bumblebee-pollinated wild plants (Holzschuh et al., 2011). Other bee (non-*Bombus*), non-bee and honeybee abundance in non-crop habitats did not decline with mass-flowering crop cover. The majority of other bees occurring in non-crop habitats during the early season are likely not attracted by mass-flowering crop resources, relying on resources within their more restricted foraging ranges compared to bumblebees (Fijen et al., 2019; Rollin et al., 2013). Non-bee pollinators, on the other hand, such as hoverflies and other dipterans, are non-central-place foragers and highly mobile as adults (Jauker et al., 2009), lowering the probability of dilution and potentially increasing spillover to nearby habitats, as non-bee pollinators might be attracted to mass-flowering crops from larger distances. Honeybee abundance in non-crop habitats was marginally positively related to mass-flowering crop cover, potentially leading to competition with other flower visitors, particularly wild bees, in non-crop habitats when floral resources are limited (e.g. reducing wild bees pollen and nectar collection) (González-Varo & Vilà, 2017; Herbertsson et al., 2016).

Flower availability in crop and non-crop habitats in temperate regions is often lower in summer than in spring (Persson & Smith, 2013; Scheper et al., 2014; Timberlake et al., 2019); therefore, we expected that later in the season, the dilution of wild pollinator in crop and non-crop habitats with mass-flowering crop cover would be weaker compared to early in the season. In line with expectations, other bee abundance in non-crop habitats increased with mass-flowering crop cover late in the season. The positive relationship between mass-flowering crop cover and other bee abundance in non-crop habitats late in the season became somewhat weaker when pan-trap data was excluded, likely due to reduced statistical power. Other bee abundance in non-crop habitats might have increased as a result of released competition from crop-adapted species (e.g. honeybee and bumblebee) that are attracted to late-flowering crops (Fijen et al., 2019; Page & Williams, 2022), such as clover and faba bean. In addition, increased availability of flower resources could benefit other bees that forage in mass-flowering crop habitats (Holzschuh et al., 2013). For other bees, there was no difference in abundance between seasons. Therefore, seasonal differences in abundances

cannot explain the contrasting responses of other bees to mass-flowering crop cover early versus late in the season. Honeybee abundance in crop habitats also increased with mass-flowering crop cover late in the season, and so did non-bee abundance when pan-trap data was excluded. While the positive effects of mass-flowering crops late in the season for non-bees and honeybees that reproduce within the season could be due to population-/colony-level effects, abundances were not higher later in the season, suggesting concentration effects. Honeybees and non-bees, such as hoverflies, are strong fliers and likely to fly several kilometres for rewarding resources (Jauker et al., 2009; Steffan-Dewenter & Kuhn, 2003). Honeybees and non-bees are therefore likely concentrated in crop habitats from adjacent habitats and landscapes (Guezen & Forrest, 2021) late in the season. Furthermore, honeybee hives are placed nearby mass-flowering crops in the spring, and some are still present later in the season, leading to concentration in late-season mass-flowering crops (González-Varo & Vilà, 2017). Thus, early flowering crop cover impacts pollinator dynamics later in the season, and this should be further investigated (Riedinger et al., 2014). Finally, early and late seasonal patterns could also be due to the unavoidable relationship between crop identity and flowering season.

Bumblebee richness in crop habitats declined with mass-flowering crop cover early, but not late in the season. Late-season mass-flowering crops include legumes, which are attractive to bumblebees, and their bloom coincides with bumblebee colony reproduction. Therefore, late-season mass-flowering crops such as clover could attract and sustain bumblebee species at a time of low flower availability (Riggi et al., 2021). The species richness of other bees in crop habitats decreased with mass-flowering crop cover. This could be a consequence of increased competition with a few dominant pollinator species associated with mass-flowering crop cultivation (i.e. honeybees and short-tongued bumblebees; Magrach et al., 2017). Alternatively, declines in other bee richness could be a consequence of dilution effects on bee populations, such that rare species become harder to detect with increasing mass-flowering crop cover. No declines in wild pollinator richness with mass-flowering crop cover were found in non-crop habitats, indicating that many species occurring in non-crop habitats rely more on resources within these habitats (Rollin et al., 2013) and might benefit as honeybees and bumblebees are attracted to mass-flowering crop habitats (Bänsch et al., 2021).

We found positive relationships between non-crop habitat cover and bumblebee abundance in crop habitats and non-bee abundance when pan-trap data was excluded, underlying the role of non-crop habitat as source habitats for these groups (Öckinger & Smith, 2007). In contrast to our expectation, higher non-crop habitat cover did not increase other bee abundances (Holzschuh et al., 2016). Non-crops encompassed a broad range of habitats, including forests and field borders, which might each favour or disfavour specific species, thus leading to inconsistent effects. Primarily crop-adapted bumblebee species, which form large colonies, and mobile non-bee species might benefit from the wide range of non-crop habitats included in these studies. Bumblebee richness in non-crop habitats

TABLE 2 Model summary results for (A) non-crop and (B) crop habitats, with estimates (est), standard errors (se) and p-values (p).

Non-crop habitat

(A)

Response		MFC cover	Non-crop cover	Season (late)	Bloom (post)	Collection (T)	MFC*season	Obs	DS	R
Bumblebee abundance	Est±SE	−0.01±0.005	0.002±0.005	−0.14±0.13	0.35±0.10	NI		484	14	4
	p	**0.013**	0.661	0.257	**0.001**					
Bumblebee richness	Est±SE	−0.01±0.01	0.01±0.007	−0.02±0.15	0.73±0.12	NI		265	6	14
	p	0.346	**0.016**	0.891	**<0.001**					
Other bee abundance*	Est±SE	−0.003±0.004	0.001±0.004	0.11±0.14	0.01±0.11	0.16±0.26	0.03±0.01	562	15	2
	p	0.454	0.751	0.427	0.907	0.552	**0.006**			
Other bee richness*	Est±SE	−0.003±0.009	−0.006±0.006	0.26±0.18	0.05±0.13	0.20±0.24		343	7	2
	p	0.749	0.376	0.157	0.699	0.398				
Non-bee abundance	Est±SE	−0.0001±0.006	0.0004±0.005	−0.20±0.14	−0.12±0.11	0.0002±0.15		508	13	0
	p	0.980	0.935	0.167	0.296	0.999				
Non-Bee richness	Est±SE	0.01±0.01	0.006±0.006	−0.47±0.16	−0.25±0.12	−0.02±0.13		299	5	5
	p	0.406	0.304	**0.003**	**0.040**	0.856				
Honeybee abundance*	EST±SE	0.008±0.004	0.004±0.004	0.23±0.17	−0.09±0.12	NI		454	13	2
	p	0.057	0.282	0.179	0.451					

Crop habitat

(B)

Response		MFC cover	Non-crop cover	Season (late)	Collection (T)	MFC*season	MFC*non-crop cover	Obs	DS	R
Bumblebee abundance**	Est±SE	−0.02±0.006	0.01±0.008	0.53±0.21	NI		−0.0005±0.0004	300	18	7
	p	**<0.001**	**0.050**	**0.011**			0.214			
Bumblebee richness**	Est±SE	−0.03±0.008	0.0009±0.01	0.40±0.14	NI	0.05±0.01		197	10	13
	p	**<0.001**	0.926	**0.005**		**0.002**				
Other bee abundance	Est±SE	−0.03±0.005	−0.0004±0.004	0.10±0.38	−0.04±0.29	0.04±0.02		297	18	13
	p	**<0.001**	0.907	0.787	0.875	**0.049**				
Other bee richness	Est±SE	−0.02±0.007	0.006±0.005	−0.42±0.38	0.18±0.35			184	9	10
	p	**<0.001**	0.193	0.276	0.606					
Non-bee abundance**	Est±SE	−0.01±0.01	0.002±0.009	−0.05±0.33	−0.19±0.39	0.04±0.02		186	14	2
	p	0.153	0.767	0.860	0.626	**0.040**				
Non-bee richness	Est±SE	0.008±0.01	0.02±0.007	0.50±0.44	−0.87±0.44			81	6	17
	p	0.590	**0.003**	0.250	0.052					
Honeybee abundance	Est±SE	−0.01±0.007	0.007±0.005	−0.11±0.31	NI	0.06±0.02		300	18	3
	p	0.058	0.167	0.723		**0.008**				

Note: Bumblebees and honeybees were analysed only in the transect dataset. Significant results ($p < 0.05$) are shown in bold and marginal results ($0.05 < p < 0.08$) in italic. The best fit model included:

(*) a covariance structure (diag(Study+0|unit)), (**) random slope (non-crop habitat cover||Study).

Abbreviations: DS, number of studies included; NI, predictor not included; Obs, number of observations (i.e. sampling sites); R, marginal R^2 (%); T, transect collection.
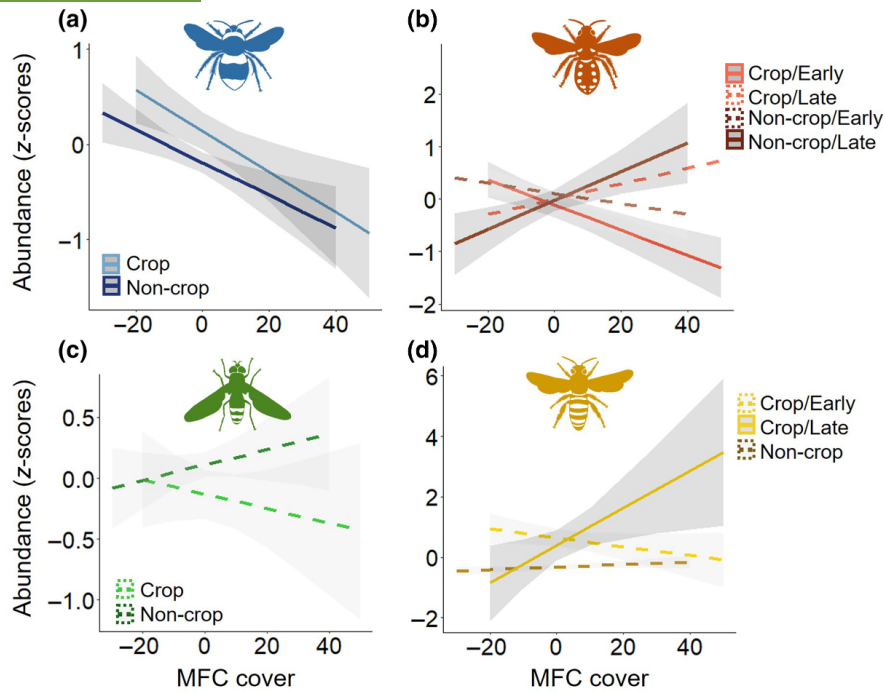
FIGURE 2 Model predictions of the relationships between mean pollinator abundance (scaled and centred, z-scores) and mass-flowering crop cover (centred, %) in 1-km radius landscapes (combined transect and pan-trap data). (a) Bumblebee abundance decreased with mass-flowering crop cover in crop and non-crop habitats. (b) Other bee abundance decreased with mass-flowering crop cover in crop habitats early in the season (early (trend±se:−0.03±0.008, CI:−0.04/−0.01); late (0.02±0.01, −0.009/0.05)) and increased with mass-flowering crop cover in non-crop habitat late in the season (early (−0.003±0.004, −0.01/0.005); late (0.03±0.01, 0.007/0.05)), 95% CI only shown for significant relationships. (c). Non-bee abundance was not related to mass-flowering crop cover despite a significant interaction (early (−0.01±0.01, −0.03/0.005); late (0.03±0.02, −0.007/0.007)). (d) Honeybee abundance marginally increased ($p=0.057$) with mass-flowering crop cover in non-crop habitats, while in crop habitats abundance increased with mass-flowering crop cover late in the season (early (−0.01±0.007, −0.02/0.0005); late (0.04±0.02, 0.003/0.08)). Shaded areas represent the 95% confidence interval (CI), solid lines indicate a significant relationship and dashed lines indicate a non-significant/marginal interaction.
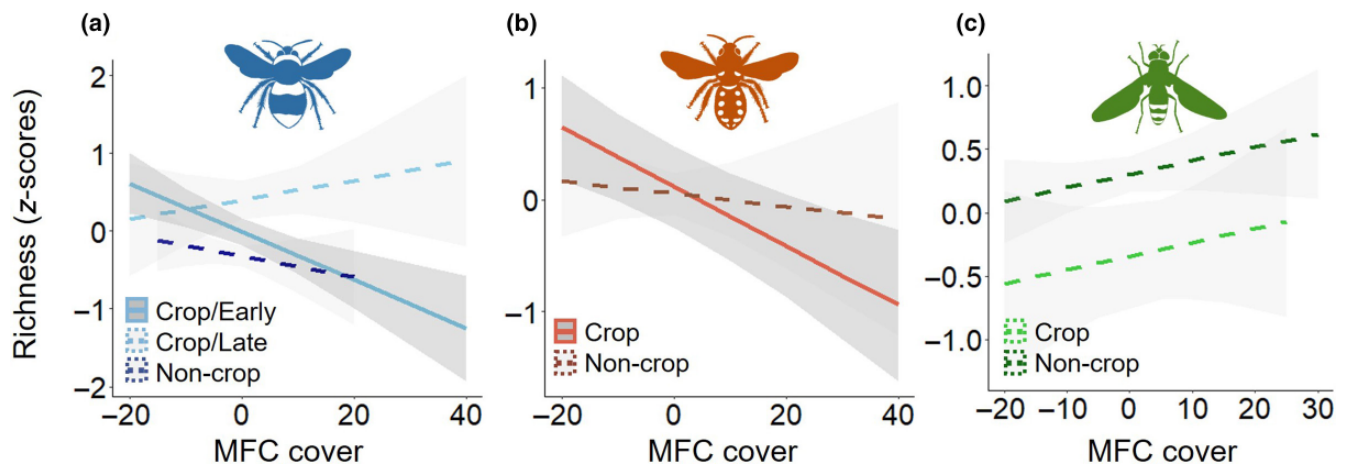

FIGURE 3 Model predictions of the relationships between mean pollinator richness (scaled and centred) and mass-flowering crop cover (centred, %) in 1-km radius landscapes (combined pan-trap and transect data). (a) Bumblebee species richness in crop habitats declined with mass-flowering crop cover early in the season (early (trend±SE = −0.03±0.008, CI: −0.04/−0.01); late (0.02±0.01, −0.009/0.05)). (b) Other bee richness in crop habitats declined with mass-flowering crop cover. (c) Non-bee richness was not related to mass-flowering crop cover. Shaded areas represent the 95% CI, dark grey shading indicates a significant relationship and dashed lines indicate a non-significant/marginal interaction.

and non-bee richness in crop habitats increased with non-crop habitat cover. Other bee richness in crop habitats also increased with non-crop habitat cover, but only when pan-trap data was excluded, which could be because studies using pan-traps were conducted in landscapes with a high proportion of non-crop habitats (>10% cover) and the positive effects of non-crop habitat cover might saturate at higher levels of non-crop habitat cover (i.e. species–area relationships). Positive effects of non-crop habitats on wild pollinator richness were expected, as many species require resources for nesting and larval development (e.g. litter, tree holes) that are provided by non-crop habitats.

We did not detect positive relationships between mass-flowering crop cover and wild pollinator abundance or richness in non-crop habitats after crop bloom. This is in line with previous findings that suggest that the effect of mass-flowering crop bloom is short-lived and that there is little spillover of wild pollinators from crop to non-crop habitats after crop bloom (Hanley et al., 2011; Montero-Castaño et al., 2016). Studies that found positive effects of mass-flowering crop cover after crop bloom indicate that primarily pollinator species that are adapted to the focal mass-flowering crop increase in the landscape after crop bloom (e.g. long-tongued bumblebee species after legume bloom or honeybees; Beyer et al., 2020; Riggi et al., 2021). Only six out of 22 studies included data after crop bloom, which meant that we had limited statistical power to analyse post-bloom effects. To better understand the temporal effects of mass-flowering crops on wild pollinator communities, we need more studies comparing landscapes with and without focal crop during and after bloom. The temporal effects of mass-flowering crop cover across seasons would also be important to consider. For example, in landscapes with perennial flowering crops, such as orchards, which were included in our study, mass-flowering crop cover effects in the current season could be intertwined with legacy effects from previous seasons.

This study provides insights on the seasonal effects of mass-flowering crop cover on different pollinator groups. A major finding is that increasing mass-flowering crop cover dilutes wild pollinator abundance and richness in crop habitats, primarily early in the season. A notable exception is bumblebee abundance, which declined with mass-flowering crop cover irrespective of season. Late in the season, mass-flowering crop cover effects were mostly absent or even positively related to the abundance of honeybees in crop habitats and of other bees in non-crop habitats. The positive effects of increasing late-season mass-flowering crop cover might be due to increased flower availability at a time when flower resources are scarce, leading to a concentration of mobile species in mass-flowering crops and decreased competition in non-crop habitats. Including different flowering crops as part of carefully designed diverse crop rotations or mixtures (e.g. intercropping, undersowing), could provide resources at times of pollen and nectar shortages in non-crop habitats and support wild pollinators in agricultural landscapes. Further studies are needed to understand which pollinator traits (e.g. foraging range, specialisation and sociality) benefit from

mass-flowering crop cultivation and whether late-season crops can reduce resource competition in non-crop habitats (Guezen & Forrest, 2021). To assess the role of mass-flowering crop cultivation for pollinator conservation in agricultural landscapes, it is imperative to disentangle transient pollinator distribution within season (dilution and concentration effects) from population-level effects, for example the reproductive supporting effect of mass-flowering crop (Carvell et al., 2017). While mass-flowering crop cultivation is unlikely to be sufficient for conserving pollinators alone, combined with the preservation of permanent non-crop habitats with diverse floral resources, it might provide valuable supplementary food resources for crop-adapted pollinators, particularly late in the season when alternative flower resources are limited.

CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

Data available via the Swedish National Data Service (https://doi.org/10.5878/9vfz-ca92; Riggi, 2023).

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REFERENCES

Bänsch, S., Tscharntke, T., Gabriel, D., & Westphal, C. (2021). Crop pollination services: Complementary resource use by social vs solitary bees facing crops with contrasting flower supply. *Journal of Applied Ecology*, *58*(3), 476–485. https://doi.org/10.1111/1365-2664.13777

Beyer, N., Gabriel, D., Kirsch, F., Schulz-Kesting, K., Dauber, J., & Westphal, C. (2020). Functional groups of wild bees respond differently to faba bean *Vicia faba* L. cultivation at landscape scale. *Journal of Applied Ecology*, *57*(12), 2499–2508. https://doi.org/10.1111/1365-2664.13745

Beyer, N., Kirsch, F., Gabriel, D., & Westphal, C. (2021). Identity of mass-flowering crops moderates functional trait composition of pollinator communities. *Landscape Ecology*, *36*(9), 2657–2671. https://doi.org/10.1007/s10980-021-01261-3

Boyer, K. J., Fragoso, F. P., Dieterich Mabin, M. E., & Brunet, J. (2020). Netting and pan traps fail to identify the pollinator guild of an agricultural crop. *Scientific Reports*, *10*(1), 13819. https://doi.org/10.1038/s41598-020-70518-9

Carvell, C., Bourke, A. F. G., Dreier, S., Freeman, S. N., Hulmes, S., Jordan, W. C., Redhead, J. W., Sumner, S., Wang, J., & Heard, M. S. (2017). Bumblebee family lineage survival is enhanced in high-quality landscapes. *Nature*, *543*(7646), Article 7646. https://doi.org/10.1038/nature21709

EU. (2018). *EU Pollinators Initiative*. https://ec.europa.eu/environment/nature/conservation/species/pollinators/policy_en.htm

FAOSTAT. (2022). *FAOSTAT*. https://www.fao.org/faostat/en/#home

Fijen, T. P. M., Scheper, J. A., Boekelo, B., Raemakers, I., & Kleijn, D. (2019). Effects of landscape complexity on pollinators are moderated by pollinators' association with mass-flowering crops. *Proceedings of the Royal Society B: Biological Sciences*, *286*(1900), 20190387. https://doi.org/10.1098/rspb.2019.0387

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

Guezen, J. M., & Forrest, J. R. K. (2021). Seasonality of floral resources in relation to bee activity in agroecosystems. *Ecology and Evolution*, *11*(7), 3130–3147. https://doi.org/10.1002/ece3.7260

Hanley, M. E., Franco, M., Dean, C. E., Franklin, E. L., Harris, H. R., Haynes, A. G., Rapson, S. R., Rowse, G., Thomas, K. C., Waterhouse, B. R., & Knight, M. E. (2011). Increased bumblebee abundance along the margins of a mass flowering crop: Evidence for pollinator spill-over. *Oikos*, *120*(11), 1618–1624. https://doi.org/10.1111/j.1600-0706.2011.19233.x

Herbertsson, L., Lindström, S. A. M., Rundlöf, M., Bommarco, R., & Smith, H. G. (2016). Competition between managed honeybees and wild bumblebees depends on landscape context. *Basic and Applied Ecology*, *17*(7), 609–616. https://doi.org/10.1016/j.baae.2016.05.001

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*(10), 1228–1236. https://doi.org/10.1111/ele.12657

Holzschuh, A., Dormann, C. F., Tscharntke, T., & Steffan-Dewenter, I. (2011). Expansion of mass-flowering crops leads to transient pollinator dilution and reduced wild plant pollination. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1723), 3444–3451. https://doi.org/10.1098/rspb.2011.0268

Holzschuh, A., Dormann, C. F., Tscharntke, T., & Steffan-Dewenter, I. (2013). Mass-flowering crops enhance wild bee abundance. *Oecologia*, *172*(2), 477–484. https://doi.org/10.1007/s00442-012-2515-5

IPBES. (2016). *Assessment report of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services on pollinators, pollination and food production*. IPBES.

Jauker, F., Diekötter, T., Schwarzbach, F., & Wolters, V. (2009). Pollinator dispersal in an agricultural matrix: Opposing responses of wild bees and hoverflies to landscape structure and distance from main habitat. *Landscape Ecology*, *24*(4), 547–555. https://doi.org/10.1007/s10980-009-9331-2

Kendall, L. K., Mola, J. M., Portman, Z. M., Cariveau, D. P., Smith, H. G., & Bartomeus, I. (2022). The potential and realized foraging movements of bees are differentially determined by body size and sociality. *Ecology*, *103*, e3809. https://doi.org/10.1002/ecy.3809

Knapp, J. L., Bates, A., Jonsson, O., Klatt, B., Krausl, T., Sahlin, U., Svensson, G. P., & Rundlöf, M. (2022). Pollinators, pests and yield—Multiple trade-offs from insecticide use in a mass-flowering crop. *Journal of Applied Ecology*, *59*(9), 2419–2429. https://doi.org/10.1111/1365-2664.14244

Lenth, R. V., Buerkner, P., Herve, M., Love, J., Riebl, H., & Singmann, H. (2021). *Emmeans* (1.5.5-1) [Computer software]. https://CRAN.R-project.org/package=emmeans

Lowe, E. B., Groves, R., & Gratton, C. (2021). Impacts of field-edge flower plantings on pollinator conservation and ecosystem service delivery—A meta-analysis. *Agriculture, Ecosystems & Environment*, *310*, 107290. https://doi.org/10.1016/j.agee.2020.107290

Magnusson, A., Skaug, H., Nielsen, A., Berg, C., Kristensen, K., Maechler, M., van Bentham, K., Bolker, B., Sadat, N., Lüdecke, D., Lenth, R., O'Brien, J., Geyer, C. J., McGillycuddy, M., & Brooks, M. (2021). *GlmmTMB* (1.1.2.3) [Computer software]. https://CRAN.R-project.org/package=glmmTMB

Magrach, A., Gonzalez-Varo, J. P., Boiffier, M., Vila, M., & Bartomeus, I. (2017). Honeybee spillover reshuffles pollinator diets and affects plant reproductive success. *Nature Ecology & Evolution*, *1*(9), 1299–1307. https://doi.org/10.1038/s41559-017-0249-9

Montero-Castaño, A., Ortiz-Sánchez, F. J., & Vilà, M. (2016). Mass flowering crops in a patchy agricultural landscape can reduce bee abundance in adjacent shrublands. *Agriculture, Ecosystems & Environment*, *223*, 22–30. https://doi.org/10.1016/j.agee.2016.02.019

Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, *4*(2), 133–142. https://doi.org/10.1111/j.2041-210x.2012.00261.x

Öckinger, E., & Smith, H. G. (2007). Semi-natural grasslands as population sources for pollinating insects in agricultural landscapes. *Journal of Applied Ecology*, *44*(1), 50–59. https://doi.org/10.1111/j.1365-2664.2006.01250.x

O'Connor, R. S., Kunin, W. E., Garratt, M. P. D., Potts, S. G., Roy, H. E., Andrews, C., Jones, C. M., Peyton, J. M., Savage, J., Harvey, M. C., Morris, R. K. A., Roberts, S. P. M., Wright, I., Vanbergen, A. J., & Carvell, C. (2019). Monitoring insect pollinators and flower visitation: The effectiveness and feasibility of different survey methods. *Methods in Ecology and Evolution*, *10*(12), 2129–2140. https://doi.org/10.1111/2041-210X.13292

Page, M. L., & Williams, N. M. (2022). Honey bee introductions displace native bees and decrease pollination of a native wildflower. *Ecology*, *104*, e3939. https://doi.org/10.1002/ecy.3939

Persson, A. S., & Smith, H. G. (2013). Seasonal persistence of bumblebee populations is affected by landscape context. *Agriculture, Ecosystems & Environment*, *165*, 201–209. https://doi.org/10.1016/j.agee.2012.12.008

Potts, S. G., Biesmeijer, J. C., Kremen, C., Neumann, P., Schweiger, O., & Kunin, W. E. (2010). Global pollinator declines: Trends, impacts and drivers. *Trends in Ecology & Evolution*, *25*(6), 345–353. https://doi.org/10.1016/j.tree.2010.01.007

R Core Team. (2020). *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org/

Riedinger, V., Renner, M., Rundlöf, M., Steffan-Dewenter, I., & Holzschuh, A. (2014). Early mass-flowering crops mitigate pollinator dilution in late-flowering crops. *Landscape Ecology*, *29*(3), 425–435. https://doi.org/10.1007/s10980-013-9973-y

Riggi, L. (2023). Data from: Early season mass-flowering crop cover dilutes wild bee abundance and species richness in temperate regions: A quantitative synthesis. Swedish National Data Service https://doi.org/10.5878/9vfz-ca92

Riggi, L. G. A., Lundin, O., & Berggren, Å. (2021). Mass-flowering red clover crops have positive effects on bumblebee richness and diversity after bloom. *Basic and Applied Ecology*, *56*, 22–31. https://doi.org/10.1016/j.baae.2021.06.001

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 & Environment*, *179*, 78–86. https://doi.org/10.1016/j.agee.2013.07.007

Rundlöf, M., Stuligross, C., Lindh, A., Malfi, R. L., Burns, K., Mola, J. M., Cibotti, S., & Williams, N. M. (2022). Flower plantings support wild bee reproduction and may also mitigate pesticide exposure effects. *Journal of Applied Ecology*, *59*(8), 2117–2127. https://doi.org/10.1111/1365-2664.14223

Scheper, J., Reemer, M., van Kats, R., Ozinga, W. A., van der Linden, G. T. J., Schaminée, J. H. J., Siepel, H., & Kleijn, D. (2014). Museum specimens reveal loss of pollen host plants as key factor driving wild bee decline in The Netherlands. *Proceedings of the National Academy of Sciences of the United States of America*, *111*(49), 17552–17557. https://doi.org/10.1073/pnas.1412973111

Shaw, R. F., Phillips, B. B., Doyle, T., Pell, J. K., Redhead, J. W., Savage, J., Woodcock, B. A., Bullock, J. M., & Osborne, J. L. (2020). Mass-flowering crops have a greater impact than semi-natural habitat on crop pollinators and pollen deposition. *Landscape Ecology*, *35*(2), 513–527. https://doi.org/10.1007/s10980-019-00962-0

Steffan-Dewenter, I., & Kuhn, A. (2003). Honeybee foraging in differentially structured landscapes. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *270*(1515), 569–575. https://doi.org/10.1098/rspb.2002.2292

Timberlake, T. P., Vaughan, I. P., & Memmott, J. (2019). Phenology of farmland floral resources reveals seasonal gaps in nectar availability for bumblebees. *Journal of Applied Ecology*, *56*(7), 1585–1596. https://doi.org/10.1111/1365-2664.13403

Tuerlings, T., Buydens, L., Smagghe, G., & Piot, N. (2022). The impact of mass-flowering crops on bee pathogen dynamics. *International Journal for Parasitology: Parasites and Wildlife*, *18*, 135–147. https://doi.org/10.1016/j.ijppaw.2022.05.001

USDA. (2020). *USDA: Conservation reserve program—pollinators*. USDA: Conservation Reserve Program-Pollinators. https://fsa.usda.gov/programs-and-services/economic-and-policy-analysis/natural-resources-analysis/pollinators/index

Westerberg, L., Berglund, H.-L., Jonason, D., & Milberg, P. (2021). Color pan traps often catch less when there are more flowers around.

Ecology and Evolution, *11*(9), 3830–3840. https://doi.org/10.1002/ece3.7252

Westphal, C., Steffan-Dewenter, I., & Tscharntke, T. (2003). Mass flowering crops enhance pollinator densities at a landscape scale. *Ecology Letters*, *6*(11), 961–965. https://doi.org/10.1046/j.1461-0248.2003.00523.x

Westphal, C., Steffan-Dewenter, I., & Tscharntke, T. (2009). Mass flowering oilseed rape improves early colony growth but not sexual reproduction of bumblebees. *Journal of Applied Ecology*, *46*(1), 187–193. https://doi.org/10.1111/j.1365-2664.2008.01580.x

Zuur, A., Ieno, E. N., Walker, N., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. Springer Science & Business Media.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Supplementary Material A. Overview of published and selected papers.

Figure A1. Overview of published papers on mass-flowering crops (MFC) and pollinators in Web of Science ($N = 157$, search string: TS=("flower* crop*" AND "pollin*" AND "landscape*") in August 2021).

Figure A2. PRISMA flow diagram for literature review on mass-flowering crops and pollinators densities and species richness in Web of Science (string: ("flower* crop*" AND "pollin*" AND "landscape*") on 4 August 2021).

Table A1. Table of publications included ($n = 13$, Figure S2) with descriptive habitat information.

Supplementary Material B. Landscape and pollinator data.

Table B1. Pearson correlation values between SNH and mass-flowering crop (%) cover for crop and non-crop habitats within and across datasets (p-value).

Table B2. Mean ($\pm$SD) of species richness per transect or pan trap within each pollinator group in non-crop and crop habitats within each study.

Table B3. Mean ($\pm$SD) abundance of pollinator group per 100m^2 transect or pan trap day in non-crop and crop habitats within each study.

Supplementary Material C. Supplementary results and analyses.

Table C1. Anova results for wild pollinators abundance and richness in A. Non-crop and B. Crop habitats in the transect dataset, including honeybee (A. mel) abundance (scaled and centred within datasets) as a covariate.

Figure C1. Model prediction (merged datasets) showing the positive relationship between % non-crop habitat cover (centered, %) at 1-km and (a) bumblebee abundance (scaled and centred, z-scores) in crop habitats. (b) Bumblebee richness (scaled and centred, z-scores) in non-crop habitats. (c) Non-bee richness (scaled and centred, z-scores) in crop habitats. Shaded area represent 95% CI.

Figure C2. Model predictions (transect dataset, excluding pan-traps) showing the results for the interaction between mass-flowering crop cover (% MFC, centred) and season on (a) other bee abundance (scaled and centred, z-scores) in crop habitats

(Early (trend ± SE = −0.03 ± 0.006, CI: −0.05/−0.02) and Late (0.007 ± 0.02, −0.03/0.04)) and in non-crop habitats (Early (trend ± SE = −0.002 ± 0.007, CI: −0.01/0.01) and Late (0.03 ± 0.01, −0.004/0.07)). (b). Non-bee abundance (scaled and centred, z-scores) in crop habitats (Early (trend ± SE = −0.03 ± 0.01, CI: −0.05/−0.006) and Late (0.02 ± 0.008, 0.005/0.03)). Shaded areas represent 95% confidence interval (CI), shading indicate a significant relationship, and no shading indicate a non-significant/marginal interaction.

Table C2. Models summary results for A. non-crop and B. crop habitats for other bees and non-bees in transect datasets only. Table includes estimates (est), standard errors (SE) and p-values (p).