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Article

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RESEARCH ARTICLE

Bees increase seed set of wild plants while the proportion of arable land has a variable effect on pollination in European agricultural landscapes

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Background and aims – Agricultural intensification and loss of farmland heterogeneity have contributed to population declines of wild bees and other pollinators, which may have caused subsequent declines in insect-pollinated wild plants.

Material and methods – Using data from 37 studies on 22 pollinator-dependent wild plant species across Europe, we investigated whether flower visitation and seed set of insect-pollinated plants decline with an increasing proportion of arable land within 1 km.

Key results – Seed set increased with increasing flower visitation by bees, most of which were wild bees, but not with increasing flower visitation by other insects. Increasing proportion of arable land had a strongly variable effect on seed set and flower visitation by bees across studies.

Conclusion – Factors such as landscape configuration, local habitat quality, and temporally changing resource availability (e.g. due to mass-flowering crops or honey bee hives) could have modified the effect of arable land on pollination. While our results highlight that the persistence of wild bees is crucial to maintain plant diversity, we also show that pollen limitation due to declining bee populations in homogenized agricultural landscapes is not a universal driver causing parallel losses of bees and insect-pollinated plants.

Keywords – Habitat loss; landscape complexity; landscape simplification; pollination; pollinating insects; semi-natural.

INTRODUCTION

Agricultural intensification threatens the richness and abundance of vascular plants in European agricultural landscapes, likely because of a combination of drivers such as nitrogen deposition, weed control, and the loss and degradation of semi-natural habitats (Robinson & Sutherland 2002; Bobbink et al. 2010; Bilz et al. 2011).

Although plant communities are strongly influenced by the availability of water, light, and minerals, which determine the degree of stress and interspecific competition (e.g. Theodose & Bowman 1997; Qi et al. 2018), the regeneration of plants in a community is also affected by seed production (Turnbull et al. 2000), which in turn depends on pollen transfer (Burd 1994). Consequently, loss of suitable pollinators can distort plant regeneration and reshape plant communities (Fontaine et al. 2005). Thus, because about 90% of the flowering plant species are pollinated by insects (Ollerton et al. 2011), observed declines of pollinators, such as butterflies (van Swaay et al. 2006), bees (Scheper et al. 2014), and hoverflies (Hallmann et al. 2021), could exacerbate the threat to plant populations (Clough et al. 2014; Papanikolaou et al. 2017).

A major driver of the pollinator decline is agricultural intensification, which is associated with loss of habitat and increased exposure to agrochemicals (IPBES 2016). In agricultural landscapes where semi-natural habitats have been converted to arable land (hereafter: homogeneous landscapes), pollinators can suffer from a lack of forage plants (Wallisdevries et al. 2012; Scheper et al. 2014). Depending on their specific needs, groups of pollinators, such as bees, butterflies, and hoverflies, may also suffer from lack of nesting habitats (Persson et al. 2015), larval host plants (Kuussaari et al. 2007), and larval microhabitats (Power et al. 2016). In addition to high-quality habitats (e.g. semi-natural habitats and low-intensive permanent grasslands), pollinators often use complementary resources from field borders and arable fields (Smith et al. 2014). Therefore, they do not only suffer from loss of high-quality habitat, but also from the general loss of flower resources at a landscape scale (Persson & Smith 2013; Mallinger et al. 2016).

Pollinators respond differently to variation in landscape homogeneity (Jauker et al. 2009; Ekroos et al. 2010; Ekroos et al. 2013). For example, population declines and scarcity in homogeneous landscapes are biased towards species with high habitat specificity, narrow diet requirements, or low mobility (Biesmeijer et al. 2006; Ekroos et al. 2010; Bommarco et al. 2012), and some generalist species can even benefit from certain aspects of modern agricultural landscapes (Westphal et al. 2003). Therefore, it is possible that the lack of certain pollinators in homogeneous landscapes can be mitigated by the presence of other pollinators, and thus have little impact on wild plant pollination and regeneration.

Parallel declines of bees and insect-pollinated plants may indicate loss of pollination in contemporary landscapes (Biesmeijer et al. 2006) and correlations between species loss in wild bees and insect-pollinated plants have been observed along gradients of land-use intensity (Clough et al. 2014) and agricultural intensification (Gabriel & Tscharntke 2007). This could simply reflect the fact that bees need flowers, or that the two groups respond negatively to an external factor, such as intensive agriculture (Biesmeijer et al. 2006). Yet, the fact that insect-pollinated plants show steeper declines over time and landscape-scale land-use gradients than wind- or self-pollinated plants indicates that loss of suitable pollinators plays a role (Biesmeijer et al. 2006; Clough et al. 2014).

It is important to consider that more homogenous landscapes not only support fewer pollinators, but that there are also fewer flowers to visit (Persson & Smith 2013). Therefore, it is possible that the net number of visits per flower or per plant is only weakly or not at all affected by increasing landscape homogenisation and that the loss of insect-pollinated plants is driven entirely by factors unrelated to pollination, such as reduced mowing and grazing of permanent grasslands (Tyler et al. 2018), or management changes (Kleijn & Snoeijing 1997; Honová et al. 2007). For example, herbicides and fertilisers can benefit the relative abundance of grasses at the expense of forbs (Kleijn & Snoeijing 1997; Honová et al. 2007). This calls for an assessment of whether flower visitation and seed set of insect-pollinated wild plants decline with increasing landscape homogeneity.

In this study, we aimed to address this knowledge gap. Ideally, this requires time-series data from landscapes characterized by different trajectories of change over time, which unfortunately is not available. We therefore capitalized on studies using a time-for-space substitution approach, in which the proportion of arable land varied between different study landscapes. We compiled data from such studies from eight European countries, on 22 highly pollinator-dependent native plant taxa. Using these data, we assessed the relationships between (i) flower visitation and seed set, (ii) the proportion of arable land and flower visitation, and (iii) the proportion of arable land and seed set. We expected (i) seed set to increase with flower visitation, and both (ii) flower visitation and (iii) seed set to decline with increasing proportion of arable land. By selecting a meta-analytical tool to address this aim, we were able to assess the general directions of the relationships, but also if these varied more than expected among studies.

MATERIAL AND METHODS

Data

Following an initial screening of the published literature, we contacted European researchers investigating wild plant pollination. We did this in 2015. We requested published and unpublished data from studies where seed set of a native insect-pollinated plant species had been measured at a minimum of five sites, which were separated by at least 1 km. Data should be from Europe, and most of the sites should be situated in landscapes (1 km radius) where at least 50% of the land was covered by agriculture, including arable land, permanent crops, pastures, etc. In addition, while there was no requirement that the original aim of the studies was to assess the effect of landscape homogeneity, we required variation in landscape homogeneity among the sites within each study. We identified suitable data for 22 plant taxa (for details, see supplementary file 1A), from both potted plants in experimental field studies (15 studies, 10 taxa) and naturally occurring plant populations (22 studies, 15 taxa). The data were collected in eight European countries (supplementary file 1A) between the years 2000 and 2015. When the identified studies included data on more than one plant species, we treated the data for each species as a separate study. All studies from the same country were later grouped (see statistical methods).

Flower visitation of the focal plants (i.e. focal observations of the study plants) was recorded in 14 of the studies, but we excluded one because bees and other flower visitors were not distinguished in that study. In another study, only bees had visited the flowers during the observations. In nine studies, flower visitation was quantified as the number of observed visitors divided by the number of flowers at the site, or sub-site for studies including replication within sites. In the four remaining studies, the number of observed flower visitors was recorded per group of plants, using the same number of plants at all sites within a study. To keep the data as homogeneous and comparable among studies as possible, we did not include other types of estimates on pollinator densities such as data deriving from e.g. transect walks and pan traps, which we considered less relevant from a pollination perspective. To account for differences in sampling effort (sampling time and the number of observed flowers or plants) among the studies, we z-transformed flower visitation within each study (see statistical methods).

We extracted land-cover information for landscape sectors with 1 km radius around each site, or sub-site for studies with replications within sites. This radius corresponds to a common foraging distance of wild bees (Walther-Hellwig & Frankl 2000; Greenleaf et al. 2007) and has been shown to be relevant when assessing landscape effects on flower visitation by bees (e.g. Steffan-Dewenter et al. 2001). We extracted data from the CORINE online database (https://www.eea.europa.eu/data-and-maps/data/corine-biotopes) with a minimum mapping unit of 25 ha for polygon data from 2006. We expected that the proportion of arable land had remained rather stable during the time span in this study (2000–2015), because for example in the UK, only around 1% of the total area was reclassified between 2006 and 2012, and the changes were biased towards forested land (Cole et al. 2018).

Statistical methods

To analyse the relationships between (i) flower visitation and seed set, (ii) proportion of arable land and flower visitation, and (iii) proportion of arable land and seed set, we used hierarchical meta-analyses (R package metafor; Viechtbauer 2010) in R v.4.1.0 (R Core Team 2021). This is a meta-analytical tool that allows the use of factors to group data that are not independent, such as studies from the same country.

We estimated seed set as the proportional seed set per fruit, or as the number of seeds per fruit when the total number of ovules had not been measured (supplementary file 1B). To account for the different scales at which these estimates were reported (supplementary file 1B), we z-transformed (mean = 0, SD = 1) seed set within each study. For the same reason (supplementary file 1B), we z-transformed flower visitation by bees and other insects (after log-transforming the latter two), respectively, within each study. For studies where pollinator data included zeros, we added the minimum non-zero value (1 or smaller) for that particular study, before the log-transformation.

To prepare for the meta-analyses, we calculated effect sizes and variances for each study using either linear models when data were collected from independent sites, or linear mixed-effects models when we needed to specify random factors to account for geographical dependence among sub-sites from the same study site. For each of the studies (supplementary file 1A) with enough data we tested the following relationships:

- Flower visitation by bees and seed set (13 studies)
- Flower visitation by other insects and seed set (12 studies)

Table 1 – Results from the meta-analyses. Interrelations between the proportion of arable land, abundance of flower-visiting bees, as well as other flower-visiting insects, and seed set. For each meta-analysis, the number of studies (Studies (n)), the overall estimates (Pearson's r), their associated 95% confidence intervals (CI_{95}) and p values are shown, in addition to Q statistics and the associated significance (Q_p) that indicates if effect sizes are heterogeneous; column I^2 (%) shows how much of the variability is caused by among study variation, rather than by sampling error. Potted: potted plants; nat. occ.: naturally occurring plants.

Variable	**Studies (n)**	**Q**	**Q_p**	**I^2 (%)**	**Pearson's r**	**CI_{95}**	**p**
Flower visitation by bees							
Proportion of arable land	13	26.65	< 0.01	30.00	0.02	-1.12–1.08	0.97
Flower visitation by other insects							
Proportion of arable land	12	9.59	0.57	25.41	-0.66	-1.78–0.45	0.24
Seed set							
Flower visitation by bees	13	9.34	0.67	< 0.01	0.19	0.32–0.34	0.02
Flower visitation by other insects	12	17.05	0.11	23.14	-0.05	-0.26–0.16	0.64
Proportion of arable land (potted)	15	15.20	0.36	< 0.01	-0.002	-0.73–0.73	> 0.99
Proportion of arable land (nat. occ.)	22	48.32	< 0.01	10.20	-0.44	-1.25–0.36	0.28

- Proportion of arable land and flower visitation by bees (13 studies)
- Proportion of arable land and flower visitation by other insects (12 studies, because in one study, only bees visited the flowers)
- Proportion of arable land and seed set:
    - in potted plants (15 studies)
    - in naturally occurring plants (22 studies)

For each of these relationships, we then ran a separate random-effects meta-analysis, using the effect sizes and variances obtained in the previous step. In these meta-analyses, we specified country as a grouping factor to account for non-independence among studies from the same country, since we expected land-use history, climate, and political decisions to have shaped the landscape similarly within, but not necessarily among, countries. Since the shared phylogenetic history of plant species can pose a potential bias in meta-analyses (Vamosi et al. 2006; Chamberlain et al. 2012), we ran extra models with plant family as grouping factor, which had no qualitative impact on the results (supplementary file 2A). Because the plant species were all insect-pollinated, and therefore did not represent a random selection of angiosperms, we did not find it necessary to further control for the phylogeny of the plants. When extracting effect sizes and variances, some of the sub-replicated studies, for which we used linear mixed models, had a random variance close to zero. We therefore aggregated data from these studies and instead used mean values per site (aggregation of plant, insect, and landscape data from all sub-sites within a site). This had no qualitative impact on the results (supplementary file 2B). Because it is possible that potted plants and plants from naturally occurring populations respond differently to pollination-related effects of variation in the proportion of arable land, we ran the meta-analysis on the proportion of arable land and seed set separately for these two groups. For flower visitation by bees and other insects, we were not able to make this distinction due to the lower number of studies (n = 13 and n = 12, respectively).

We used Wald's test, with restricted maximum likelihood, to evaluate if the effect differed from zero. We used Q statistics to evaluate if the heterogeneity among effect sizes was larger than expected by chance (Higgins & Thompson 2002), which would indicate that an important moderator is missing from the model (Del Re 2015). In addition, we used the inconsistency index I^2 to evaluate the proportion of total variation resulting from heterogeneity among studies rather than sampling error (Higgins & Thompson 2002). To ease interpretation of fig. 1, we used Fisher's z-transformation and transformed the z values that had been used in the meta-analyses, to Pearson's r correlations (Batáry et al. 2018).

RESULTS

Bees constituted 57 ± 29% (mean ± SD) of the total number of flower visitors across the studies where pollinator data had been collected and bees had been distinguished from other insects. The remaining 43% (referred to as other insects) were butterflies, moths, hoverflies, bee flies, and other unidentified flower-visiting insects. Only eight of the studies distinguished between honey bees and other bees. In these studies, wild bees were more common than honey bees, with honey bees constituting 11 ± 11% (mean ± SD) of the individual flower-visiting bees.

Seed set increased with increasing flower visitation by bees, but not with other insects (table 1, fig. 1). We found no overall relationship between the proportion of arable land and flower visitation by bees or by other insects ($p > 0.05$, table 1, fig. 2). The effect of the proportion of arable land on flower visitation by bees was significantly context-dependent, as shown by heterogeneous effect sizes among studies ($Q_p < 0.05$, table 1, fig. 2). The inconsistency index I^2 showed that true heterogeneity among studies explained 30% of the variation (table 1). Flower visitation by other insects was unrelated to the proportion of arable land in a consistent manner across studies ($Q_p > 0.05$, $p > 0.05$, table 1, fig. 2).

The proportion of arable land did not have a significant relationship with seed set for either naturally occurring or potted plants ($p > 0.05$, table 1, fig. 2). However, seed set of naturally occurring plants was significantly heterogeneously related to the proportion of arable land among studies ($Q_p < 0.05$, table 1, fig. 2) and the inconsistency index I^2 shows that true heterogeneity explained 10.2% of the variation. Notably, we observed considerable variation in the direction of the effect across studies, even within species or genera (fig. 2). This was not the case concerning potted plants ($Q_p > 0.05$, $p > 0.05$, table 1, fig. 2). For seed set of naturally occurring plants, we tested if the heterogeneous effect sizes related to mean latitude (per study) and mean proportion of arable land (per study), but the addition of these moderators did not explain the heterogeneity (supplementary file 2C). We did not test if the addition of the above moderators explained the heterogeneity in the relationship between the proportion of arable land and flower visitation by bees, because of the low number of studies (n = 13).

DISCUSSION

As expected, seed set in the study plants increased with flower visitation by bees, but not by other insects, possibly because of a biased choice of bee pollinated plants among researchers. When splitting the different groups of bees, more than 90% of the flower-visiting bees were wild bees (similar to Hung et al. 2018), likely reflecting that honey bees tend to aggregate on mass-flowering resources (Rasmussen et al. 2021). This highlights the importance of maintaining these insects for the pollination of wild plants in agricultural landscapes. Despite that the abundance of wild bees often declines with the proportion of arable land in the surrounding landscape (Da Encarnação Coutinho et al. 2018), neither seed set, nor flower visitation declined with the proportion of arable land across all studies. For naturally occurring plants as well as flower-visiting bees, the relationship with increasing proportions of arable land instead varied strongly among the studies, as shown by a significantly heterogeneous response (table 1), including strongly positive as well as strongly negative effects of increasing proportion of arable land in individual studies (fig. 2). Similar patterns for bees and seed set suggest that the effect on seed set is driven by flower-visitation and pollen transfer.

For potted plants, we found no relationship at all between increasing proportions of arable land and seed set, neither consistent ($p > 0.05$), nor inconsistent ($Q_p > 0.05$). Based on our results it is, however, unclear whether the observed difference between potted and naturally occurring plants is explained by a true difference between them or reflects a difference in sample size between the groups (n = 15 for potted plants, compared to n = 22 for naturally occurring plants).

Habitat fragmentation can disrupt flower visitation and pollination (Steffan-Dewenter & Tscharntke 1999; Aguilar et al. 2006; Cranmer et al. 2011; Aguilar et al. 2019), but we show that an increasing proportion of arable land instead has a strongly variable impact on flower visitation by bees and seed set of wild plants, at least for the subset of plants that is covered in this study. While a complete lack of effect could have been explained by an inappropriate landscape gradient (Winfree et al. 2009) or scale (Westphal et al. 2006), or by the fact that both wild bees and the flowers they visit are rare in homogeneous landscapes (i.e. similar per capita flower visitation as in heterogeneous landscapes, cf. Persson & Smith 2013), a strongly variable effect needs a further explanation. We suggest that it results from variation in the extent to which the proportion of arable land reflects pollinator-relevant effects in the different study landscapes.

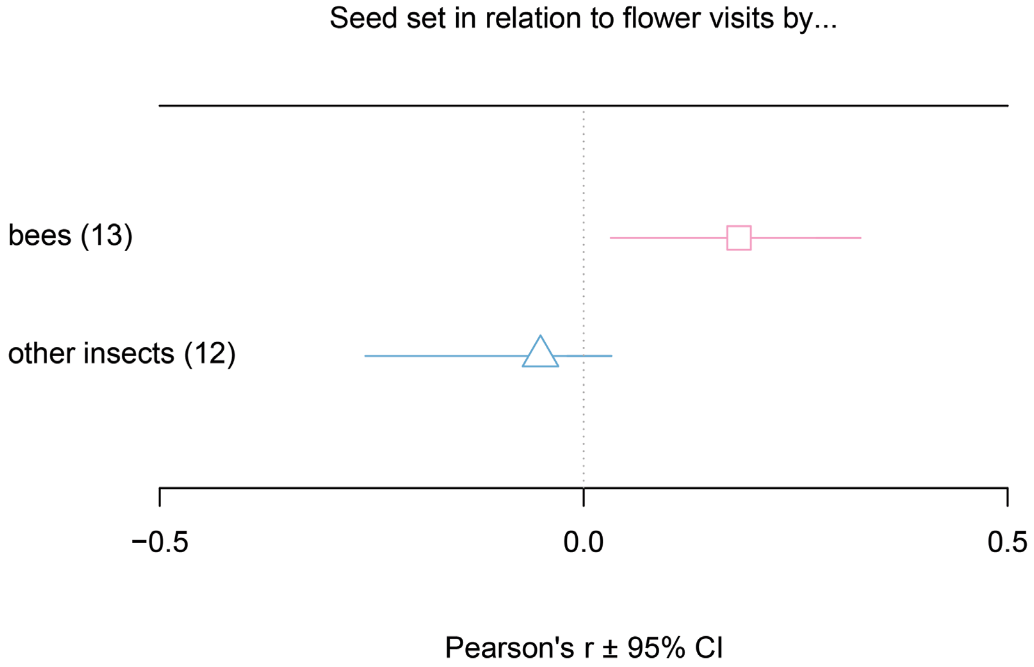

Figure 1 – Seed set in the tested plant species increased with flower visitation by bees (pink square), but not with other insects (blue triangle). Estimated mean values (squares and triangles) and 95% confidence intervals (error bars) from the meta-analyses are shown.

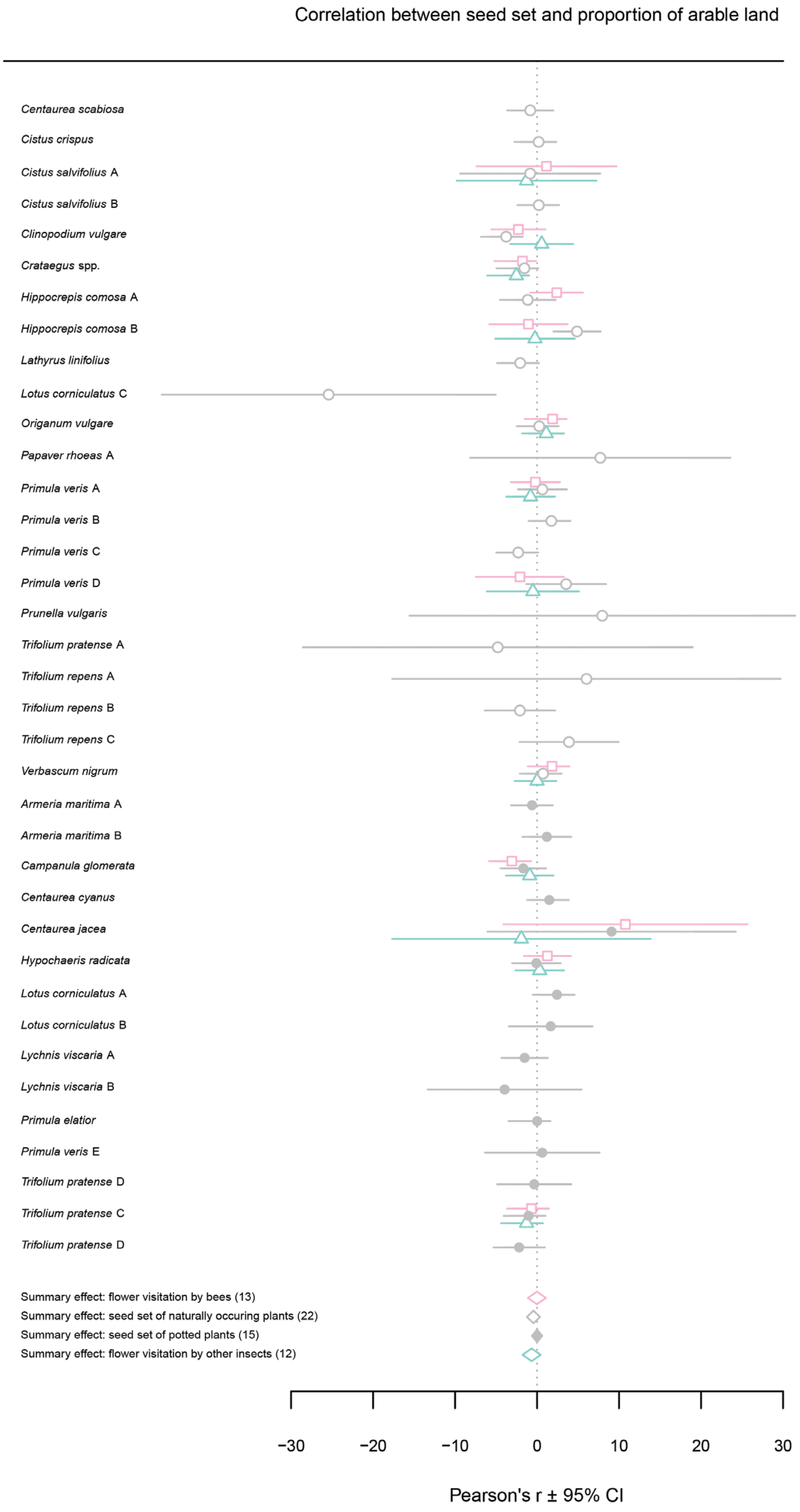

Figure 2 – Forest plot showing the relationship with proportion of arable land for flower visitation by bees (open pink squares), flower visitation by other insects (open blue triangles), and seed set (grey circles) in naturally occurring (open circles) and potted (filled circles) plants. The estimated correlation coefficients (squares, circles, and triangles) and 95% confidence intervals (error bars) for each of the included studies are shown. The summary effects (mean ± 95% CI) of increasing proportion of arable land are shown as diamonds.

Land-use change can affect pollinators in very different ways depending on how it alters floral resource availability (Winfree et al. 2011). While an increasing proportion of arable land often has a negative effect on wild bees when it occurs at the expense of flower-rich semi-natural habitat (Kennedy et al. 2013; Clough et al. 2014), it can instead have a positive effect when it substitutes flower-poor habitats, such as forests (Winfree et al. 2011). In addition, resource availability is not always low in landscapes dominated by arable land but depends on crop management (Tuck et al. 2014) and the configuration of arable land (Martin et al. 2019). When fields are small, or subject to organic farming, landscapes with high proportions of arable land can contain sufficient floral resources to maintain high bee densities (Rundlöf et al. 2008; Carrié et al. 2018; Hass et al. 2018; Martin et al. 2019). Therefore, the way in which increasing proportions of arable land affect seed set and flower visitation by bees depends on the type of arable land as well as the land-cover type it replaces.

Furthermore, while flower densities are usually higher in heterogeneous landscapes than in homogeneous landscapes, the characteristics of co-flowering plants themselves can affect each other in contrasting ways (Carvalheiro et al. 2014). They can either facilitate pollination by simultaneously attracting pollinators to a spot or compete for flower visitors (Hegland et al. 2009) and suffer from intraspecific pollen transfer (Morales & Traveset 2008). Hence, the effect of increasing proportion of arable land on flower visitation and seed set may depend on flower availability in the local habitat (cf. Herbertsson et al. 2018) and differ between plant species depending on their relative attractiveness to bees (Mesgaran et al. 2017). The focus on individual plant species in this study, compared to averaging over a whole plant community as in Clough et al. (2014), may thus have resulted in a larger heterogeneity of landscape effects.

Common flowering crops, such as oilseed rape and red clover, can increase bee densities (Westphal et al. 2003; Rundlöf et al. 2014), alter the bumble bee community composition (Diekötter et al. 2010), and redistribute bees across the landscape (Kovács-Hostyánszki et al. 2013; Holzschuh et al. 2016; Marja et al. 2018). Consequently, their effect on flower visitation depends on the location and phenology of the wild plants relative to the crop and on the extent to which they share pollinators with the crop (Cussans et al. 2010; Kovács-Hostyánszki et al. 2013; Herbertsson et al. 2017; Magrach et al. 2018). Flowering crops are often supplemented with honey bees, so that the abundance of honey bees on natural vegetation in agricultural landscapes increases with cultivation of bee-pollinated crops (Holzschuh et al. 2016; Magrach et al. 2017), affecting pollination networks (Magrach et al. 2017) and flower visitation of wild plants. In this study, we had no information on the extent to which flowering crops and bee hives occurred in the surrounding landscapes, and we could therefore not test if any of these variables caused the heterogeneity.

CONCLUSION

To conclude, we show that the relation between increasing proportion of arable land and pollination of wild plants is highly context-dependent. We found no consistent evidence that an increasing proportion of arable land reduces per capita flower visitation and seed set, which instead varied across the studies. While this suggests that other factors, such as habitat degradation, are stronger drivers of the loss of insect-pollinated plants in landscapes dominated by arable land, we also show that lack of flower-visiting bees can harm seed set in such plants, which could affect their long-term persistence. In order to develop adequate conservation solutions for wild insect-pollinated plants, it is therefore important to identify why the increasing proportion of arable land has a variable, and sometimes contrasting, effect on flower visitation and seed set.

DATA AVAILABILITY STATEMENT

All data used in the analyses are presented in supplementary file 3.

SUPPLEMENTARY FILES

Supplementary file 1 – Contains information about the data sets used in the meta-analyses.

https://doi.org/10.5091/plecevo.2021.1884.2525

Supplementary file 2 – Contains extended results.

https://doi.org/10.5091/plecevo.2021.1884.2527

Supplementary file 3 – Contains all data used in the meta-analyses.

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AUTHOR CONTRIBUTIONS

HGS, MR, and RB formulated the original idea; LH and JE developed the idea with contribution from HGS; LH compiled and analyzed the data with input from HGS, JE, PC, and PB. AH, ALH, AKH, AJ, AS, BJ, EÖ, HGS, IB, ISD, JE, JCS, JME, JPGV, LH, MA, MHE, MR, NF, PB, RB, SF, SH, SL, SP, TD, TTe, TTj, VS, VG, WK, and WEK provided data. LH interpreted the data and wrote the manuscript with contributions from all authors.

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