

RESEARCH ARTICLE

Mass-flowering lupin has positive, but limited, effect on wild bee conservation in agricultural landscapes

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Abstract

1. Mass-flowering crops have the potential to benefit pollinator conservation while still contributing to agricultural production, but their effects on pollinators can be variable and remain uncertain. Lupin could be particularly suitable for pollinator conservation because it is a late-flowering legume crop, but its effects on pollinators have never been investigated.
2. We tested the intra- and interannual effects of lupin cultivation on wild bees in landscapes with no history of lupin cultivation. To do this, we surveyed bees in semi-natural habitats before, during, and after lupin bloom and in the following year in landscapes with and without the experimental addition of 1 ha of lupin (*Lupinus albus* or *Lupinus angustifolius*). We also surveyed bees within lupin fields during bloom to understand which species use lupin floral resources.
3. We found positive effects of lupin cultivation on the abundance of bumblebees in the wider landscape after lupin bloom, likely due to increased bumblebee colony growth. However, this was only the case for the three common species that used lupin floral resources. In addition, this effect did not carry over into the following year.
4. Some large-bodied solitary bees, namely, *Megachile* spp., also utilized lupin floral resources but were not numerous enough in the surrounding landscape to determine an effect. This could be due to a general lack of large-flowered leguminous floral resources in agricultural landscapes.
5. *Synthesis and applications.* Our results indicate that lupin can potentially support the few common, abundant bee species that preferentially visit it. However, to effectively support the entire bee community, conservation management should focus on improving the quality of existing semi-natural habitats by increasing floral availability and diversity, possibly of Fabaceae floral resources in particular.

KEYWORDS

agricultural landscape, Agri-environment, Fabaceae, floral resources, mass-flowering crops, pollinator conservation, wild bees

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1 | INTRODUCTION

Decades of agricultural transformation to maximize crop production has created monoculture-dominated landscapes relatively barren of natural habitats (Robinson & Sutherland, 2002). Such landscape simplification drives declines in pollinator biodiversity (Wagner, 2020), a species group that contributes to the production of three-fourths of the leading global food crops (Klein et al., 2007). To curb this decline, agricultural policies have introduced conservation measures that aim to diversify and extensify agroecosystems (Batáry et al., 2015). Creation of flowering habitats has been shown to benefit pollinators (Lowe et al., 2021), but these biodiversity-friendly measures typically cover very small proportions of the landscape (Baude et al., 2016), and tend to be less implemented by intensive producers (Klebl et al., 2023). Despite conservation efforts, pollinators are still in decline (Powney et al., 2019), which suggests that flowering habitats need to be implemented on a much larger scale. Mass-flowering crops offer the possibility of large-scale floral enhancement while still contributing to agricultural production, which may be a more attractive option to farmers. However, if these crops can reliably contribute to pollinator conservation, and therefore should be incorporated into biodiversity measures, remains less certain.

A recent synthesis of the effects of mass-flowering crops on pollinators revealed effects that varied with season, blooming period, species group, and habitat type, but suggested that late-flowering crops have the largest potential to support pollinator populations (Riggi et al., 2023). These inconsistent relationships between mass-flowering crops and pollinator abundances could be because relatively few studies have considered post-bloom and across-year effects on pollinators in the wider landscape (Riggi et al., 2023), despite these being the key periods for assessing changes in pollinator populations. Typically, the biodiversity benefits of conservation measures are most effectively evaluated using a before-after control-impact design (Kleijn et al., 2006), but this approach is very difficult to apply to mass-flowering crop research due to the legacies of crop rotations. To better understand the potential for mass-flowering crops to be used as conservation measures, the intra- and interannual responses of pollinators should be monitored in relation to the introduction of a mass-flowering crop. Furthermore, these relationships should be examined for both local densities and predicted landscape-level population sizes, since these responses are meaningful to conservation outcomes (Kleijn et al., 2018).

One late-flowering crop that could be particularly suitable for biodiversity measures is lupin (*Lupinus* spp.), a leguminous plant that is known to have been utilized by rare and declining bee species in the past (Kleijn & Raemakers, 2008). Four species of lupin (*Lupinus albus*, *Lupinus angustifolius*, *Lupinus luteus* and *Lupinus mutabilis*) are commercially grown for food and fodder globally (Lucas et al., 2015). However, agricultural specialization and intensification have greatly reduced the cultivation of leguminous crops (Zander et al., 2016), which likely has contributed to the disproportionate decline of bee species that preferentially forage on leguminous plants (Scheper et al., 2014) and indicates that cultivating these crops might benefit

bee conservation. In contrast to more abundant spring-flowering crops like oilseed rape, lupin blooms in mid-to-late summer, which provides floral resources during a relative dearth period in agricultural landscapes (Bishop, Fijen, et al., 2024; Timberlake et al., 2019). Lupin is visited by bees for its pollen (Fijen et al., 2021), which bees use primarily as provision for their brood, but it does not produce nectar (Fijen et al., 2021), so possible benefits to bee reproduction are uncertain. Lupin has a high protein content similar to soy (Bähr et al., 2014), and the demand for plant protein is rapidly increasing (Committee on Agriculture and Rural Development, 2023), so it may be attractive as a crop for plant protein production. Legumes are incorporated into the greening measures under the EU Common Agricultural Policy, but they are perceived to have limited benefits to biodiversity (Pe'er et al., 2017). However, these benefits may be underestimated due to the mass-flowering resources that grain and pulse legumes provide to bees (Cole et al., 2020). Understanding if lupin can benefit bee conservation would contribute to determining the suitability of mass-flowering crops, and of leguminous crops in particular, as biodiversity conservation measures with both farm and ecosystem benefits.

Here we tested the landscape-scale effects of lupin cultivation on wild bees to understand the potential of lupin as a tool for bee conservation in agroecosystems, which is currently unknown. We surveyed bees in landscapes with and without the experimental addition of lupin cultivation at four different time points to measure intra- and interannual effects: before, during, and after lupin bloom; and in the late spring of the following year. We also surveyed bees inside of lupin fields during lupin bloom to understand which species utilize lupin floral resources and therefore which species can be expected to benefit from lupin as a biodiversity measure. Finally, we determined how possible effects of lupin on local bee densities translate into landscape-scale differences by extrapolating densities to total pollinator community sizes, which although representing a fundamental measure of effectiveness of conservation efforts, has not been previously examined in mass-flowering crop research. We hypothesized that densities of bees that use lupin resources are greater after lupin bloom and in the following year in lupin landscapes than in control landscapes due to the positive impacts of pollen availability on reproduction. We furthermore expected that these effects are more pronounced when extrapolating to landscape-level bee community sizes.

2 | MATERIALS AND METHODS

The study was conducted in south Limburg, the Netherlands (Figure 1), an agricultural area characterized by mixed arable and dairy farming and by generally little cultivation of mass-flowering crops, aside from a small proportion of fruit orchards. We studied 13 organically or extensively managed lupin (*L. angustifolius* $n=5$ and *L. albus* $n=8$; 1.08 ± 0.55 ha, mean $\pm$ SD) fields to test the effects of the addition of lupin floral resources on wild bees in the surrounding landscape. Lupin was cultivated from 2021 to 2023,

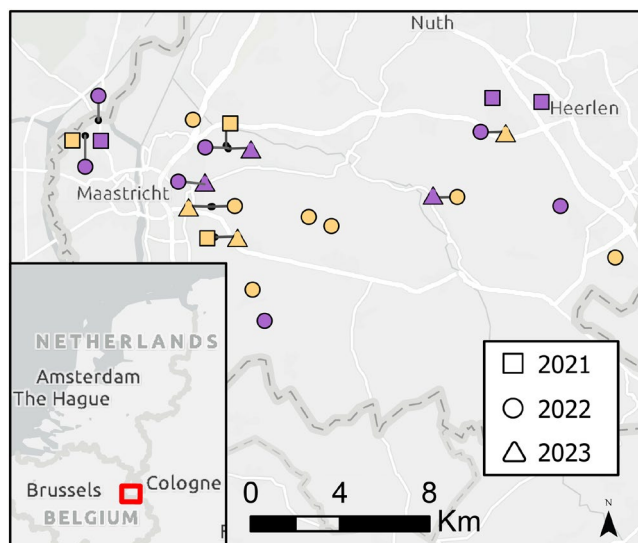


FIGURE 1 Map of study fields. Purple symbols indicate lupin fields and yellow control. Fields in close proximity are marked with indicator lines and were not sampled in the same year.

with a varying number of fields in each year (2021 $n=3$, 2022 $n=7$, 2023 $n=3$), but landscapes had no history of lupin cultivation prior to 2021, with the exception of one field. Because lupin cannot be cultivated successively on the same field, locations of fields vary across years even if cultivated by the same farmer. For each landscape with lupin cultivation, a control landscape was selected centred on an organically or extensively managed grain field to represent a typical and similar landscape without the experimental addition of lupin. Control landscapes were selected to have approximately equal coverage of surrounding semi-natural habitat (Netherlands National Land Use; Hazeu et al., 2020) as lupin landscapes (control $7.66 \pm 8.30\%$, lupin $7.52 \pm 8.06\%$; 500 m radius) to ensure similar landscape contexts. All fields sampled in the same year were minimum 1 km apart, but on average inter-site distances were larger (2.1 ± 1.2 km including distances between sites of the same treatment, and 3.8 ± 3.2 km between sites of different treatments). The average foraging distances of the largest bees in our study (bumblebees) are typically 500 m, but maximum foraging ranges exceed this distance (Redhead et al., 2016). Greater inter-site distances were not possible due to the selection of lupin-growing locations by the participating farmers, but we tested for possible spatial independence issues in our models (see Section 2.2).

2.1 | Surveys

Standardized transects (Westphal et al., 2008) were conducted by 1–2 observers before, during, and after the bloom of lupin (May–August), and in the spring following lupin cultivation (May) to determine baseline bee densities within landscapes and the effect of lupin cultivation thereafter. There were on average 4 weeks between each

sampling period within the same year (27.7 ± 11.7 days, mean $\pm$ SD). We only performed one survey in the year after lupin cultivation due to the likelihood of within-year resource dynamics having a large effect on observed bee abundances later in the summer, and because crop rotation of lupin in the vicinity of some fields would confound possible interannual effects. In each survey round, four 150 m² transects were selected in accessible flower-rich pollinator habitats in the landscapes surrounding focal fields. Where possible, an effort was made to equally distribute transects 0–500 m from the field. Selected habitats were most often roadside verges, but sometimes included extensive grasslands or mass-flowering resources such as wildflower strips or radish (*Raphanus sativus*) cover crops to ensure that the most attractive floral patches were covered by our surveys. Transects were 150 $\times$ 1 m, but dimensions were allowed to vary to accommodate the size of habitat patches shorter than 150 m in length. On dry days with $\geq 12^\circ\text{C}$, low winds and low cloud cover, transects were surveyed for 15 min excluding catching and handling time, and all bees encountered were recorded or collected with an insect net for later identification (total survey effort 2400 m² and 4 h per landscape). *Bombus terrestris* and *Bombus lucorum* queens and workers were grouped into one complex (*B. terrestris* agg.) as they cannot be separated without molecular techniques in our study area (Alferink et al., 2020). Floral resources were also recorded within the transect area by identifying all forbs in flower to species using ObsIdentify and relevant keys (Streeter & Hart-Davies, 2016) and by counting all individual flowers (or heads for Asteraceae) for each species. Flower counts were multiplied by an average flower area for each species, which was then summed across species and divided by the transect area to calculate the percentage flower cover (Scheper et al., 2015). No permits or ethical approval were required for the surveys in this study.

Transects were additionally carried out within lupin fields to identify the species utilizing lupin as a resource and their relative abundances. Four transects of 75 m² were placed at equal intervals between field edge and centre and were surveyed for 7.5 min excluding catching and handling time twice during the blooming period (total survey effort of 600 m² and 1 h per field). All bees visiting lupin flowers were recorded or collected for later identification.

2.2 | Analyses

First, we split our bee observations into three groups according to their observed interaction with lupin floral resources. In our surveys within lupin fields, three bumblebee species constituted 68% of all bee visitors of lupin flowers: *Bombus lapidarius*, *B. terrestris* agg., and *Bombus pascuorum* (see Table S1). Other bumblebees were not observed (except one single *Bombus hortorum* in 13 h of surveys, so we did not consider this species as lupin-visiting), and solitary bees made up 7% of observations. The remaining percentage was *Apis mellifera*, which are managed and so are not analysed here. We assumed that lupin would have the largest potential effect on lupin-visiting bumblebees, since bumblebees grow their colonies within one season,

while solitary bees are more likely to be affected by across-year resource dynamics (Roulston & Goodell, 2011). We did not further separate solitary bees into lupin-visiting and not lupin-visiting categories because the most frequent visitors to lupin, *Megachile willughbiella* and *Megachile ericetorum* (77% of solitary bee visitors), were seldom observed in the wider landscape in any survey round, which prevented sufficient counts for a separate analysis. Accordingly, we analysed the effect of lupin cultivation on the summed abundances of lupin-visiting bumblebees, other bumblebees, and solitary bees separately.

All analyses were conducted in R version 4.1.2 (R Core Team, 2021). We constructed a linear mixed model for each bee group using the glmmTMB package (Brooks et al., 2017) to estimate the effect of lupin cultivation on landscape bee densities before, during, and after bloom. We analysed bee densities recorded in the spring following lupin cultivation separately with linear models because these observations were not independent of the within-year observations due to some overlapping landscapes across years, but we used the same general approach. In preliminary models using only data from lupin landscapes, we confirmed that lupin field size did not affect the density of bees in the landscape ($p \geq 0.2$ for all models), and thus did not further consider this variable in our analyses. For each bee group, we used bee densities averaged across transects within sites as our response variable, because models constructed using transect-level data were spatially autocorrelated and could not converge with the inclusion of a spatial correlation structure. Bee densities were square root transformed to achieve residual normality. We tested the interaction between treatment (lupin or control) and round to answer our main research question. For following year models, there was only one survey round, so only treatment was included. We included average transect flower cover, average transect flower richness, landscape semi-natural habitat (%), alternative (i.e. non-lupin) landscape mass-flowering resources (%) (Nationaal Georegister, 2024), and year as covariates to control for other possible influences on bee densities. All continuous fixed effects were centred and scaled (z-scores) to standardize beta coefficients. For within-year models, the site was used as a random effect to account for repetition across sampling rounds. For final model structures, see Table S2.

We inspected residual plots and ensured that model assumptions were met, including the absence of VIFs >3 and unmodelled interactions, using the DHARMA (Hartig & Lohse, 2022), effects (Fox & Weisberg, 2018, 2019) and performance (Lüdecke et al., 2021) packages. We also checked for spatial autocorrelation in our models using the DHARMA package, because bees flying >500 m from study sites could have introduced non-independence between sites, which would have influenced the comparison of lupin and control landscapes in our models. There was no significant spatial autocorrelation present in our residuals, indicating that our observations can be considered spatially independent. The landscape mass-flowering resource variable was dropped from all following year models because it produced VIFs >4 due

to correlation with flower cover. For the solitary bee model, we excluded a single outlier transect because the extreme number of bees recorded there could not readily be explained by our measured environmental parameters (Figure S1). We evaluated model fixed effects using log-likelihood ratio tests, but tested our main hypothesis, that lupin cultivation increases bee densities after bloom, through a priori contrasts between treatments in each round using the emmeans package (Lenth et al., 2024). We applied this method to all models because a priori contrasts do not require a significant ANOVA test (Quinn & Keough, 2002), and we did not adjust p -values because the contrasts were planned and orthogonal (Lenth, 2024; Quinn & Keough, 2002).

To estimate how possible effects of lupin cultivation on bee densities at the transect level translate into changes in landscape-scale community sizes, we extrapolated our modelled bee densities by multiplying them by the area of semi-natural habitat in the landscape (Kleijn et al., 2018; Persson & Smith, 2013), assuming a linear abundance–area relationship (Taki et al., 2018). First, we iteratively predicted bee densities in each treatment-round combination across the entire range of semi-natural habitat coverage observed in our study (1% increments up to 25%). Then we multiplied the density per m² (predicted density/150) by the respective coverage of semi-natural habitat (% semi-natural habitat/100 $\times \pi \times 500^2$) to calculate landscape-level bee abundance under varying landscape contexts. This allowed us to visualize the effect of lupin cultivation on bee populations while accounting for the influence of the local and landscape variables included in our models.

Plots were constructed using the ggplot2 (Wickham, 2009), viridis (Garnier et al., 2023), ggeffects (Lüdecke, 2018) and gridExtra (Auguie & Antonov, 2017) packages.

3 | RESULTS

Across the 4 years of the study, 5563 wild bees from 111 species were recorded (Table S3), and 14 of these species were observed to visit lupin (Table S1). Within lupin fields, *B. terrestris* agg. ($n=382$) and *B. lapidarius* ($n=382$) were the most commonly observed bumblebees, while *M. willughbiella* ($n=50$) and *M. ericetorum* ($n=17$) were the most commonly observed solitary bees. In semi-natural habitats in the surrounding landscape, the most common lupin-visiting bumblebees were *B. pascuorum* ($n=825$) and *B. lapidarius* ($n=712$), and the most common other bumblebees were *B. hortorum* ($n=129$) and *Bombus pratorum* ($n=62$). *Lasioglossum pauxillum* ($n=338$) and *Halictus scabiosae* ($n=181$) were the most common solitary bees. Flower species encountered are presented in Table S4.

3.1 | Intra-annual effects

In the wider landscape, lupin-visiting bumblebee densities were significantly higher in lupin landscapes after bloom (Figure 2a;

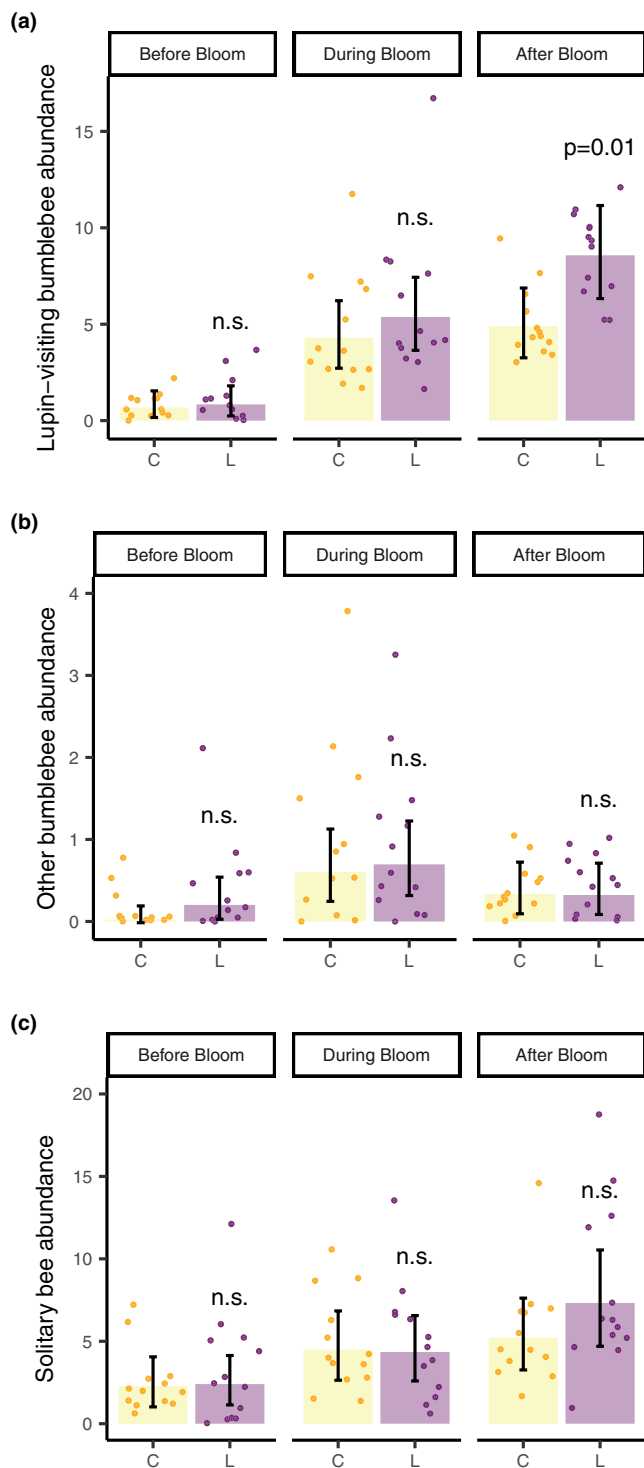


FIGURE 2 Estimate marginal mean $\pm$ 95% CI abundance of (a) lupin-visiting bumblebees, (b) other bumblebees, and (c) solitary bees in semi-natural habitats before, during, and after lupin bloom (back transformed from the square root scale). C, control; L, lupin. Abundances expressed per 150 m² per 15 min. Points represent partial residuals.

Table S6), but did not differ between lupin and control landscapes before or during bloom. In addition, lupin-visiting bumblebee

densities were significantly predicted by transect flower cover (Table S5; $\text{Chisq}=8.117$, $\text{df}=1$, $p=0.004$), but not by other local and landscape habitat variables.

Other bumblebee and solitary bee densities did not significantly differ between treatments in any survey round, or overall (Tables S7–S10; Figure 2b,c). Other bumblebee densities were not significantly related to any local or landscape habitat variable, but solitary bee densities were significantly positively predicted by both transect flower cover and richness (Table S9; $\text{Chisq}=5.494$, $\text{df}=1$, $p=0.019$; $\text{Chisq}=6.177$, $\text{df}=1$, $p=0.013$).

The differences in transect-level densities of lupin-visiting bumblebees between lupin and control landscapes after lupin bloom resulted in large differences in bumblebee abundances at the landscape scale (Figure 3). For example, in landscapes with an average cover of semi-natural habitat (7%), landscapes with lupin cultivation were predicted to support 1339 more bumblebees than control landscapes after lupin bloom. These differences were not present for other bumblebees or solitary bees (Figures S1 and S2).

3.2 | Interannual effects

In the spring following lupin cultivation, there were no significant differences between control and lupin landscapes in the densities of lupin-visiting bumblebees or solitary bees (Tables S11–S13), but other bumblebee densities in lupin landscapes were marginally higher than those in control landscapes (Table S12; $\text{Chisq}=2.774$, $\text{df}=1$, $p=0.096$). Lupin-visiting bumblebee densities were significantly predicted by flower cover (Table S11; $\text{Chisq}=23.619$, $\text{df}=1$, $p<0.001$), while other bumblebee densities were significantly related to flower richness (Table S12; $\text{Chisq}=5.759$, $\text{df}=1$, $p=0.016$). Solitary bee densities were marginally related to landscape semi-natural habitat cover (Table S13; $\text{Chisq}=3.662$, $\text{df}=1$, $p=0.056$).

4 | DISCUSSION

Our results suggest that lupin can possibly benefit bee populations, but these effects are limited to the subset of the bee community that preferentially visits it. In our study area, this subset primarily comprised three common bumblebee species that are not directly of conservation concern. Lupin likely supported colony growth and reproduction for these species by providing resources during a key period. However, these effects were not detected in the year following lupin cultivation. Lupin may also benefit solitary bees that prefer to forage on large Fabaceae, but the low counts of these species in the wider landscape prevented us from testing this empirically, which could indicate that these floral resources might be lacking in agricultural areas. Though the cultivation of legume crops like lupin can provide abundant floral resources to certain bee species, conservation strategies should instead emphasize measures to increase the quality of semi-natural habitats in agricultural landscapes to support the entire bee community.

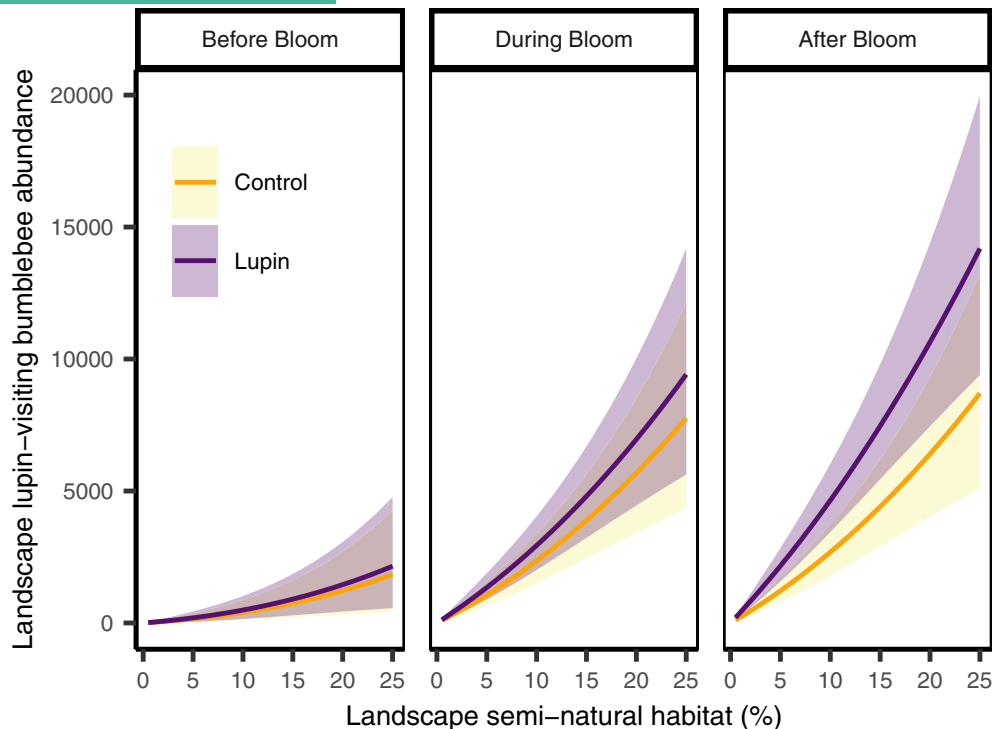


FIGURE 3 The effect of lupin cultivation on landscape-scale lupin-visiting bumblebee abundance across different landscape contexts before, during, and after lupin bloom. Back-transformed bee abundances and 95% CIs are extrapolated from transect densities to the landscape scale.

4.1 | Intra- and interannual effects of lupin on bumblebees

After bloom, lupin supported greater landscape bumblebee densities and in turn community sizes for lupin-visiting bumblebees, suggesting that mass-flowering crops can benefit the conservation of pollinators that preferentially visit them. These bumblebee species were likely able to take advantage of the lupin floral resources because they are abundant, common species that are likely relatively well adapted to resource perturbations in agricultural landscapes (Hemberger et al., 2023). During our study, lupin typically bloomed from mid-June to early July, which is a low point in floral resource availability due to agricultural and land management in the study area (Bishop, Fijen, et al., 2024), as well as likely the approximate peak egg-laying period for these common bumblebee species (Cumber, 1949; Duchateau & Velthuis, 1988). Lupin increased the continuity of floral resource availability in these landscapes, which has been shown to improve bumblebee colony performance (Hemberger et al., 2022). The increase in lupin-visiting bumblebee abundance in lupin landscapes after bloom can thus likely be explained by the use of lupin pollen resources by these species to rear brood, resulting in larger bumblebee community sizes in the landscape later in the season.

The differences in landscape-level bumblebee abundance shown in our extrapolations suggest that the addition of lupin resources supports larger bumblebee colonies, which can increase colony reproductive output (production of queens and males) (Westphal et al., 2009). Our extrapolations assumed no limitation of lupin

resources with increasing landscape complexity, which in theory might be the case if more complex landscapes had greater resident bumblebee communities (Persson & Smith, 2013). Nesting resources could also possibly limit bumblebee communities, but nesting density likely linearly increases with landscape complexity (Stanley et al., 2013). There was no effect of lupin field size on bumblebee densities, so the amount of lupin available was likely not limiting. Previous research has shown that late-flowering red clover crops can increase densities of bumblebee queens and males in agricultural landscapes (Rundlöf et al., 2014) but that early-flowering oilseed rape does not enhance bumblebee colony reproduction (Westphal et al., 2009). Since our results imply that bumblebee colony size was enhanced late in the season (July–August), it is possible that lupin contributed to increased bumblebee reproduction.

However, we did not observe this possible positive effect on reproduction in the spring following lupin cultivation. It may be difficult to detect a legacy effect of mass-flowering crops after only 1 year due to the many ways that land use and habitat quality influence queen production, overwintering survival, and spring nest establishment (Carvell et al., 2017) because these processes could have diminished any effect of lupin from the previous year. While it was a strength of the study that there was no history of lupin cultivation in our study area, which allowed the implementation of a before-after control-impact design, multi-year legacies may be better suited to detecting effects of past mass-flowering crops due to the gradual buildup of populations across years (Beyer et al., 2021). Furthermore, the springtime abundances of *B. pascuorum* were

relatively higher than those of *B. terrestris* agg. and *B. lapidarius* ($n=150$, 67 and 36, respectively). The densities of this species in lupin fields were relatively lower than those of the two other species (Table S1), so this relatively lower potential for benefiting from lupin might have obscured any effect on bumblebee densities in the following year. These differences can likely be explained by the differential foraging behaviours of these three species (Walther-Hellwig & Frankl, 2000).

4.2 | Fabaceae resources and the conservation of the entire bee community

Some solitary bee species did visit lupin, and *M. willughbiella* and *M. ericetorum* visited lupin in particularly high numbers, suggesting that these species might also benefit from lupin cultivation. Despite these bees being attracted to lupin from the surrounding landscape, they were not frequently detected in the landscape semi-natural habitat patches themselves, which limited our ability to analyse the effect of lupin on solitary bees. Bees that preferentially forage on Fabaceae were found to have declined in the Netherlands during the past century (Scheper et al., 2014), likely due to the loss of Fabaceae-rich grassland habitats and the decrease in cultivation of Fabaceae for fodder (Scheper et al., 2014). The low presence of these *Megachile* species outside of lupin fields could thus indicate that landscapes in general lack leguminous forage, in which case the addition of lupin could greatly benefit bees that prefer large-flowered Fabaceae species. The other solitary bees observed on lupin were far fewer in number, despite being relatively common bees in the wider landscape, which is likely because their smaller size prevents them from being able to trip the flowers enough to collect pollen (Fijen et al., 2021). Other large, but rare, solitary bees might also benefit from lupin cultivation, as one *Anthophora retusa* individual was observed collecting pollen in a lupin field (although outside of the study transects) (Bishop, 2023). Even though our results do not provide evidence for the effect of lupin cultivation on solitary bees, we cannot rule out a possible effect on species that seem to preferentially visit it, like *M. willughbiella* and *M. ericetorum*.

Other bumblebee species were not affected by lupin cultivation but were affected by alternative floral resources in the surrounding landscape. The marginal difference in other bumblebee densities across treatments in the spring following lupin cultivation seemed to be due to flower species composition in the survey areas. Landscapes with lupin cultivation had slightly higher cover of *Lamium* spp. and *Trifolium* spp. in surveyed transects (total 3.71% and 1.94% in lupin landscapes, and 3.13% and 1.45% in control landscapes, respectively), which are among the preferred plants of the most common non-lupin-visiting bumblebees observed in this sampling round, *B. hortorum* and *B. pratorum* (Kleijn & Raemakers, 2008). These observations highlight the importance of *Lamium* spp. for bumblebees in springtime (Fussell & Corbet, 1992), and might additionally suggest that *Trifolium* spp. should be prioritized in biodiversity-friendly agricultural measures (Cole et al., 2022).

Because lupin primarily supported only three common bumblebee species, our results emphasize the need for high-quality semi-natural habitat patches in agricultural landscapes to maintain pollinator populations, which aligns with the recommendations of previous mass-flowering crop research (Beyer et al., 2020). The majority of the species observed in the wider landscape did not visit lupin (88%), meaning they rely principally on resources in semi-natural habitats or other biodiversity-friendly agricultural areas. In addition, we found positive effects of flower richness on non-lupin-visiting bee groups, indicating that habitat quality determined the suitability of these habitat patches to support bees. While our measurements focused on floral resources, nesting resources also contribute to habitat quality and thus suitability for bees, and should therefore also be incorporated into conservation actions. Since mass-flowering crops cannot benefit the majority of the bee community, and since arable fields cannot provide stable nesting habitats for bees, conservation should likely be focused on measures that increase the quality of semi-natural habitats and their resource continuity, ideally by targeting large permanent herbaceous habitats such as pastures (Baude et al., 2016; Bishop, Fijen, et al., 2024), as opposed to arable crops.

4.3 | Management recommendations

Our study suggests that lupin could positively impact common, crop-visiting bumblebee species when used as a crop diversification measure. As a late-flowering Fabaceae crop, lupin has the potential to be more beneficial to bees compared with other mass-flowering crops, because it possibly fills an existing resource gap in time and in preferred forage. This potential for positive biodiversity impacts would likely be enhanced when combined with a diversity of flowering crops (Martins et al., 2018). However, policies that support the enhancement of semi-natural habitats should likely be further incentivized to improve their uptake, so that the majority of the bee community that does not visit crops can be supported. While a wide diversity of floral species should be enhanced, increasing the cover and richness of Fabaceae floral resources in semi-natural habitats might be particularly beneficial, since these species are relatively lacking in agricultural areas. Small-flowered species such as clovers (*Trifolium* spp.) and lucerne (*Medicago sativa*) are already regularly incorporated into conservation strategies, but large-flowered species, such as *Lathyrus* spp., *Vicia* spp., and *Lotus* spp. could be further promoted (Carvell et al., 2006). In conclusion, diversification at the field scale can still likely improve the overall functionality of agricultural landscapes, but diversification measures need to encompass both production and non-production areas to achieve landscape-scale support of biodiversity.

AUTHOR CONTRIBUTIONS

Gabriella A. Bishop, David Kleijn, and Thijs P. M. Fijen conceived the ideas and designed the methodology; Gabriella A. Bishop, Inês I. Vicente, and Thijs P. M. Fijen collected the data; Gabriella A. Bishop

analysed the data; Gabriella A. Bishop led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication. Statement on inclusion: This study was conducted in collaboration with farmers and land management organizations in south Limburg, the Netherlands. Results and feedback were discussed regularly with all stakeholders.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data available via Zenodo <https://doi.org/10.5281/zenodo.11352983> (Bishop, Kleijn, et al., 2024).

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REFERENCES

- Alferink, L., Marshall, L., Jonghe, R. D., & Biesmeijer, J. (2020). Distinguishing white-tailed bumblebees in the Netherlands: Morphology, ecology and DNA-barcoding. *Authorea*. <https://doi.org/10.22541/au.159969685.50828819>
- Auguie, B., & Antonov, A. (2017). *gridExtra: Miscellaneous functions for 'grid' graphics*. CRAN.
- Bähr, M., Fechner, A., Hasenkopf, K., Mittermaier, S., & Jahreis, G. (2014). Chemical composition of dehulled seeds of selected lupin cultivars in comparison to pea and soya bean. *LWT—Food Science and Technology*, 59, 587–590. <https://doi.org/10.1016/j.lwt.2014.05.026>
- Batáry, P., Dicks, L. V., Kleijn, D., & Sutherland, W. J. (2015). The role of agri-environment schemes in conservation and environmental management. *Conservation Biology*, 29, 1006–1016. <https://doi.org/10.1111/cobi.12536>
- Baude, M., Kunin, W. E., Boatman, N. D., Conyers, S., Davies, N., Gillespie, M. A., Morton, R. D., Smart, S. M., & Memmott, J. (2016). Historical nectar assessment reveals the fall and rise of floral resources in Britain. *Nature*, 530, 85–88. <https://doi.org/10.1038/nature16532>
- 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, 2499–2508. <https://doi.org/10.1111/1365-2664.13745>
- Beyer, N., Gabriel, D., & Westphal, C. (2021). Contrasting effects of past and present mass-flowering crop cultivation on bee pollinators shaping yield components in oilseed rape. *Agriculture, Ecosystems and Environment*, 319, 107537. <https://doi.org/10.1016/j.agee.2021.107537>
- Bishop, G. A. (2023). *Zwarte sachembij—Anthophora retusa* [WWW document]. Waarneming.nl. <https://waarneming.nl/observation/280601660/>
- Bishop, G. A., Fijen, T. P. M., Raemakers, I., van Kats, R. J. M., & Kleijn, D. (2024). Bees go up, flowers go down: Increased resource limitation from late spring to summer in agricultural landscapes. *Journal of Applied Ecology*, 61, 431–441. <https://doi.org/10.1111/1365-2664.14576>
- Bishop, G. A., Kleijn, D., Vicente, I. I. G. P. P., & Fijen, T. P. M. (2024). Data from: Mass-flowering lupin has positive, but limited, effect on wild bee conservation in agricultural landscapes. *Zenodo*, <https://doi.org/10.5281/zenodo.11352983>
- Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Mächler, M., & Bolker, B. M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R Journal*, 9, 378. <https://doi.org/10.32614/RJ-2017-066>
- 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, 547–549. <https://doi.org/10.1038/nature21709>
- Carvell, C., Roy, D. B., Smart, S. M., Pywell, R. F., Preston, C. D., & Goulson, D. (2006). Declines in forage availability for bumblebees at a national scale. *Biological Conservation*, 132, 481–489.
- Cole, L., Kleijn, D., Dicks, L., Stout, J., Potts, S., Albrecht, M., Balzan, M., Bartomeus, I., Bebeli, P., Bevk, D., Biesmeijer, J., Chlebo, R., Dautarte, A., Emmanouil, N., Hartfield, C., Holland, J., Holzschuh, A., Knoben, N., & Scheper, J. (2020). A critical analysis of the potential for EU common agricultural policy measures to support wild pollinators on farmland. *Journal of Applied Ecology*, 57, 681–694. <https://doi.org/10.1111/1365-2664.13572>
- Cole, L. J., Baddeley, J. A., Robertson, D., Topp, C. F. E., Walker, R. L., & Watson, C. A. (2022). Supporting wild pollinators in agricultural landscapes through targeted legume mixtures. *Agriculture, Ecosystems and Environment*, 323, 107648. <https://doi.org/10.1016/j.agee.2021.107648>
- Committee on Agriculture and Rural Development. (2023). *European protein strategy* [WWW document]. https://www.europarl.europa.eu/doceo/document/AGRI-PR-742624_EN.html
- Cumber, R. A. (1949). The biology of humble-bees, with special reference to the production of the worker caste. *Transactions of the Entomological Society of London*, 100, 1–45. <https://doi.org/10.1111/j.1365-2311.1949.tb01420.x>
- Duchateau, M. J., & Velthuis, H. H. W. (1988). Development and reproductive strategies in *Bombus terrestris* colonies. *Behaviour*, 107, 186–207.
- Fijen, T. P. M., Morra, E., & Kleijn, D. (2021). Pollination increases white and narrow-leaved lupin protein yields but not all crop visitors contribute to pollination. *Agriculture, Ecosystems and Environment*, 313, 107386. <https://doi.org/10.1016/j.agee.2021.107386>
- Fox, J., & Weisberg, S. (2018). Visualizing fit and lack of fit in complex regression models with predictor effect plots and partial residuals. *Journal of Statistical Software*, 87, 1–27. <https://doi.org/10.18637/jss.v087.i09>
- Fox, J., & Weisberg, S. (2019). *An R companion to applied regression* (3rd ed.). SAGE.
- Fussell, M., & Corbet, S. A. (1992). Flower usage by bumblebees: A basis for forage plant management. *Journal of Applied Ecology*, 29, 451–465.

- Garnier, S., Ross, N., Rudis, B., Camargo, A. P., Sciaini, M., & Scherer, C. (2023). Rvision—Colorblind-friendly color maps for R. *Zenodo*, <https://doi.org/10.5281/ZENODO.4679423>
- Hartig, F., & Lohse, L. (2022). *DHARMA: Residual diagnostics for hierarchical (multi-level/mixed) regression models*. CRAN.
- Hazeu, G. W., Vitek, M., Schuiling, R., Bulens, J. D., Storm, M. H., Roerink, G. J., & Meijninger, W. M. L. (2020). *LGN2018: een nieuwe weergave van het grondgebruik in Nederland (No. 1566–7197)*. Wageningen Environmental Research.
- Hemberger, J., Bernauer, O. M., Gaines-Day, H. R., & Gratton, C. (2023). Landscape-scale floral resource discontinuity decreases bumble bee occurrence and alters community composition. *Ecological Applications*, 33, e2907. <https://doi.org/10.1002/eap.2907>
- Hemberger, J., Witynski, G., & Gratton, C. (2022). Floral resource continuity boosts bumble bee colony performance relative to variable floral resources. *Ecological Entomology*, 47, 703–712. <https://doi.org/10.1111/een.13154>
- Klebl, F., Feindt, P. H., & Piorr, A. (2023). Farmers' behavioural determinants of on-farm biodiversity management in Europe: A systematic review. *Agriculture and Human Values*, 41, 831–861. <https://doi.org/10.1007/s10460-023-10505-8>
- Kleijn, D., Baquero, R. A., Clough, Y., Díaz, M., De Esteban, J., Fernández, F., Gabriel, D., Herzog, F., Holzschuh, A., Jöhl, R., Knop, E., Kruss, A., Marshall, E. J. P., Steffan-Dewenter, I., Tschardtke, T., Verhulst, J., West, T. M., & Yela, J. L. (2006). Mixed biodiversity benefits of agri-environment schemes in five European countries. *Ecology Letters*, 9, 243–254. <https://doi.org/10.1111/j.1461-0248.2005.00869.x>
- Kleijn, D., Linders, T. E. W., Stip, A., Biesmeijer, J. C., Wäckers, F. L., & Bukovinsky, T. (2018). Scaling up effects of measures mitigating pollinator loss from local- to landscape-level population responses. *Methods in Ecology and Evolution*, 9, 1727–1738. <https://doi.org/10.1111/2041-210X.13017>
- Kleijn, D., & Raemakers, I. (2008). A retrospective analysis of pollen host plant use by stable and declining bumble bee species. *Ecology*, 89, 1811–1823.
- Klein, A. M., Vaissiere, B. E., Cane, J. H., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C., & Tschardtke, T. (2007). Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B*, 274, 303–313.
- Lenth, R. (2024). *Basics of estimated marginal means* [WWW document]. <https://cran.r-project.org/web/packages/emmeans/vignettes/basics.html#pvalues>
- Lenth, R. V., Bolker, B., Buerkner, P., Giné-Vázquez, I., Herve, M., Jung, M., Love, J., Miguez, F., Riebl, H., & Singmann, H. (2024). *Emmeans: Estimated marginal means, aka least-squares means*.
- 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 and Environment*, 310, 107290. <https://doi.org/10.1016/j.agee.2020.107290>
- Lucas, M. M., Stoddard, F. L., Annicchiarico, P., Frias, J., Martinez-Villaluenga, C., Sussmann, D., Duranti, M., Seger, A., Zander, P. M., & Pueyo, J. J. (2015). The future of lupin as a protein crop in Europe. *Frontiers in Plant Science*, 6, 705. <https://doi.org/10.3389/fpls.2015.00705>
- Lüdecke, D. (2018). Ggeffects: Tidy data frames of marginal effects from regression models. *Journal of Open Source Software*, 3, 772. <https://doi.org/10.21105/joss.00772>
- Lüdecke, D., Ben-Shachar, M., Patil, I., Waggoner, P., & Makowski, D. (2021). Performance: An R package for assessment, comparison and testing of statistical models. *Journal of Open Source Software*, 6, 3139. <https://doi.org/10.21105/joss.03139>
- Martins, K. T., Albert, C. H., Lechowicz, M. J., & Gonzalez, A. (2018). Complementary crops and landscape features sustain wild bee communities. *Ecological Applications*, 28, 1093–1105. <https://doi.org/10.1002/eap.1713>
- Nationaal Georegister. (2024). *Basisregistratie Gewaspercelen (BRP)* [WWW document]. Nationaal Georegister. <https://www.nationaalgeoregister.nl/geonetwork/srv/api/records/b812a145-b4fe-4331-8dc6-d914327a87ff>
- Pe'er, G., Zingrebe, Y., Hauck, J., Schindler, S., Dittrich, A., Zingg, S., Tschardtke, T., Oppermann, R., Sutcliffe, L. M. E., Sirami, C., Schmidt, J., Hoyer, C., Schleyer, C., & Lakner, S. (2017). Adding some green to the greening: Improving the EU's ecological focus areas for biodiversity and farmers. *Conservation Letters*, 10, 517–530. <https://doi.org/10.1111/conl.12333>
- Persson, A. S., & Smith, H. G. (2013). Seasonal persistence of bumblebee populations is affected by landscape context. *Agriculture, Ecosystems and Environment*, 165, 201–209. <https://doi.org/10.1016/j.agee.2012.12.008>
- Powney, G. D., Carvell, C., Edwards, M., Morris, R. K. A., Roy, H. E., Woodcock, B. A., & Isaac, N. J. B. (2019). Widespread losses of pollinating insects in Britain. *Nature Communications*, 10, 1018. <https://doi.org/10.1038/s41467-019-08974-9>
- Quinn, G. P., & Keough, M. J. (2002). *Experimental design and data analysis for biologists*. Cambridge University Press.
- R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.
- Redhead, J. W., Dreier, S., Bourke, A. F. G., Heard, M. S., Jordan, W. C., Sumner, S., Wang, J., & Carvell, C. (2016). Effects of habitat composition and landscape structure on worker foraging distances of five bumble bee species. *Ecological Applications*, 26, 726–739. <https://doi.org/10.1890/15-0546>
- Riggi, L. G. A., Raderschall, C. A., Fijen, T. P. M., Scheper, J., Smith, H. G., Kleijn, D., Holzschuh, A., Aguilera, G., Badenhauer, I., Bänisch, S., Beyer, N., Blitzer, E. J., Bommarco, R., Danforth, B., González-Varo, J. P., Grab, H., Le Provost, G., Poveda, K., Potts, S. G., ... Lundin, O. (2023). Early-season mass-flowering crop cover dilutes wild bee abundance and species richness in temperate regions: A quantitative synthesis. *Journal of Applied Ecology*, 61, 452–464. <https://doi.org/10.1111/1365-2664.14566>
- Robinson, R. A., & Sutherland, W. J. (2002). Post-war changes in arable farming and biodiversity in Great Britain. *Journal of Applied Ecology*, 39, 157–176. <https://doi.org/10.1046/j.1365-2664.2002.00695.x>
- Roulston, T. H., & Goodell, K. (2011). The role of resources and risks in regulating wild bee populations. *Annual Review of Entomology*, 56, 293–312. <https://doi.org/10.1146/annurev-ento-120709-144802>
- Rundlöf, M., Persson, A. S., Smith, H. G., & Bommarco, R. (2014). Late-season mass-flowering red clover increases bumble bee queen and male densities. *Biological Conservation*, 172, 138–145. <https://doi.org/10.1016/j.biocon.2014.02.027>
- Scheper, J., Bommarco, R., Holzschuh, A., Potts, S. G., Riedinger, V., Roberts, S. P. M., Rundlöf, M., Smith, H. G., Steffan-Dewenter, I., Wickens, J. B., Wickens, V. J., & Kleijn, D. (2015). Local and landscape-level floral resources explain effects of wildflower strips on wild bees across four European countries. *Journal of Applied Ecology*, 52, 1165–1175. <https://doi.org/10.1111/1365-2664.12479>
- 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, 17552–17557. <https://doi.org/10.1073/pnas.1412973111>
- Stanley, D. A., Knight, M. E., & Stout, J. C. (2013). Ecological variation in response to mass-flowering oilseed rape and surrounding landscape composition by members of a cryptic bumblebee complex. *PLoS One*, 8, e65516. <https://doi.org/10.1371/journal.pone.0065516>
- Streeter, D., & Hart-Davies, C. (2016). *Collins wild flower guide* (2nd ed.). William Collins.
- Taki, H., Murao, R., Mitai, K., & Yamaura, Y. (2018). The species richness/abundance-area relationship of bees in an early successional tree

- plantation. *Basic and Applied Ecology*, 26, 64–70. <https://doi.org/10.1016/j.baae.2017.09.002>
- 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, 1585–1596. <https://doi.org/10.1111/1365-2664.13403>
- Wagner, D. L. (2020). Insect declines in the Anthropocene. *Annual Review of Entomology*, 65, 457–480. <https://doi.org/10.1146/annurev-ento-011019-025151>
- Walther-Hellwig, K., & Frankl, R. (2000). Foraging habitats and foraging distances of bumblebees, *Bombus* spp. (Hym., Apidae), in an agricultural landscape. *Journal of Applied Entomology*, 124, 299–306. <https://doi.org/10.1046/j.1439-0418.2000.00484.x>
- Westphal, C., Bommarco, R., Carre, G., Lamborn, E., Morison, N., Petanidou, T., Potts, S. G., Roberts, S. P. M., Szentgyorgyi, H., Tscheulin, T., Vaissiere, B. E., Woyciechowski, M., Biesmeijer, J. C., Kunin, W. E., Settele, J., & Steffan-Dewenter, I. (2008). Measuring bee diversity in different European habitats and biogeographical regions. *Ecological Monographs*, 78, 653–671. <https://doi.org/10.1890/07-1292.1>
- Westphal, C., Steffan-Dewenter, I., & Tscharnkte, T. (2009). Mass flowering oilseed rape improves early colony growth but not sexual reproduction of bumblebees. *Journal of Applied Ecology*, 46, 187–193.
- Wickham, H. (2009). *ggplot2: Elegant graphics for data analysis*. Springer. <https://doi.org/10.1007/978-0-387-98141-3>
- Zander, P., Amjath-Babu, T. S., Preissel, S., Reckling, M., Bues, A., Schläfke, N., Kuhlman, T., Bachinger, J., Uthes, S., Stoddard, F., Murphy-Bokern, D., & Watson, C. (2016). Grain legume decline and potential recovery in European agriculture: A review. *Agronomy for Sustainable Development*, 36, 26. <https://doi.org/10.1007/s13593-016-0365-y>

SUPPORTING INFORMATION

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

Table S1: Relative abundance of bee visitors to lupin.

Table S2: Final model structures.

Table S3: All bee species encountered in landscape transects.

Table S4: All flower species encountered in landscape transects.

Table S5: Evaluation of model fixed effects for lupin-visiting bumblebees by log-likelihood ratio tests.

Table S6: Estimated marginal mean lupin-visiting bumblebee density across treatments in each survey round, with within-round contrasts.

Table S7: Evaluation of model fixed effects for other bumblebees by log-likelihood ratio tests.

Table S8: Estimated marginal mean other bumblebee density across treatments in each survey round, with within-round contrasts.

Table S9: Evaluation of model fixed effects for solitary bees by log-likelihood ratio tests.

Table S10: Estimated marginal mean solitary bee density across treatments in each survey round, with within-round contrasts.

Table S11: Evaluation of model fixed effects for lupin-visiting bumblebees by log-likelihood ratio tests (following-year model).

Table S12: Evaluation of model fixed effects for other bumblebees by log-likelihood ratio tests (following-year model).

Table S13: Evaluation of model fixed effects for solitary bees by log-likelihood ratio tests (following-year model).

Figure S1: The outlier transect in the solitary bee data, which was excluded from the model.

Figure S2: The effect of lupin cultivation on landscape-scale other bumblebee population size across different landscape contexts before, during, and after lupin bloom.

Figure S3: The effect of lupin cultivation on landscape-scale solitary bee population size across different landscape contexts before, during, and after lupin bloom.

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