



# Annual flower strips and honeybee hive supplementation differently affect arthropod guilds and ecosystem services in a mass-flowering crop

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## ABSTRACT

Intensively managed agricultural landscapes have degraded the provisioning of diverse and continuous forage and shelter habitats for arthropods and weakened the delivery of ecosystem services such as insect crop pollination and biological pest control. In response, farmers are incentivised to sow flower strips along field margins to counteract resource bottlenecks. Yet, it is poorly understood how effective this diversification practice is when combined with the supplementation of honeybee (*Apis mellifera* L.) hives, which is commonly used to boost insect pollination in flowering crops. Honeybees share floral resources with wild pollinators and natural enemies of pests, which could lead to competition for food resources. We sampled pollinators, natural enemies and their pests as well as estimated the benefit of insect pollination in 17 organic faba bean (*Vicia faba minor* L.) fields in southern Sweden either with or without sown annual flower strips and with or without added honeybee hives. In fields with flower strips, bumblebee (*Bombus* spp.) densities were redistributed from field edges to interiors but without affecting their overall densities. Flower strips enhanced silver Y moth (*Autographa gamma* L.) densities and carabid beetle Shannon diversity along the field edge, and overall spider activity density. The supplementation of honeybee hives enhanced honeybee densities, overall ladybird beetle densities, black bean aphid (*Aphis fabae* Scop.) densities along field edges, but deterred silver Y moths and pushed bumblebees towards the field interior. Bean mass per plant was higher in insect pollinated plants compared with bagged, self-pollinated plants. This insect pollination benefit was independent of honeybee hive supplementation and the flower strip treatment suggesting that faba bean fields were not deficient in pollinator visits. We conclude that flower strips did not provide sufficient floral resources to increase overall wild pollinator densities in faba bean fields. Yet, annual flower strips attracted and facilitated ground-dwelling predators, especially spiders, to faba bean fields, likely by providing beneficial shelter habitats. It is worth noting that 2018, in which we collected our data, was characterised by late frosts in spring followed by an unusually hot and dry summer. While these unforeseen weather conditions together with a relatively small sample size might limit the generalisation of our results, we argue that conducting experiments under such conditions provide insights into the effectiveness of agri-environmental schemes under climate change, especially considering that such weather conditions are becoming increasingly more frequent.

## 1. Introduction

Balancing the requirements for increasing demands for agricultural products alongside the conservation of ecosystems and biodiversity, and the regenerative production capacity of agroecosystems, is one of the utmost challenges of our time (Jägermeyr, 2020; Rockström et al., 2017). While agricultural intensification over the last century has greatly increased agricultural production per unit land area (Mann, 1999; Pingali, 2012) this intensification has also contributed to reduced

biodiversity (Dainese et al., 2019; Foley et al., 2005). One of the main drivers responsible for the biodiversity decline, of which insects are a major component (Raven and Wagner, 2021), is the transformation of semi-natural habitats such as grasslands, forests or field borders into large agricultural fields (Cousins et al., 2007), and the associated loss of continuous and diverse food resources, nesting or shelter habitats (Carvell et al., 2017; Kremen et al., 2002; Rivers-Moore et al., 2020). This simplification of intensively used agricultural landscapes can be severe enough to not only reduce species abundances and richness of

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beneficial arthropods, such as pollinators or natural enemies of pests, but also degrade ecosystem services they provide such as insect pollination and biological pest control (Dainese et al., 2019). Environmentally-friendly farming methods are needed to support biodiversity to ensure sustainable agricultural production. Ecological intensification seeks to sustainably intensify agriculture by, for example, enhancing beneficial arthropods and harness the ecosystem functions they provide by diversifying agriculture and providing shelter and forage resources for beneficial organisms throughout their life cycle (Bommarco et al., 2013; Schellhorn et al., 2015).

Enhancing forage and habitat resources by sowing flower strips along field margins is a commonly applied measure to support beneficial arthropods and harness ecosystem services (Albrecht et al., 2020). Flower strips can facilitate higher numbers of natural enemies of pests in adjacent crop fields (Holland et al., 2016; Tschumi et al., 2016), and support pollinators (Lowe et al., 2021; Zamorano et al., 2020), which in some cases are also facilitated to the adjacent crop fields (Blaauw and Isaacs, 2014; Rundlöf et al., 2018). Flower strips can also enhance biological pest control (Tschumi et al., 2016) and insect pollination in adjacent crop fields (Blaauw and Isaacs, 2014; Sutter et al., 2018), and in some cases increase crop yield (Pywell et al., 2015; Rundlöf et al., 2018).

However, the effect of flower strips on ecosystem services delivered to the focal field are variable, with flower strips often failing to facilitate pollination or pest control services despite attracting more beneficial insects compared to unenhanced field edges (Albrecht et al., 2020). Flower strips can both facilitate beneficial insects to a neighbouring crop or compete with the crop by attracting them away from the field. As such flower strips sown alongside insect pollinated fields might potentially weaken the provision of crop pollination in the focal field (Lowe et al., 2021; Nicholson et al., 2019). In addition, the effectiveness of sown flower strips can also depend on the surrounding landscape structure and the created ecological contrast they provide (Scheper et al., 2013). As such, the benefits of flower strips are crop and region specific and more studies are needed to better understand in which context they are most effective (Sardiñas and Kremen, 2015).

The addition of managed honeybee (*Apis mellifera* L.) hives to fields during crop flowering is an additional common management practice to supply stable crop pollination in regions, especially where pollination by wild pollinators is inadequate (Breeze et al., 2014; Cunningham and Le Feuvre, 2013; Marini et al., 2012). Honeybees are reported to pollinate the greatest variety of crop species (Klein et al., 2007), but evidence suggests that wild pollinators are just as important service providers, and for certain crop species deliver even superior pollination than managed honeybees (Garibaldi et al., 2013). Increased densities of managed honeybees can, however, decrease the densities of wild bees within the adjacent crop field (Artz et al., 2011; Lindström et al., 2016) due to competition for floral resources (Wojcik et al., 2018), and lead to lower fruit set in flowering crops (Angelella et al., 2021). Similarly, many natural enemies of pests including ladybird beetles, hoverflies and parasitic wasps are pollen and nectar feeders and thus share flower resources with honeybees (Lundgren, 2009a; Hogg et al., 2011; Lundin et al., 2019). The natural enemies could be negatively affected by high densities of honeybees due to competition for resources. However, evidence for resource competition between honeybees and natural enemies of pests has not been examined. If high densities of honeybees suppress natural enemies of pests then honeybee hives near flowering fields could lead to increased pest densities, which subsequently might attract more ground-dwelling predators such as carabid beetles and spiders.

Experiments manipulating local bee densities and floral resources concurrently have not been done, making it difficult to predict if and when sown wild flower strips can mitigate the negative effects of resource competition from honeybee hives on wild pollinator visits to crop plants, and potential competition with flower visiting natural enemies of pests.

Faba bean (*Vicia faba minor* L.) is a mass-flowering, nitrogen-fixating crop grown worldwide for food and fodder (Karkanis et al., 2018). Black

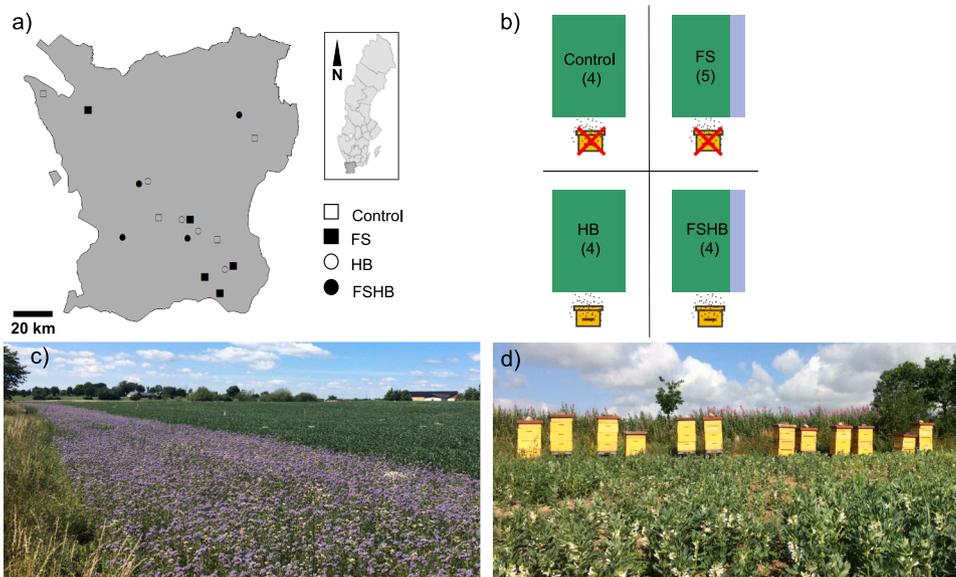
bean aphids (*Aphis fabae* Scop.) and broad bean beetles (*Bruchus rufimanus* L.) are among the most severe pests in faba bean and can drastically reduce seed yield (Hansen et al., 2008; Stoddard et al., 2010) and quality (Segers et al., 2021). Occasionally, also pea aphids (*Acyrtosiphon pisum* Harris) attack faba bean plants (Sanders et al., 2018). Faba bean is self-fertile but benefits from pollination by insects (Bishop and Nakagawa, 2021). Due to their deep corollas, which make it difficult to access pollen and nectar, faba bean flowers are predominantly visited by honeybees and bumblebees (Free, 1993). In addition, their extrafloral nectaries (EFN), which secrete nectar on stipules below the flowers, are attractive for natural enemies such as ladybird beetles and insect pollinators when floral resources are unavailable (Stoddard and Bond, 1987). Bees exhibit different foraging behaviours when visiting faba bean flowers. While pollen collection requires legitimate visits, where bees enter the corolla through the front and transfer pollen, nectar foragers can visit flowers legitimately or rob nectar through a pierced hole in the back of the corolla (Marzinzig et al., 2018; Tasei, 1976). Since only legitimately visiting pollinators contribute to cross-pollination, legitimate visitation is the foraging behaviour that most enhances faba bean pollination (Kendall and Smith, 1975). Nonetheless, nectar robbing can enhance self-pollination by tripping faba bean flowers and thereby contribute more to pollination than if flowers are not visited at all (Kendall and Smith, 1975). Predominant foraging behaviours depend on floral resource availability of the crop (Marzinzig et al., 2018) and the amount of semi-natural habitat in the landscape (Raderschall et al., 2021a). Flower resource availability near crops and wild bee densities can influence honeybee visitation rates and movement behaviours within crops (Brittain et al., 2013; Carvalheiro et al., 2011; Eeraerts et al., 2020), but it remains unclear if flower resource availability and honeybee densities affect whether pollinators predominantly visit flowers legitimately or rob nectar. Likewise, it is unknown if combining flower strips with increased honeybee densities in faba bean affect natural enemies of pests, pests themselves and biological pest control.

We experimentally manipulated local flower resources by sowing annual flower strips, and resource competition by supplementing managed honeybee hives to faba bean fields in a crossed design. We hypothesised that 1) flower strips enhance the densities of wild pollinators, insect pollination and natural enemies, and reduce pest densities in adjacent faba bean fields, 2) added honeybee hives displace wild pollinators and natural enemies from faba bean fields due to competition for shared flower resources, and subsequently promote pest densities in faba bean fields, 3) the negative effect of honeybee hives on beneficial insects and ecosystem services is counteracted by flower strips by mediating forage resource competition. Finally, since both the flower strips and the honeybee hive supplementation were applied along the edge of the faba bean fields, we hypothesised that the treatment effects were more pronounced closer to the field edge compared with the field interior.

## 2. Methods

### 2.1. Experimental design

We selected 17 organically managed faba bean fields in 2018 in Skåne, a region dominated by agriculture in southern Sweden. While each faba bean field was sown with a single cultivar, several cultivars were grown among our experimental crop fields. Faba bean cultivars differ in their reliance on insect pollination (Bishop and Nakagawa, 2021) and broadly belong two types with either white or coloured flowers, that differ in tannin levels (Duc, 1997) and thus might influence herbivory. Since it was not possible to find sufficient crop fields of a single cultivar, we balanced flower colour type across all treatments: white-flowered cultivars (4 fields) and coloured-flowered cultivars (13 fields) (Table S1). Presence of honeybee hives and flower strips were manipulated in a fully crossed design, with four or five fields in each treatment (Fig. 1). Field sizes of experimental fields (mean: 14.5 ha,



**Fig. 1.** (a) Field locations in Skåne, Sweden (inset) for the four treatments: Circles = fields with honeybee hives (HB), squares = fields without honeybee hives, filled symbols = fields with flower strips (FS), open symbols = fields without flower strips. (b) Schematic of the four treatments and the respective number of replications within parenthesis. Top left: faba bean control field, top right: faba bean field with sown flower strip and without honeybee hives (FS); bottom left: faba bean field without flower strip and with honeybee hives (HB) and bottom right: faba bean field with flower strip and honeybee hives (FSHB). (c) Photo of a faba bean field with a sown flower strip. (d) Photo of a faba bean field supplemented with honeybee hives.

range: 2–38 ha) were similar among treatments (Tables S1 and S2). Due to the drought in 2018 (Wilcke et al., 2020), two farmers irrigated their faba bean fields, both of which had flower strips, and one of each honeybee hive treatment.

The landscape composition surrounding focal faba bean fields was characterised within a 2 km radius. Pasture and crop information, and field perimeter length data, which was used as a proxy for field border density, were extracted from the Integrated Administration and Control System, administered by the Swedish Board of Agriculture. Forest cover information was obtained from a digitised map layer (Terrängkartan, Lantmäteriet, 2018). Land use data was analysed in ArcMap 10.4.1 (ESRI, 2015). The percentage of arable land (mean: 74%, range: 44–90%), semi-natural habitat, including pastures and forest (mean: 13%, range: 2–32%), winter oilseed rape (*Brassica napus* L.) and turnip rape (*Brassica rapa* L.) (mean: 4%, range: 0–12%), and average field perimeter length were balanced among our treatments (Tables S1 and S2). Other mass-flowering crops constituted less than 2% across all 2 km landscape buffers and were therefore not further analysed.

## 2.2. Supplementing and removing honeybee hives

Honeybee hives are common in Skåne and beekeepers are required to report the location of their beehives to the County Administrative Board. We followed the method from Lindström et al. (2016) (for details see supplementary material) to manipulate honeybee densities around each focal field. Using hive location information from the County Administrative Board, together with information from farmers, local residents, beekeepers and personal observations, we mapped all honeybee hives within a 2 km radius from our focal faba bean fields. Based on whether there were high or low abundances of honeybee hives in the landscape, we assigned the focal fields to either the honeybee hive or the honeybee control treatment. For the honeybee control treatments, we further reduced stationary honeybee hives by asking beekeepers to remove hives away from focal fields. For the eight focal fields located in landscapes with a high density of stationary honeybee hives, we placed additional hives along the edge of the field at the onset of faba bean flowering. We aimed for adding ten full-strength hives per field, but because some of beekeepers used recently split hives with fewer honeybees, we compensated for this by adding double the number of hives, such that each field was supplemented with the equivalent of ten full-strength honeybee hives. To the best of our knowledge, honeybee control fields ended up with on average 2 hives within 1 km from the crop field and 9 hives within 2 km, while honeybee supplemented fields

ended up with 13 hives within 1 km (of which three hives were stationary and 10 supplemented during faba bean bloom) and 31 hives within 2 km from focal faba bean field centres.

## 2.3. Adding annual flower strips

Flower strips were sown along the edge of nine faba bean fields in spring 2018. We aimed to scale the size of the flower strip depending on field size, but the actual proportion of flower strip to field area varied depending on field configuration and machine widths used for sowing flower strips, with on average 167 m<sup>2</sup> of sown flower strip per hectare focal faba bean field (range: 83–338 m<sup>2</sup>). The area of flower strip per hectare faba bean field was balanced among the two levels of the honeybee hive treatment (Tables S1b and Table S2a). Flower strips were between 200 and 800 m long and 2–6 m wide and had a total area of 0.1–0.5 ha (Table S1a). The flower mixture was designed to include flower species that attract both wild pollinators and natural enemies to aphids and broad bean beetles, and to contain a variety of floral morphologies and flowering times such that the flower strip would provide nectar and pollen throughout faba bean flowering and beyond until late summer. The plant species sown and their seeding rates were: dill (*Anethum graveolens* L., Apiaceae, 1 kg ha<sup>-1</sup>), cornflower (*Centaurea cyanus* L., Asteraceae, 0.5 kg ha<sup>-1</sup>), buckwheat (*Fagopyrum esculentum* Moench, Polygonaceae, 5 kg ha<sup>-1</sup>), crimson clover (*Trifolium incarnatum* L., Fabaceae, 3 kg ha<sup>-1</sup>), Persian clover (*Trifolium resupinatum* L., Fabaceae, 5 kg ha<sup>-1</sup>) and phacelia (*Phacelia tanacetifolia* Benth, Boraginaceae, 5 kg ha<sup>-1</sup>). The seeds were mixed and sown at 1–2 cm soil depth. Most flower strips were cut after flowering. In fields without a flower strip, a 5 m wide area of faba bean served as a control strip, such that the sampling transects were located at comparable distances from the outer field edge (Fig. S1).

## 2.4. Sampling design

Pollinators, foliage-dwelling natural enemies of pests (hereafter natural enemies), ground-dwelling predators (hereafter ground predators), insect pests (hereafter pests) were sampled once per week from faba bean bloom onset in early June (crop stage BBCH 60; Weber and Bleiholder, 1990) until early pod set in mid-July (BBCH 72), which is the period when aphids (Stoddard et al., 2010) and broad bean beetles (Segers et al., 2021) colonise the plants and flower visitors pollinate the flowers. Data was collected along two transects placed at 10 m and 50 m from the inner flower strip or control strip edge. Ground predators were

also sampled within the strips (Fig. S1). Each transect was divided into four segments of 25 m length and 1 m width (S1: 50–75 m from the nearest perpendicular field edge; S2: 75–100 m; S3: 100–125 m; S4: 125–150 m).

#### 2.4.1. Pollinators and floral resources

We sampled faba bean pollinators weekly along each segment for 10 min net collection time. Depending on faba bean bloom duration, pollinators were sampled 1–3 times (mean: 2.2) per field. We counted all flower- and EFN-visiting insects and noted their foraging behaviour: 1) legitimately pollinating, 2) nectar robbing, or 3) EFN-visiting. All pollinators, except bumblebee queens, honeybees and silver Y moths, were collected and brought to the laboratory to be identified to species-level using Løken (1973), Edwards and Jenner (2005) and Falk (2015). At the end of each sampling round, we measured the flower resource abundance by randomly placing a 0.36 m<sup>2</sup> quadrat in each transect segment in the faba bean field. We also quantified the flower resource of the flower strip by placing four quadrats along an additional transect in the flower strip, using the same segment distances as in the crop field. Within each quadrat, we counted the number of flower units for faba bean, each of the six sown plant species and flowering weeds. Depending on flower morphology, a flower unit could either constitute a solitary flower (e.g. faba bean, Rosaceae), umbels (e.g. Apiaceae, Brassicaceae), a raceme (e.g. Polygonaceae), an inflorescence (e.g. clovers, Asteraceae), a cyme (e.g. Boraginaceae) or a flower stalk (e.g. Lamiaceae). We measured the flower unit width and length for each species such that flower unit areas could be recalculated and expressed as flower area (cm<sup>2</sup>) per unit ground area (m<sup>2</sup>).

#### 2.4.2. Pests and their natural enemies

We surveyed faba bean foliage weekly for natural enemies and pests. Fields were sampled 2–4 times (mean: 3.2), depending on crop maturation rate. In each transect segment, we randomly selected 20 plants (i. e., 160 per field), which were screened for ladybird beetles (Coccinellidae, egg clusters, larvae, pupae and adults), lacewings (Chrysopidae, eggs and larvae), hoverflies (Syrphidae, larvae and pupae) and the common faba bean pests pea aphids, black bean aphids and broad bean beetles (Stoddard et al., 2010; Segers et al., 2021). Because black bean aphids are highly aggregated and individuals therefore are time consuming to count, we estimated their abundance by grouping them into five categories: C0 = no aphids, C1 = 0–50 aphids (midpoint count of 25), C2 = 51–100 (midpoint: 75), C3 = 101–500 (midpoint: 300) and C4 > 500 (midpoint set at 750). The midpoint in the highest category was set by multiplying its lower range limit (500) by 1.5 (Gordy et al., 2019). We also counted parasitised pea aphids (mummies) as a measure of aphid biological control.

#### 2.4.3. Ground predators

Ground predators, including carabid beetles (Carabidae), rove beetles (Staphylinidae) and spiders (Araneae), were sampled using pitfall traps. We placed three pitfall traps in each transect at 10 m and 50 m from the inner flower strip or control strip edge and along an additional transect inside the flower strip or control strip (nine pitfall traps per field). Pitfall traps were made from polypropylene beakers (12 cm diameter) filled with 200 mL of soap water. Pitfall traps were placed 50 m apart. We emptied and refilled traps on average every 7.0 days (sd: 1.1 day) and conducted between 1 and 4 sampling rounds (mean: 1.8). Carabid beetles, rove beetles and spiders were stored in ethanol and later identified to species or genus level.

#### 2.4.4. Insect pollination

We estimated the benefit of insect pollination in faba bean by selecting one plant pair in each segment (eight per field), where one of the plants in each pair was covered with a tulle net (2 mm mesh size) just before anthesis, to exclude insect pollinators. The other plant remained uncovered and was open to insect pollinators. The plants in each pair

were close to each other and similar in height and bud numbers. Nets were adjusted weekly for plant growth and flowers that started wilting were uncovered to minimise netting effects on pod development. At pod maturity, all pods of netted and open plants were harvested. Plants that were infested by black bean aphids (N = 12 (bagged) and N = 7 (open)), were harvested but excluded from analyses since black bean aphid infestation negatively affects faba bean yield components (Raderschall et al., 2021b). We counted pods per plant and beans per pod. We dried beans at 65 °C for 48 h and weighed the dry bean mass per plant. Individual bean weight was calculated by dividing bean mass with the total number of beans per plant.

#### 2.4.5. Broad bean beetle infestation and parasitisation

To quantify the level of broad bean beetle infestation and parasitisation, we collected 20 mature faba bean pods in each segment just before harvest. Since infestation rate is highest on the lowest pod bearing nodes (Seidenglanz and Huñady, 2016), we collected pods exclusively from the 2nd or 3rd lowest pod bearing nodes. The collected pods were transferred into cardboard tubes for 3–4 months until all broad bean beetles and parasitoids had emerged. Pods were opened and the number of broad bean beetle and parasitoid emergence holes, which differ in size (Seidenglanz and Huñady, 2016), counted. A subsample of emerged parasitoids in the cardboard tubes were all determined as *Triaspis thoracicus* Curtis, which is a known parasitoid of *Bruchus rufimanus* (Seidenglanz and Huñady, 2016). Since bean density varied among transects and fields, thereby potentially influencing the infestation rate, we placed a 0.36 m<sup>2</sup> quadrat in each transect segment, and collected all pods and counted the number of beans per quadrat. The total number of beans per quadrat was added as a covariate in the analysis (for details see section 2.5).

### 2.5. Statistical analysis

We used linear mixed models or generalised linear mixed models to conduct the statistical analyses (package: “glmmTMB”; Brooks et al., 2017) in R version 3.6.1 for Windows (R Core Team, 2019). The amount of variance associated with a sample by the explanatory variables was analysed with a type III Anova (package: “car”; Fox and Weisberg, 2019). To verify that models were not overdispersed and to obtain residual diagnostics for models with Poisson, negative binomial and binomial error distributions, we used the testDispersion and the simulateResidual functions (package: “DHARMA”; Hartig, 2019). Marginal R-square values were calculated for each model using the r2\_nakagawa function (package: “performance”; Lüdtke et al., 2021), which calculates the r-square values for mixed effects models based on Nakagawa et al. (2017). For the analyses, data was summed across segments within transects. Full models included the honeybee hive treatment (HB or C), the flower strip treatment (FS or C), the distance from the strip (10 m or 50 m, or within the strip for the pitfall trap data) and their two-way interactions as explanatory variables unless specified otherwise. We used honeybee hive treatment rather than honeybee visitation counts as an explanatory variable, because it better reflects the factorial design of the experiment, and because honeybee counts were only done on a few occasions such that the hive treatment factor provides a better proxy for honeybee densities over the whole season. We simplified models by removing interactions between explanatory variables if  $p > 0.10$ . Remaining models with interactions were tested against models without interactions using a likelihood ratio test via the anova function (R Core Team, 2019), and the more complex models including interactions were only kept if their predictive power was significantly ( $p < 0.050$ ) better than that of the simplified model without the interaction (Zuur et al., 2009). Field identity was used as a random effect in all models unless specified otherwise to account for data being collected along multiple transects within each field. Wherever final models included interactions between explanatory variables, we conducted a post-hoc analysis to obtain the estimated marginal means with the emmeans function and

their pair-wise comparisons using the pairs function and visualised the results using the emmip function (package: “emmeans” (Lenth, 2019)). The p-values were adjusted with the Tukey method for multiple testing where necessary. One field with the treatments of flower strip and added honeybees, was heavily impacted by black bean aphids and water stress and did not produce any pods. It was therefore excluded from all analyses dependent on presence of mature pods, i.e. insect pollination benefit, broad bean beetle infestation and parasitisation rate.

The densities of pollinators were summed across all sampling rounds for each transect and analysed with three separate models using either honeybees, bumblebees or silver Y moths as response variable. We observed one solitary bee legitimately pollinating faba bean flowers. Due to the low sample size we excluded this single observation from the analysis. We used Poisson error distribution with a log link and added the log-transformed number of sampling rounds as an offset to account for differential sampling effort among fields (Zuur et al., 2009). The Shannon diversity of bumblebees was first calculated for each sampling round and transect separately to account for the different sampling efforts. We then calculated the mean Shannon diversity across all sampling rounds for each transect and assumed a normal error distribution to analyse the Shannon diversity of bumblebees. The foraging behaviour of bumblebees was analysed using the number of legitimately pollinating and nectar robbing bumblebees per total number of pollinators summed across sampling rounds in two separate models with either the proportion of legitimately pollinating, or the proportion of nectar robbing bumblebees as the response variable. The number of EFN visitors was too low ( $N = 34$ ) to be analysed. We used a binomial distribution with a logit link to analyse foraging behaviours.

The pollination treatment effect was analysed by comparing the yield components between open pollinated and bagged plant pairs (107 bagged and 112 open plants) in four separate models using either bean mass per plant, pods per plant, beans per pod, or individual bean weight as response variable. In addition to the honeybee treatment, flower strip treatment and transect distance, we included the pollination treatment as an explanatory variable. We tested all two- and three-way interactions between the pollination treatment and the other explanatory variables. The three-way interaction, which included the pollination treatment, was replicated within the two-way interaction and therefore did not use up additional degrees of freedom. We used plant pair nested within transect, within field identity as random effects. The square root transformed bean mass per plant and log-transformed individual bean weight were analysed assuming a normal error distribution. The number of pods per plant was analysed with a Poisson error distribution and a log link. The number of beans per pod was analysed as the number of beans per plant with the log-transformed number of pods as an offset and with a Poisson error distribution and a log link.

The densities of natural enemies and pests were summed across all sampling rounds for each transect and analysed in seven separate models using number of ladybird beetles, hoverflies, lacewings, pea aphids, parasitised pea aphids (mummies), black bean aphids and broad bean beetles as response variables. We added the average black bean aphid infestation category as an additional explanatory variable to all the models except the one for black bean aphids. This was necessary for the ladybird beetle model to meet model assumptions and was kept for the other natural enemies and pests for consistency. In contrast to pea aphids that occur relatively evenly distributed among plants, black bean aphid infestation is patchy with highly aggregated colonies that reach large numbers that attract natural enemies. For the analysis of ladybird beetles, hoverflies and broad bean beetles we used a Poisson error distribution with a log link. For the analysis of black bean aphids we used a zero-inflated model by applying a single zero-inflation parameter to all observations using the (ziformula  $\sim 1$ ). The densities of lacewings and pea aphids were analysed with a negative binomial error distribution to account for overdispersion of the Poisson model. The log-transformed number of sampling rounds was added as an offset to account for differential sampling effort among fields for all models with Poisson and

negative binomial distribution. Pea aphid parasitisation rate was analysed as the number of parasitised pea aphids (mummies) per pea aphid using a binomial error distribution with a logit link.

The activity density of ground predators (hereafter ground predator density) was summed per transect and across all sampling rounds. Ground predator densities were analysed in three separate models with carabid beetle density, spider density or rove beetle density as response variable and with a negative binomial error distribution, as Poisson models were overdispersed. The log-transformed number of pitfall days was added as an offset. The Shannon diversity of ground predators was also analysed in separate models for each species group with an assumed normal error distribution.

Broad bean beetle infestation and parasitisation was summed per transect. Broad bean beetle infestation was analysed using the number of broad bean beetle emergence holes as response variable and with a Poisson error distribution and a log-link. The log-transformed number of the sum of all beans (infested or not) from the 80 pods per transect was added as an offset. We added the mean number of beans per quadrat and transect as an additional explanatory variable to the model to account for differential bean density among transects and fields. Broad bean beetle parasitisation rate was analysed using the number of parasitoid emergence holes per broad bean beetle emergence holes using a binomial error distribution with a logit link.

### 3. Results

#### 3.1. Flower strip and honeybee hive treatment

Due to late frost, which delayed sowing of the flower strip in spring, the flower strip bloom was later than planned. In addition, a record drought and heatwave (Wilcke et al., 2020) caused early and shortened flowering of the faba bean fields in 2018. Among the six sown plant species in the flower strip, only phacelia and buckwheat co-flowered with the faba bean fields and the peak bloom of the flower strip was in mid-July, after faba bean flowering had ended (Fig. S2, Table S3).

We observed 1052 honeybees visiting faba bean flowers or EFN. The density of honeybees was overall higher in fields with honeybee hives, and was explained by an interaction between the honeybee hive treatment and the transect distance from the flower strip (Fig. S3, Table 1). In fields without honeybee hives, the honeybee density was higher at 10 m (mean: 7.4, s.e.: 2.2) compared with 50 m (mean: 4.8, s.e.: 1.4) distance from the strip, whereas in fields with honeybee hives, honeybee density was lower at 10 m (mean: 17.5, s.e.: 5.1) compared with 50 m (mean: 20.2, s.e.: 5.9) distance from the strip (Fig. S3).

#### 3.2. Bumblebee densities and Shannon diversity

We observed a total of 610 bumblebees representing 10 species or species groups visiting faba bean flowers and EFN (Table S4). The density of bumblebees was explained by both an interaction between the flower strip treatment and the transect distance, as well as between the honeybee hive treatment and the transect distance (Table 1). In fields without honeybee hives, bumblebee density was higher at 10 m compared with 50 m from the strip, whereas in fields with honeybee hives, bumblebee density was higher at 50 m compared with 10 m distance from the strip (Fig. 2a). In fields with flower strips, the bumblebee density was higher at 50 m compared to 10 m from the strip, while there was no effect of transect distance on bumblebee density in fields without flower strips (Fig. 2b). Bumblebee Shannon diversity ranged between 0 and 0.64 (mean: 0.31) across transects and was not affected by any of the treatments (Table 1).

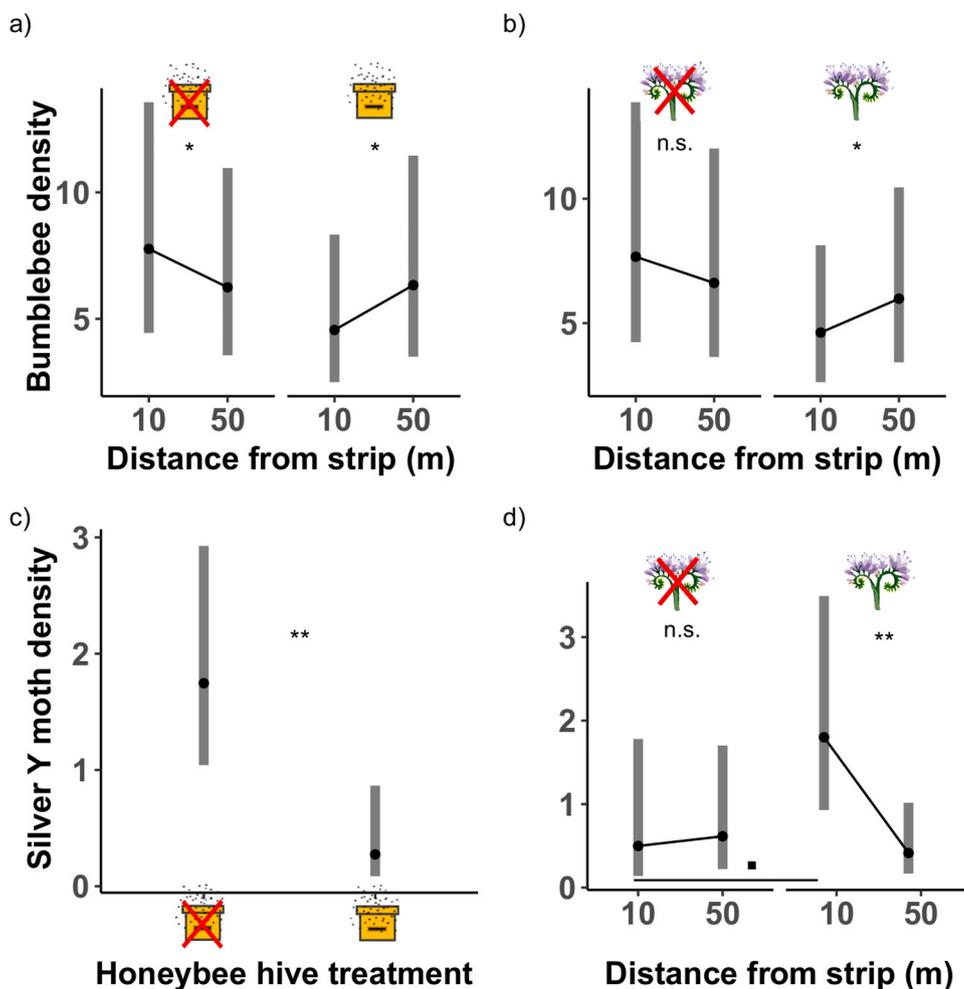
#### 3.3. Silver Y moth densities

We observed a total of 82 silver Y moths, which exclusively visited faba bean flowers legitimately. The silver Y moth density was explained

**Table 1**

Chi-Square ( $\chi^2$ ) and p-values (p) from mixed-effect models for the densities of honeybees, bumblebees and silver Y moths (moths), bumblebee (BB) (Shannon) diversity, and the proportions of legitimately visiting and nectar robbing bumblebees. Explanatory variables were honeybee hive treatment (HB), flower strip treatment (FS) and transect distance (transect) and their two-way interactions. P-values in bold are significant at the 0.05 level. Marginal R-square values ( $R^2$ ) are given for each model to represent the variance explained by the fixed effects.

Predictors	Honeybees		Moths		Bumblebees		BB diversity		Legitimate BB		Nectar robbing BB	
Marginal $R^2$	$R^2 = 0.36$		$R^2 = 0.52$		$R^2 = 0.082$		$R^2 = 0.072$		$R^2 = 0.043$		$R^2 = 0.046$	
	$\chi^2$	p	$\chi^2$	p	$\chi^2$	p	$\chi^2$	p	$\chi^2$	p	$\chi^2$	p
Intercept	<b>35.25</b>	<b>&lt; 0.001</b>	0.17	0.68	<b>42.46</b>	<b>&lt; 0.001</b>	<b>17.20</b>	<b>&lt; 0.001</b>	0.76	0.38	0.52	0.47
HB	<b>4.35</b>	<b>0.037</b>	<b>10.61</b>	<b>0.0011</b>	1.74	0.19	0.17	0.68	2.70	0.10	2.21	0.14
FS	0.79	0.38	<b>4.20</b>	<b>0.041</b>	1.59	0.21	1.42	0.23	2.70	0.10	<b>4.47</b>	<b>0.035</b>
Transect	<b>15.36</b>	<b>&lt; 0.001</b>	0.11	0.74	<b>8.15</b>	<b>0.0043</b>	0.47	0.50	0.98	0.32	2.62	0.11
HB x FS												
HB x Transect	<b>18.80</b>	<b>&lt; 0.001</b>			<b>10.29</b>	<b>0.0013</b>						
FS x Transect			<b>5.36</b>	<b>0.021</b>	<b>5.86</b>	<b>0.016</b>			<b>5.73</b>	<b>0.017</b>	<b>5.96</b>	<b>0.015</b>



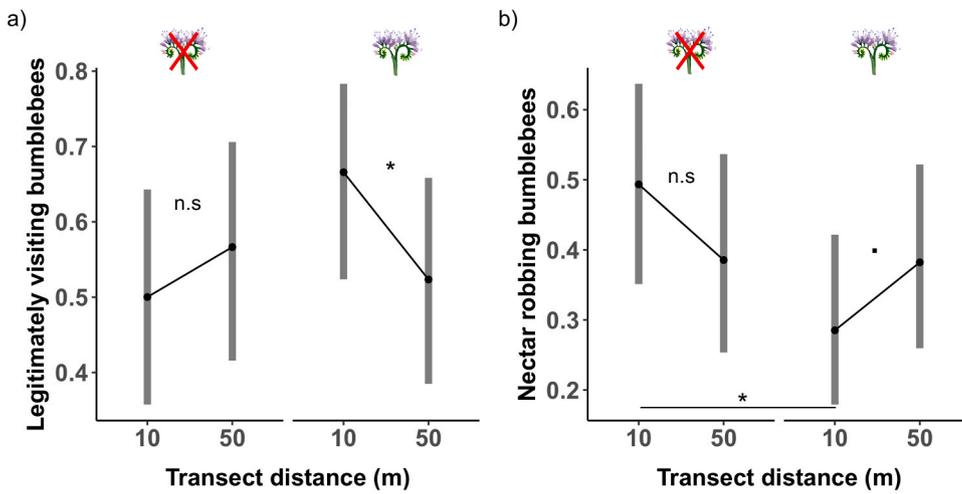
**Fig. 2.** Estimated marginal means of the densities of (a, b) bumblebees and (c, d) silver Y moths per transect (100 m<sup>2</sup>) in fields without flower strips (crossed out flower symbol) and with flower strips (flower symbol), without honeybee hives (crossed out hive symbol) and with honeybee hives (hive symbol). Whiskers represent 95% confidence intervals. Alpha levels of pair-wise comparisons of the estimated marginal means of post-hoc tests (a, b, d) and main effects (c) are indicated by \*\* < 0.010, \* < 0.050 ■ > 0.050 and n.s. > 0.10. Figures with raw data points are provided in Fig. S4.

by the honeybee hive treatment, and an interaction between the flower strip treatment and the transect distance (Table 1). Silver Y moth density was higher in fields without honeybee hives (Fig. 2c). In addition, silver Y moth density was higher in fields with flower strips, but only at 10 m distance from the strip (Fig. 2d). There was no effect of transect distance on silver Y moth density in fields without flower strips.

### 3.4. Bumblebee foraging behaviour

In total we observed 300 bumblebees legitimately visiting faba bean flowers and 251 bumblebees robbing nectar (Table S4). Among the nectar robbers, 94% of the observations were from individuals

belonging to the *B. terrestris* complex (Table S4). Both the proportion of legitimately visiting bumblebees and nectar robbing bumblebees was explained by an interaction between the flower strip treatment and the transect distance (Table 1). In fields with a flower strip, the proportion of legitimately visiting bumblebees was higher at 10 m distance compared with 50 m distance from the strip and the proportion of nectar robbers tended to be lower at 10 m compared with 50 m distance from the strip (Fig. 3a, b). Also, the proportion of nectar robbing bumblebees was lower in fields with a flower strip compared with fields without a flower strip but only at 10 m from the strip (Fig. 3b).



**Fig. 3.** Estimated marginal means of the proportion of legitimately visiting bumblebees (a) and nectar robbing bumblebees (b) per transect (100 m<sup>2</sup>) in fields without flower strips (crossed out flower symbol) and with flower strips (flower symbol), and at different transect distances (10 m and 50 m). Whiskers represent 95% confidence intervals. Alpha levels of pairwise comparisons of the estimated marginal means of post-hoc tests are indicated by \* < 0.050, ■ > 0.050 and n.s. > 0.10. Figures with raw data points are provided in Fig. S5.

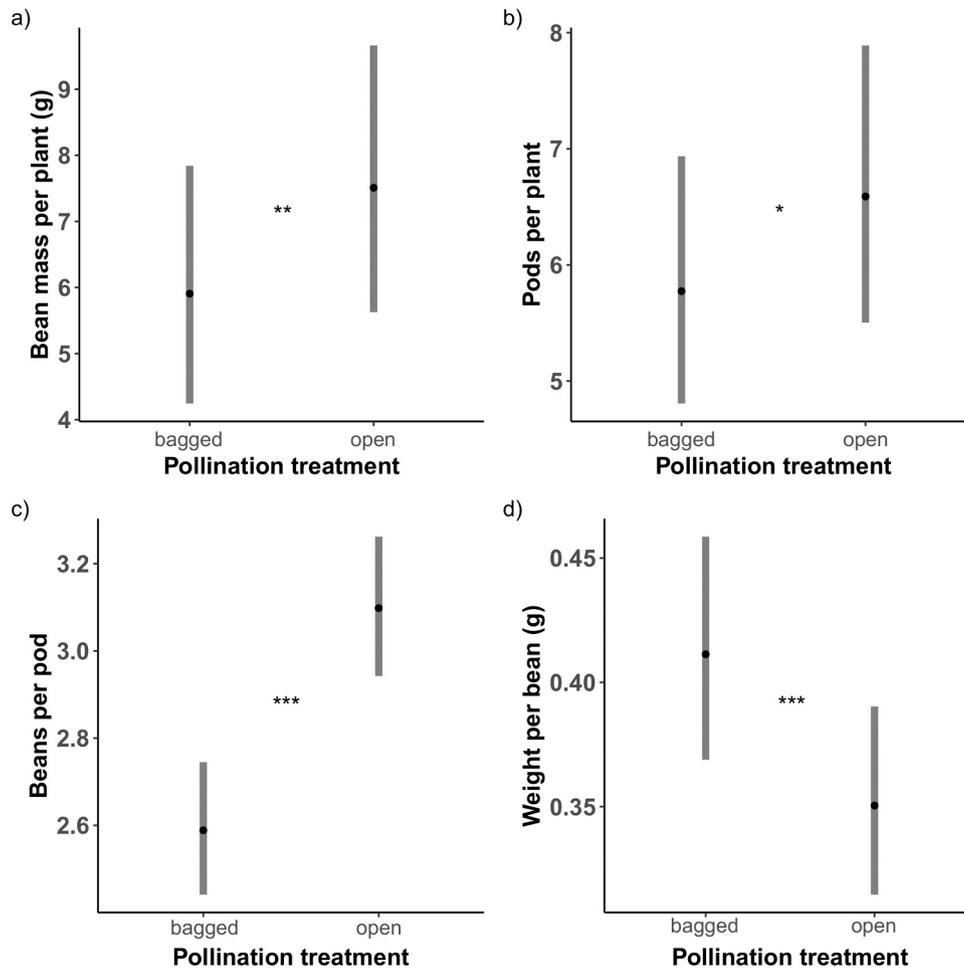
3.5. The effect of insect pollination on yield components

Bean mass per plant (g) (Fig. 4a), number of pods per plant (Fig. 4b) and number of beans per pod (Fig. 4c) were higher, whereas individual bean weight was lower (Fig. 4d) in open pollinated compared with bagged plants (Table 2). Bean mass per plant was also higher in fields with flower strips, independently of the pollination treatment (Fig. S7,

Table 2).

3.6. Natural enemies and pests

We counted a total of 1492 ladybird beetles, 197 hoverflies, 1398 lacewings, 14,470 pea aphids, 341 parasitised pea aphid mummies, 187,675 black bean aphids and 53 broad bean beetles on faba bean



**Fig. 4.** Estimated marginal means of the effect of insect pollination on yield components in bagged and open-pollinated plants: (a) bean mass per plant (grams), (b) number of pods per plant, (c) number of beans per pod and (d) individual bean weights (grams). Whiskers represent 95% confidence intervals. Alpha levels of main effects are indicated by \*\*\* < 0.0010, \*\* < 0.010, \* < 0.050. Figures with raw data points are provided in Fig. S6.

**Table 2**

Chi-Square ( $\chi^2$ ) and p-values (p) from mixed-effect models for bean mass per plant (grams), number of pods per plant, number of beans per pod, and individual bean weight (grams). Explanatory variables were honeybee hive treatment (HB), flower strip treatment (FS), transect distance (transect) and pollination treatment (bagged versus open (Poll)) and two- and three-way interactions including pollination treatment. P-values in bold are significant at the 0.05 level. Marginal R-square values ( $R^2$ ) are given for each model to represent the variance explained by the fixed effects.

	Bean mass per plant		Number of pods		Beans per pod		Individual bean weight	
Marginal $R^2$	$R^2 = 0.16$		$R^2 = 0.17$		$R^2 = 0.027$		$R^2 = 0.20$	
	$\chi^2$	p	$\chi^2$	p	$\chi^2$	p	$\chi^2$	p
Intercept	<b>40.73</b>	<b>&lt; 0.001</b>	<b>98.67</b>	<b>&lt; 0.001</b>	<b>381.64</b>	<b>&lt; 0.001</b>	<b>140.81</b>	<b>&lt; 0.001</b>
HB	1.82	0.18	0.56	0.45	0.92	0.34	1.36	0.24
FS	<b>5.18</b>	<b>0.023</b>	3.15	0.076	< 0.01	0.97	3.64	0.057
Transect	1.00	0.32	1.02	0.31	0.03	0.87	0.09	0.76
Poll	<b>9.15</b>	<b>0.0025</b>	<b>5.70</b>	<b>0.017</b>	<b>31.12</b>	<b>&lt; 0.001</b>	<b>20.25</b>	<b>&lt; 0.001</b>
HB x Poll								
FS x Poll								
Transect x Poll								
HB x FS x Poll								
HB x Transect x Poll								
FS x Transect x Poll								

plants.

The ladybird beetle density was explained by both the honeybee hive treatment and an interaction between the flower strip treatment and the transect distance (Table 3). The ladybird beetle density was higher in fields with honeybee hives (Fig. 5a), and in fields with flower strips, ladybird beetle density was higher at 50 m from the strip (Fig. 5b). The density of hoverflies and lacewings was not affected by any of the treatments (Table 3). Both ladybird beetles and hoverflies were more abundant in fields with a high density of black bean aphids (Table 3).

The pea aphid density was positively correlated with the black bean aphid infestation category (Table 3). Both the pea aphid density and parasitisation rate were explained by an interaction between the honeybee hive treatment and the transect distance (Table 3). In fields with honeybee hives, the pea aphid density was higher at 50 m compared to 10 m from the strip (Fig. 5c). In contrast, the pea aphid parasitisation rate was higher at 10 m from the strip in fields with honeybee hives but tended to be higher at 50 m from the strip when there were no honeybee hives (Fig. 5d). The black bean aphid density was also explained by an interaction between the honeybee hive treatment and the transect distance (Table 3). The black bean aphid density was higher along the field edges in fields with honey bee hives (Fig. 5e). Bean aphid densities also increased from the field edge towards the field interior in fields without honey bees, but decreased towards the field interior in fields with honey bee hives (Fig. 5e). The broad bean beetle density was not affected by any treatment (Table 3).

### 3.7. Ground predators

We collected a total of 11897 carabid beetles from 61 species

**Table 3**

Chi-Square ( $\chi^2$ ) and p-values (p) from mixed-effect models for ladybird beetles, hoverflies, lacewings, pea aphids, pea aphid parasitisation rate, black bean aphids (bean aphids) and broad bean beetles. Explanatory variables included in models were honeybee hive treatment (HB), flower strip treatment (FS) and transect distance (transect) and their two-way interactions, and black bean aphid infestation category. P-values in bold are significant at the 0.05 level. Marginal R-square values ( $R^2$ ) are given for each model to represent the variance explained by the fixed effects.

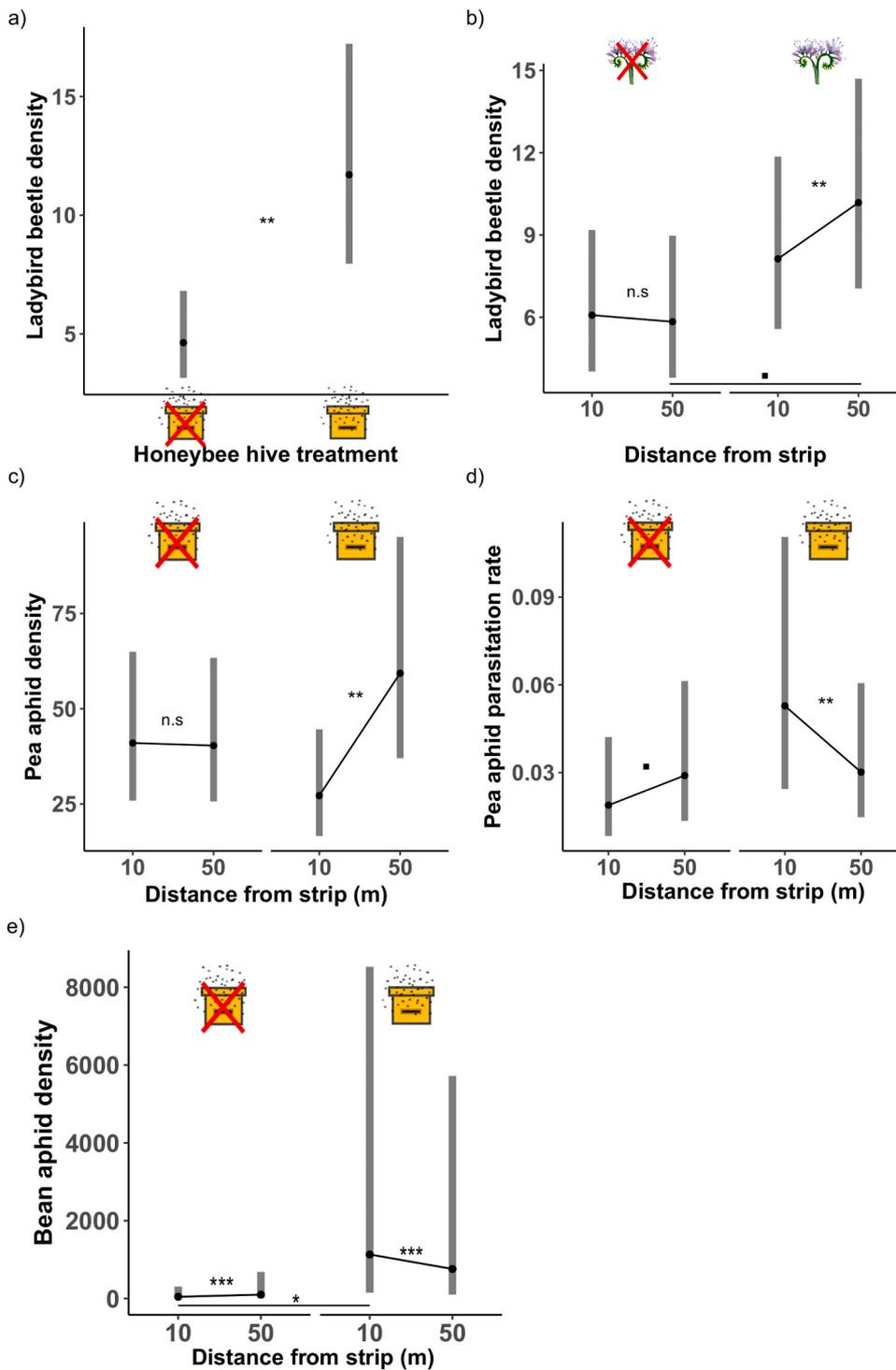
	Ladybird beetles		Hoverflies		Lacewings		Pea aphids		Pea aphid parasitisation rate		Bean aphids		Broad bean beetles	
Marginal $R^2$	$R^2 = 0.64$		$R^2 = 0.15$		$R^2 = 0.051$		$R^2 = 0.74$		$R^2 = 0.054$		$R^2 = 0.081$		$R^2 = 0.047$	
	$\chi^2$	p	$\chi^2$	p	$\chi^2$	p	$\chi^2$	p	$\chi^2$	p	$\chi^2$	p	$\chi^2$	p
Intercept	<b>18.50</b>	<b>&lt; 0.001</b>	0.47	0.49	<b>64.25</b>	<b>&lt; 0.001</b>	<b>114.46</b>	<b>&lt; 0.001</b>	<b>52.36</b>	<b>&lt; 0.001</b>	<b>152.07</b>	<b>&lt; 0.001</b>	0.88	0.35
HB	<b>11.65</b>	<b>&lt; 0.001</b>	1.23	0.27	0.70	0.40	1.43	0.23	3.25	0.071	2.82	0.093	0.12	0.73
FS	1.13	0.29	1.39	0.24	< 0.01	0.94	0.97	0.33	0.22	0.64	< 0.01	0.93	0.32	0.57
Transect	0.11	0.74	0.72	0.40	0.61	0.44	0.02	0.90	3.14	0.076	<b>1173.50</b>	<b>&lt; 0.001</b>	< 0.01	0.93
Bean aphids	<b>35.47</b>	<b>&lt; 0.001</b>	<b>13.95</b>	<b>&lt; 0.001</b>	0.05	0.82	<b>60.31</b>	<b>&lt; 0.001</b>	3.28	0.070			0.19	0.67
HB x FS														
HB x Transect							<b>17.79</b>	<b>&lt; 0.001</b>	<b>10.37</b>	<b>0.0013</b>	<b>9643.32</b>	<b>&lt; 0.001</b>		
FS x Transect														

(Table S5). Carabid beetle density did not differ among treatments nor with distance from the strip (Table 4). Carabid beetle Shannon diversity ranged between 1.33 and 2.47 (mean: 1.80) and was explained by an interaction between the flower strip treatment and transect location (Table 4). In fields with flower strips, carabid beetle diversity was higher within the flower strip and at 10 m distance from the flower strip compared with 50 m from the flower strip (Fig. 6a). In fields without flower strips, carabid beetle diversity did not differ among transect locations. We collected a total of 1189 rove beetles from 21 genera (Table S5). Rove beetle Shannon diversity ranged between 0 and 2.09 (mean: 1.30). Neither rove beetle abundance nor Shannon diversity were affected by any of the treatments (Table 4).

We collected a total of 3346 spiders from 52 species (Table S5). Spider abundance was higher in fields with flower strips, independently of transect location and honeybee hive treatment (Fig. 6b, Table 5). Spider Shannon diversity ranged between 0.69 and 2.31 (mean: 1.60) and was higher within the strip and at 10 m distance from the strip compared with 50 m from the strip, irrespective of whether fields had flower strips or honeybee hives (Fig. 6c).

### 3.8. Broad bean beetle infestation rate

We observed a total of 1153 broad bean beetle emergence holes and 51 parasitoid emergence holes. The number of broad bean beetle emergence holes per bean was explained by an interaction between the honeybee hive and flower strip treatment (Table 5). Post-hoc tests did, however, not reveal any significant differences between group means. There was a tendency ( $p = 0.090$ ) that the infestation rate per bean was higher in fields with flower strips and honeybee hives compared to fields



**Fig. 5.** Estimated marginal means of natural enemies and pests per transect in fields without flower strips (crossed out flower symbol) and with flower strips (flower symbol), without honeybee hives (crossed out hive symbol) and with honeybee hives (hive symbol): (a, b) ladybird beetles, (c) pea aphid density, (d) pea aphid parasitization rate, (e) black bean aphid density. Whiskers represent 95% confidence intervals. Alpha levels of p-values for main effects (a) and pair-wise comparisons of the estimated marginal means of post-hoc tests (b–e) are indicated by \*\*\* < 0.0010, \*\* < 0.010, \* < 0.050, ■ < 0.10 and n.s. > 0.10. Figures with raw data points are provided in Fig. S8.

without a flower strip and with honeybee hives, which was driving the interaction (Fig. 7a). The broad bean beetle parasitization rate was explained by an interaction between the flower strip treatment and the transect distance (Table 5). The parasitization rate was higher at 10 m compared with 50 m from the strip, but only in fields without flower strips (Fig. 7b). There was a tendency for the parasitization rate to be lower in fields with a flower strip, but only at 10 m distance from the strip (Fig. 7b).

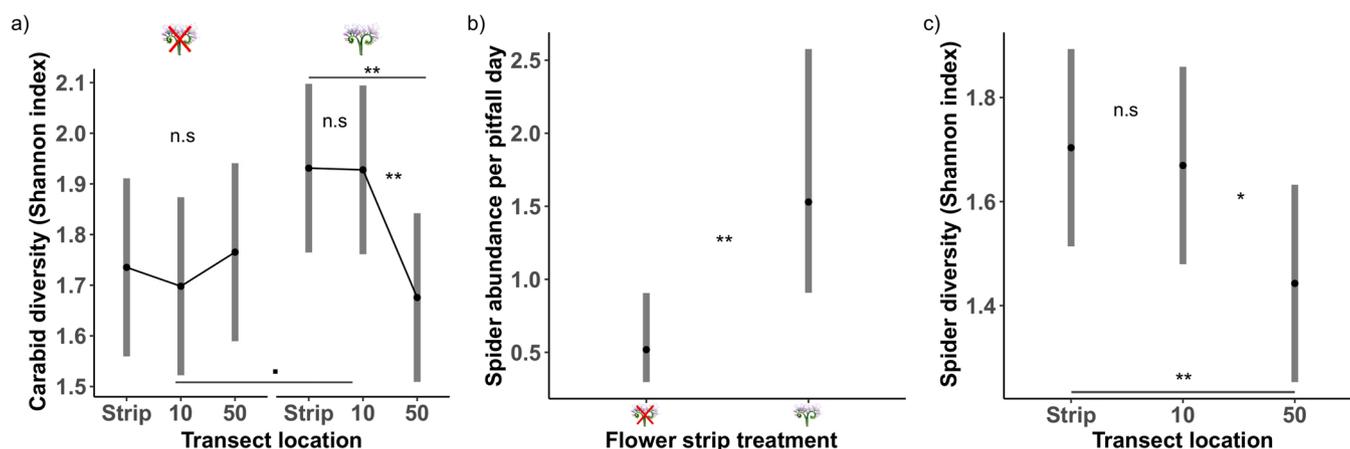
#### 4. Discussion

Sowing annual flower strips and supplementing honeybee hives along field edges affected arthropod guilds and the ecosystem services they provide differently. Annual flower strips promoted pollinator silver Y moths near the strip and redistributed bumblebees from faba bean field edges to interiors without affecting their overall densities, did not affect foliage-dwelling natural enemies, but enhanced ground spider abundance, and near the strip also increased carabid Shannon diversity. Interestingly, adding honeybee hives enhanced overall ladybird beetle densities, enhanced black bean aphids along field edges, pushed

**Table 4**

Chi-Square ( $\chi^2$ ) and p-values (p) from mixed-effect models for carabid beetle density, carabid beetle (Shannon) diversity, spider density, spider (Shannon) diversity, rove beetle density, and rove beetle (Shannon) diversity. Explanatory variables included in models were honeybee hive treatment (HB), flower strip treatment (FS) and transect distance (transect) and their two-way interactions. P-values in bold are significant at the 0.05 level. Marginal R-square values ( $R^2$ ) are given for each model to represent the variance explained by the fixed effects.

	Carabid beetle density		Carabid diversity		Spider density		Spider diversity		Rove beetle density		Rove beetle diversity	
Marginal $R^2$	$R^2 = 0.020$		$R^2 = 0.26$		$R^2 = 0.19$		$R^2 = 0.11$		$R^2 = 0.032$		$R^2 = 0.063$	
	$\chi^2$	p	$\chi^2$	p	$\chi^2$	p	$\chi^2$	p	$\chi^2$	p	$\chi^2$	p
Intercept	<b>41.56</b>	<b>&lt; 0.001</b>	<b>199.66</b>	<b>&lt; 0.001</b>	3.62	0.057	<b>117.62</b>	<b>&lt; 0.001</b>	<b>3.90</b>	<b>0.048</b>	<b>46.19</b>	<b>&lt; 0.001</b>
HB	0.39	0.53	2.56	0.11	0.11	0.74	0.51	0.48	0.44	0.51	0.52	0.47
FS	0.24	0.63	<b>7.09</b>	<b>0.0077</b>	<b>8.10</b>	<b>0.0044</b>	0.05	0.82	0.47	0.49	1.42	0.23
Transect	0.32	0.85	0.81	0.67	2.75	0.25	<b>12.07</b>	<b>0.0024</b>	3.64	0.16	0.60	0.74
HB x FS			2.91	0.088								
HB x Transect												
FS x Transect			<b>11.58</b>	<b>0.0031</b>								



**Fig. 6.** Estimated marginal means of (a) carabid Shannon diversity, (b) spider abundance per pitfall day, and spider Shannon diversity in fields without flower strips (crossed out flower symbol) and with flower strips (flower symbol) and along different transect distances (within the strip, at 10 m and 50 m from the strip). Whiskers represent 95% confidence intervals. Alpha levels of pair-wise comparisons of the estimated marginal means of post-hoc tests (a) and main effects (b-c) are indicated by \*\* < 0.010, \* < 0.050, ■ < 0.10 and n.s. > 0.10. Figures with raw data points are provided in Fig. S9.

**Table 5**

Chi-Square ( $\chi^2$ ) and p-values (p) from mixed-effect models for broad bean beetle infestation per bean (infestation) and broad bean beetle parasitisation rate (parasitisation). Explanatory variables were honeybee hive treatment (HB), flower strip treatment (FS) and transect distance (transect) and their two-way interactions, and the average number of beans in a 0.36 m<sup>2</sup> quadrat per transect (beans per quadrat). P-values in bold are significant at the 0.05 level. Marginal R-square values ( $R^2$ ) are given for each model to represent the variance explained by the fixed effects.

	Infestation		Parasitisation rate	
Marginal $R^2$	$R^2 = 0.078$		$R^2 = 0.099$	
	$\chi^2$	p	$\chi^2$	p
Intercept	<b>8.42</b>	<b>0.0037</b>	<b>15.67</b>	<b>&lt; 0.001</b>
HB	2.82	0.093	< 0.01	0.95
FS	1.12	0.29	3.78	0.052
Transect	1.40	0.24	<b>5.24</b>	<b>0.022</b>
Beans per quadrat	2.12	0.15		
HB x FS	<b>4.04</b>	<b>0.044</b>		
HB x Transect				
FS x Transect			<b>4.35</b>	<b>0.037</b>

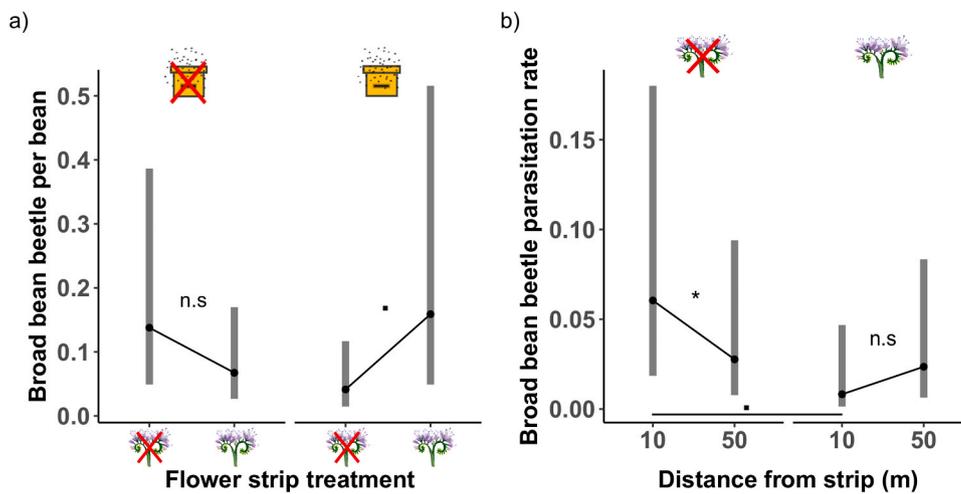
bumblebees towards the interior of the field and depressed overall densities of silver Y moths. Pea aphid parasitisation rate tended to be higher in fields with honeybee hives, but decreased towards the interior of the field.

#### 4.1. Local effects of flower strips on pollinator densities and bumblebee foraging behaviour

Annual flower strips influenced the distribution of pollinator densities and bumblebee foraging behaviours within faba bean fields. Bumblebee densities were lower at 10 m from the strip compared with 50 m when flower strips were present while there was no effect of transect distance on bumblebee densities in fields without a flower strip. At the time of faba bean bloom, phacelia was the dominant flowering species in the flower strip (Fig. S2, Table S3). Phacelia is highly attractive to bumblebees (Williams and Christian, 1991). It is thus possible that phacelia attracted bumblebees from the faba bean field edge into the flower strip, a phenomenon in line with the “concentrator hypothesis”, where flower plantings temporarily compete with flowering crops for pollinator visits (Albrecht et al., 2020; Kremen et al., 2019). This hypothesis would need to be confirmed by sampling bumblebees in both the field and the flower strip. In contrast to bumblebees, silver Y moth densities were higher at 10 m compared with 50 m from the flower strip, suggesting that flower strips facilitated moths into the crop.

We found a higher proportion of legitimately pollinating bumblebees at 10 m compared with 50 m from the flower strip. More bumblebees might be visiting the phacelia for nectar, which is more easily accessible due to their shorter corolla, and use the adjacent faba bean for pollen, which is particularly rich in protein (Pamminger et al., 2019) and must be collected legitimately. As such, the presence of flower strips decreased bumblebee density, but selected for legitimately visiting bumblebees along the faba bean field edge.

Even though flower strips redistributed bumblebees and silver Y



**Fig. 7.** Estimated marginal means of (a) broad bean beetle infestation per bean and (b) parasitism rate in fields without flower strips (crossed out flower symbol) and with flower strips (flower symbol), and without honeybee hives (crossed out hive symbol) and with honeybee hives (hive symbol), and at two transect distances of 10 m and 50 m from strips. Whiskers represent 95% confidence intervals. Alpha levels for pair-wise comparisons of the estimated marginal means of post-hoc tests are indicated by \* < 0.050, ■ > 0.050 and n.s. > 0.10. Figures with raw data points are provided in Fig. S10.

moths within the field, we found no effect of flower strips on the overall densities of these wild pollinators in the crop fields. It is possible that the relatively small areas of flower strips (range: 0.1–0.5 ha) did not provide sufficient resources to attract pollinators from the wider landscape. The effectiveness of flower strips to attract pollinators depends on the ecological contrast in floral resources they provide compared with that in the surrounding landscape (Scheper et al., 2013). Alternatively, pollinators were attracted to the flower strips, but did not spill over into the crop fields. The flower strip blooming period might also have occurred too late to affect the pollinators visiting faba bean. The hot and dry summer delayed flower strip bloom and shortened faba bean crop bloom, giving a very short bloom overlap between the two.

#### 4.2. Honeybee hives redistribute bumblebees within fields and deter silver Y moths

As expected, supplementing honeybee hives to faba bean fields increased the overall density of honeybees foraging within the faba bean fields. Against our hypothesis, the honeybee hive treatment did not affect overall bumblebee densities in faba bean fields. It is possible that the number of honeybee hives supplemented in our experimental landscapes was not high enough to induce resource depletion and deter bumblebees from crop fields as previously observed (Angelella et al., 2021; Lindström et al., 2016). However, the presence of honeybee hives counteracted the positive effects of flower strips on the abundance of bumblebee queens and males in linear habitats in the same landscapes as here (Bommarco et al., 2021). Instead, we found lower bumblebee densities at 50 m from the strip in fields without honeybee hives, and higher bumblebee densities at 50 m from the strips in fields with honeybee hives, suggesting that high numbers of honeybees pushed bumblebees farther into the field centres. Redistribution of bumblebee foragers within fields, rather than deterrence from fields, in response to higher honeybee densities has previously been observed (Walthers-Hellwig et al., 2006). Silver Y moth densities on the other hand, were lower in fields with honeybee hives indicating that they were deterred from faba bean fields by high honeybee densities.

#### 4.3. Benefit of insect pollination on yield components

Insect pollination increased bean mass per plant in open pollinated compared with bagged plants on average by 27% as a result of more pods per plant and beans per pod. Insect pollination benefits in faba bean are commonly observed but vary substantially among experiments and among cultivars (Bishop and Nakagawa, 2021). The insect pollination benefit on bean mass per plant, pods per plant and beans per pod were independent of the flower strip and honeybee hive treatment,

suggesting that faba bean fields were not pollinator limited, where increased visitation by honeybees and legitimately visiting bumblebees and silver Y moths did not enhance pollination. Bean mass per plant was, however, higher in fields with flower strips, but the effect was independent of the pollination treatment. Since bean mass was higher in both bagged and open pollinated plants in field with flower strips, this effect could have been driven by two fields, with flower strips, which were irrigated due to the extreme drought. The individual bean weight was lower in open pollinated plants. Higher individual bean weight in faba bean plants excluded from insect pollination is not uncommon and might be a way for the plant to compensate for inadequate cross-pollination (Lundin and Raderschall, 2021).

#### 4.4. Honeybee hives promote ladybird beetles and black bean aphids while flower strips have weak effects

Against our expectations, adding honeybee hives promoted overall ladybird beetle densities and black bean aphids along the field edge. To our knowledge, our finding that adding honeybee hives benefits natural enemies of pests is unique. Ladybird beetle densities were higher in fields with honeybee hives even though the number of black bean aphid infestation was added as a covariate to the models. Thus, factors independent of black bean aphids associated to the addition of honeybee hives promote ladybird beetles. Ladybird beetles regularly feed on pollen (Lundgren, 2009b; Triltsch, 1997). Therefore, it could be that honeybees spill pollen when flying between faba bean flowers and so make more pollen available for ladybird beetles. Due to the flower morphology, faba bean pollen might otherwise be difficult to access for ladybird beetles. The pea aphid parasitism rate was lower in the field interior compared with the field edge in fields with added honey bee hives. This is probably because pea aphid densities were higher but not the parasitism was densities leading to a lower parasitism rate.

Among foliage-dwelling pests and natural enemies, flower strips only had a positive effect on ladybird beetles at 50 m from the strip. It could be that at 10 m from the flower strip, ladybird beetles were attracted into the flower strip, though we did not confirm this by sampling inside the flower strip. We found no effect on any other foliage-dwelling natural enemies in the adjacent faba bean fields. This is in contrast to previous findings of flower strips facilitating higher numbers of foliage-dwelling natural enemies into adjacent crop fields (Tschumi et al., 2015, 2016). The relatively late flower strip bloom might have prevented sufficiently large colonisation of natural enemies to detect a spill-over effect into the faba bean field.

#### 4.5. Flower strips benefit ground-dwelling predators

Carabid beetle Shannon diversity, but not overall density, was higher inside flower strips and at 10 m from the flower strips compared with fields without flower strips. This suggests that flower strips did not generate overall higher carabid beetle numbers, but benefited certain carabid beetle species more than others. There was no effect of flower strips on rove beetle density or Shannon diversity. Carabid and rove beetles require heterogeneous landscapes (Sutter et al., 2018) and vicinity to semi-natural habitats (Duflo et al., 2016), as overwintering habitats (Pywell et al., 2005). The fact that annual flower strips cannot provide such overwintering habitat might explain why overall carabid and rove beetle densities were not affected by flower strips. Spider abundances, on the other hand, increased in their overall density irrespective of distance from the flower strip. Flower strips most likely benefited spiders by providing more complex vegetation structure and a different microclimate rather than providing food resources (Ditner et al., 2013). The strong positive effect of flower strips on spiders could be because such structural and microclimatic benefits already establish soon after sowing rather than just at flowering, which gave spider populations more time to establish and spill into the adjacent crop.

#### 4.6. Interactions between honeybee hive and flower strip treatments explain broad bean beetles infestation and parasitation

Broad bean beetle infestation was explained by an interaction between the honeybee hive and the flower strip treatments. Post-hoc tests did however only reveal a tendency for increased broad bean beetle infestation in fields with honeybee hives and flower strips compared with fields with honeybee hives but without flower strips. Broad bean beetles regularly feed on EFN and pollen of faba bean, but also consume pollen of other plants such as dill, buckwheat, phacelia, cornflower and clover, which were growing in the flower strips (Pölitiz and Reike, 2019). The influence of honeybee hives and flower strips on broad bean beetle infestation could be better understood by investigating the number of broad bean beetles in the flower strips or by further exploring the effect of pollinators on broad bean beetles in faba beans. We found that broad bean beetle parasitation rate was influenced by an interaction between the flower strip treatment and transect distance. The parasitation rate was higher along field edges in fields without a flower strip but tended to be lower along field edges in fields with flower strips. This suggests that flower strips might attract parasitoids away from the crop rather than promoting broad bean beetle parasitation, a hypothesis that can be tested by sampling parasitoids in both the field and the flower strip.

## 5. Conclusions

Annual flower strips in landscapes dominated by arable fields did not provide sufficient resources to attract higher overall densities of wild pollinators. The strips did affect the local distribution and foraging behaviour of bumblebees possibly by providing alternative nectar resources. The unusual weather in 2018 likely hampered facilitation of pollinators and foliage-dwelling natural enemies of pests from flower strips to faba bean fields. This because the onset of the flower strip bloom was delayed due to a late frost in early spring, while the faba bean bloom was preceded and hastened due to the hot and dry summer, leading to a very short bloom overlap between the two habitats. In contrast, annual flower strips were beneficial for spiders and enhanced carabid diversity possibly by providing more diverse shelters and beneficial microclimate soon after sowing. The addition of honeybee hives had no detrimental effect on bumblebees visiting faba bean flowers, suggesting that resource competition was not severe enough to deter bumblebees from the crop fields. Increased honeybee densities had an unexpected positive effect on ladybird beetle density, an effect that deserves more attention in future research. Insect pollination increased faba bean yield components independently of the flower strip and

honeybee hive treatments, suggesting that faba bean fields were not short on insect pollination this year. Our research took place under an unusual drought year. These unforeseen weather conditions might limit the generalisation of our results under less extreme weather conditions. On the other hand, we believe that our work provides insights into the effectiveness of flower strips, and the interaction between floral resource provision and potential resource competition under climate change, which is expected to cause an increasing frequency of exactly the kind of dry and hot weather that occurred during our sampling (Toreti et al., 2019).

#### CRediT authorship contribution statement

RB, OL and SAML conceived the idea and secured funding. All authors designed and planned the experiment. CAR supervised and conducted the field work with support from co-authors. CAR led data analysis, interpretation of results and the manuscript writing with support from OL and RB. All authors contributed to the revisions of the manuscript.

#### Data accessibility statement

Data is available online at the Swedish National Data Service at : <http://doi.org/10.5878/e50m-9547>

#### Declaration of Competing Interest

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

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#### Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.agee.2021.107754](https://doi.org/10.1016/j.agee.2021.107754).

#### References

- Albrecht, M., Kleijn, D., Williams, N., Tschumi, M., Blaauw, B., Bommarco, R., Campbell, A., Dainese, M., Drummond, F., Entling, M., Ganser, D., De Groot, A., Goulson, D., Grab, H., Hamilton, H., Herzog, F., Isaacs, R., Jacot, K., Jeanneret, P., Jonsson, M., Knop, E., Kremen, C., Landis, D., Loeb, G., Marini, L., McKeerchar, M., Morandin, L., Pfister, S., Potts, S., Rundlöf, M., Sardiñas, H., Sciligo, A., Thies, C., Tschamtko, T., Venturini, E., Veromann, E., Vollhardt, I., Wäckers, F., Ward, K., Wilby, A., Woltz, M., Wratten, S., Sutter, L., 2020. The effectiveness of flower strips and hedgerows on pest control, pollination services and crop yield: a quantitative synthesis. *Ecol. Lett.* 23, 1488–1498. <https://doi.org/10.22541/au.158618502.29242370>.
- Angelella, G.M., McCullough, C.T., Rourke, M.E.O., 2021. Honey bee hives decrease wild bee abundance, species richness, and fruit count on farms regardless of wildflower strips. *Sci. Rep.* 11, 3202. <https://doi.org/10.1038/s41598-021-81967-1>.
- Artz, D.R., Hsu, C.L., Nault, B.A., 2011. Influence of honey bee, *Apis mellifera*, hives and field size on foraging activity of native bee species in pumpkin fields. *Environ. Entomol.* 40, 1144–1158. <https://doi.org/10.1603/EN10218>.
- Bishop, J., Nakagawa, S., 2021. Quantifying crop pollinator dependence and its heterogeneity using multi-level meta-analysis. *J. Appl. Ecol.* 58, 1030–1042. <https://doi.org/10.1111/1365-2664.13830>.

- Blaauw, B.R., Isaacs, R., 2014. Flower plantings increase wild bee abundance and the pollination services provided to a pollination-dependent crop. *J. Appl. Ecol.* 51, 890–898. <https://doi.org/10.1111/1365-2664.12257>.
- Bommarco, R., Kleijn, D., Potts, S.G., 2013. Ecological intensification: harnessing ecosystem services for food security. *Trends Ecol. Evol.* 28, 230–238. <https://doi.org/10.1016/j.tree.2012.10.012>.
- Bommarco, R., Lindström, S.A.M., Raderschall, C.A., Gagic, V., Lundin, O., 2021. Flower strips enhance abundance of bumble bee queens and males in landscapes with few honey bee hives. *Biol. Conserv.* 263, 109363 <https://doi.org/10.1016/j.biocon.2021.109363>.
- Breeze, T.D., Vaissière, B.E., Bommarco, R., Petanidou, T., Seraphides, N., Kozák, L., Scheper, J., Biesmeijer, J.C., Kleijn, D., Gyldenkerne, S., Moretti, M., Holzschuh, A., Steffan-Dewenter, I., Stout, J.C., Pärtel, M., Zobel, M., Potts, S.G., 2014. Agricultural policies exacerbate honeybee pollination service supply-demand mismatches across Europe. *PLoS One* 9, e82996. <https://doi.org/10.1371/journal.pone.0082996>.
- Brittain, C., Williams, N., Kremen, C., Klein, A.M., 2013. Synergistic effects of non-Apis bees and honey bees for pollination services. *Proc. R. Soc. B Biol. Sci.* 280, 20122767 <https://doi.org/10.1098/rspb.2012.2767>.
- Brooks, M.E., Kristensen, K., Koen, J., Magnusson, A., Berg, C., Nielsen, A., Skaug, H., Maechler, M., Bolker, B., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R. J.* 9, 378–400.
- Carvalho, L.G., Veldtman, R., Shenkute, A.G., Tesfay, G.B., Pirk, C.W.W., Donaldson, J.S., Nicolson, S.W., 2011. Natural and within-farmland biodiversity enhances crop productivity. *Ecol. Lett.* 14, 251–259. <https://doi.org/10.1111/j.1461-0248.2010.01579.x>.
- 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>.
- Cousins, S.A.O., Ohlson, H., Eriksson, O., 2007. Effects of historical and present fragmentation on plant species diversity in semi-natural grasslands in Swedish rural landscapes. *Landsc. Ecol.* 22, 723–730. <https://doi.org/10.1007/s10980-006-9067-1>.
- Cunningham, S.A., Le Feuvre, D., 2013. Significant yield benefits from honeybee pollination of faba bean (*Vicia faba*) assessed at field scale. *Field Crop. Res.* 149, 269–275. <https://doi.org/10.1016/j.fcr.2013.05.019>.
- Daigne, M., Martin, E.A., Aizen, M.A., Albrecht, M., Bartomeus, I., Bommarco, R., Carvalho, L.G., Chaplin-Kramer, R., Gagic, V., Garibaldi, L.A., Ghazoul, J., Grab, H., Jonsson, M., Karp, D.S., Kennedy, C.M., Kleijn, D., Kremen, C., Landis, D.A., Letourneau, D.K., Marini, L., Poveda, K., Rader, R., Smith, H.G., Tscharntke, T., Andersson, G.K.S., Badenhausser, I., Baensch, S., Bezerra, C.-L., Cavigliasso, P., Cetkovic, A., Chacoff, N.P., Classen, A., Cusser, S., da Silva e Silva, F.D., de Groot, G.A., Dudenhöffer, J.H., Ekroos, J., Fijen, T., Franck, P., Freitas, B.M., Garratt, M.P.D., Gratton, C., Hipolito, J., Holzschuh, A., Hunt, L., Iverson, A.L., Jha, S., Kaesar, T., Kim, T.N., Kishinevsky, M., Klatt, B.K., Klein, A.-M., Krewenka, K.M., Krishnan, S., Larsen, A.E., Lavigne, C., Liere, H., Maas, B., Malling, R.E., Martinez Pachon, E., Martinez-Salinas, A., Meehan, T.D., Mitchell, M.G.E., Molina, G.A.R., Nesper, M., Nilsson, L., O'Rourke, M.E., Peters, M.K., Plegas, M., Potts, S.G., Ramos, D., de, L., Rosenheim, J.A., Rundlöf, M., Rusch, A., Saez, A., Scheper, J., Schleuning, M., Schmack, J.M., Sciligo, A., Seymour, C., Stanley, D.A., Stewart, R., Stout, J.C., Sutter, L., Takada, M.B., Taki, H., Tamburini, G., Tschumi, M., Viana, B.F., Westphal, C., Willcox, B.K., Wratten, S.D., Yoshioka, A., Zaragoza-Trello, C., Zhang, W., Zou, Y., Steffan-Dewenter, I., 2019. A global synthesis reveals biodiversity-mediated benefits for crop production. *Sci. Adv.* 5, eaax0121.
- Ditner, N., Balmer, O., Beck, J., Blick, T., Nagel, P., Luka, H., 2013. Effects of experimentally planting non-crop flowers into cabbage fields on the abundance and diversity of predators. *Biodivers. Conserv.* 22, 1049–1061. <https://doi.org/10.1007/s10531-013-0469-5>.
- Duc, G., 1997. Faba bean (*Vicia faba* L.). *Field Crop. Res.* 53, 99–109. [https://doi.org/10.1016/S0378-4290\(97\)00025-7](https://doi.org/10.1016/S0378-4290(97)00025-7).
- Duflot, R., Ernout, A., Burel, F., Aviron, S., 2016. Landscape level processes driving carabid crop assemblage in dynamic farmlands. *Popul. Ecol.* 58, 265–275. <https://doi.org/10.1007/s10144-015-0534-x>.
- Edwards, E., Jenner, M., 2005. *Field Guide to the Bumblebees of Great Britain and Ireland*. Ocelli Limited, Eastbourne.
- Eeraerts, M., Smagghe, G., Meeus, I., 2020. Bumble bee abundance and richness improves honey bee pollination behaviour in sweet cherry. *Basic Appl. Ecol.* 43, 27–33. <https://doi.org/10.1016/j.baec.2019.11.004>.
- ESRI (Environmental Systems Research Institute), 2015. ArcMap 10.4.1, Redlands, CA, USA.
- Falk, S.J., 2015. *Field Guide to the Bees of Great Britain and Ireland*. Blombury, London.
- Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N., Snyder, P.K., 2005. Global consequences of land use. *Science* 309, 570–574. <https://doi.org/10.1126/science.1111772>.
- Fox, J., Weisberg, S., 2019. *An {R} Companion to Applied Regression*, third ed. Sage, Thousand Oaks CA <https://socialsciences.mcmaster.ca/jfox/Books/Companion/>.
- Free, J.B., 1993. *Insect Pollination of Crops*. Chapter 34. Leguminosae: *Vicia*. Academic Press, London, UK.
- Garibaldi, L.A., Steffan-Dewenter, I., Winfree, R., Aizen, M.A., Bommarco, R., Cunningham, S.A., Kremen, C., Carvalho, L.G., Harder, L.D., Afik, O., Bartomeus, I., Benjamin, F., Boreux, V., Cariveau, D., Chacoff, N.P., Dudenhöffer, J.H., Freitas, B.M., Ghazoul, J., Greenleaf, S., Hipolito, J., Holzschuh, A., Howlett, B., Isaacs, R., Javorek, S.K., Kennedy, C.M., Krewenka, K.M., Krishnan, S., Mendelike, Y., Mayfield, M.M., Motzke, I., Muryli, T., Nault, B.A., Otieno, M., Petersen, J., Pisanty, G., Potts, S.G., Rader, R., Ricketts, T.H., Rundlöf, M., Seymour, C.L., Schüepp, C., Szentgyörgyi, H., Taki, H., Tscharntke, T., Vergara, C.H., Viana, B.F., Wanger, T.C., Westphal, C., Williams, N., Klein, A.M., 2013. Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *Science* 339, 1608–1611.
- Gordy, J.W., Brewer, M.J., Bowling, R.D., Buntin, G.D., Seiter, N.J., Kerns, D.L., Reay-Jones, F.P.F., Way, M.O., 2019. Development of economic thresholds for sugarcane aphid (Hemiptera: Aphididae) in susceptible grain sorghum hybrids. *J. Econ. Entomol.* 112, 1251–1259. <https://doi.org/10.1093/jeet/toz028>.
- Hansen, L.M., Lorentsen, L., Boelt, B., 2008. How to reduce the incidence of black bean aphids (*Aphis fabae* Scop.) attacking organic growing field beans (*Vicia faba* L.) by growing partially resistant bean varieties and by intercropping field beans with cereals. *Acta Agric. Scand. Sect. B Soil Plant Sci.* 58, 359–364. <https://doi.org/10.1080/09664710701788844>.
- Hartig, F., 2019. DHARMA: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models. R Package Version 0.2.4. (<https://CRAN.R-project.org/package=DHARMA>).
- Hogg, B.N., Bugg, R.L., Daane, K.M., 2011. Attractiveness of common insectary and harvestable floral resources to beneficial insects. *Biol. Control* 56, 76–84. <https://doi.org/10.1016/j.biocontrol.2010.09.007>.
- Holland, J.M., Bianchi, F.J., Entling, M.H., Moonen, A.C., Smith, B.M., Jeanneret, P., 2016. Structure, function and management of semi-natural habitats for conservation biological control: a review of European studies. *Pest Manag. Sci.* 72, 1638–1651. <https://doi.org/10.1002/ps.4318>.
- Jägermeyr, J., 2020. Agriculture's historic twin-challenge toward sustainable water use and food supply for all. *Front. Sustain. Food Syst.* 4, 35. <https://doi.org/10.3389/fsufs.2020.00035>.
- Karkanis, A., Ntasi, G., Lepse, L., Fernández, J.A., Vågen, I.M., Rewald, B., Alsina, I., Kronberga, A., Balliu, A., Olle, M., Bodner, G., Dubova, L., Rosa, E., Savvas, D., 2018. Faba bean cultivation – revealing novel managing practices for more sustainable and competitive European cropping systems. *Front. Plant Sci.* 9, 1115. <https://doi.org/10.3389/fpls.2018.01115>.
- Kendall, A.D.A., Smith, B.D., 1975. The pollinating efficiency of honeybee and bumblebee visits to field bean flowers (*Vicia faba* L.). *J. Appl. Ecol.* 12, 709–717.
- Klein, A.-M., Vaissière, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Tscharntke, T., 2007. Importance of pollinators in changing landscapes for world crops. *Proc. R. Soc. B Biol. Sci.* 274, 303–313. <https://doi.org/10.1098/rspb.2006.3721>.
- Kremen, C., Williams, N.M., Thorp, R.W., 2002. Crop pollination from native bees at risk from agricultural intensification. *Proc. Natl. Acad. Sci. USA* 99, 16812–16816. <https://doi.org/10.1073/pnas.262413599>.
- Kremen, C., Albrecht, M., Ponisio, L., 2019. Restoring pollinator communities and pollination services in hedgerows in intensively managed agricultural landscapes. In: Dover, J.W. (Ed.), *The Ecology of Hedgerows and Field Margins*. Routledge, New York, USA, pp. 163–185.
- Lenth, R., 2019. Emmeans: Estimated Marginal Means, Aka Least-Squares Means. R Package Version 1.4.2. (<https://CRAN.R-project.org/package=emmeans>).
- Lindström, S.A.M., Herberthsson, L., Rundlöf, M., Bommarco, R., Smith, H.G., 2016. Experimental evidence that honeybees depress wild insect densities in a flowering crop. *Proc. R. Soc. B Biol. Sci.* 283, 20161641 <https://doi.org/10.1098/rspb.2016.1641>.
- Løken, A., 1973. *Studies on Scandinavian bumble bees (Hymenoptera, Apidae)*. *Nor. J. Entomol.* 20, 1–218.
- Lowe, E.B., Groves, R., Gratton, C., 2021. Impacts of field-edge flower plantings on pollinator conservation and ecosystem service delivery – a meta-analysis. *Agric. Ecosyst. Environ.* 310, 107290 <https://doi.org/10.1016/j.agee.2020.107290>.
- Lüdtke, D., Ben-Shachar, M., Patil, I., Waggoner, P., Makowski, D., 2021. Performance: an R package for assessment, comparison and testing of statistical models. *J. Open Source Softw.* 6, 3139. <https://doi.org/10.21105/joss.03139>.
- Lundgren, J.G., 2009a. *Relationships of Natural Enemies and Non-Prey Foods*. Springer, Dordrecht, Netherlands.
- Lundgren, J.G., 2009b. Nutritional aspects of non-prey foods in the life histories of predaceous Coccinellidae. *Biol. Control* 51, 294–305. <https://doi.org/10.1016/j.biocontrol.2009.05.016>.
- Lundin, O., Raderschall, C., 2021. Landscape complexity benefits bumble bee visitation in faba bean (*Vicia faba* minor L.) but crop productivity is not pollinator-dependent. *Agric. Ecosyst. Environ.* 314, 107417.
- Lundin, O., Ward, K.L., Williams, N.M., 2019. Identifying native plants for coordinated habitat management of arthropod pollinators, herbivores and natural enemies. *J. Appl. Ecol.* 56, 665–676. <https://doi.org/10.1111/1365-2664.13304>.
- Mann, C.C., 1999. Crop scientists seek a new revolution. *Science* 283, 310–314.
- Marini, L., Quaranta, M., Fontana, P., Biesmeijer, J.C., Bommarco, R., 2012. Landscape context and elevation affect pollinator communities in intensive apple orchards. *Basic Appl. Ecol.* 13, 681–689. <https://doi.org/10.1016/j.baec.2012.09.003>.
- Marzinig, B., Brinjes, L., Biagioni, S., Behling, H., Link, W., Westphal, C., 2018. Bee pollinators of faba bean (*Vicia faba* L.) differ in their foraging behaviour and pollination efficiency. *Agric. Ecosyst. Environ.* 264, 24–33. <https://doi.org/10.1016/j.agee.2018.05.003>.
- Nakagawa, S., Johnson, P.C.D., Schielzeth, H., 2017. The coefficient of determination R<sup>2</sup> and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. *J. R. Soc. Interface* 14. <https://doi.org/10.1098/rsif.2017.0213>.
- Nicholson, C.C., Ricketts, T.H., Koh, I., Smith, H.G., Lonsdorf, E.V., Olsson, O., 2019. Flowering resources distract pollinators from crops: model predictions from landscape simulations. *J. Appl. Ecol.* 56, 618–628. <https://doi.org/10.1111/1365-2664.13333>.

- Pamlinger, T., Becker, R., Himmelreich, S., Schneider, C.W., Bergtold, M., 2019. Pollen report: quantitative review of pollen crude protein concentrations offered by bee pollinated flowers in agricultural and non-agricultural landscapes. *PeerJ* 7, e7394. <https://doi.org/10.7717/peerj.7394>.
- Pingali, P.L., 2012. Green revolution: impacts, limits, and the path ahead. *Proc. Natl. Acad. Sci. USA* 109, 12302–12308. <https://doi.org/10.1073/pnas.0912953109>.
- Pöhlitz, B., Reike, H.P., 2019. Studies on biology and infestation dynamics of the bean seed beetle (Coleoptera, Bruchidae: *Bruchus rufimanus*) in Saxony. *Gesunde Pflanz.* 71, 79–85. <https://doi.org/10.1007/s10343-019-00459-5>.
- Pywell, R.F., James, K.L., Herbert, I., Meek, W.R., Carvell, C., Bell, D., Sparks, T.H., 2005. Determinants of overwintering habitat quality for beetles and spiders on arable farmland. *Biol. Conserv.* 123, 79–90. <https://doi.org/10.1016/j.biocon.2004.10.010>.
- Pywell, R.F., Heard, M.S., Woodcock, B.A., Hinsley, S., Ridding, L., Nowakowski, M., Bullock, J.M., Varennes, Y.D., Boyer, S., Wratten, S.D., 2015. Wild-life friendly farming increases crop yield: evidence for ecological intensification. *Proc. R. Soc. B Biol. Sci.* 282, 20151740 <https://doi.org/10.1098/rspb.2015.1740>.
- R Core Team, 2019. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. URL: (<http://www.R-project.org/>).
- Raderschall, C.A., Bommarco, R., Lindström, S.A.M., Lundin, O., 2021a. Landscape crop diversity and semi-natural habitat affect crop pollinators, pollination benefit and yield. *Agric. Ecosyst. Environ.* 306, 107189 <https://doi.org/10.1016/j.agee.2020.107189>.
- Raderschall, C.A., Vico, G., Lundin, O., Taylor, A.R., Bommarco, R., 2021b. Water stress and insect herbivory interactively reduce crop yield while the insect pollination benefit is conserved. *Glob. Chang. Biol.* 27, 71–83. <https://doi.org/10.1111/gcb.15386>.
- Raven, P.H., Wagner, D.L., 2021. Agricultural intensification and climate change are rapidly decreasing insect biodiversity. *Proc. Natl. Acad. Sci. USA* 118, 1–6. <https://doi.org/10.1073/pnas.2002548117>.
- Rivers-Moore, J., Andrieu, E., Vialatte, A., Ouin, A., 2020. Wooded semi-natural habitats complement permanent grasslands in supporting wild bee diversity in agricultural landscapes. *Insects* 11, 1–21. <https://doi.org/10.3390/insects11110812>.
- Rockström, J., Williams, J., Daily, G., Noble, A., Matthews, N., Gordon, L., Wetterstrand, H., DeClerck, F., Shah, M., Steduto, P., de Fraiture, C., Hatibu, N., Unver, O., Bird, J., Sibanda, L., Smith, J., 2017. Sustainable intensification of agriculture for human prosperity and global sustainability. *Ambio* 46, 4–17. <https://doi.org/10.1007/s13280-016-0793-6>.
- Rundlöf, M., Lundin, O., Bommarco, R., 2018. Annual flower strips support pollinators and potentially enhance red clover seed yield. *Ecol. Evol.* 8, 7974–7985. <https://doi.org/10.1002/ece3.4330>.
- Sanders, D., Thébault, E., Kehoe, R., Frank van Veen, F.J., 2018. Trophic redundancy reduces vulnerability to extinction cascades. *Proc. Natl. Acad. Sci. USA* 115, 2419–2424. <https://doi.org/10.1073/pnas.1716825115>.
- Sardiñas, H.S., Kremen, C., 2015. Pollination services from field-scale agricultural diversification may be context-dependent. *Agric. Ecosyst. Environ.* 207, 17–25. <https://doi.org/10.1016/j.agee.2015.03.020>.
- Schellhorn, N.A., Gagic, V., Bommarco, R., 2015. Time will tell: resource continuity bolsters ecosystem services. *Trends Ecol. Evol.* 30, 524–530. <https://doi.org/10.1016/j.tree.2015.06.007>.
- Scheper, J., Holzschuh, A., Kuussaari, M., Potts, S.G., Rundlöf, M., Smith, H.G., Kleijn, D., 2013. Environmental factors driving the effectiveness of European agri-environmental measures in mitigating pollinator loss – a meta-analysis. *Ecol. Lett.* 16, 912–920. <https://doi.org/10.1111/ele.12128>.
- Segers, A., Caparros Megido, R., Lognay, G., Francis, F., 2021. Overview of *Bruchus rufimanus* Boheman 1833 (Coleoptera: Chrysomelidae): biology, chemical ecology and semiochemical opportunities in integrated pest management programs. *Crop Prot.* 140, 105411 <https://doi.org/10.1016/j.cropro.2020.105411>.
- Seidenglanz, M., Huňady, I., 2016. Effects of faba bean (*Vicia faba*) varieties on the development of *Bruchus rufimanus*. *Czech J. Genet. Plant Breed.* 52, 22–29. <https://doi.org/10.17221/122/2015-CJGPB>.
- Stoddard, F.L., Bond, D.A., 1987. The pollination requirements of the faba bean. *Bee World* 68, 144–152. <https://doi.org/10.1080/0005772X.1987.11098923>.
- Stoddard, F.L., Nicholas, A.H., Rubiales, D., Thomas, J., Villegas-Fernández, A.M., 2010. Integrated pest management in faba bean. *Field Crop. Res.* 115, 308–318. <https://doi.org/10.1016/j.fcr.2009.07.002>.
- Sutter, L., Albrecht, M., Jeanneret, P., 2018. Landscape greening and local creation of wildflower strips and hedgerows promote multiple ecosystem services. *J. Appl. Ecol.* 55, 612–620. <https://doi.org/10.1111/1365-2664.12977>.
- Tasei, J.-N., 1976. Les insectes pollinisateurs de la féverole d'hiver (*Vicia faba equina* L.) et la pollinisation des plantes mâle-stérile en production de semence hybride. *Apidologie* 7, 1–38.
- Toreti, A., Belward, A., Perez-Dominguez, I., Naumann, G., Luterbacher, J., Cronie, O., Seguíni, L., Manfron, G., Lopez-Lozano, R., Baruth, B., van den Berg, M., Dentener, F., Ceglar, A., Chatzopoulos, T., Zampieri, M., 2019. The exceptional 2018 European water seesaw calls for action on adaptation. *Earth's Future* 7, 652–663. <https://doi.org/10.1029/2019EF001170>.
- Triltsch, H., 1997. Gut contents in field sampled adults of *Coccinella septempunctata* (Col.: Coccinellidae). *Entomophaga* 42, 125–131. <https://doi.org/10.1007/BF02769889>.
- Tschumi, M., Albrecht, M., Entling, M.H., Jacot, K., 2015. High effectiveness of tailored flower strips in reducing pests and crop plant damage. *Proc. Biol. Sci.* 282, 20151369 <https://doi.org/10.1098/rspb.2015.1369>.
- Tschumi, M., Albrecht, M., Collatz, J., Dubsky, V., Entling, M.H., Najar-Rodriguez, A.J., Jacot, K., 2016. Tailored flower strips promote natural enemy biodiversity and pest control in potato crops. *J. Appl. Ecol.* 53, 1169–1176. <https://doi.org/10.1111/1365-2664.12653>.
- Walther-Hellwig, K., Fokul, G., Frankl, R., Büchler, R., Ekschmitt, K., Wolters, V., 2006. Increased density of honeybee colonies affects foraging bumblebees. *Apidologie* 37, 517–532.
- Weber, E., Bleiholder, H., 1990. Explanations of the BBCH decimal codes for the growth stages of maize, rape, faba beans, sunflowers and peas - with illustrations. *Gesunde Pflanz.* 42, 308–332.
- Wilcke, R., Kjellström, E., Lin, C., Matei, D., Moberg, A., 2020. The extremely warm summer 2018 in Sweden – set in a historical context. *Earth Syst. Dyn.* 11, 1107–1121. <https://doi.org/10.5194/esd-2020-25>.
- Williams, I.H., Christian, D.G., 1991. Observations on *Phacelia tanacetifolia* Bentham (Hydrophyllaceae) as a food plant for honey bees and bumble bees. *J. Apic. Res.* 30, 3–12. <https://doi.org/10.1080/00218839.1991.11101227>.
- Wojcik, V.A., Morandin, L.A., Davies Adams, L., Rourke, K.E., 2018. Floral resource competition between honey bees and wild bees: is there clear evidence and can we guide management and conservation? *Environ. Entomol.* 47, 822–833. <https://doi.org/10.1093/ee/nvy077>.
- Zamorano, J., Bartomeus, I., Grez, A.A., Garibaldi, L.A., 2020. Field margin floral enhancements increase pollinator diversity at the field edge but show no consistent spillover into the crop field: a meta-analysis. *Insect Conserv. Divers.* 13, 519–531. <https://doi.org/10.1111/icad.12454>.
- Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. *Mixed Effects Models and Extensions in Ecology with R*. Springer, New York, USA.