



Flower strips enhance abundance of bumble bee queens and males in landscapes with few honey bee hives

Riccardo Bommarco^{a,*}, Sandra A.M. Lindström^b, Chloé A. Raderschall^a, Vesna Gagic^c, Ola Lundin^a

^a Swedish University of Agricultural Sciences, Department of Ecology, SE-750 07 Uppsala, Sweden

^b Swedish Rural Economy and Agricultural Society, SE-291 09 Kristianstad, Sweden

^c Queensland Department of Agriculture and Fisheries, Ecosciences Precinct, Dutton Park, QLD 4102, Australia

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ABSTRACT

Wild bee declines in agricultural landscapes have led farmers to supplement crops with honey bees. Simultaneously, environmental subsidy and conservation programmes have incentivized farmers to establish flower strips to support wild and managed pollinators. To find out if flower strips enhance, and competition from honey bees suppresses, wild bees in the landscape and across seasons, we surveyed bumble bee and honey bee abundances in 16 sites in Sweden in summer 2018. The centre of each site (2 km radius) was with or without an annual flower strip, and with or without added honey bee hives. We surveyed bees in each flower strip and in linear habitats in the landscape around each site, such as field edges and road verges. In the following spring, we surveyed bumble bee queen abundance in each site. We show that adding flower strips benefits bumble bee queen abundance the following year, but this effect is diminished if honeybee hives are added. In sites with flower strips, added honey bee hives reduced male bumble bee abundance. Our relatively small flower strip areas bolstered bumble bee population growth across seasons, probably by relieving a resource bottleneck. Adding honey bee hives in combination with flower strips to landscapes with few floral resources should be avoided as it cancelled the positive effect of flower strips.

1. Introduction

Agricultural intensification is a main driver for biodiversity decline (Diaz et al., 2019). In some landscapes, species loss has degraded ecosystem services, possibly diminishing crop production (Dainese, 2019). For instance, the loss of wild bees (Bartomeus et al., 2013; Biesmeijer et al., 2006; Zattara and Aizen, 2021) has weakened crop pollination in intensively cropped landscapes (Kennedy et al., 2013; Potts et al., 2016) deprived of semi-natural habitat and with large fields of few crop species (Senapathi et al., 2015). Such homogeneous landscapes are problematic for wild pollinators as they lose continuity of nesting and foraging resources needed for them to complete their life cycle (Carvell et al., 2006; Schellhorn et al., 2015). Bumble bees are important crop pollinators (Kleijn et al., 2015). They are central-place foragers that routinely forage within 1.5 km from their nests (Osborne et al., 2008) and require access to pollen and nectar within flight range throughout the season. These flower resources are needed to produce workers in spring and early summer, but also to produce reproductive

castes (queens and males) later in summer (Crone and Williams, 2016; Rundlöf et al., 2014; Westphal et al., 2009). Reproductive castes, in contrast to workers, ultimately contribute to bumble bee population persistence, thus making it important to measure caste-specific effects of interventions on bumble bees.

Farmers can reintroduce flower resources into landscapes by establishing hedges and flower strips along field borders (Haaland et al., 2011), a practice that is also subsidised in the EU and USA (Albrecht et al., 2020; Kremen et al., 2019). Such flower strips enhance pollinator abundance and diversity locally within the strip (Scheper et al., 2015), and colony growth and reproduction of reared bumble bees are higher when colonies are closer to flower strips (Klatt et al., 2020). It is less well understood if flower strips provide sufficient resources to enhance landscape level bumble bee population abundance. But in one example of this, bumble bee abundance in field borders was enhanced by flower strip plantings at the centre of the landscape (Jönsson et al., 2015). However, it is not known if establishing flower strips increases abundance of queens and thereby affects population growth across seasons.

* Corresponding author.

E-mail address: Riccardo.Bommarco@slu.se (R. Bommarco).

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Furthermore, flower strips could affect how bumble bees distribute themselves between flower strips and other linear habitats, such as field edges and road verges in the landscape, and this might differ for workers, males and queens due to caste-specific habitat and foraging preferences (Goulson, 2010; Roswell et al., 2019), but this is poorly understood.

Although honey bees are less efficient per flower visit than wild bees (Földesi et al., 2021), they are important pollinators of many crops due to their numerical dominance and high flower visitation rates (e.g., Aizen and Harder, 2009; Rader et al., 2012). Their managed hives are often placed near flowering crops to bolster crop pollination (Breeze et al., 2014) and compensate for loss of wild pollinators (e.g., Marini et al., 2012). However, honey bees can competitively displace wild bees and deplete floral resources (Thomson, 2004; Wojcik et al., 2018; but see Paine, 2004; Wojcik et al., 2018). Competition might be stronger in intensively cropped landscapes, where foraging resources are scarce. For instance, honey bees displace bumble bees in and near crop fields (Herbertsson et al., 2016; Lindström et al., 2016), which can reduce fruit set (Angelella et al., 2021). Whether this displacement by honey bees affects castes differently, bumble bee queen abundance the next season, and whether it can be mitigated by flower strips has not been examined (Mallinger et al., 2017; Thomson and Page, 2020).

Here, we investigate the effects of two management actions that manipulate flower resource availability and/or honey bee abundance on population dynamics of bumble bees within the landscape and across seasons. We surveyed bumble bee abundance in 2018 in southern Sweden in 16 sites. Each site had an organic faba bean field at its centre, with or without a flower strip, and with or without added honey bee hives. To assess if effects of flower strips and honey bee hives carry over into the next season, we sampled bumble bee queen abundance in the following spring in the landscape within a 2 km radius around each site. We tested the hypothesis that landscape level bumble bee abundance will increase with flower strips and be suppressed by higher abundance of honey bees. We expected these effects to be more pronounced for the late season reproductive castes of males and queens, than for early season workers, because resource limitation is highest in late summer when mass-flowering crops have finished their bloom (Timberlake et al., 2019). Further, we hypothesised bumble bees to aggregate in the flower strips, but that this effect would be less pronounced when honey bee hives are present because abundant honey bees displace bumble bees from the flower strips.

2. Material and methods

2.1. Site selection and experimental design

In spring of 2018, we selected 16 sites with a radius of 2 km centred around an organically managed faba bean field (*Vicia faba* minor L.) in the province of Skåne in southernmost Sweden (Fig. S1). All fields were at least 4 km apart. We examined the effect of adding a flower strip, and adding or removing honey bees from these sites on bumble bees in a crossed two by two design. Each of the four treatments was replicated four times (Fig. S1).

The focal faba bean field sizes varied between 5 and 38 ha and were sown with several both coloured and white-flowered cultivars (Duc, 1997; Table S1). The proportions land cover of arable land, and semi-natural pastures, forests, and field borders (mean field perimeter length was used as a proxy), and winter oilseed rape were quantified within a radius of 2 km from each faba bean field centre (Table S1). Pastures, forest patches, field borders and winter oilseed rape provide important nesting and foraging resources for bumble bees in agricultural landscapes (Öckinger and Smith, 2007; Söber et al., 2020; Westphal et al., 2009). Winter oilseed rape accounts for ca. 95% of the mass-flowering crop area in the study region (Rundlöf et al., 2014). Proportions of arable land, pasture and winter oilseed rape, and mean field perimeter lengths were calculated using data obtained from the

Integrated Administration and Control System, administered by the Swedish Board of Agriculture (Jönköping). Proportion forest was calculated from Terrängkartan, a digitised map layer provided by Lantmäteriet (Gävle). Mean focal field sizes, the distribution of cultivar types and landscape characteristics were similar across the experimental treatments (Tables S1, S2).

2.2. Flower strip treatment

Flower strips were sown in the spring of 2018 along field edges of eight faba bean fields. Flower strips were 200 to 800 m long, 2 to 6 m wide and had an area of 0.1 to 0.5 ha. The flower strips were sown with a mix of the annual flowering plant species buckwheat (*Fagopyrum esculentum*), cornflower (*Centaurea cyanus*), crimson clover (*Trifolium incarnatum*), dill (*Anethum graveolens*), phacelia (*Phacelia tanacetifolia*) and Persian clover (*Trifolium resupinatum*). The seeding rate was 5 kg ha⁻¹ for buckwheat, phacelia and Persian clover, 3 kg ha⁻¹ for crimson clover, 1 kg ha⁻¹ for dill and 0.5 kg ha⁻¹ for cornflower. The seeds were mixed and sown at 1–2 cm depth. Due to a record drought in 2018 (Toreti et al., 2019), two of the faba bean fields containing flower strips were irrigated during summer.

2.3. Honey bee treatment

Beekeepers in Sweden are required to report the location of their hives to the County Administrative Board. With this information, contacts with local beekeepers and personal observations, we divided the focal faba bean fields into either high or low abundance of stationary honey bee hives within 2 km. For eight fields with low numbers of stationary honey bee hives, we decreased honey bee hive numbers further by asking beekeepers to remove their colonies from the area before faba bean bloom. For eight fields with already high numbers of stationary honey bee hives, we added ten full-strength honey bee hives to the faba bean fields at the onset of crop bloom. The added hives were placed as a group along an edge of the faba bean field. In cases where beekeepers used colony splits instead of full-strength hives, we compensated for the lower honey bee activity by adding extra hives using the approximate exchange rate of two splits per full-strength hive. Added honey bee hives remained in place for the duration of the faba bean bloom. To the best of our knowledge, honey bee control sites, i.e., with low honey bee abundance, had on average 1 and 5 hives within 1 and 2 km, respectively, throughout the season. Sites with honey bee hives had 13 and 31 hives within 1 and 2 km, respectively, during faba bean bloom. Ten of these hives were supplemented by us during faba bean bloom as part of the experiment, and these were then removed after bloom. Irrespective of our supplemented and subsequently removed hives, sites with honey bee hives had consistently more hives (with on average 3 and 21 hives within 1 and 2 km, respectively) than the honey bee control sites throughout the season.

In one control site with a low number of honey bee hives, we recorded (see “Bee and flower sampling” below) high honey bee abundance late in the season. We suspect that beekeepers moved hives near the faba bean field late in the season of 2018. As production of reproductive castes is mainly conditioned in the earlier part of the season (Malfi et al., 2020), we expected the low abundance of honey bees in early season at this site to have a greater effect on bumble bees than the higher numbers of honey bees observed later on in the season. We therefore excluded late season samples from this site when analysing the 2018 data, but we analysed and present 2019 data both with and without this site included, consistently classifying it as a control site with low numbers of honey bee hives.

2.4. Bee and flower sampling

In the summer of 2018, we sampled two to three 50 m long and 1 m wide transects in flower-rich uncultivated linear habitats in the

landscape in each site for bumble bee and honey bee abundances. These were field and road edges. The transects were situated within 50 to 500 m from the focal faba bean field. In addition, in sites with flower strips, bees were surveyed in a 50 m long and 1 m wide transect within the flower strip each time the landscape linear habitats of the site were surveyed. Each transect was surveyed four times after faba bean bloom, between June 25 and July 27 2018. We originally planned surveys both during and after faba bean bloom, but bloom was unusually brief in 2018 (only two weeks), and we surveyed after bean bloom in order to cover all sites under comparable conditions. Bees were sampled between 9 am and 7 pm, when the vegetation was dry, temperatures were at least 17 °C, wind speeds less than 8 m s⁻¹ (four or lower on the Beaufort scale) and skies partly sunny or brightly overcast. Flower-visiting and flying bumble bees were collected with a net for later identification in the laboratory. Honey bees and bumble bee queens were not collected but instead identified directly in the field. *Bombus terrestris*, *B. lucorum*, *B. cryptarum* and *B. magnus* were treated as one species complex, denoted as *B. terrestris* agg. (Murray et al., 2008).

Flower resources were quantified in the transects each time bees were surveyed. The number and area of flower units was estimated throughout the transect for each flowering plant species that had potential nectar or pollen resources for bumble bees (Table A2 in Persson and Smith, 2013) and for all plant species sown in the flower strips. Depending on flower type, a flower unit was an individual flower (Papaveraceae, Rosaceae, Violaceae, Campanulaceae, Caprifoliaceae, Caryophyllaceae, Convolvulaceae, Dipsacaceae, Ranunculaceae, Scrophulariaceae), number of flower clusters (Brassicaceae, Clusiaceae), number of inflorescences (Asteraceae, Apiaceae, Boraginaceae, Myrsinaceae), number of racemes (Fabaceae) or number of flower stalks (Lamiaceae, Plantaginaceae, Polygonaceae, Lythraceae, Onagraceae) (Persson and Smith, 2013).

In flower strips, flower resources were subsampled in four 0.6 m by 0.6 m quadrats due to the high number of flowers, while flowers in linear landscape habitats were sampled in the full extent of the two 50 by 1 m transects in each site and survey. We measured the length and width of one representative flower unit per plant species using callipers, and then summed up and calculated the total flower area per ground area unit in each transect and survey round (Williams et al., 2015).

Each site was surveyed again five times in spring 2019 between April 1 and May 29 for bumble bee queens. Initially, we sampled the same 50 m long transects along field and road edges as in summer 2018, but due to low bumble bee queen sightings, we added transects along these edges and also added stone walls and ditches sequentially to increase the sample sizes (mean: 10 transects per survey round in each site). Transect widths varied between 1 and 6 m. In total, 125,225 m² of transects were covered and divided among treatments as follows: 29,475 m² no flower strip, no added hives; 28,350 m² flower strip, no added hives; 37,400 m² no flower strip, hives added; and 30,000 m² flower strip, hives added. All transects were within 50 to 500 m from the focal faba bean field in the previous year. Sampling was conducted between 9 am and 8 pm, when the vegetation was dry, temperatures were at least 8 °C, wind speeds less than 8 m s⁻¹ (four or lower on the Beaufort scale). Flying, nest-searching and flower-visiting bumble bee queens were counted and identified directly in the field. Flowering resources were quantified along transects each time bumble bees were surveyed using the same methodology as in 2018.

2.5. Statistical analyses

We first compared flower area and flower species richness between linear landscape habitats and flower strips using a generalised mixed-effects model with a gamma distribution (log link function) in the model for flower area, and Poisson distribution (log link function) for flower species richness, including site and sampling round as crossed random effects.

We analysed honey bees and bumble bees abundance in 2018

separately. First, we tested whether honey bee and bumble bee abundance in linear landscape habitats were affected by the presence or absence of a flower strip in the site in interaction with the honey bee hive treatment. Standardised flower area (subtracted mean and divided by standard deviation) was not included in these analyses, due to a high collinearity between habitat type and flower area, i.e., there was greater flower area per square meter in flower strips than in the linear landscape habitats.

Second, selecting only sites with flower strips we compared the abundance distribution of pollinators between habitat types, i.e., between within the flower strip and in the linear landscape habitats in the surrounding landscape, and in interaction with the honey bee hive treatment. Here, we included standardised flower area as a covariate to account for differences in the local flower resources when testing honey bee and bumble bee abundance in linear landscape habitats.

We used generalised linear mixed-effects models with negative binomial distribution. Models had site identity (1:16) crossed with survey round (1:4) in the random structure. Added to this, the model for comparing bumble bee abundance in flower strips and landscape linear habitats had the additional term of habitat type nested in the site identity to account for multiple bumble bee samples within each habitat type.

We also tested whether the aforementioned responses differed by bumble bee caste (workers and males). We excluded unidentified castes and queens from this analysis since we found very few queens in 2018 (Table S3). The models were the same as above, but with caste included as an additional explanatory variable, together with its two-way interaction with other variables in the models.

To test how abundance of overwintered queens changed with presence or absence of flower strips and the honey bee hives treatment, we used a generalised mixed-effects model with Poisson distribution, using data sampled in 2019. Flower area (log transformed) and type of linear landscape habitat (field edge, road edge, stone wall or ditch) were included as additional explanatory variables. To account for differences in the width of the sampled transects we used log transformed transect width in the model offset. Linear landscape habitat type nested in the site identity and crossed with the survey round was included in the random structure. We performed this analysis both with and without the honey bee control site where large numbers of honey bees occurred late in the season 2018 (Fig. S1).

We checked and validated model assumptions for all models, including testing for over- or underdispersion, zero inflation, spatial and temporal autocorrelation, non-linearity and collinearity. We performed residual diagnostics through visual inspection of the scaled residuals simulated from the model fit, i.e., deviation from uniformity and observed against predicted residuals. We simplified models by removing interactions between explanatory variables or removing the covariate flower area if $p > 0.10$. We compared Akaike information criterion corrected for small sample size (AICc) and performed likelihood ratio test between full and simplified models. All data were analysed using R.4.0.3 (R Core Team, 2020) and packages “glmmTMB” (Brooks et al., 2017), “DHARMA” (Hartig, 2020), “ncf” (Bjornstad, 2020) and “car” (Fox and Weisberg, 2019). Parameter significance was tested using Type III Wald z-test. The code for the full and the final simplified models for each analysis of honey bee and bumble bee abundance are presented in the Supplementary materials.

3. Results

In 2018 we observed 1,019 honey bees and 2,001 bumble bee individuals belonging to 10 species. Among the bumble bees, *Bombus terrestris* agg. dominated (67.4%), followed by *B. subterraneus* (2.4%) (Table S3a). Around a quarter of the bumble bees (25.4%) could not be identified to species. We observed 1,247 bumble bee workers, 174 males and 8 queens. The caste for 572 individuals could not be identified (Table S3a). In the spring of 2019 we observed a total of 121 queens

belonging to 13 species (Table S3b).

Flower area was relatively stable across the season in linear landscape habitats (Fig. S4) (mean 73.61 cm² m⁻², SE 9.36, N 139). The flower strips had a higher flower area (mean 882.35, SE 129.93, N 32), which declined in the two final rounds (Fig. S5). The linear landscape habitats in 2018 were dominated by Asteraceae species (Table S4a) and the flower strip by *Phacelia tanacetifolia*. (Table S4b). In 2019, the linear landscape habitats were dominated by *Taraxacum spp.*, *Prunus spp.*, *Capsella bursa-pastoris*, *Lamium purpureum*, *Anthriscus sylvestris*, and *Lamium album* (Table S5).

Flower area was lower in linear landscape habitats compared with flower strips (estimates at link scale, -2.7185 ± 0.1866, p < 0.001) and flower species richness did not differ between habitat types.

3.1. Honey bee responses

In 2018, honey bee abundance in linear landscape habitats was higher in sites to which we had added hives, confirming that the honey bee hive treatment succeeded (Fig. S2a, Table 1). Analysing only sites with flower strips, we found that the honey bee hive treatment increased honey bee abundance, and did so more in the flower strip than in the linear landscape habitats (Fig. S2b, Table 2).

3.2. Bumble bee responses in 2018

In 2018, there was a tendency, i.e., there was a significant difference at the 10% but not at the 5% probability level, for bumble bee abundance in linear landscape habitats in landscapes with a flower strip at their centre to be lower when honey bee hives were added (Fig. 1a, Table 1).

Analysing only sites with flower strips, we found that bumble bees were less abundant in linear landscape habitats than within flower strips, especially when honey bee hives were added (Fig. 1b, Table 2).

Analysing castes (workers and males), we found workers to be more abundant than males, and there was no difference between caste abundances within linear landscape habitats in response to our treatments, i.e., no significant interactions (Table 1). In the sites with flower strips, there were fewer workers and males in the linear landscape habitats compared with flower strips (Table 2). Workers were more abundant than males and were similarly abundant irrespective of honey bee hive treatment. Male bumble bees occurred at lower abundance in sites with than without added honey bee hives (Fig. 2, Table 2).

3.3. Bumble bee queen responses in 2019

Bumble bee queen abundance in spring 2019 was higher in sites with a flower strip and without added honey bee hives in the previous season (Fig. 3, Table 1). Exclusion of the site, which despite having low numbers of honey bee hives had a high abundance of honey bees late in the season of 2018, gave similar estimated means and variances (Fig. S3), but no statistically significant effect of flower strips and honey bee hives or their interaction on bumble bee queen abundance (Table S6).

4. Discussion

We show positive legacy effects of annual flower strips on queen bumble bee abundance in the subsequent spring, but honey bee hives counteracted this effect. Although not statistically significantly different, sites with flower strips but without added hives had over twice the number of bumble bee males as sites without flower strips in the summer of 2018 (Fig. 1a). This is similar to the ca. 2.5 times higher bumble bee abundance in sites with a flower strip in the same region found in 2011–2012, although with a larger area of 0.3–4.8 ha of flower strips and honey bee abundance not reported (Jönsson et al., 2015).

In the following spring, we observed higher bumble bee queen

Table 1 Test statistics with estimates and their standard errors (SE), and z- and p-values for models including all sites that tested for effects on honey bee and abundance of all bumble bees including all castes and those of unidentified caste in 2018, abundance of bumble bees identified to caste as male or worker in 2018 and bumble bee queens in 2019 (with all 16 sites included). Explanatory variables were flower strip (FS) and honey bee hive (HB) treatments, flower area in the linear landscape habitat, bumble bee caste (workers or males) and linear landscape habitat type (field edge, road, stone wall or ditch). Dash indicates a variable that was tested but removed during model simplification, whereas blank values indicate that the variable was not included in the model. Statistically significant (p < 0.05) results are in bold and trends (0.05 < p < 0.10) are in italics. The intercept is set at sites without flower strips and honey bee hive supplementation, caste at males and linear landscape habitat type at ditch.

| Variable | Honey bees 2018 | | | Bumble bees 2018 | | | Bumble bee castes 2018 | | | Bumble bee queens 2019 | | |
|-------------|-----------------|------|--------|------------------|------|-------|------------------------|------|-------|------------------------|------|---------|
| | Estimate | SE | p | Estimate | SE | p | Estimate | SE | p | Estimate | SE | p |
| Intercept | -0.17 | 0.61 | | -0.83 | 0.46 | 0.073 | -2.00 | 0.90 | 0.026 | -5.05 | 0.58 | <0.0010 |
| FS | -1.28 | 0.71 | 0.78 | 0.81 | 0.62 | 0.19 | -0.08 | 0.89 | 0.93 | 1.64 | 0.56 | 0.0037 |
| HB | 1.87 | 0.71 | 0.0083 | 0.24 | 0.62 | 0.70 | -0.19 | 0.89 | 0.83 | 0.46 | 0.58 | 0.43 |
| FS*HB | - | - | - | -1.48 | 0.89 | 0.098 | - | - | - | -1.52 | 0.78 | 0.049 |
| Flower area | - | - | - | - | - | - | 1.22 | 0.28 | 4.41 | 0.16 | 0.05 | 0.0030 |
| Caste (C) | - | - | - | - | - | - | - | - | - | - | - | - |
| C*FS | - | - | - | - | - | - | - | - | - | - | - | - |
| C*HB | - | - | - | - | - | - | - | - | - | - | - | - |
| LE type | - | - | - | - | - | - | - | - | - | - | - | - |
| field edge | - | - | - | - | - | - | - | - | - | 0.88 | 0.65 | 1.36 |
| road edge | - | - | - | - | - | - | - | - | - | 0.82 | 0.42 | 1.96 |
| stone wall | - | - | - | - | - | - | - | - | - | 0.57 | 0.42 | 1.37 |

Table 2

Test statistics with estimates and their standard errors (SE) and z- and p-values for models including only sites with flower strips that tested for effects on honey bee abundance and abundance of all bumble bees including all castes and those of unidentified caste in 2018, abundance of bumble bees identified to caste as male or worker in 2018. Explanatory variables were honey bee hive supplementation (HB), habitat type (flower strip or linear landscape habitat) and bumble bee caste (workers or males). Dash indicates a variable that was tested but removed during model simplification, whereas blank values indicate that the variable was not included in the model. Statistically significant ($p < 0.05$) results are in bold and trends ($0.05 < p < 0.10$) are in italics. The intercept is set at sites without honey bee hive supplementation, habitat type at flower strip and caste at males.

| Variable | Honey bees 2018 | | | | Bumble bees 2018 | | | | Bumble bee castes 2018 | | | |
|------------------|-----------------|-------------|--------------|-------------------|------------------|-------------|--------------|---------------|------------------------|-------------|--------------|-------------------|
| | Estimate | SE | z | p | Estimate | SE | z | p | Estimate | SE | z | p |
| Intercept | -0.19 | 0.75 | -0.25 | 0.80 | 1.60 | 0.57 | 2.80 | 0.0052 | <i>1.41</i> | <i>0.80</i> | <i>1.76</i> | <i>0.079</i> |
| HB | 4.01 | 1.03 | 3.90 | <0.0010 | 0.91 | 0.77 | 1.18 | 0.24 | -1.36 | 0.93 | -1.47 | 0.14 |
| Habitat type (H) | <i>-1.09</i> | 0.64 | <i>-1.70</i> | <i>0.090</i> | -1.64 | 0.76 | -2.15 | 0.032 | -3.59 | 0.85 | -4.24 | <0.0010 |
| HB*H | -2.19 | 0.86 | -2.55 | 0.011 | -2.21 | 1.09 | -2.02 | 0.043 | - | - | - | - |
| Caste (C) | | | | | | | | | 1.42 | 0.38 | 3.80 | <0.0010 |
| C*HB | | | | | | | | | 1.44 | 0.57 | 2.52 | 0.012 |
| C*H | | | | | | | | | - | - | - | - |

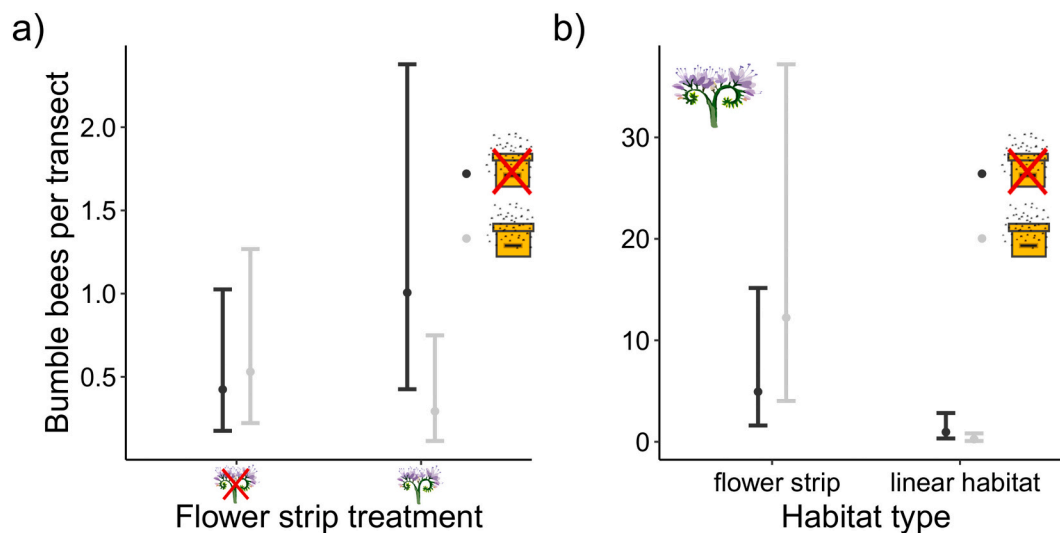


Fig. 1. Bumble bee abundance in (a) linear landscape habitats in the landscape in 2018 tended to be higher in sites with flower strips but with honey bee hives removed, and (b) in sites with flower strips were overall higher in the flower strips compared with in linear landscape habitats in the landscape, and interacted with the honey bee treatment such that adding honey bees increased bumble bee densities in the flower strips and decreased them in the linear landscape habitats in the landscape, respectively. Each transect was 50 m². Black bars denote control sites with honey bee hives removed and light grey bars denote sites with honey bee hives added. Error bars indicate 95% confidence intervals.

abundance in sites that had a flower strip in the previous summer in sites with no added honey bee hives. This result, together with the finding that more male bumble bees were found in flower strip sites in which honey bee hives were not added, suggest that flower strips can increase bumble bee reproduction as long as resource competition with honey bees is limited, and that the positive effect is maintained until the next season. A positive relationship between floral resources in the previous summer and overwintered bumble bee queen abundance has been shown in temperate deciduous forest ecosystems (Inari et al., 2012), but such links have, to our knowledge, not been assessed specifically for flower strips. There are, nonetheless, congruent findings. Bumble bee family lineage survival from one season to the next is enhanced by high quality forage, including planted wildflower mixtures in agricultural landscapes (Carvell et al., 2017), and nectar available in late summer has been shown to increase bumble bee colony density in the following spring (Timberlake et al., 2020). Bumble bee queen production occurs in late summer, when floral resources tend to be limited in agricultural landscapes (Timberlake et al., 2019). The flower strips have likely prolonged nectar availability and increased pollen diversity, thereby reducing a critical resource gap across the life cycle of the bees (Schellhorn et al., 2015; Ganser et al., 2018; Timberlake et al., 2020; Vaudo et al., 2015). Another possibility is that a late season nectar-rich diet from the flower strips (Costa et al., 2020) enhanced the queen bee

body sizes (Costa et al., 2020; Grab et al., 2019), which increases their overwintering survival (Beekman et al., 1998). It is possible that these effects were accentuated by the dry and hot summer of 2018 (Wilcke et al., 2020), which may have further reduced the already depleted late season bee foraging resources due to long term land use change and agricultural intensification in the region.

Higher abundance of honey bees counteracted the positive effect of flower strips on the abundance of bumble bee queens in spring of 2019. Honey bees can displace and negatively affect within-season abundance and reproduction of wild bees (Angelella et al., 2021; Wojcik et al., 2018). It is possible that the honey bees compete with wild bees, in our case bumble bees, for pollen and nectar needed for their reproduction (Roulston and Goodell, 2010; Thomson, 2004). Such resource competition from honey bees is particularly pronounced in landscapes with limited floral resources such as intensively cropped agricultural landscapes (Herbertsson et al., 2016). Further, analysing only sites with flower strips, we found that adding honey bee hives reduced male but not worker abundance. We detected no such differences in response between castes in the analysis including sites without flower strips. It is possible that the overall higher bumble bee abundance within the flower strips compared with linear landscape habitats, increased the probability of detecting a late season negative impact of honey bees on male bumble bees that generally occurred at low abundance. This finding is in



Fig. 2. Analysing caste abundances only in sites with flower strips, males were more abundant in sites with honey bee hives removed. Each transect was 50 m². Black bars denote control sites with honey bee hives removed and light grey bars denote sites with honey bee hives added. Error bars indicate 95% confidence intervals.

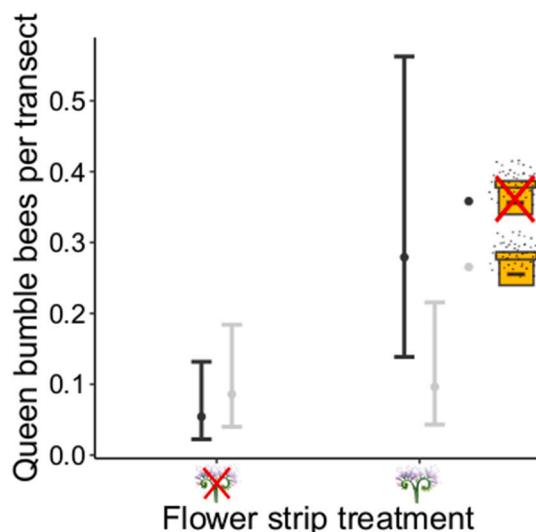


Fig. 3. In the spring of 2019, bumble bee queen densities were higher in sites with flower strips but with honey bee hives removed. Black bars denote control sites with honey bee hives removed and light grey bars denote sites with honey bee hives added. Error bars indicate 95% confidence intervals.

line with our hypothesis that negative effects from competition with honey bees is more pronounced for late season bumble bee reproductive castes compared with workers.

We confirm that flower strips attract both bumble bees (Blaauw and Isaacs, 2014; Jönsson et al., 2015) and honey bees (Lundin et al., 2017), with abundance of both honey bees and bumble bees being higher in flower strips compared with linear habitats in the landscape. Contrary to our expectation, bumble bee abundance was higher in flower strips than in linear landscape habitats even when honey bees were also abundant in flower strips. The plant species that provided most of the floral area in the flower strips was *Phacelia tanacetifolia*, which is attractive for both bumble bees and honey bees (Williams and Christian, 1991). It is possible that the rich foraging resources in the flower strip can support high numbers of both honey bees and bumble bees together, while the increased numbers of honey bees in linear landscape habitats displace bumble bees from that habitat. Honey bees are known to affect the

distribution of the bumble bees in linear habitats (e.g. Herbertsson et al., 2016), and might have pushed the bumble bees from linear landscape habitats into the flower strips where they had more opportunity of collecting flower rewards. This proposition is partially supported by observations, where abundant short-tongued bumble bee species, such as *B. terrestris*, only showed weak responses to higher honey bee abundance in phacelia patches, whereas especially long-tongued bumble bee species were displaced by higher honey bee abundance in wild flower patches (Walther-Hellwig et al., 2006).

We found statistically significant differences among treatments in reproductive caste production despite the small area of the flower strips, limited replication, low bumble bee densities in the linear landscape habitats and the repeatedly observed time-lag of several years between flower strip establishment and positive effects on wild bee abundance and crop pollination services (Albrecht et al., 2020; Blaauw and Isaacs, 2014; Scheper et al., 2015). Furthermore, the mass-flowering faba bean fields have likely contributed to increasing bumble bee population size across sites (Beyer et al., 2020). Positive effects on bumble bees from adding flower strips should thereby increase in landscapes lacking faba beans, but adding also honey bees to such landscapes could again intensify resource competition. Annual flower strips offer flexibility and can be relocated on a farm from year to year depending on land availability and crop pollination needs. Future research should assess the effects of annual flower strips across consecutive years. That we find a positive effect on bumble bee queen abundance in the following spring from sowing comparably small areas of annual flower strips is in this respect highly encouraging, but we also show that high honey bee abundance can cancel this effect. Our findings suggest that land managers should avoid combining adding honey bee hives and flower strips to landscapes with few floral resources, as the added hives cancelled the positive effect of flower strips.

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Data accessibility statement

Data and r-script are available online at the Swedish National Data Service at <https://doi.org/10.5878/s2bx-3j34>.

CRediT authorship contribution statement

RB,SL,OL,CR Conceptualization.
 SL,OL,VG Data curation.
 RB,VG Formal analysis.
 RB,SL,OL Funding acquisition.
 RB,SL,OL,CR,VG Investigation.
 RB,SL,CR Methodology.
 RB,OL,SL Project administration.
 RB Resources.
 VG Software.
 RB,OL,SL,CR Supervision; Validation.
 VG,CR Visualization.
 RB Roles/Writing - original draft.
 RB,OL,SL,CR,VG Writing - review & editing.

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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