



Efficiency of flower strips for bumblebee colonies depends on nesting habitat and interactions with semi-natural habitats and mass-flowering crops

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Abstract

Context Pollinator populations are generally sensitive to landscape fragmentation, but the contribution of habitat types at different area proportion to the development of bumblebee colonies at landscape scale is unclear.

Objectives We contribute to this field of landscape ecological research by analysing how the area proportions of semi-natural habitats, flower strips and mass-flowering crops affect the density of bumblebee colonies in artificial landscapes with a simulation model.

Methods We created different artificial landscapes (1 km × 1 km) with gradients of the area proportions of the different habitat types in a fully crossed design (landscape composition). Additionally, we created a

gradient of habitat fragmentation by modifying the number of fields per landscape and, thus, the number of habitat patches (landscape configuration). Then, we applied the open source model BumbleBEEHAVE to simulate the population development of *Bombus terrestris* over five years in the artificial landscapes.

Results Each habitat type showed a significant positive effect on the simulated number of bumblebee colonies with increasing area proportion in the landscapes. In contrast, the effect of the number of habitat patches (habitat fragmentation) was negative. The efficiency of flower strips was higher in landscapes with low area proportions of semi-natural habitats and oilseed rape. Both food (nectar) and nesting habitat were limiting resources for the density of bumblebee colonies in the landscapes.

Conclusions Our results show that additional food and nesting resources provided by flower strips are particularly important for bumblebees in landscapes with low proportions of semi-natural habitats and oilseed rape as mass-flowering crop. To substantially increase the number of bumblebee colonies, not only more food but also more nesting habitat is required. This result is in line with previous results from real landscapes with and without biodiversity measures.

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Introduction

Transforming agricultural practices to address declining biodiversity is urgently needed and has to be an issue of policy and society likewise (Mupepele et al. 2021). The decline of pollinators, including wild bee diversity and abundance, has been described as a consequence of the loss and fragmentation of semi-natural habitats, caused by an increasing intensification and homogenization of agricultural landscapes across Europe (Goulson et al. 2008; Kleijn et al. 2011; Kovács-Hostyánszki et al. 2017; Potts et al. 2010). More specifically, the causes of pollinator decline are loss of nesting, mating and hibernation sites and insufficient supply of food (pollen and nectar) regarding both quantity and temporal continuity (Kleijn and van Langevelde 2006; Carvell et al. 2007; Roulston and Goodell 2011). Bumblebees, such as our target species *Bombus terrestris*, belong to the most important pollinator taxa in the agricultural landscapes of Central Europe (Ollerton 2017). However, since the 1980s this species was also domesticated (Velthuis and van Doorn 2006), but we only focussed on non-domesticated bumblebees. Thus, the landscape structure determines the availability of nesting sources. They need continuous food resources to establish and maintain their colonies (Persson and Smith 2013; Timberlake et al. 2019; Hemberger et al. 2022).

Semi-natural habitats, such as hedgerows and field margins, can play an important role in sustaining bumblebees in agricultural landscapes as they provide both food resources and nesting, hibernating and mating sites (Marshall and Moonen 2002; Hopfenmüller et al. 2014; Cole et al. 2020), whereas agricultural fields do not present suitable habitat due to frequent disturbances and low amounts of floral resources (Greenleaf et al. 2007; Holzschuh et al. 2007; Kremen et al. 2007). Hedges that offer floral resources throughout the summer increase the abundance of bumblebees (Königslöw et al. 2022). During the period of colony foundation, field margins are even more attractive nesting habitats than hedgerows for spring queens (Lye et al. 2009). However, field margins are often degraded due to intense management (Neumüller et al. 2020), which may reduce their habitat quality for bumblebees.

Other previous studies found that also mass-flowering crops can increase the abundance of solitary bee species and short-tongued bumblebees, such

as *B. terrestris*, in addition to semi-natural habitats (Walther-Hellwig and Frankl 2000; Westphal et al. 2003). Especially, bumblebee density and colony growth can benefit from large areas of oilseed rape (Westphal et al. 2006, 2009; Riedinger et al. 2014). However also negative correlations of bumblebees with early mass-flowering crops, such as the oilseed rape, have been observed (Hovestadt et al. 2019; Riggi et al. 2024). Hence, the potential effects of oilseed rape and other mass-flowering crops on bumblebee colonies remain unclear.

Beside semi-natural habitats and mass-flowering crops, perennial flower strips may be important flower-rich and extensively managed habitats for bumblebees (Pywell et al. 2005; Carvell et al. 2007; Goulson et al. 2008) that can increase the nectar and pollen supply in agricultural landscapes (Potts et al. 2003; Ebeling et al. 2008; Scheper et al. 2013; Blaauw and Isaacs 2014). Additionally, perennial flower strips can provide nesting habitat for ground-nesting bees (e.g., Schubert et al. 2022). Owing to these attributes, flower strips have been incorporated into the Common Agricultural Policy (CAP) of the European Union as agri-environmental measures since the early 1990s. They are meant to counteract the decline of pollinators and to promote biological diversity in agricultural landscapes (Batáry et al. 2010; Pe'er et al. 2019). The positive influence of flower strips or flower areas on wild bees, for example, has already been shown by previous studies (Haaland et al. 2011; Dicks et al. 2015; Ouvrard and Jacquemart 2018), also for bumblebees, such as *B. terrestris*, in terms of increasing abundances (Buhk et al. 2018; Geppert et al. 2020; Piko et al. 2021).

Habitat types, such as semi-natural habitats, flower strips and mass-flowering crops, have different plant communities and, therefore, differ in overall quantity and in temporal distribution of food supply throughout the year (Cole et al. 2020; Maurer et al. 2022). Hence, floral resources vary within and across years depending on landscape features and farming practice on the fields (Bishop et al. 2024). In consequence, the landscape composition, particularly the area proportions of different habitat types, influences bee communities (Kennedy et al. 2013; Neumüller et al. 2020) as it determines the availability and temporal continuity of floral resources at local and landscape scale (Scheper et al. 2015). Therefore, the effect of biodiversity measures, such as flower strips, on pollinators

depends on the landscape context (Carvell et al. 2011; Haas 2018; Kleijn et al. 2018; Hellwig et al. 2022).

Furthermore, the spatial configuration of habitats in the landscape may have an influence on pollinator abundance (Kleijn and van Langevelde 2006; Martin et al. 2019; Scheper et al. 2013; Beyer et al. 2021). For example, the fragmentation of habitats, i.e., the subdivision of habitat area into separate patches, affects the foraging travel distances (e.g., Harmon-Threatt and Anderson 2023). In agricultural landscapes, the number of habitat patches on semi-natural hedges and field margins as well as on arable land is largely determined by the size of fields with smaller fields causing a higher number of patches and, thus, stronger fragmentation of habitat. Thus, field size appears to be an important factor of spatial configuration. Previous research found that large fields could limit the reproduction of bumblebees within the landscape (Geppert et al. 2020).

In general, the response of wild bees to floral resources depends on foraging distances and life history traits (Wood et al. 2017; Grab et al. 2018). Despite these findings, there is a lack of knowledge on how landscape composition and configuration influence the efficiency of different floral resources for pollinator populations at landscape scale (Pérez-Sánchez et al. 2023). Due to its relatively high flight distance, *B. terrestris* may be able to buffer effects of spatial configuration of habitat patches (Osborne et al. 2008a) and, theoretically, as a mobile species should respond to habitat quantity at larger spatial scales than less mobile species (Steffan-Dewenter et al. 2002). Hence, a landscape scale approach was chosen for this study.

Studying the development of pollinator populations along gradients of area proportions and spatial configuration of different habitat types in experimental field designs is nearly impossible due to high costs and limited availability of land and of farmers who would participate in such projects, particularly considering sufficient repetitions of different landscapes that would allow to test interactive effects (Oppermann et al. 2019). However, simulation models, such as the agent-based model BumbleBEEHAVE (Becher et al. 2018b), are suitable for detailed studies of pollinator response to numerous variants of landscape composition and configuration in crossed designs of multiple factors. In Baden-Böhm et al. (2023), we used BumbleBEEHAVE to investigate

the effect of biodiversity measures in case studies of three different real landscapes and found that biodiversity measures providing food and nesting habitats had a positive effect on the number of bumblebee colonies. However, these case studies did not allow to build response functions of the number of bumblebee colonies to increasing habitat area or fragmentation (Baden-Böhm et al. 2023). In the present study, we created artificial landscapes of 1 km × 1 km with gradients of landscape composition and configuration by controlling the area proportions of semi-natural habitats, mass-flowering crops and flower strips as well as the number of fields in the landscapes, respectively. Here, the number of fields was a design factor determining the degree of landscape fragmentation in terms of number of habitat patches. The aim was to assess the response of the number of bumblebee colonies, as a measure of bumblebee abundance at landscape level, to the gradients of habitat amounts and fragmentation. Specifically, we aimed to answer the following research questions:

- (I) What is the relationship between area proportions of semi-natural habitats (hedges, field margins), mass-flowering crops (oilseed rape) and flower strips with the density of bumblebee colonies? How is the shape of the relationship (i.e., linear/non-linear) and the effect size?
- (II) Does fragmentation of habitats (subdivision of habitat area into more separate habitat patches) affect densities of bumblebee colonies?
- (III) (A) Is the effectiveness of flower strips for bumblebee colonies modified by area proportions of semi-natural habitat and/or mass-flowering crops? (B) In which landscape settings are flower strips particularly effective? (C) Can mass-flowering crops obviate the need for flower strips?
- (IV) Is density of bumblebee colonies affected more strongly by amount of food resources or by area of nesting habitat?

Material and methods

Landscape scenarios

We created artificial landscapes of 1 km × 1 km to represent agricultural landscapes that comprise both

patchy and linear habitat types (habitats) (Fig. 1). The size of the landscape is identical to the size of the actual examined landscapes in the research project F.R.A.N.Z.. We chose this size, because it corresponded to the mobility of most wild bee species including bumblebees (Westrich 2019). Patchy habitat types were crop fields differentiated into two categories: (i) matrix area without profitable food resource for the bumblebees such as cereal fields and (ii) mass-flowering crop, here oilseed rape as an example, which is the most typical mass-flowering crop cultivated in Germany (BLE 2024). Linear habitat types included hedges and field margins as semi-natural habitats and flower strips as biodiversity measures.

Three different classes of scenarios were developed and compared (Table 1):

- ‘Business as usual’ with matrix, oilseed rape as mass-flowering crop and semi-natural habitats (SNH);
- SNH with flower strips that provide food but **no** nesting habitat (Biodiv);
- SNH with flower strips that additionally provide nesting habitat (Biodiv + nest).

In the SNH scenarios, only semi-natural habitats were functioning as nesting habitat for bumblebees. Food was provided by the mass-flowering crops and the semi-natural habitats. In the Biodiv scenarios flower strips were included as additional food source, while in the Biodiv + nest scenarios flower strips provided both nesting and food habitat.

For each scenario class, we created a large number of landscape scenarios with different landscape compositions and configurations. We used a fully crossed design of different area proportions of the three habitat types to create gradients of landscape composition (Table 1). Further, each variant of landscape composition was crossed with three levels of the number of fields per landscape in order to create an additional gradient of habitat fragmentation (number of habitat patches in the landscapes). Based on combinations of landscape compositions and number of fields, we created 120 SNH and 480 Biodiv landscape scenarios. For each landscape scenario, we produced four stochastically different repetitions of artificial landscapes and, thus, created 2400 different landscapes altogether. For the Biodiv + nest scenario class, we used the same 1920 landscapes as for the Biodiv scenario class, so that finally, we conducted 4320 simulation runs of

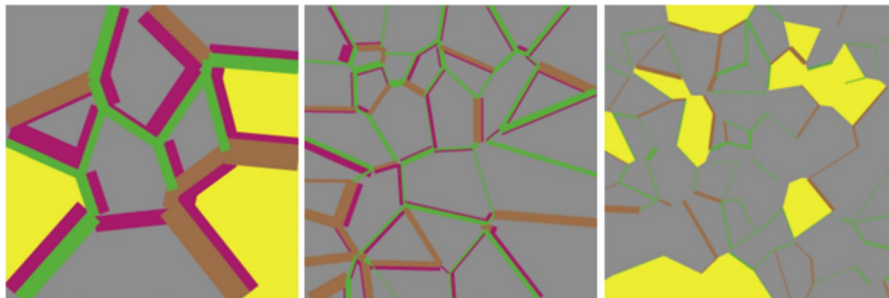


Fig. 1 Examples of artificial landscapes with different numbers of fields and habitats: From left to right: 10–33–66 fields. The habitat types: hedges (brown) and field margins (green)

as semi-natural habitats, oilseed rape (yellow) as mass-flowering crop and flower strips (magenta) as biodiversity measure. Matrix is shown in grey

Table 1 Gradients of the area proportions of habitat types and of the number of fields used for creating landscape scenarios

Scenario class	Semi-natural habitats (%) (linear)	Oilseed rape (%) (patchy)	Flower strips (%) (linear)	Number of fields	Number of landscape scenarios
SNH	0.5, 1.0, 1.5, 2, 3, 6, 9, 15, 20, 30	0, 5, 20, 40	0	10, 33, 66	120
Biodiv/Biodiv + nest	0.5, 1.0, 1.5, 2, 3, 6, 9, 15, 20, 30	0, 5, 20, 40	2.5, 5, 7, 15	10, 33, 66	480

the development of bumblebees in total. The models are time-consuming and needed a high server capacity, therefore we only could do simulations for five years and in a parallel processing way.

The maximum area proportions of the habitat types (Table 1) reached beyond the values that can usually be observed in real agricultural landscapes e.g., from the F.R.A.N.Z. project in order to reduce uncertainty of modelled response of bumblebees within the realist ranges of habitat areas. Regarding area proportion of semi-natural habitats, a minimum of 0.5% was required, because at least one nesting habitat must be present in order to avoid extinction of the bumblebee colonies in the simulations of population development (Becher et al. 2018b). The area proportions of semi-natural habitats were divided into equal shares of hedges and field margins. Furthermore, we refrained from implementing a crop rotation, although we simulated a period of five years.

We implemented different numbers of fields in the landscapes to assess the effect of habitat fragmentation. A higher number of fields leads to a higher number of patches of both patchy habitats (oilseed rape) and linear habitats (semi-natural and flower strips) where the latter are located on the edges of the fields. The gradient of number of fields per landscapes, was chosen based on the real landscapes of the project F.R.A.N.Z. (Baden-Böhm et al. 2023). Landscapes with 66 fields per square kilometre represented small-featured landscapes, whereas 10 fields corresponded to landscapes with the largest fields among the study areas of the project. The means and min–max ranges of the numbers of habitat patches in the landscape scenarios with 10, 33 and 66 fields were 30.1 (2–47), 94.3 (7–163) and 160.8 (9–331), respectively.

All artificial landscapes were created with R 4.3.2 (R Core Team 2023) using a custom R script which was based on the landscape generator included in the model SpatSam_1.0 (Thiele et al. 2023). As compared to SpatSam_1.0, we added flower strips as an additional type of linear feature which is located at field edges either instead of semi-natural habitats (i.e., hedges and field margins) or next to them (Fig. 1). The R script for the creation of artificial landscapes can be found in the Supplementary Material. The landscapes were stored in raster format with a spatial resolution of 1 m.

Model process and modelling of population development

For the simulation of bumblebee population development, we used the agent-based model BumbleBEEHAVE (Becher et al. 2018b) which is implemented in NetLogo 5.3.1 (Wilensky 1999). The model is freely available and open source under <https://beehave-model.net/>. The model BumbleBEE SCOUT, which generates input data for BumbleBEEHAVE, could be ignored, because we generated the input data using custom R scripts.

In particular, the input data for BumbleBEEHAVE comprised information about the plant composition of the habitat types which is required to determine the daily nectar and pollen amounts. The plant composition of each habitat type were the same for every landscape scenario. Compared to Baden-Böhm et al. (2023), the plant composition of the hedges was revised and comprised both a shrub and herb layer. The field margin, the flower strip and oilseed rape were the same as for the study area Havelland in Baden-Böhm et al. (2023). So, oilseed rape was chosen as a mass-flowering crop during spring, while the field margin has a lower number of flowers than the hedges or flower strips (Supplementary material: Plant species per habitat). The different plant species and the number of flowers determine temporal variability of nectar and pollen. The plant composition of the different habitats based on field studies (semi-natural habitats), regional German seed mixtures (flower strips) or literature (oilseed rape). In other studies, we tested different plant compositions adapted to the regional conditions and could see the temporal variability of floral resources (cf. Baden-Böhm et al. 2022b, 2023). However, not all plant species that occurred in the plant composition were integrated in the FloRes Database (Baden-Böhm et al. 2022a) and, therefore, could be used to calculate available pollen and nectar. In this study, we focussed on the areal proportion (spatial variability of food resource) and not on the temporal variability of food resources.

BumbleBEEHAVE can simulate the population development, behaviour and survival of six bumblebee species. In our present study, we focussed on *Bombus terrestris*, one of the most common bumblebee species in Germany (Westrich 2019). In the model, the life cycle started on the 1st January (more details in Becher et al. (2018b) and Baden-Böhm

et al. (2023)). A landscape is beneficial for bumblebees, when there are suitable food and nesting habitats. Here, we wanted to quantify the thresholds of habitats by proportion. For this, we looked at the number of colonies, because they are an indicator for a successful reproductivity of bumblebees after hibernation (Westphal et al. 2009; Hemberger et al. 2022).

We reduced the simulation period to five years, because the model is time consuming (although we did parallel processing). As in the default settings of *BumbleBEEHAVE*, the number of bumblebee queens was set to 500 at the 1st January of year one, which is sufficient to avoid extinction of the population during the first year (Becher et al. 2018b). This corresponds to previous studies where densities of all bumblebee species in linear and non-linear countryside habitats in the United Kingdom ranged between 1100 and 3700 nests km⁻² (Osborne et al. 2008b).

We ran the model *BumbleBEEHAVE* at daily time steps. Weather was not explicitly implemented in the model although it modifies the foraging time of bumblebees. For simplicity, the foraging time was set to a constant value of eight hours per day. Climate and weather conditions were implicitly integrated in the model through the timing of queens emerging from hibernating and the phenology of flowering plant species (Becher et al. 2018b).

Data analysis

For statistical analyses, we used the number of *B. terrestris* colonies in the landscapes after five years of simulation as target variable in Generalized Linear Models that we calculated with the package *glmmTMB* 1.1.8 in R 4.3.0 (R Core Team 2023). To answer our research questions, we built two model variants with different sets of predictor variables.

The first model variant, hereafter called ‘habitat model’, included the areas of habitat types (semi-natural habitat, oilseed rape, flower strips) and the total number of habitat patches as main predictor variables and, further, the number of fields in the landscape (categorical; 10, 33 or 66 fields) and the scenario classes (SNH, Biodiv, Biodiv+nest) as co-factors. This model was used to answer research questions I–III. In addition to the main effects, it also included interactions of the areas of semi-natural habitats and flower strips and of oilseed rape and flower strips (research question III).

The second model variant, hereafter called ‘resources model’, included the daily mean amount of nectar, i.e., the yearly sum of nectar divided by the number of days with bumblebee colonies present, and the area of nesting habitat as main predictors and ‘scenario class’ as co-factor. The co-factor ‘number of fields’ was not included in this model as it caused convergence problems. We also tested variables that assessed the temporal distribution of nectar during the year, namely nectar ‘permanency’ (mean of daily nectar amount during the season divided by the standard deviation of daily nectar amount) and monthly sums of nectar in periods with generally low nectar availability (June, September). However, the predictors of temporal nectar distribution did not provide meaningful results and, therefore, were excluded from the final ‘resources model’.

Both model variants were set up with negative binomial distribution and log-link. As validations of preliminary models indicated zero-inflation and heterogeneous variances, the models also included submodels of zeros and dispersion. The best fitting predictors and transformations for these submodels were identified by manual model building based on AIC.

In order to find suitable models of the shapes of the relationships between metric predictor variables and number of colonies, we tried different transformations of the predictors using for-loops iterating over the predictors and a set of predefined transformations (log, ^0.25, ^0.50, ^0.75, ^1.5, ^2.0). A transformation was included in the model, replacing the previous transformation of the same predictor, if it reduced the ‘significant AIC’ from Jamil et al. (2012).

After identifying the best transformations, we added the interactions described above to the ‘habitat model’. In the ‘resources model’, we tried to include the interaction of nectar and area of nesting habitat which, however, lead to convergence failure of the model and, therefore, was discarded.

We used the R package *DHARMA* 0.4.6 (Hartig 2022) for validating the distribution, link function, linearity and homogeneity of variance of the models. Further, we used the R package *performance* 0.10.8 (Lüdtke 2021) for assessing model fit (‘posterior predictive check’) and collinearity of predictors. The validation showed no substantial deviation from linearity and there was also no collinearity among the main effects in the models. We found significant deviations of the model residuals from the assumed

distribution and dispersion which could not be fully eliminated through model optimizations (setup of zero-inflation model and dispersion submodels, transformations of predictors). As posterior predictive checks indicated good model fit and given the large sample size, we decided to accept the final models in spite of these deviations from model assumptions.

Results

Relationships between habitat areas and bumblebee colonies

In general, we observed the maximum number of bumblebee colonies of the target model species *Bombus terrestris* in the fifth year, the last simulation year, which was used for all statistical analyses.

The relationships of semi-natural habitats (hedges and field margins), oilseed rape as mass-flowering crop and flower strips with bumblebee colonies were analysed with the habitat model (Fig. 2A–C).

All habitat types showed a significant positive effect on the number of bumblebee colonies with increasing area proportion in the landscapes (Online Appendix 1 Table 1). Area of semi-natural habitats had the strongest effect on the number of colonies and showed a log-power relationship with an exponent of 0.75 (Fig. 2A; Online Appendix 1 Table 1). The relationship of area proportion of oilseed rape with number of colonies was log-square root (Fig. 2B), while that of flower strips was log-power with an exponent of 0.25 and, thus, was the most non-linear one (Fig. 2C).

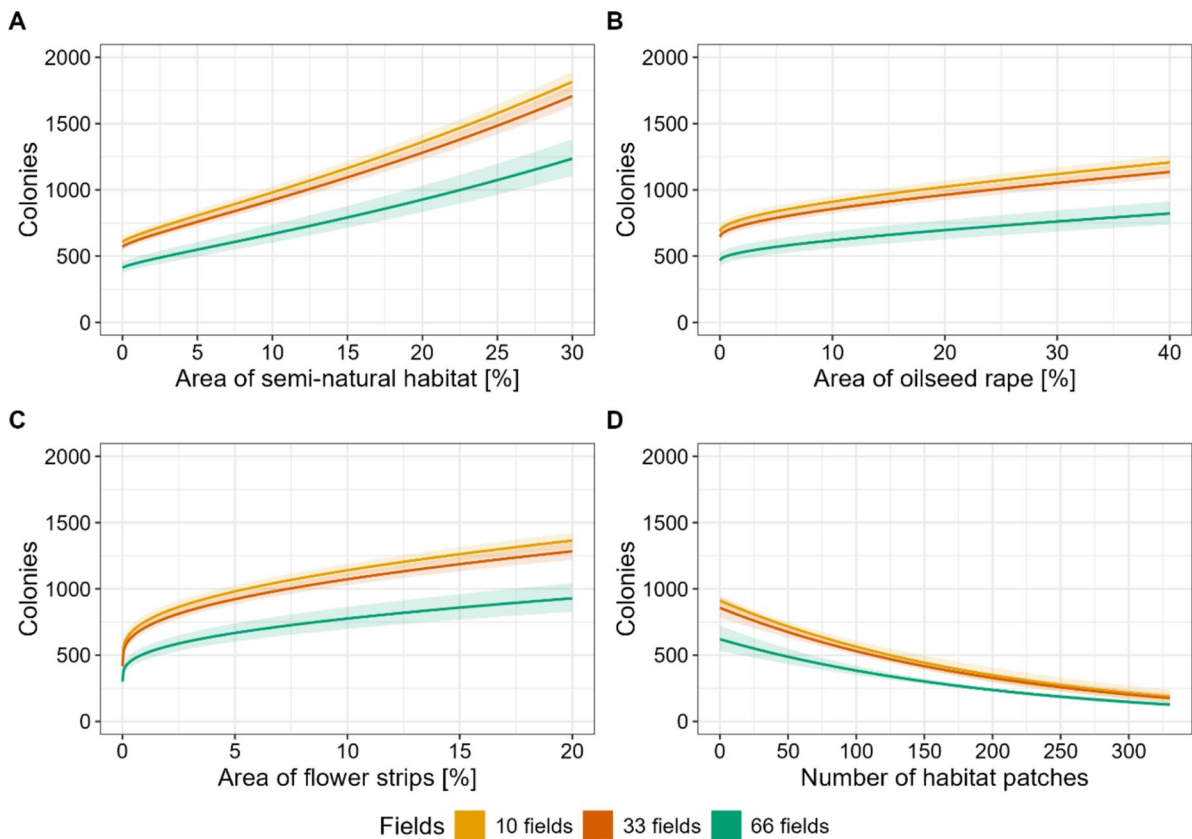


Fig. 2 Relationships of habitat area proportion (given as percentage of the landscape) and habitat fragmentation (number of habitat patches) with the density of bumblebee colonies

according to predictions from a Generalized Linear Model ('habitat model') based on simulation results

Effects of habitat fragmentation

Fragmentation of habitats (number of habitat patches) had a negative impact on bumblebees. Hence, the number of bumblebee colonies decreased significantly with increasing number of habitat patches in a log-linear relationship (Fig. 2D, Online Appendix 1 Table 1). Additionally, the intercept of number of colonies decreased significantly from landscape scenarios with the lowest number of fields (10 fields) to the landscapes with the highest number of fields (66 fields) (Online Appendix 1 Table 1).

Interactions between flower strip area and other habitats

The relationship of flower-strip area and bumblebee colonies was modified by the proportion of semi-natural habitats and oilseed rape in the landscapes (Fig. 3) as evidenced by the negative interactions in the habitat model (Online Appendix 1 Table 1). Thus, flower strips were more efficient in landscapes with low area proportions of semi-natural habitats and oilseed rape (Fig. 4). An area proportion of 5% of flower

strips led to a doubling of the number of bumblebee colonies when there were 10% semi-natural habitats and 10% oilseed rape in the landscape, whereas it led to a four-fold increase at 1% of each of the other two habitats (Fig. 4). The increase of bumblebee colonies due to flower strips stagnated when there were 30% of semi-natural habitats and more than 20% of oilseed rape in the landscape (Fig. 3).

Further, flower strips had a stronger effect per area unit than oilseed rape in landscapes with up to 25% of semi-natural habitats (Fig. 5). However, the difference in effect size decreased with increasing area of semi-natural habitats, and 30% of oilseed rape in landscapes with 30% semi-natural habitats even had a stronger effect than the maximum, i.e., 20% of flower strips.

Relative importance of food and nesting resources

Regarding food and nesting resources, we found that number of colonies increased near-linearly with the amount of available nectar (Fig. 6) while the relationship with area proportion of nesting habitat was log-quadratic (Fig. 7). In landscapes with low or

Fig. 3 Relationship of area proportion of flower strips with density of bumblebee colonies modified by semi-natural habitats and mass-flowering crop (oilseed rape) according to predictions from a Generalized Linear Model ('habitat model') based on simulation results

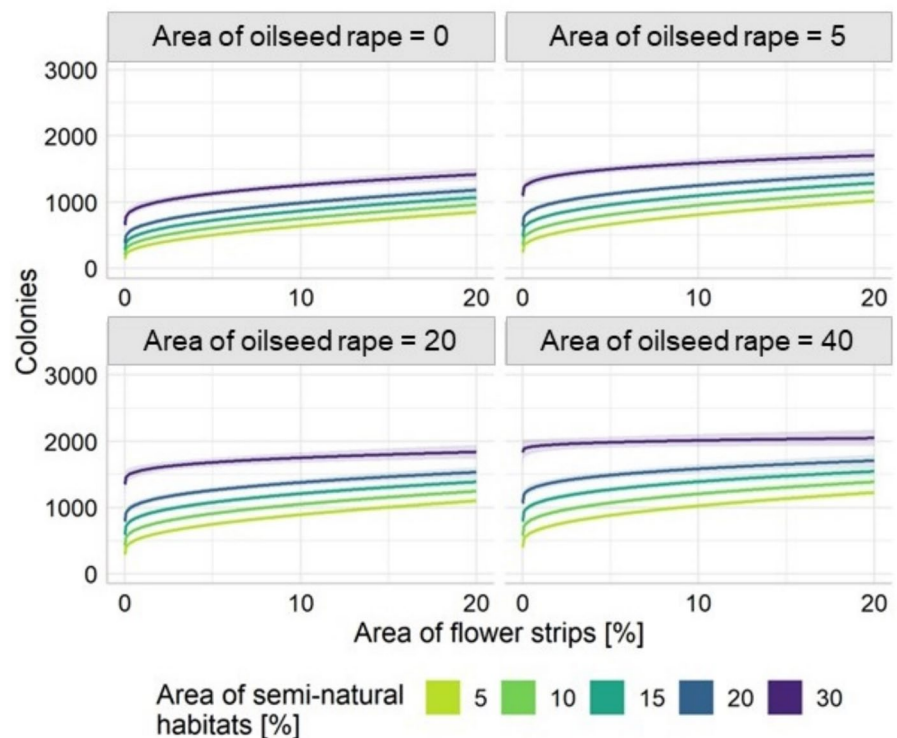


Fig. 4 Effect size of area of flower strips on density of bumblebee colonies in the landscape depending on area of semi-natural habitat and mass-flowering crops (oilseed rape). Effect size is given as ratio between predicted values at 5% area proportion of flower strips vs. 0% according to a Generalized Linear Model ('habitat model') based on simulation results

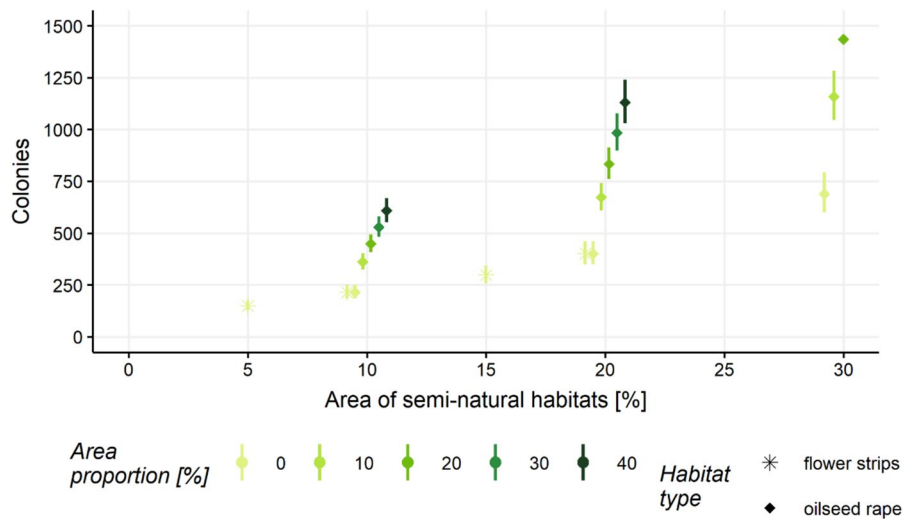
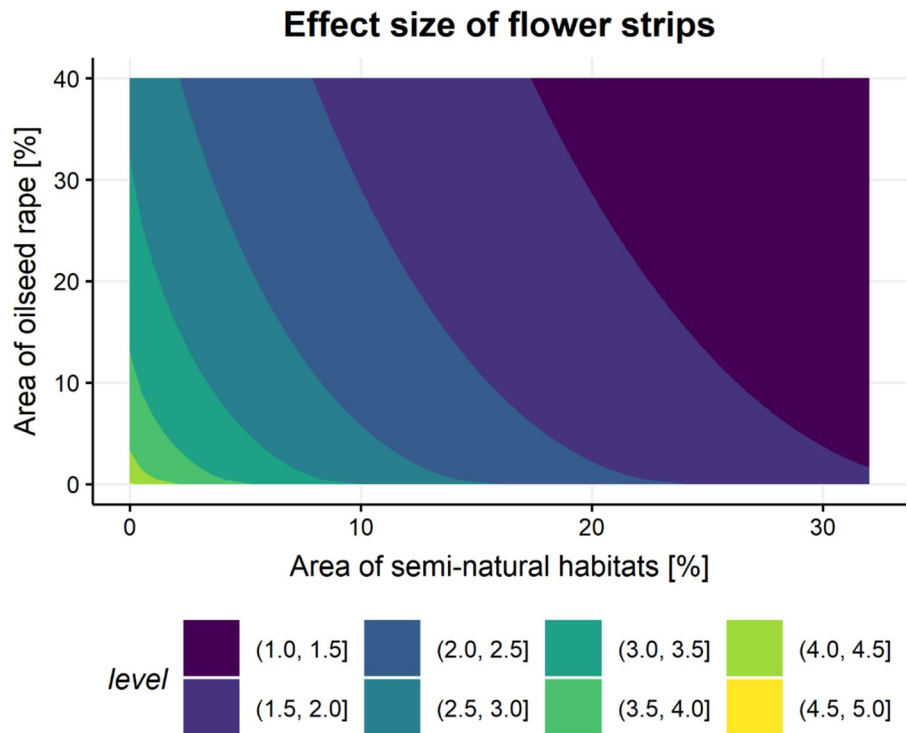


Fig. 5 Comparison of effects of flower strips and mass-flowering crop (oilseed rape) on density of bumblebee colonies in the landscape at different area proportions of semi-natural habitats (5, 10, 15, 20 and 30%) according to predictions from a Generalized Linear Model ('habitat model') based on simulation results. For predictions of number of colonies at different area

proportions of flower strips, the area of oilseed rape was set to zero, and vice versa. Predictions were made for landscape scenarios with 33 fields and no additional nesting habitat due to flower strips. Note that positions of data points were shifted along the x-axis so as to avoid overlap of plotting symbols

Fig. 6 Relationships of amount of available nectar (daily mean) with density of bumblebee colonies at different levels of the area of nesting habitat in the landscape according to predictions from a Generalized Linear Model ('resources model') based on simulation results

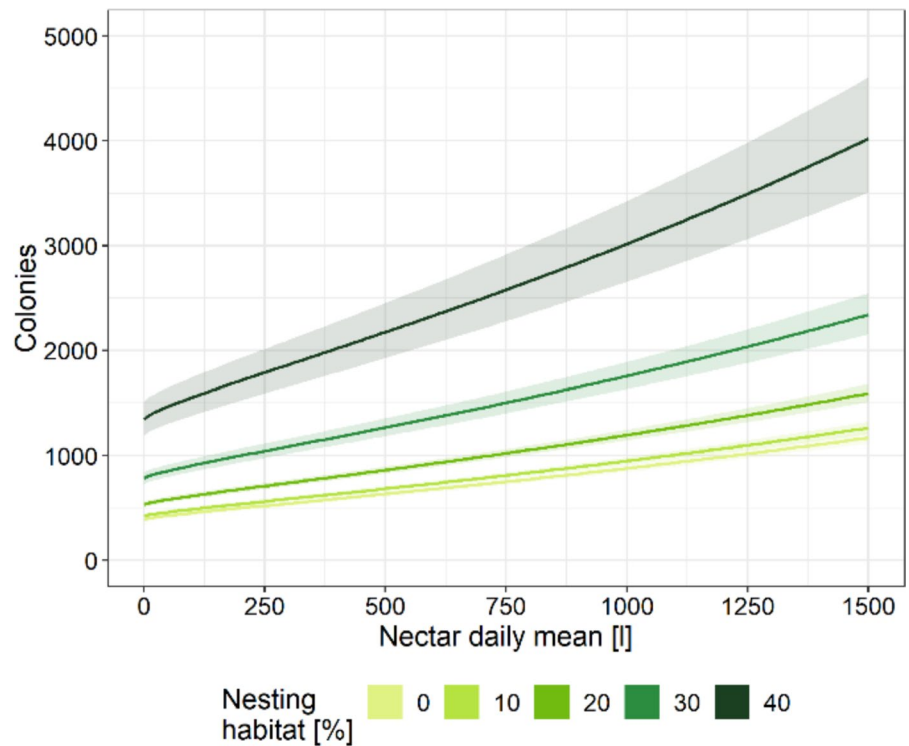
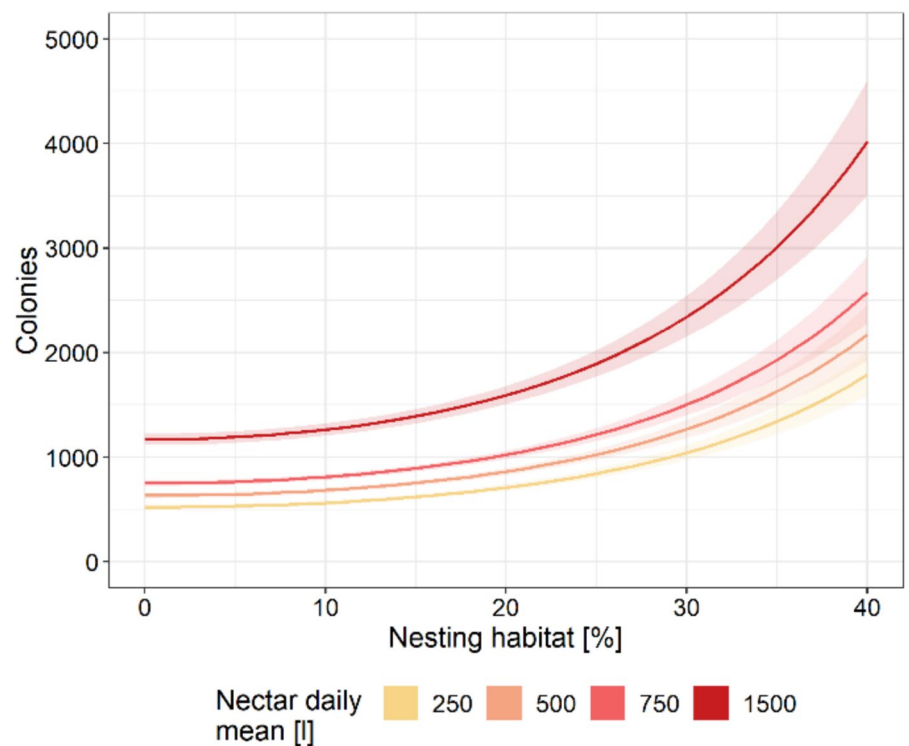


Fig. 7 Relationships of proportion of nesting habitat (% of the landscape) with density of bumblebee colonies at different levels of available nectar in the landscape according to predictions from a Generalized Linear Model ('resources model') based on simulation results



moderate amounts of resources, the density of bumblebee colonies was affected more strongly by additional nectar, whereas the effect of additional nesting habitat became stronger in landscapes that already had high proportions of food habitats (Online Appendix Table 2). Overall, we found synergistic effects of amount of nectar and area proportion of nesting habitat on the number of bumblebee colonies (Online Appendix 1 Fig. 2).

Discussion

Relationships between habitat areas and bumblebee colonies

Our study showed that area of semi-natural habitats in the landscape had a positive near-linear relationship with density of bumblebee colonies, whereas the relationships of flower strips and, particularly, mass-flowering crops (oilseed rape) with density of bumblebee colonies levelled off with increasing area of those respective habitats. Altogether, semi-natural habitats had a stronger effect than flower strips and oilseed rape. The difference in effect size and shape can be explained by the fact that semi-natural habitats also provided nesting habitats for bumblebees, while oilseed rape per se was only food habitat and flower strips were only food habitat in 50% of the scenarios with biodiversity measures. Thus, the flattening of the curves with increasing area of flower strips and oilseed rape indicates that nesting habitat becomes a limiting factor when only food supply increases. When considering only scenarios with flower strips providing both food and nesting habitat, the resulting relationship with density of bumblebee colonies was similar to that of semi-natural habitats. Thus, in the model, flower strips become as effective as semi-natural habitats for bumblebee colony density if they provide nesting habitat in addition to flowering habitat. This is important, if we assume that farmers or land owners have a choice of either implementing annual or perennial flower strips or other flowering habitats. The annual ones provide food but do not offer nesting habitat, whereas the perennial ones provide both.

Nesting sites are largely missing in intensive agricultural landscapes (Westrich 1996), because the arable land use implicates frequent disturbances of the soil (Greenleaf et al. 2007; Holzschuh et al. 2007;

Kremen et al. 2007). This impairs many bee species because 75% of them nest below ground (Antoine and Forrest 2021), including our target species *Bombus terrestris*. Consequently, bumblebees have to nest and hibernate in semi-natural habitats, such as field margins and hedges.

Field margins and hedges are attractive nesting habitats and affect the development and abundance of bumblebees (Lye et al. 2009; Pfiffner et al. 2018; Königslöw et al. 2022). According to Herrmann et al. (2007) the proportion of semi-natural habitats had a minor positive impact on bumblebee abundance, while other studies found slightly negative effects on bumblebee abundance (Hass et al. 2019). Further, a high amount of semi-natural habitats decreased the abundance of bumblebees in intensive agricultural landscapes (Kulow et al. unpublished), whereby the abundance of wild bees increased in heterogeneous landscapes and with higher area proportion of semi-natural habitats (Steffan-Dewenter et al. 2002; Ricketts et al. 2008). This is the opposite to our results, where the number of bumblebee colonies (abundance) was higher at low area proportion of semi-natural habitats and oilseed rape in a landscape with low number of fields, so resembling a homogenous landscape.

Using a similar approach as in the present study, Baden-Böhm et al. (2023) found that the same types of semi-natural habitats, i.e. field margins and hedges, have a stronger effect than the investigated biodiversity measures. In both studies, semi-natural habitats providing food and nesting source are the base of all scenarios, whereby the flower composition and also the quality (pollen and nectar supply) of hedges is modified in the present study. Furthermore, Baden-Böhm et al. (2023) could show that the implementation of biodiversity measures had in all landscapes a positive effect on the number of bumblebee colonies as food and as food and nesting habitat and these results were in line with the field study results of Kulow et al. (unpublished). However, the number of bumblebee colonies showed the same trend not the actual measured number (Baden-Böhm et al. 2023).

The positive effect of flower strips in our simulations is in line with field studies of biodiversity measures, such as flower strips (Haaland et al. 2011; Scheper et al. 2013). Kulow et al. (unpublished) found that bumblebees and common species benefit from biodiversity measures. They suggest that there is no

significant positive effect because bumblebees have a large flight radius (Osborne et al. 2008a) and are not dependent on resources in the immediate vicinity such as additional food sources like from biodiversity measures (Kulow et al. unpublished).

Field studies attribute the effectiveness of flower strips mainly to the provisioning of floral resources (Scheper et al. 2013). However, our results suggest that the importance of providing additional nesting habitat on flower strips or similar biodiversity measures may have been underestimated. In order to improve the effectiveness of flower strips on pollinators, biodiversity measures should be established over several years without intermittent tillage (Blaauw and Isaacs 2014; Buhk et al. 2018), so that they have the potential to provide nesting sites for ground-nesting bees throughout their active phase. Artificial nesting hills are relative new biodiversity measures which provide successfully nesting and food habitats in landscapes with a low cover of semi-natural habitat. They were successively colonized and should therefore also be implemented over several years (Neumüller et al. 2022).

Mass-flowering crops are particularly attractive for generalist and mobile bumblebees, such as *B. terrestris*, because they forage especially on open flowers (Walther-Hellwig and Frankl 2000; Alanen et al. 2011; Gayer et al. 2021). Also in this study, bumblebee colonies increased due to the food supply of oilseed rape in agricultural landscapes (Baden-Böhm et al. 2023). Further, according to Haas (2018) and Westphal et al. (2009) oilseed rape enhance the density and colony growth of bumblebees. The present study suggests that temporary massive food supply through oilseed rape does have a positive effect, but it also shows that its effectiveness is limited and dependent on other habitats that provide nesting sites.

Effects of landscape fragmentation

Increasing fragmentation of landscape (number of habitat patches) had a negative effect on bumblebees. Additionally, the landscape scenarios with many and, consequently, smaller fields generally showed lower densities of colonies (Fig. 2D). Bumblebees have a large flight radius between 1750 and 3000 m compared to, e.g., solitary bees (Walther-Hellwig and Frankl 2000; Westphal et al. 2003; Osborne et al. 2008a). Haas (2018) mentioned that *B. terrestris* as

high mobile generalist species was little affected by habitat fragmentation. Further previous studies, which investigated the number of patches, edge length, or interpatch connectivity of semi-natural habitats per landscape, found no or only weak effects (Kennedy et al. 2013; Steckel et al. 2014). However, our result on fragmentation is in line with an earlier simulation study using BumbleBEEHAVE (Baden-Böhm et al. 2023), where the landscape with the largest fields and fewest habitat patches also had the highest number of colonies when controlling for habitat area. The reason for lower densities of colonies with highly fragmented habitats in the simulations is likely a higher flight distance and, therefore, higher energy expenditure leaving fewer resources for the brood and the mortality risk increase (Becher et al. 2018a). Also the abstraction of the habitat patches as point coordinates can influence the effect of spatial distribution. It may be possible, that the model overestimates costs of travelling between patches compared to costs of foraging on the patches. However, the possibility that more aggregated habitat might be beneficial for bumblebees should be considered in future field studies.

Interactions between flower strip area and other habitats

The efficiency of flower strips for bumblebee colonies decreases in landscapes with high area-proportions of semi-natural habitats and mass-flowering crops. In the present study, we found a stagnation of growth of bumblebee colonies, when semi-natural habitats were higher than 30%. For instance, in a landscape with 40% oilseed rape and 5% semi-natural habitat, an increase of flower strips from 0 to 10% would lead to a doubling of the number of colonies, while the same increase of flower strips would have no effect if the area-proportion of semi-natural habitat was as high as 30%, according to the simulations. The reason for reduced efficiency of additional food resources is likely again the limitation of colony development by lack of nesting habitat when food supply is high.

In line with our results, Krimmer et al. (2019) found that only small flower fields may be important in landscapes with high proportion of semi-natural habitats and larger ones in landscapes with low proportion of semi-natural habitats. Two studies showed that, in structurally simple landscapes with intermediate levels of semi-natural habitats,

the impact of biodiversity measures is the strongest (Tscharntke et al. 2005; Baden-Böhm et al. 2023). Hence, both field and simulation studies underline that flower strips are particularly rewarding in landscapes that are poor in semi-natural habitats. We conclude that biodiversity measures likely have an effect on bumblebees, but proportion of semi-natural habitat is also essential (Kennedy et al. 2013; Steckel et al. 2014).

The results that an increase of oilseed rape from 0 to 40% in a landscape with an amount of semi-natural habitats (5%) would almost yield a doubling of colonies and that efficiency of flower strips decreases in landscapes with high proportions of oilseed rape, raises the question, whether costly agri-environmental schemes could simply be replaced by highly productive mass-flowering crops. In North-East and East of Germany, a high proportion of mass-flowering crops is typical (cf. landscape “Havelland” in Baden-Böhm et al. 2023). In the same landscapes, semi-natural habitats and biodiversity measures can reach proportions of up to almost 9%. However, oilseed rape only has effect sizes comparable to 5–10% flower strips in landscapes with > 15% semi-natural habitats, which are rather exceptions in agricultural regions of Central Europe and elsewhere. Thus, oilseed rape cannot obviate the need for flower strips in intensively used agricultural landscapes. Comparable studies are difficult to find because semi-natural habitats are interpreted and summarised differently in these respective studies. For example, extensive grassland and forest are often counted as semi-natural habitat. This was not possible in this study due to a lack of precise information about the type of grassland or forest.

In contrast to oilseed rape, flower strips offer pollen and nectar throughout the vegetation period. Further, they provide most food resources in summer (Königslöw et al. 2022), while oilseed rape and semi-natural habitats have their flowering peak in spring. For instance, red clover and sunflower are late mass-flowering crops (Rundlöf et al. 2014; Königslöw et al. 2022). Thus, flower strips augment the food resources (Königslöw et al. 2022). In line with this, an empirical study found that the reproduction rate of bumblebees in oilseed rape was enhanced with flower strips compared to oilseed rape alone (Adler et al. 2020).

Relative importance of food and nesting resources

In general, our results are limited by the definition of resources that habitat types can provide for bumblebees in our model (i.e., the plant composition per habitat, which determines the food resources, and which habitat provides nesting resources). These definitions are spatially constant and constant across different years. This means that spatial variability or heterogeneity within habitat types (e.g., hedges with abundant flowers next to hedges with sparse flowers) and weather influences within the simulated 5-year-period cannot be considered. Raising the amounts of both available nectar and area of nesting habitat increased the number of colonies. Thus, both are limiting factors. For a high number of bumblebee colonies a high amount of nectar is necessary. When provisioning of large amounts of nesting habitat (30–40% of the landscape area) is required, the number of colonies is also markedly higher. To achieve this in real landscapes, we have to implement, beside flower strips, extensive grasslands or orchards in the landscape, which are also good nesting sites for bumblebees and other pollinators (Goulson et al. 2010; Riedinger et al. 2014). The effect size of nesting habitat increases above ca. 10% of the landscape area. Either the area proportion and nectar of semi-natural habitat increase or other additional food and/or nesting sources in form of flower strips and oilseed rape were added in the scenarios.

It is well-known that especially floral resources influence the bees on local and landscape scales (Holzschuh et al. 2008; Carvell et al. 2011; Scheper et al. 2015; Hass et al. 2019). Plant phenology and the composition and management of different habitats affect the presence of floral resources in the landscape (Cole et al. 2017; Maurer et al. 2022). Bumblebees need high flower diversity, nectar and pollen as parameters of floral resources in the active period of the colony (from late April to September) and for reproductive success (Carvell et al. 2006; Hass et al. 2019; Klaus et al. 2021). In the present study, we analysed the daily nectar amount instead of pollen, but there is a high collinearity between nectar and pollen. Higher nectar together with increasing nesting habitat increased the density of colonies. The diversity of nectar (or pollen) increased due to the implementation of flower strips. On the contrary, gaps in flowering because

of the flowering phenology or farmers' practice can negatively influence colony development (Carvell et al. 2006; Klaus et al. 2021). In the present study, we did not test scenarios like this, because a minimum of area proportion of semi-natural habitats as nesting and food habitat always has to be implemented in the landscape scenarios. However, these landscape scenarios showed that only a low area proportion of semi-natural habitats did not allow a survival of bumblebee colonies above 5 years.

Conclusion

The present study showed that all habitat types, flower strips, semi-natural habitats (field margins and hedges) and oilseed rape had a significant positive effect on the number of bumblebee colonies (*Bombus terrestris*) with increasing area proportion in the artificial landscapes (1 km × 1 km). Assuming a constant total area of habitat patches, the density of bumblebee colonies was negatively affected by the number of habitat patches (habitat fragmentation). The effectiveness of flower strips was higher in landscapes with low area proportions of semi-natural habitats and oilseed rape. Flower strips that also provide nesting sites can be as effective as semi-natural habitats. Hence, we would recommend that farmers and land users rather implement perennial flower strips or other perennial flowering habitats instead of annual biodiversity measures, because those provide food and nesting habitat, whereas the annual ones offer only food habitat. Moreover, nectar and nesting habitat are both limiting factors for the bumblebee density in landscapes and, together, have synergistic effects.

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Author contributions F.B.B. and J.T. devised and designed the study. F.B.B., N.H. and J.T. created data and performed the data collection. F.B.B. and J.T. analyzed the data. F.B.B., N.H., J.D. and J.T. wrote the paper.

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Data availability All data supporting the findings of this study are available within the paper and supplementary files.

Declarations

Competing interests The authors declare no competing interests.

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