



## Biodiversity measures providing food and nesting habitat increase the number of bumblebee (*Bombus terrestris*) colonies in modelled agricultural landscapes

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### ABSTRACT

Individual biodiversity measures in agricultural landscapes such as flower strips are reported to promote the diversity and abundance of pollinating insects. Those biodiversity measures can be important food sources increasing the amount and continuity of pollen and nectar supply besides sometimes also offering nesting and hibernation sites. Still little is known about combined effects of biodiversity measures at the landscape scale and their long-term impact on pollinator population development. We used the agent-based simulation model BumbleBEEHAVE to investigate, if biodiversity measures have a positive effect on bumblebee populations at landscape scale in terms of the number of colonies per hectare. For this purpose, we chose *Bombus terrestris*, the most common bumblebee species in Germany, as target species. We used three real landscapes located in different regions of Germany as landscape settings for the simulations. The landscapes had strongly different farming systems regarding crop diversity and rotations and, consequently, different spatial structure and areal proportions of land-use types and semi-natural habitats. Between 2017 and 2020, distinct combinations of biodiversity measures, such as flower strips, flowering headland and fallows, were established by farmers on different areal proportions of the three landscapes. The biodiversity measures differed in plant-seed mixtures and, thus, the pollen and nectar supply by plants. We simulated the development of bumblebee colonies in the landscapes with and without the implemented biodiversity measures over eight years (four years in a twice repetition). We found that the implementation of biodiversity measures had a significant positive effect on the number of colonies. Further analysis showed that the pollen and nectar supplied by biodiversity measures had positive effects in all three landscapes, while the effect of additional nesting habitat differed among landscapes. Mass-flowering crops had little to no significant effect on the number of bumblebee colonies, whereas semi-natural habitats had a markedly positive effect. Our study underlines that not only biodiversity measures are likely to affect the bumblebee population, but that the overall landscape composition, particularly proportion of semi-natural habitats, is also important. So, to achieve high effectiveness of biodiversity measures, landscape context may be taken into account.

### 1. Introduction

Across Europe, biodiversity measures have been implemented with the aim to counteract habitat loss in intensively-used agricultural landscapes and, thus, to promote many declining species including pollinators, such as bumblebees (Carvell et al., 2015). For bumblebees, flower-rich and extensively managed habitats are essential components of agricultural landscapes that provide food resources as well as nesting, mating and hibernation sites (Carvell et al., 2007; Goulson et al., 2008;

Pywell et al., 2005). Especially, continuity of food supply throughout the season is important for long-lived bumblebee species and their colony establishment, growth and colony success (Hemberger et al., 2020; Kevan and Baker, 1983; Persson and Smith, 2013; Timberlake et al., 2019). In comparison to most solitary bees, they are particularly dependent on resources availability at the period of their activity time due to their shorter life cycles (Beyer et al., 2021). Therefore, flower-rich biodiversity measures should promote the development of bumblebee colonies in intensively-used agricultural landscapes that are in short

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supply of extensively managed land and semi-natural habitats.

Several agri-environment schemes have been incorporated in the Common Agricultural Policy (CAP) of the European Union since the early 1990 s (Batáry et al., 2010; Pe'er et al., 2019), including extensive grassland and field edges, set-aside land, and wildflower patches or strips (Jönsson et al., 2015; Scheper et al., 2013). In the present study, we analysed the effect of annual and/or perennial biodiversity measures on the density of bumblebee colonies in intensively-used agricultural landscapes using three real landscapes as case studies. In addition to food resources, perennial biodiversity measures also offer nesting sites for bumblebees. Using a simulation modelling approach allowed us to separately explore the effects of food and nesting habitats on colony density of bumblebees at the landscape level.

We used the simulation model BumbleBEEHAVE (Becher et al., 2018) and the model species *Bombus terrestris* which is the most common bumblebee species in Germany (Westrich, 2018). The agent-based model BumbleBEEHAVE simulates bumblebees on individual, colony and population level (Becher et al., 2018). The only published study which applied the model BumbleBEEHAVE deals with the importance of courgette as a mass-flowering food source for bumblebees (Knapp et al., 2019). However, there are no current studies about the importance of food and nesting habitats at landscape level for bumblebees.

Therefore, we formulate these research questions:

1. Do biodiversity measures effectively increase the number of bumblebee colonies in the case-study landscapes through provisioning of a.) food resources and b.) nesting habitat?
2. Does the effectiveness of biodiversity measures vary among agricultural landscapes with different landscape composition and configuration?

3. What is the effect of a.) areas of different food habitats, i.e., semi-natural habitats, mass-flowering crops and biodiversity measures and b.) amount of food and nesting resources on the number of bumblebee colonies?

## 2. Materials and methods

### 2.1. Study areas

To analyse the effects of biodiversity measures on bumblebee colony development in landscapes differing in landscape composition and configuration, we located three 1 × 1 km study landscapes in the regions Havelland (HVL: 52°37' N; 12°45'E), Lower Bavaria (BAV: 48°36' N, 12°36' E) and Rhine-Hesse (RHS: 49°56' N, 8°7'E). The three regions represent types of intensive agricultural farming common in Germany (Sutcliffe and Leuschner, 2022). For instance, the average field size was 6.3 ha in the 1 × 1 km study area in Havelland, 2.5 ha in Lower Bavaria and 1.4 ha in Rhine-Hesse. The landscape in Havelland was comprised of agricultural land by 75% of the area with maize, oilseed rape and cereals as dominant crops in the crop rotation. Lower Bavaria had 56% of agricultural land and 25% of forest. Maize and cereals were the most cultivated crops. In Rhine-Hesse, arable land represented 88% of the landscape and the main crops were sugar beet, cereals and oilseed rape. Additionally, the Rhine-Hesse landscape comprised orchards with drupe and pome (6.8%). In all three case study regions, grasslands were usually managed very intensively. As no detailed information of grassland management was available at the level of parcels, we assumed that all grassland were silage meadows and, thus, did not provide semi-natural habitat, except for those parcels that were listed as being under a biodiversity measure, such as “extensive grassland”. The proportions of semi-natural habitats, such as hedgerows, field margins, ditch margins

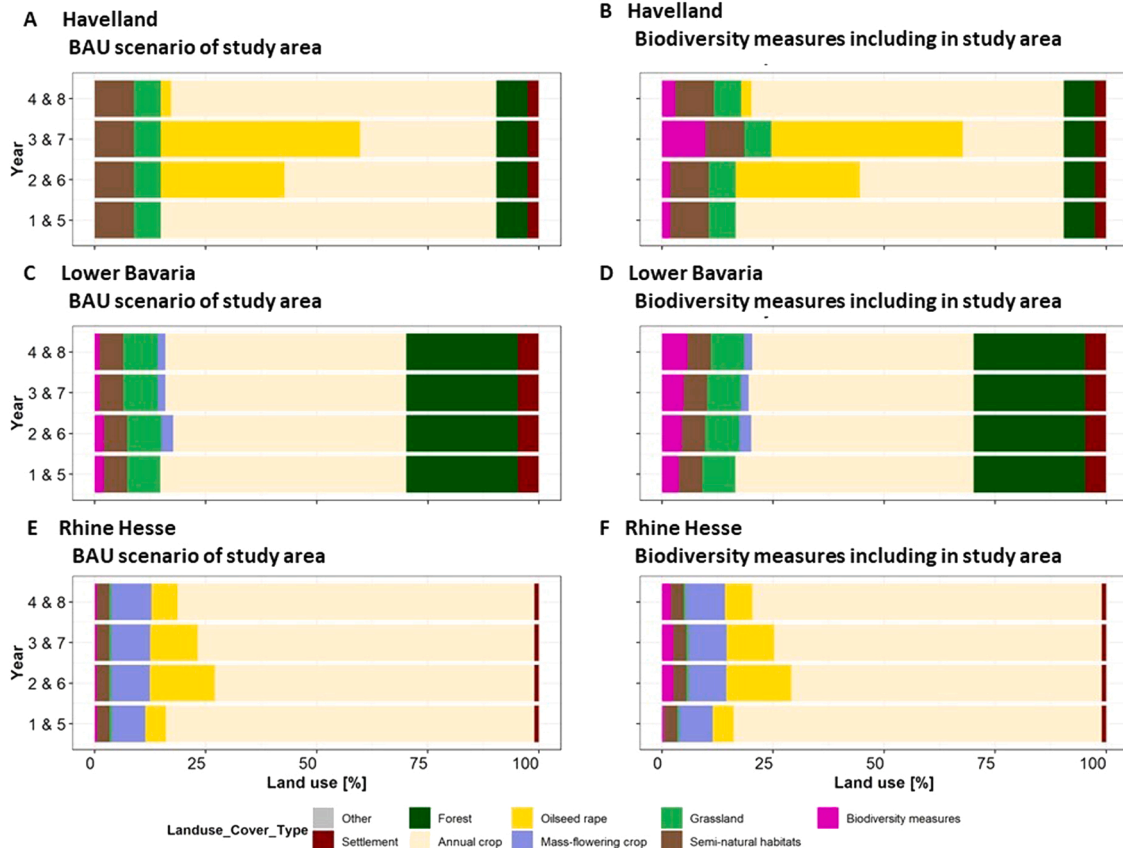


Fig. 1. Proportions of land use for the business as usual scenario in the study areas (A, C, E) and for the scenarios with biodiversity measures implemented in the study areas (B, D, F). The category ‘annual crop’ summarizes the crops not providing resources for bumblebees.

and unpaved dirt tracks, varied between 3.0% and 8.8% of the landscapes (Fig. 1).

The landscapes were located to cover the land of conventional farms which had joined the project F.R.A.N.Z. (Future Resources, Agriculture & Nature Conservation, [Umweltstiftung Michael Otto, 2022](#)) and had established and developed biodiversity measures between the years 2017 and 2020 and allowed the monitoring of wild bees and mapping of land use on their farmland. Next to the biodiversity measures from the project F.R.A.N.Z., there could be other biodiversity measures in the landscapes implemented by farms in the frame of their farming practices. Hence, the mix of biodiversity measures varied and these determined the area proportion in this study. As we aimed to analyse the effect of biodiversity measures at landscape level, we also considered these additional biodiversity measures in the simulations of bumblebee populations.

## 2.2. Landscape scenarios

For each of the three landscapes we developed three types of scenarios:

- Business as usual (BAU) scenario of study area, i.e., the original landscapes incl. crops and semi-natural habitats without implementation of biodiversity measures;
- Biodiversity measures implemented in the study area offering food resources but no additional nesting habitats (Biodiv);
- Biodiversity measures implemented in the study area offering both food resources and additional nesting habitats (Biodiv nest).

We used project data from land-use mappings of the years 2017, 2018 and 2020 for the information about composition of crops (Appendix 1, Fig. S2). The crops of 2019 were derived based on information about the crop rotation from farmers in the region. Some of the crops, such as oilseed rape, provided food resources for bumblebees, i.e., pollen and nectar, but none except for orchards offered nesting habitats (Table 1). The BAU scenarios are the study areas without the additional biodiversity measures which were implemented by the farmers of the project. Hence, the BAU scenarios could include some biodiversity

**Table 1**

Food (yellow) and nesting (green) habitats for bumblebees in the three scenario types. In the table “Land use per region” in appendix 2 all habitat types were listed, also the habitats which were neither food nor nesting habitat, e.g., maize or cereals.

Scenario	BAU	Biodiv	Biodiv nest
<b>Crops</b>			
Oilseed rape	Yellow	Green	Green
Faba bean	Yellow	Green	Green
Sunflower	Yellow	Green	Green
Drupe (Prune) *	Green	Green	Green
Pome (Apple) *	Green	Green	Green
Clover	Yellow	Green	Green
<b>Semi-natural habitats</b>			
Hedges *	Green	Green	Green
Field margins *	Green	Green	Green
Ditch margins *	Green	Green	Green
Dirt track *	Green	Green	Green
<b>Biodiversity measures</b>			
Flower strips *	Yellow	Green	Green
Flowering headland *	Yellow	Green	Green
Fallows *	Yellow	Green	Green
Extensive grassland *	Yellow	Green	Green
Extensive cereals	Yellow	Green	Green
Maize-bean mixture	Yellow	Green	Green

measures as food sources. This was the case in the study area Lower Bavaria (0–2.0%; Appendix 1, Table S1) and Rhine Hesse (0.4%; Appendix 1, Table S1). In the BAU scenario In Lower Bavaria there were fallows and flowering areas and in Rhine Hesse a fallow already established (Appendix 2). At least some nesting habitat was present due to semi-natural habitats, such as hedgerows and field margins, in all scenario types.

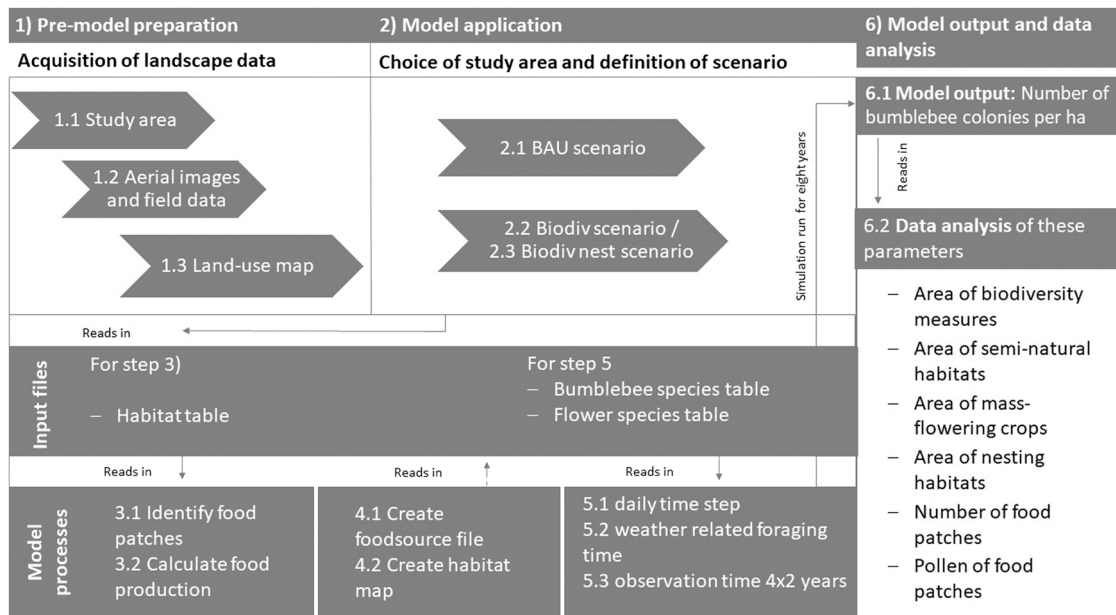
The scenarios with biodiversity measures (Biodiv and Biodiv nest) contained those biodiversity measures that were implemented in the years 2017 until 2020, which comprised annual and perennial as well as production-integrated and non-production-integrated measures (Appendix 2, Table 1 and Fig. S4). Flower strips and flowering headlands can be annual or perennial. Other perennial biodiversity measures comprised extensive grassland, fallows and flowering headlands, whereas, maize-bean mixture and extensive cereals were annual biodiversity measures. The landscape scenarios contained a mix of different biodiversity measures and the area covered by biodiversity measures varied among years and study areas. The mix of biodiversity measures differed between landscapes, because scenarios followed the adaptation to the respective farming practice and the landscape surroundings as undertaken in the establishment of measures by farmers in the real project landscapes. Therefore, not all biodiversity measures were implemented in all landscapes and annual biodiversity measures were only temporally implemented. Further, the specific land use of the fields changed over the years due to crop rotation. Thus, for each landscape, we created four digital maps of the BAU scenario and four maps of the BAU plus biodiversity measures scenario (Biodiv and Biodiv nest) respectively, which represented the years 2017 until 2020. Biodiv and Biodiv nest scenarios were identical in composition and configuration, but in the latter scenarios, information about nest site suitability of measures was added in the model input information about habitat quality.

These scenarios were implemented technically as habitat maps based on digital aerial images and the digital basic landscape model ‘ATKIS’ (BKG, 2018b, 2018a) and self-provided land-cover layers in ArcMap 10.7.1 (ESRI, 2019). The land-cover layers comprised digitalized records of crops, semi-natural habitats and biodiversity measures (Table 1) which were based on land-use mapping in the years 2017, 2018 and 2020. Subsequently, we classified all land-cover types as ‘food habitat’, ‘food and nesting habitat’ or ‘no habitat’ in order to create the habitat maps (Fig. 2).

## 2.3. Modelling approach

We applied the spatially explicit agent-based models BumbleBEEHAVE and the submodel BEESCOUT 2.0 (Becher et al., 2018), which is implemented in the software NetLogo (Wilensky, 1999). BEESCOUT 2.0 calculates the abundance of flowers on food patches in the landscape and, then, BumbleBEEHAVE simulates the development of bumblebee colonies. In contrast to the previous model BEEHAVE that simulates effects of diverse farmland practices, Varroa mites and pesticide use on honeybees (Baden-Böhm et al., 2022b; Horn et al., 2021; Schödl et al., 2022), the model BumbleBEEHAVE has not been applied much so far (Knapp et al., 2019). The models are open source and freely available under <https://beehave-model.net/>. We adjusted both models for our research (Appendix 3). The model is a tool that can support decision-making processes from researchers up to practitioners or advisor of land management, in order to compare the effects of bee-friendly interventions on bumblebee populations over several years. But we did not only deliver information on a temporal scale, but also on spatial scales like on landscape level. We started with our research before the model BEE-STEWART was published which combined BEESCOUT and BumbleBEEHAVE and is more user-orientated (Twiston-Davies et al., 2021).

BumbleBEEHAVE can simulate the behaviour, life-cycle and population development of six bumblebee species in rasterized landscapes on



**Fig. 2.** The acquisition of landscape data started with the choice of study areas. The land-use maps were created based on aerial images and field data (1). For each study area the business as usual scenario and the scenarios with biodiversity measures implemented in study areas were defined (2). The scenarios and the habitat table are the model input of BEESCOUT 2.0 (3). In BEESCOUT the food patches were identified and food (pollen and nectar amount) were calculated (3.1-3.2). After the model run of BEESCOUT 2.0 the foodsource-file tables and habitat maps were created (4.1 and 4.2). These outputs and the tables about the observed bumblebee species and the flower tables were read into the model BumbleBEEHAVE (5). In BumbleBEEHAVE the daily time step, foraging time of 8 h and observation time of eight years ( $4 \times 2$ ) were set (5.1-5.3). Run and output of the model BumbleBEEHAVE and the number of bumblebee colonies and landscapes parameters over multiple years was stored in text files and analysed (6.1-6.2).

daily time steps. In the present study, we focussed on *Bombus terrestris*, the most common bumblebee species in Germany (Westrich, 2018). In BumbleBEEHAVE, the life cycle starts with the emergence of hibernated queens in spring. After emergence, the initial queens search for suitable nesting sites. If they are successful, they start to collect pollen and nectar and lay eggs. The eggs develop to larvae and then to pupae. Emerged adults forage for pollen and nectar for the colony, while the queens stop foraging and specialize on egg laying. New queens are developed, when a sufficient number of workers relative to larvae is present. In autumn, the young queens go into hibernation and will not be active until they emerge in the spring of the following year and the life cycle starts again (Becher et al., 2018).

The model BEESCOUT 2.0 requires habitat maps provided as raster image files as a basis for modelling the spatial and temporal distribution of food resources (Becher et al., 2018). Therefore, we rasterized the habitat maps of our study areas with a spatial resolution of 1 m. On the raster images, all habitat types received a specific NetLogo colour code. In this way, different types of habitat patches could be discerned in the landscapes by BEESCOUT 2.0.

BEESCOUT 2.0 allows to simulate the food provisioning of multiple flower species on the same habitat patch. Thus, the plant-species composition of each habitat type (biodiversity measures, semi-natural habitats and mass flowering crops) was defined in an auxiliary file ('habitat table') that contained the abundance of shoots per square meter and the number of flowers per shoot of the different plant species present. The habitat-specific plant-species compositions allowed to differentiate between different seed mixtures of biodiversity measures. Each landscape had a specific habitat table, because the presence and abundance of flowers on biodiversity measures varied due to different seed mixtures, because regional autochthonous seed mixtures were used in the project. For the biodiversity measures, we supposed that the plant species' cover percentage was equal to the percentage of their seeds in the mixture, because we did not have a complete data set on the number of flowers per square meter. Finally, the output of BEESCOUT 2.0 is a text file with a list of food patches. For each food patch, it lists location,

size and the abundance of flowers per plant species.

Before modelling of population development, BumbleBEEHAVE calculates the quality and quantity of nectar and pollen on the food patches for each day of the year. This is done with the help of a table of floral traits of the plant species ('flower species table'). It contains the following traits: pollen amount (g pollen/ flower), nectar amount (ml nectar/ flower), proportion of protein in pollen (%), sugar concentration in nectar (mol), flowering start (day of the year), flowering end (day of the year), depth of corolla (mm), and the constant average time to fly from one flower to the next (s). The flower species table was based on the table "5\_FloRes\_no\_corolla" from the FloRes Database (Baden-Böhm et al., 2022a). For a better representation of regional phenology, we differentiated the flowering time of oilseed rape (*Brassica napus*) as a crop in Rhine-Hesse and Havelland by calculating the regional average of flowering start over the years 2016–2019 (2020 was not yet available) as recorded by the German Meteorological Service (Deutscher Wetterdienst) using the closest weather station to the study areas (DWD Climate Data Center (DWD), 2021). The flowering end was after 44 days, which is the average of flowering days of *Brassica napus* according to (Horn, 2017).

Another input for the model BumbleBEEHAVE is a table of the bumblebee species, where the nesting sites of bumblebees were defined. In the present study, we were interested in effects of biodiversity measures as only food sources and also as additional nesting sites. Therefore, we created two bumblebee species tables, one where biodiversity measures were not established as nesting site and one in which perennial biodiversity measures as well as other biodiversity measures where no soil disturbance occurs over the winter were additional nesting sites (Table 1).

We simulated population development of *Bombus terrestris* over a course of eight years considering crop rotation and changes in biodiversity measures over time. For this purpose, we used four habitat maps per landscape scenario that represented consecutive years which we repeated once to cover the years 5–8. We ran BumbleBEEHAVE with a starting population of 500 hibernated queens which is large enough to

avoid extinction of the population after the first year (Becher et al., 2018).

We did not implement effects of daily weather conditions on foraging time of bumblebees, but used a constant foraging time of eight hours per day. However, the phenology of flower patches and the timing of the emergence of queens from hibernation implicitly reflect climate and weather conditions (Becher et al., 2018).

We repeated each scenario 30 times because of the stochasticity of BumbleBEEHAVE. Regarding model output, we focussed on the maximum number of colonies as representative indicator of population development and on the pollen and nectar amount available from the food sources per landscape and year.

#### 2.4. Data analysis

We chose the maximum number of colonies per year in order to explore the effect of enhancement of the landscape through biodiversity measures. The number of colonies represents the successful foundation of colonies by young queens. Firstly, we investigated the number of colonies at the end of the observation time, i.e., in year eight. Secondly, we analysed the development of the number of bumblebee colonies throughout the years in a time series analysis.

Data analysis was conducted in R version 4.1.0 (R Core Team, 2022) using the package nlme 3.1–155 for fitting Generalized Least Squares models (GLS) (Pinheiro et al., 2021). We used the logarithm of the number of colonies as response variable to achieve (near-)normally distributed model residuals. We used GLS models in order to account for heterogeneity of variance among the scenarios by including either a power variance structure ('varPower' in nlme) or separate variance estimates per region or landscape scenario ('varIdent'), whichever fitted better. As estimation method, we used maximum likelihood, because this is better for testing fixed effects. All metric predictor variables were z-transformed, i.e., scaled to zero mean and standard deviation of one.

We set up three separate models to investigate our research questions. Firstly, we tested the overall effectivity of biodiversity measures due to provisioning of food (question 1a), nesting habitat (question 1b) and differences among landscapes (question 2) with a GLS model that only contained 'scenario' as fixed effect. Here, 'scenario' was a factor that combined the three landscape scenarios and the three regions. Post-hoc tests for differences among scenarios were conducted using the package 'emmeans' 1.7.2 (functions 'pairs' and 'cld') with p-value adjustment according to the Tukey method and a significance level of  $p < 0.05$ .

Secondly, we evaluated the relative importance of different habitat types (question 3a) for population development of bumblebees with a model that contained the total areas of mass-flowering crops, semi-natural habitats and biodiversity measures as predictors ('habitat model'). Additionally, we included an interaction between area of biodiversity measures and 'region' to test for differences in the effectiveness between study areas. However, we did not include the main effect of 'region' because there was a high collinearity with other predictors. For calculating the area of mass-flowering crops, we summed up the area of all occurring flowering crops, which included oilseed rape (*Brassica napus*), clover (*Trifolium repens* and *T. pratense*), faba bean (*Vicia faba*), peas (*Pisum sativum*), sunflower (*Helianthus annuus*), and drupe and pome orchards with assumedly plums (*Prunus domestica*) and apples (*Malus domestica*) as fruits. Semi-natural habitat types comprised hedges, field margins, ditches and unpaved dirt tracks. With respect to biodiversity measures, we calculated the total area per landscape, regardless of whether the measure was annual or perennial. The areas of mass-flowering crops and biodiversity measures varied over the years due to crop rotation (except for orchards) and time-limited implementation, respectively. In contrast, the area of semi-natural habitats was constant over the eight years in each scenario.

Thirdly, we modelled the response of bumblebee colonies to the amount and distribution of food and nesting resources in the landscapes

(question 3b) using the sum of pollen, number of food patches and area of nesting habitat as predictors ('resource model'). Only pollen was used as measure of food supply because amounts of pollen and nectar were highly correlated. We also included the interaction between area of nesting habitat and 'region' in this model.

In the time series models, we used the same predictors as in the habitat and resource models and, additionally, included 'year' to account for trends over time'. The time-series model of food and nesting resources additionally contained the main effect of 'region'. The time-series model of habitats included interactions between 'year' and semi-natural habitats and mass-flowering crops, respectively, to improve model fit. Further, we only used scenarios where biodiversity measures did not provide nesting habitat for the time-series model of habitats. Generally, we only considered the last 4 years (year 5 – 8) of the time series to avoid effects of the starting values on the number of colonies.

### 3. Results

In the last year of the simulations, year 8, the maximum number of colonies per hectare of the modelled bumblebee species *Bombus terrestris* ranged between zero and 16. The populations of bumblebees responded differently to the biodiversity measures in the three landscapes. In Havelland (8.8% semi-natural habitats, max. 44% mass-flowering crops and max. 9.7% biodiversity measures; Fig. 1), the implementation of biodiversity measures providing food resources increased the number of colonies significantly compared to the BAU scenario, but additional nesting habitat had no effect (Fig. 3). In Lower Bavaria (5.4%, max. 2.6% and max. 5.6%; Fig. 1) and Rhine-Hesse (3.0%, max. 23.4%, 2.6%; Fig. 1), biodiversity measures had a positive effect through offering nesting habitat, in addition to the effect of food resources (Fig. 3).

The effectiveness of the biodiversity measures, as assessed with GLS models of log-transformed number of colonies, varied among the study areas with their different landscape composition and configuration. Compared to the Lower Bavarian landscape, the effect of area of biodiversity measures was significantly stronger in the Rhine-Hesse landscape, whereas the effect was significantly smaller in Havelland (Fig. 4; Appendix 1, Tables S3, S4) although the interaction of biodiversity

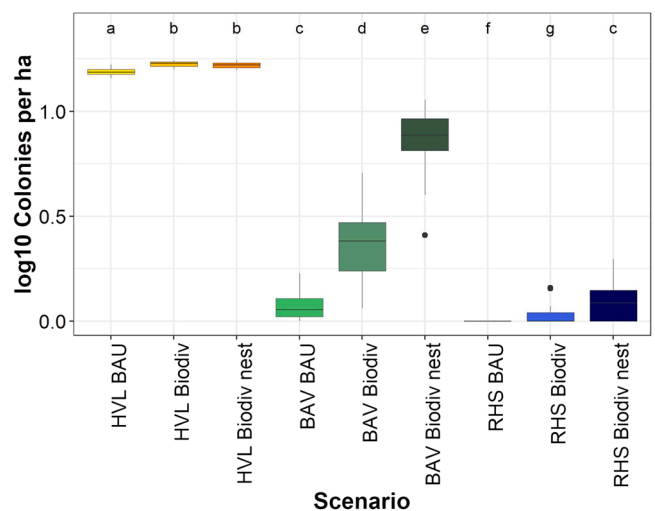


Fig. 3. Bumblebee colonies per hectare (log<sub>10</sub>-transformed, i.e., log<sub>10</sub>(colonies + 1)) in different landscape scenarios in year eight of simulation runs. Different letters indicate significant differences between the landscape scenarios. Boxes show medians and inter quartile ranges. Abbreviations of regions: HVL = Havelland; BAV = Lower Bavaria; RHS = Rhine-Hesse. Abbreviations of landscape scenarios: BAU = business as usual; Biodiv = BAU plus biodiversity measures offering food resources; Biodiv nest = BAU plus biodiversity measures offering food resources and nesting habitat.

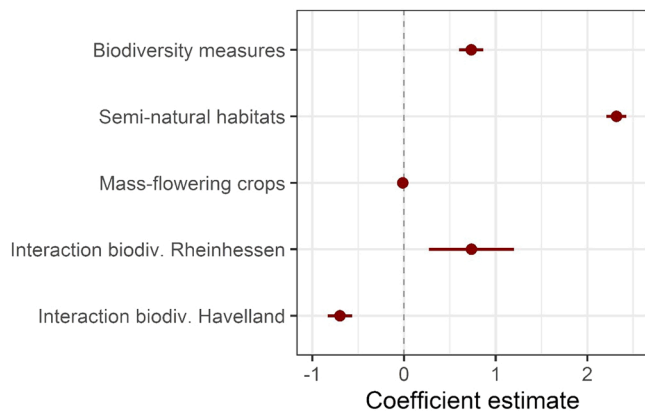


Fig. 4. Effect estimates of the areas of different habitat types on log-transformed number of bumblebee colonies in agricultural landscapes from a time-series model of years 5–8 of simulations runs.

measures and region was not significant in the model of only year 8. The area of semi-natural habitats had a stronger positive effect on number of bumblebee colonies than the area of biodiversity measures, while the area of mass-flowering crops did not have a significant effect (Fig. 4; Appendix 1, Tables S3, S4). However, in the time series model, the effect estimates of mass-flowering crops showed a significant increase over time (Appendix 1, Table S4) suggesting that a positive effect of mass-flowering crops may occur in some years. This was the case in the study area Havelland, where oilseed rape covered ca. 45% in year 7 and the number of colonies increased. The maximum numbers of colonies along the gradients of biodiversity measures, semi-natural habitats and mass-flowering crops over the years 5–8 of the simulations is shown in Fig. 5.

Analyses of effects of the quantity of food and nesting resources over all scenarios showed that the number of bumblebee colonies increased with the amount of pollen in the landscape. The number of food patches had an overall negative effect on colonies (Fig. 6, Appendix 1, Tables S5, S6), although the negative effect seemed to occur only in the study area Rhine-Hesse, while there appeared to be a positive trend of colonies with increasing number of food patches in Lower Bavaria and Havelland (Fig. 7B). However, differences in the effect of number of food patches among study areas could not be tested with the GLS model because of collinearity of predictors when including the respective interaction with ‘region’. The area of nesting habitats had a stronger positive effect than pollen on the number of colonies in the Bavarian landscape, but no effect in the other two study areas (Fig. 6; Appendix 1, Tables S5, S6).

#### 4. Discussion

The implementation of biodiversity measures aims at increasing the diversity and abundance of species in agricultural landscapes. In particular, biodiversity measures including the establishment of flowering plant species aim at pollinating insects, such as bumblebees. In our study we focussed on *Bombus terrestris*. Regarding our research questions on the effectiveness of biodiversity measures in increasing the number of colonies per hectare, the present simulations indicate a general positive effect of food resources supplied by the measures. This is in line with the field studies of the project which indicated a positive effect of biodiversity measures on abundance of bees in general and, particularly, bumblebee species, already two years after implementation (Kulow et al. unpublished). Further, the simulations suggest that also additional nesting habitat provided by biodiversity measures can increase the density of bumblebee colonies although it was not effective in the study area Havelland that already showed high population densities in the BAU scenario.

Several studies provided evidence for positive effects of biodiversity

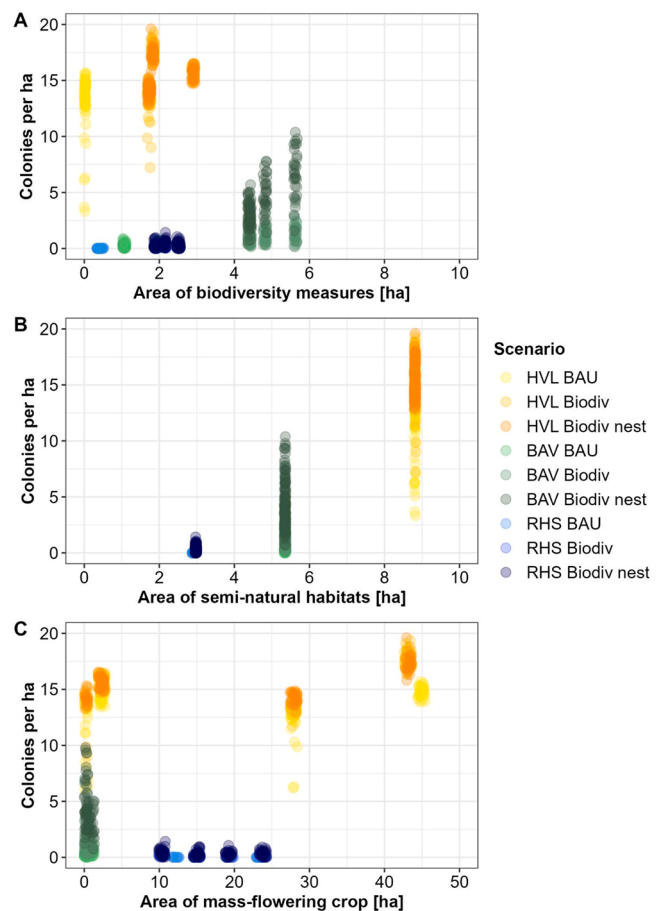


Fig. 5. Number of *Bombus terrestris* colonies per A) area of biodiversity measures (ha), B) area of semi-natural habitats (ha) and C) area of mass-flowering crop (ha) from year five to eight over all scenarios and their 30 repetitions.

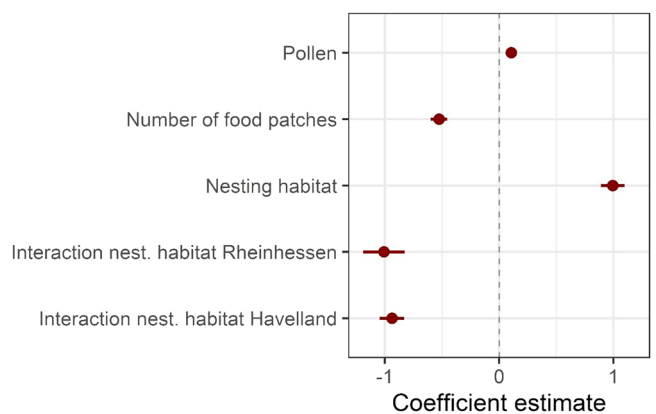


Fig. 6. Effect estimates of food and nesting resources on log-transformed number of bumblebee colonies in agricultural landscapes from a time-series model of years 5–8 of simulation runs.

measures on pollinator populations at (local and) landscape level. Biodiversity measures, such as flower strips, can improve the flower availability and, consequently, the pollen and nectar supply in intensive agricultural landscapes, which can lead to higher abundances of bumblebees, including generalist species, such as *B. terrestris*, at local and landscape scale (Blaauw and Isaacs, 2014; Buhk et al., 2018; Ebeling et al., 2008; Geppert et al., 2020; Jönsson et al., 2015; Piko et al., 2021; Potts et al., 2003; Scheper et al., 2013). Further, biodiversity measures

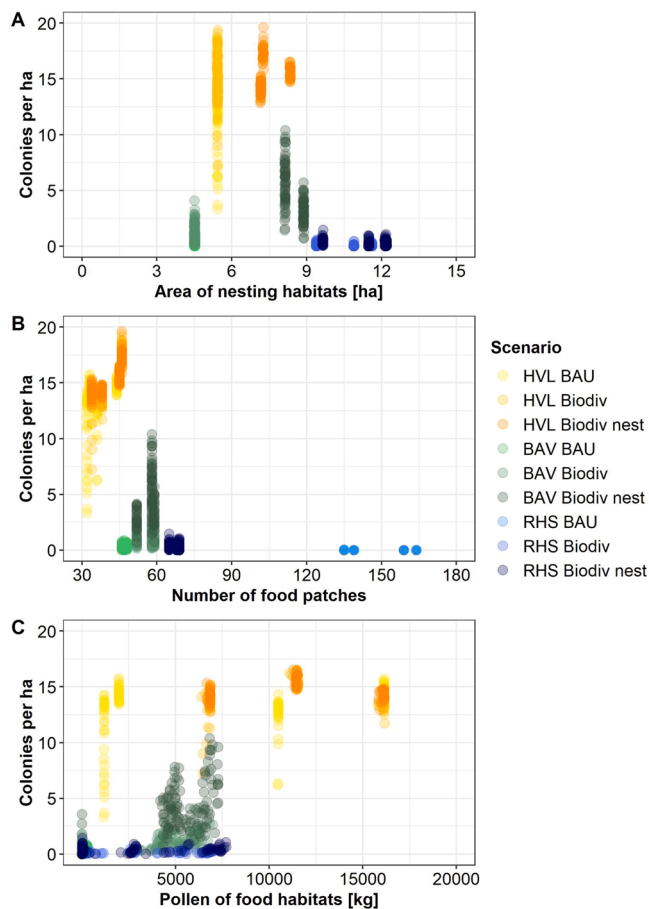


Fig. 7. Number of *Bombus terrestris* colonies per A) area of nesting habitats (ha), B) number of food patches and C) pollen of food habitats (kg) from year 5–8 over all landscape scenario types and their 30 repetitions.

can improve continuity of food supply throughout the season, which has been linked to enhanced colony establishment and population growth of long-lived bumblebee species (Hemberger et al., 2020; Kevan and Baker, 1983; Persson and Smith, 2013; Timberlake et al., 2019).

While effects of increased food supply on pollinator populations are comparatively well understood, less is known about effects of the amount of nesting habitat. According to Westrich (1996), there is a lack of favourable nesting sites in intensively managed landscapes because there is a frequent disturbance regime in agricultural fields (Greenleaf et al., 2007; Holzschuh et al., 2007; Kremen et al., 2007) and, consequently, bumblebees are forced to nest and hibernate in semi-natural habitats, such as hedges and field margins (Cole et al., 2020; Hopfenmüller et al., 2014; Kohler et al., 2008; Marshall and Moonen, 2002; Scheper et al., 2015; Svensson et al., 2000). Lye et al. (2009) showed that field margins are even more attractive nesting habitats than hedgerows for spring queens during the period of colony foundation. The question is whether the amount of nesting habitat is limiting population growths in intensive agricultural landscapes. Our simulation results suggest that, indeed, nesting habitat may be a limiting resource if only 5% or less of the landscape are suitable for nesting and, as a consequence, that biodiversity measures offering nesting possibilities may have a stronger positive effect on pollinator populations than those offering only food.

Thus, biodiversity measures such as flower-rich and extensively managed perennial habitats can be essential components of agricultural landscapes and provide food resources as well as nesting, mating and hibernation sites for bumblebees (Carvell et al., 2007; Goulson et al., 2008; Pywell et al., 2005). However, the effectiveness depends on the

landscape surrounding and the landscape composition and configuration (Carvell et al., 2011; Hass et al., 2018; Holzschuh et al., 2008; Scheper et al., 2013; Scheper et al., 2015).

Our results corroborate the hypothesis that effectiveness of biodiversity measures varies among agricultural landscapes with different landscape composition and configuration. The study area with the highest proportion of semi-natural habitat (Havelland, 8.8%) showed the highest number of bumblebee colonies and, at the same time, the least effect of biodiversity measures. In contrast, the study area with the lowest area of semi-natural habitats (Rhine Hesse, 3.0%) had the lowest density of bumblebee colonies throughout, but showed the strongest effect of biodiversity measures, while the landscape with intermediate proportion of semi-natural habitats (Lower Bavaria, 5.4%) showed intermediate effect size in terms of effect estimates from GLS on log scale. In absolute numbers, we found the strongest increase in colony density in the Lower Bavarian landscape (Appendix 1, Table S3 and S4), which is in line with other studies that found the impact of biodiversity measures to be strongest in structurally simple landscapes with intermediate levels of semi-natural habitats (Tschardt et al., 2005). Altogether, it appears that biodiversity measures may be ineffective in landscapes with comparatively high complexity and proportion of semi-natural habitats (Scheper et al., 2013; Tschardt et al., 2012).

The big potential of the simulation model is to identify and predict how biodiversity measures may affect bumblebees in context of the entire landscape. From the three parameters area of biodiversity measures, semi-natural habitats and mass-flowering crops, the other three parameters area of nesting habitat, number of food patches and pollen of the food patches were derived. Based on those parameters it was possible to evaluate the quality and quantity of habitats for the bumblebees in our study. However, conventionally managed grassland areas and forest, were not considered as food or nesting habitat for bumblebees, since no information about the plant composition was available. So, potential further food and nesting habitats for bumblebees may have been underestimated.

With respect to the importance of different habitats, we found a stronger effect of semi-natural habitats (here: mainly field margins and hedges) than of the investigated biodiversity measures (Appendix 1, Table S3 and S4). A recent study showed that hedges with high-quality herb layers where flowering starts early in the season and extends into the summer month, such as in our study, can increase the abundance of bees (Königslöw et al., 2021). Such hedges are not intrinsically less attractive for pollinators than flower strips (Piffner et al., 2018). However, another study found that the areal proportion of semi-natural habitats had minor importance for bumblebee abundance (Herrmann et al., 2007).

Also, mass-flowering crops increase the food supply for pollinators in agricultural landscapes. Especially for short-tongued bumblebees, such as *B. terrestris*, mass-flowering crops are attractive (Walther-Hellwig and Frankl, 2000). However, in our study, mass-flowering crops, mainly oilseed rape (Fig. 1), did not show a consistently positive effect on the number of bumblebee colonies. Previous studies yielded variable results. Positive effects, particularly of oilseed rape, on the density and colony growth of bumblebees were found by Westphal et al. (2006) and Westphal et al. (2009), whereas low proportions of oilseed rape lead to higher mortality rates of bumblebee queens due to the limited duration of food provisioning of oilseed rape in spring according to (Riedinger, 2014a). Regarding orchards, a recent study found a negative effect of such large, homogeneous areas on colony growth of bumble bees (Prosmans et al., 2019), because orchards offer plentiful floral resources but for only a short time span in spring (Königslöw et al., 2021; Olsson et al., 2015).

Unlike semi-natural habitats, mass-flowering crops, such as oilseed rape and orchards, only offer food resources during a short time period (Morandin and Winston, 2006). Critical time periods of nectar scarcity for bumblebees have been identified in March, June and August/September (Timberlake et al., 2019). Therefore, the effectiveness of

mass-flowering crops with limited flowering periods may depend on the amount of semi-natural habitats that provide temporally continuous floral resources (Westphal et al., 2009) and allow for temporal spill-over of bumblebees from early to late flowering crops, e.g., from oilseed rape to sunflowers (Riedinger et al., 2014b). Besides semi-natural habitats, biodiversity measures, such as flower strips, can improve the continuity of pollen and nectar supply in intensive agricultural landscapes. Further, as flower strips offer most food resources in summer, they may complement the food supply of hedges and mass-flowering crops which show peak flowering in spring (Königslöw et al., 2021).

Altogether, both the effectiveness and relative importance of biodiversity measures may vary depending on the surrounding landscape with respect to floral resources and possibility for nesting and hibernating (Krimmer et al., 2019; Scheper et al., 2015; Schubert et al., 2022). Krimmer et al. (2019) suggested that smaller flower fields should be implemented in landscapes with high proportion of semi-natural habitats and larger ones in landscapes with low proportion of semi-natural habitats. Further, authors suggested that sufficient amounts of semi-natural habitats are needed to maintain bumblebee colonies in agricultural landscapes with high proportions of mass-flowering crops (Proesmans et al., 2019). Such an interaction between mass-flowering crops and semi-natural habitats is largely missing in our study region of Rhine Hesse (low proportion of semi-natural habitat), which may explain the low density of bumblebees. According to Marja et al. (2018) changes in crop rotation, e.g., establishing mass-flowering crops, can also be an efficient solution to increase biodiversity of agricultural landscapes, because crop rotations combined with biodiversity measures determine bumblebee abundance. Especially for bumblebees, biodiversity measures and early crop cultivation as oilseed rape can provide essential resources for colony establishment and growth in spring (Scheper et al., 2015).

In conclusion, our study underlines that not only biodiversity measures are likely to affect the bumblebee population, but that the overall landscape composition, particularly proportion of semi-natural habitats, is also important (Kennedy et al., 2013; Steckel et al., 2014).

#### 4.1. Limitation

Simulation modelling can be a tool for assessing how agricultural landscapes could be improved through biodiversity measures in the most efficient way in order to promote bumblebee populations. Information about the quality of food patches in the landscape and their amount of nectar and pollen was based on literature data, which were collected in the FloRes Database (Baden-Böhm et al., 2022a). In reality, the phenology of plants is subject to annual variation depending on the weather patterns, but in the models, it is held constant in every year. Furthermore, changes in plant species composition, richness of flowering species over the years (Frank et al., 2012; Tschardt et al., 2011) or life span could not be considered in our study. Additionally, flower density depends on habitat type (Frank et al., 2012).

As in the previous study, where the effect of flower strips on honeybees was the research question (Baden-Böhm et al., 2022b), the crops were represented with a flower density of 100%. But the plant compositions of the flower-rich habitats, such as biodiversity measures or semi-natural habitats, comprised more plant species in reality than in the model, so the flower density is lower than 100% (Appendix 2). For the biodiversity measures, we additionally assumed that cover density of plant species is equal to the percentage of seeds of the respective plant species in the seed mixture.

Grassland and forest were not defined as food and/or nesting habitats. We did not have enough information about management type and intensity, so that their importance for bumblebees was likely underrated in the models.

## 5. Conclusions

We conclude that agent-based modelling with the model BumbleBEEHAVE can support the efficiency assessment of bee-friendly biodiversity measures at landscape scale. In our study, we found out that biodiversity measures providing food and nesting habitats have positive effects on the development of bumblebee colonies at landscape level. The landscape composition can modify the effect of biodiversity measures. In particular, the area of semi-natural habitats affects positively the colony density of *B. terrestris*. This is in contrast to area of mass-flowering crops that has little to no effect on the number of colonies. Mass-flowering crops are annual crops and, except for orchards, no nesting habitat. Their quality and quantity varied over the years. However, our main focus pertains particularly on the implemented biodiversity measures, which were on the one hand additional food habitats or on the other hand additional food and nesting habitats, whereby the latter include only the perennial biodiversity measures. Finally, we stress the importance of nesting habitats for the foundation of bumblebee colonies, although there are regional differences due to farming practices and surrounding landscape. The food habitats, assessed by the quantity (number of food habitats) and the quality (sum of pollen), demonstrate that the number of colonies is lower when habitat is fragmented into many small patches. The quality enhanced positively the reproductivity of bumblebees with respect to successfully founding bumblebee colonies.

### 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.

### Data availability

The authors do not have permission to share data.

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### Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.agee.2023.108649](https://doi.org/10.1016/j.agee.2023.108649).

### References

- Baden-Böhm, F., App, M., Thiele, J., 2022a. The FloRes database: a floral resources trait database for pollinator habitat-assessment generated by a multistep workflow. *Biodivers. Data J.* 10, e83523 <https://doi.org/10.3897/BDJ.10.e83523>.
- Baden-Böhm, F., Thiele, J., Dauber, J., 2022b. Response of honeybee colony size to flower strips in agricultural landscapes depends on areal proportion, spatial distribution and plant composition. *Basic Appl. Ecol.* 60, 123–138. <https://doi.org/10.1016/j.baae.2022.02.005>.
- Batáry, P., Matthiesen, T., Tschardt, T., 2010. Landscape-moderated importance of hedges in conserving farmland bird diversity of organic vs. conventional croplands



- and grasslands. *Biological Conservation* 143 (9), 2020–2027. [10.1016/j.biocon.2010.05.005](https://doi.org/10.1016/j.biocon.2010.05.005).
- Becher, M.A., Twiston-Davies, G., Penny, T.D., Goulson, D., Rotheray, E.L., Osborne, J.L., 2018. Bumble-BEEHAVE: a systems model for exploring multifactorial causes of bumblebee decline at individual, colony, population and community level. *J. Appl. Ecol.* 55 (6), 2790–2801. <https://doi.org/10.1111/1365-2664.13165>.
- Beyer, N., Kirsch, F., Gabriel, D., Westphal, C., 2021. Identity of mass-flowering crops moderates functional trait composition of pollinator communities. *Landscape Ecology* 36 (9), 2657–2671. [10.1007/s10980-021-01261-3](https://doi.org/10.1007/s10980-021-01261-3).
- BKG, 2018b. DOP40 / Digitale Orthophoto - Bodenaufklärung 40 cm. Bundesamt für Kartographie und Geodäsie (BKG).
- BKG, 2018a. Amtliches Topographisch-Kartographisches Informationssystem. Bundesamt für Kartographie und Geodäsie (BKG).
- Blaauw, B.R., Isaacs, R., 2014. Larger patches of diverse floral resources increase insect pollinator density, diversity, and their pollination of native wildflowers. *Basic Appl. Ecol.* 15 (8), 701–711. <https://doi.org/10.1016/j.baee.2014.10.001>.
- Buhk, C., Oppermann, R., Schanowski, A., Bleil, R., Lüdemann, J., Maus, C., 2018. Flower strip networks offer promising long term effects on pollinator species richness in intensively cultivated agricultural areas. *BMC ecology* 18 (1), 55. [10.1186/s12898-018-0210-z](https://doi.org/10.1186/s12898-018-0210-z).
- Carvell, C., Meek, W.R., Pywell, R.F., Goulson, D., Nowakowski, M., 2007. Comparing the efficacy of agri-environment schemes to enhance bumble bee abundance and diversity on arable field margins. *J. Appl. Ecol.* 44 (1), 29–40. <https://doi.org/10.1111/j.1365-2664.2006.01249.x>.
- Carvell, C., Osborne, L. J., Bourke, G. A. F., Freeman, N. S., Pywell, F. R., Heard, S. M., 2011. Bumble bee species' responses to a targeted conservation measure depend on landscape context and habitat quality. *Ecol. Appl.* 21 (5), 1760–1771.
- Carvell, C., Bourke, A.F.G., Osborne, J.L., Heard, M.S., 2015. Effects of an agri-environment scheme on bumblebee reproduction at local and landscape scales. *Basic Appl. Ecol.* 16 (6), 519–530. <https://doi.org/10.1016/j.baee.2015.05.006>.
- Cole, L.J., Kleijn, D., Dicks, L.V., Stout, J.C., Potts, S.G., Albrecht, M., Balzan, M.V., Bartomeus, I., Bebeli, P.J., Bevk, D., Biesmeijer, J.C., Chlebo, R., Dautartė, A., Emmanouil, N., Hartfield, C., Holland, J.M., Holzschuh, A., Knoben, N.T.J., Kovács-Hostyánszki, A., Mandelík, Y., Panou, H., Paxton, R.J., Petanidou, T., Pinheiro de Carvalho, M.A.A., Rundlöf, M., Sarthou, J.-P., Stavrínides, M.C., Suso, M.J., Szentgyörgyi, H., Vaissière, B.E., Varnava, A., Vilà, M., Zemeckis, R., Scheper, J., 2020. A critical analysis of the potential for EU common agricultural policy measures to support wild pollinators on farmland. *J. Appl. Ecol.* 57 (4), 681–694. <https://doi.org/10.1111/1365-2664.13572>.
- DWD Climate Data Center (DWD), 2021. Eintrittsdaten verschiedener Entwicklungsstadien landwirtschaftlicher Kulturpflanzen von der Bestellung bis zur Ernte (Jahresmelder, historisch), Version v007, [https://opendata.dwd.de/climate\\_environment/CDC/observations/version/phenology/annual\\_reporters/crops/historical/](https://opendata.dwd.de/climate_environment/CDC/observations/version/phenology/annual_reporters/crops/historical/).
- Ebeling, A., Klein, A.-M., Schumacher, J., Weisser, W.W., Tscharnkte, T., 2008. How does plant richness affect pollinator richness and temporal stability of flower visits? *Oikos* 117 (12), 1808–1815. <https://doi.org/10.1111/j.1600-0706.2008.16819.x>.
- ESRI, 2019. ArcGIS Desktop: ArcMap 10.7.1. Environmental Systems Research Institute (ESRI), Redlands, CA.
- Frank, T., Aeschbacher, S., Zaller, J.G., 2012. Habitat age affects beetle diversity in wildflower areas. *Agric., Ecosyst. Environ.* 152, 21–26. <https://doi.org/10.1016/j.agee.2012.01.027>.
- Geppert, C., Hass, A., Földesi, R., Donkó, B., Akter, A., Tscharnkte, T., Batáry, P., 2020. Agri-environment schemes enhance pollinator richness and abundance but bumblebee reproduction depends on field size. *J. Appl. Ecol.* 57 (9), 1818–1828. <https://doi.org/10.1111/1365-2664.13682>.
- Goulson, D., Lye, G.C., Darvill, B., 2008. Decline and conservation of bumble bees. *Annu. Rev. Entomol.* 53, 191–208. <https://doi.org/10.1146/annurev.ento.53.103106.093454>.
- Greenleaf, S.S., Williams, N.M., Winfree, R., Kremen, C., 2007. Bee foraging ranges and their relationship to body size. *Oecologia* 153 (3), 589–596. <https://doi.org/10.1007/s00442-007-0752-9>.
- Hass, A.L., Kormann, U.G., Tscharnkte, T., Clough, Y., Baillo, A.B., Sirami, C., Fahrigh, L., Martin, J.-L., Baudry, J., Bertrand, C., Bosch, J., Brotons, L., Burel, F., Georges, R., Giralt, D., Marcos-García, M.A., Ricarte, A., Siriwardena, G., Batáry, P., 2018. Landscape configurational heterogeneity by small-scale agriculture, not crop diversity, maintains pollinators and plant reproduction in western Europe. *Proceedings. Biological sciences* 285 (1872). [10.1098/rspb.2017.2242](https://doi.org/10.1098/rspb.2017.2242).
- Hemberger, J., Frappa, A., Witynski, G., Gratton, C., 2020. Saved by the pulse? Separating the effects of total and temporal food abundance on the growth and reproduction of bumble bee microcolonies. *Basic Appl. Ecol.* 45, 1–11. <https://doi.org/10.1016/j.baee.2020.04.004>.
- Herrmann, F., Westphal, C., Moritz, R.F.A., Steffan-Dewenter, I., 2007. Genetic diversity and mass resources promote colony size and forager densities of a social bee (*Bombus pascuorum*) in agricultural landscapes. *Mol. Ecol.* 16 (6), 1167–1178. <https://doi.org/10.1111/j.1365-294X.2007.03226.x>.
- Holzschuh, A., Steffan-Dewenter, I., Kleijn, D., Tscharnkte, T., 2007. Diversity of flower-visiting bees in cereal fields: effects of farming system, landscape composition and regional context. *J. Appl. Ecol.* 44 (1), 41–49. <https://doi.org/10.1111/j.1365-2664.2006.01259.x>.
- Holzschuh, A., Steffan-Dewenter, I., Tscharnkte, T., 2008. Agricultural landscapes with organic crops support higher pollinator diversity. *Oikos* 117 (3), 354–361. <https://doi.org/10.1111/j.2007.0030-1299.16303.x>.
- Hopfenmüller, S., Steffan-Dewenter, I., Holzschuh, A., 2014. Trait-specific responses of wild bee communities to landscape composition, configuration and local factors. *PLoS One* 9 (8), e104439. <https://doi.org/10.1371/journal.pone.0104439>.
- Horn, J., 2017. A modelling framework for exploration of a multi-dimensional factor causing decline in honeybee health – towards a better understanding how forage availability in agricultural landscapes affects honeybee colony persistence. PhD Thesis, Potsdam.
- Horn, J., Becher, M.A., Johst, K., Kennedy, P.J., Osborne, J.L., Radchuk, V., Grimm, V., 2021. Honey bee colony performance affected by crop diversity and farmland structure: a modeling framework. *Ecol. Appl.* 31 (1), e02216. <https://doi.org/10.1002/eap.2216>.
- Jönsson, A.M., Ekroos, J., Dänhardt, J., Andersson, G.K.S., Olsson, O., Smith, H.G., 2015. Sown flower strips in southern Sweden increase abundances of wild bees and hoverflies in the wider landscape. *Biol. Conserv.* 184, 51–58. <https://doi.org/10.1016/j.biocon.2014.12.027>.
- Kennedy, C.M., Lonsdorf, E., Neel, M.C., Williams, N.M., Ricketts, T.H., Winfree, R., Bommarco, R., Brittain, C., Burley, A.L., Cariveau, D., Carvalheiro, L.G., Chacoff, N. P., Cunningham, S.A., Danforth, B.N., Dudenhöffer, J.-H., Elle, E., Gaines, H.R., Garibaldi, L.A., Gratton, C., Holzschuh, A., Isaacs, R., Javorek, S.K., Jha, S., Klein, A. M., Krewenka, K., Mandelík, Y., Mayfield, M.M., Morandin, L., Neame, L.A., Otieno, M., Park, M., Potts, S.G., Rundlöf, M., Saez, A., Steffan-Dewenter, I., Taki, H., Viana, B.F., Westphal, C., Wilson, J.K., Greenleaf, S.S., Kremen, C., 2013. A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. *Ecology Letters* 16 (5), 584–599. [10.1111/ele.12082](https://doi.org/10.1111/ele.12082).
- Kevan, P.G., Baker, H.G., 1983. Insects as flower visitors and pollinators. *Annu. Rev. Entomol.* 28 (1), 407–453.
- Knapp, J.L., Becher, M.A., Rankin, C.C., Twiston-Davies, G., Osborne, J.L., 2019. Bombus terrestris in a mass-flowering pollinator-dependent crop: a mutualistic relationship? *Ecol. Evol.* 9 (1), 609–618. <https://doi.org/10.1002/ece3.4784>.
- Kohler, F., Verhulst, J., van Klink, R., Kleijn, D., 2008. At what spatial scale do high-quality habitats enhance the diversity of forbs and pollinators in intensively farmed landscapes? *J. Appl. Ecol.* 45 (3), 753–762. <https://doi.org/10.1111/j.1365-2664.2007.01394.x>.
- Königslöw, V. von, Fornoff, F., Klein, A.-M., 2021. Pollinator enhancement in agriculture: comparing sown flower strips, hedges and sown hedge herb layers in apple orchards. *Biodiversity and Conservation*. [10.1007/s10531-021-02338-w](https://doi.org/10.1007/s10531-021-02338-w).
- Kremen, C., Williams, N.M., Aizen, M.A., Gemmill-Herren, B., LeBuhn, G., Minckley, R., Packer, L., Potts, S.G., Roulston, T. a., Steffan-Dewenter, I., Vázquez, D.P., Winfree, R., Adams, L., Crone, E.E., Greenleaf, S.S., Keitt, T.H., Klein, A.-M., Regetz, J., Ricketts, T.H., 2007. Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. *Ecol. Lett.* 10 (4), 299–314. <https://doi.org/10.1111/j.1461-0248.2007.01018.x>.
- Krimmer, E., Martin, E.A., Krauss, J., Holzschuh, A., Steffan-Dewenter, I., 2019. Size, age and surrounding semi-natural habitats modulate the effectiveness of flower-rich agri-environment schemes to promote pollinator visitation in crop fields. *Agric., Ecosyst. Environ.* 284, 106590. <https://doi.org/10.1016/j.agee.2019.106590>.
- Lye, G., Park, K., Osborne, J., Holland, J., Goulson, D., 2009. Assessing the value of Rural Stewardship schemes for providing foraging resources and nesting habitat for bumblebee queens (Hymenoptera: Apidae). *Biol. Conserv.* 142 (10), 2023–2032. <https://doi.org/10.1016/j.biocon.2009.03.032>.
- Marja, R., Viik, E., Mänd, M., Phillips, J., Klein, A.-M., Batáry, P., 2018. Crop rotation and agri-environment schemes determine bumblebee communities via flower resources. *J. Appl. Ecol.* 55 (4), 1714–1724. <https://doi.org/10.1111/1365-2664.13119>.
- Marshall, E.J.P., Mooney, A.C., 2002. Field margins in northern Europe: their functions and interactions with agriculture. *Agric., Ecosyst. Environ.* 89, 5–21.
- Morandin, L.A., Winston, M.L., 2006. Pollinators provide economic incentive to preserve natural land in agroecosystems. *Agric., Ecosyst. Environ.* 116 (3–4), 289–292. <https://doi.org/10.1016/j.agee.2006.02.012>.
- Olsson, O., Bolin, A., Smith, H.G., Lonsdorf, E.V., 2015. Modeling pollinating bee visitation rates in heterogeneous landscapes from foraging theory. *Ecol. Model.* 316, 133–143. <https://doi.org/10.1016/j.ecolmodel.2015.08.009>.
- Pe'er, G., Zingrebe, Y., Moreira, F., Sirami, C., Schindler, S., Müller, R., Bontzorlos, V., Clough, D., Bezák, P., Bonn, A., Hansjürgens, B., Lomba, A., Möckel, S., Passoni, G., Schleyer, C., Schmidt, J., Lakner, S., 2019. A greener path for the EU common agricultural policy. *Science* 365 (6452), 449–451. <https://doi.org/10.1126/science.aax3146>.
- Persson, A.S., Smith, H.G., 2013. Seasonal persistence of bumblebee populations is affected by landscape context. *Agric., Ecosyst. Environ.* 165, 201–209. <https://doi.org/10.1016/j.agee.2012.12.008>.
- Pfiffner, L., Ostermaier, M., Stoeckli, S., Müller, A., 2018. Wild bees respond complementarily to 'high-quality' perennial and annual habitats of organic farms in a complex landscape. *J. Insect Conserv.* 22 (3–4), 551–562. <https://doi.org/10.1007/s10841-018-0084-6>.
- Piko, J., Keller, A., Geppert, C., Batáry, P., Tscharnkte, T., Westphal, C., Hass, A.L., 2021. Effects of three flower field types on bumblebees and their pollen diets. *Basic Appl. Ecol.* 52, 95–108. <https://doi.org/10.1016/j.baee.2021.02.005>.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., Heisterkamp, S., van Willigen, B., Ranke, J., 2021. Linear and nonlinear mixed effects models: Package 'nlme' [Version 3.1-149].
- Potts, S.G., Vulliamy, B., Dafni, A., Ne'eman, G., Willmer, P. At, 2003. Linking bees and flowers: how do floral communities structure pollinator communities. *Ecology* 84 (10), 2628–2642.
- Proesmans, W., Smaghe, G., Meeus, I., Bonte, D., Verheyen, K., 2019. The effect of mass-flowering orchards and semi-natural habitat on bumblebee colony performance. *Landscape Ecol.* (5), 1033–1044. <https://doi.org/10.1007/s10980-019-00836-0>.
- Pywell, R.F., Warman, E.A., Carvell, C., Sparks, T.H., Dicks, L.V., Bennett, D., Wright, A., Critchley, C.N.R., Sherwood, A., 2005. Providing foraging resources for bumblebees

- in intensively farmed landscapes. *Biol. Conserv.* 121 (4), 479–494. <https://doi.org/10.1016/j.biocon.2004.05.020>.
- R Core Team, 2022. R 4.1.0.
- Riedinger, V., 2014a. Landscape-scale spillover of pollinators from oil-seed rape to crop and semi-natural habitats on different temporal scales. Dissertation, Würzburg.
- Riedinger, V., Renner, M., Rundlöf, M., Steffan-Dewenter, I., Holzschuh, A., 2014b. Early mass-flowering crops mitigate pollinator dilution in late-flowering crops. *Landscape Ecology* 29 (3), 425–435. [10.1007/s10980-013-9973-y](https://doi.org/10.1007/s10980-013-9973-y).
- 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 (7), 912–920. <https://doi.org/10.1111/ele.12128>.
- Scheper, J., Bommarco, R., Holzschuh, A., Potts, S.G., Riedinger, V., Roberts, S.P.M., Rundlöf, M., Smith, H.G., Steffan-Dewenter, I., Wickens, J.B., Wickens, V.J., Kleijn, D., 2015. Local and landscape-level floral resources explain effects of wildflower strips on wild bees across four European countries. *J. Appl. Ecol.* 52 (5), 1165–1175. <https://doi.org/10.1111/1365-2664.12479>.
- Schödl, I., Odemer, R., Becher, M.A., Berg, S., Otten, C., Grimm, V., Groeneveld, J., 2022. Simulation of Varroa mite control in honey bee colonies without synthetic acaricides: demonstration of good beekeeping practice for Germany in the BEEHAVE model. *Ecol. Evol.* 12 (11), e9456 <https://doi.org/10.1002/ece3.9456>.
- Schubert, L.F., Hellwig, N., Kirmer, A., Schmid-Egger, C., Schmidt, A., Dieker, P., Tischew, S., 2022. Habitat quality and surrounding landscape structures influence wild bee occurrence in perennial wildflower strips. *Basic Appl. Ecol.* 60, 76–86. <https://doi.org/10.1016/j.baae.2021.12.007>.
- Steckel, J., Westphal, C., Peters, M.K., Bellach, M., Rothenwohrer, C., Erasmi, S., Scherber, C., Tschardtke, T., Steffan-Dewenter, I., 2014. Landscape composition and configuration differently affect trap-nesting bees, wasps and their antagonists. *Biol. Conserv.* 172, 56–64. <https://doi.org/10.1016/j.biocon.2014.02.015>.
- Sutcliffe, L., Leuschner, C., 2022. Auswirkungen von Biodiversitätsmaßnahmen auf die Segetalflora auf intensiv bewirtschafteten landwirtschaftlichen Flächen - Ergebnisse aus dem F.R.A.N.Z.-Projekt. *Nat. und Landsch. (NuL)* 54 (6), 22–29. <https://doi.org/10.1399/NuL.2022.06.02>.
- Svensson, B., Lagerlöf, Jan, Svensson, B.G., 2000. Habitat preferences of nest-seeking bumble bees (Hymenoptera: Apidae) in an agricultural landscape. *Agric., Ecosyst. Environ.* 77, 247–255.
- Timberlake, T.P., Vaughan, I.P., Memmott, J., 2019. Phenology of farmland floral resources reveals seasonal gaps in nectar availability for bumblebees. *J. Appl. Ecol.* 56 (7), 1585–1596. <https://doi.org/10.1111/1365-2664.13403>.
- Tschardtke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I., Thies, C., 2005. Landscape perspectives on agricultural intensification and biodiversity: ecosystem service management. *Ecol. Lett.* 8, 857–874. <https://doi.org/10.1111/j.1461-02005.00782.x>.
- Tschardtke, T., Batáry, P., Dormann, C.F., 2011. Set-aside management: How do succession, sowing patterns and landscape context affect biodiversity? *Agric., Ecosyst. Environ.* 143 (1), 37–44. <https://doi.org/10.1016/j.agee.2010.11.025>.
- Tschardtke, T., Tylianakis, J.M., Rand, T.A., Didham, R.K., Fahrig, L., Batáry, P., Bengtsson, J., Clough, Y., Crist, T.O., Dormann, C.F., Ewers, R.M., Fründ, J., Holt, R. D., Holzschuh, A., Klein, A.M., Kleijn, D., Kremen, C., Landis, D.A., Laurance, W., Lindenmayer, D., Scherber, C., Sodhi, N., Steffan-Dewenter, I., Thies, C., van der Putten, W.H., Westphal, C., 2012. Landscape moderation of biodiversity patterns and processes - eight hypotheses. *Biol. Rev. Camb. Philos. Soc.* 87 (3), 661–685. <https://doi.org/10.1111/j.1469-185X.2011.00216.x>.
- Twiston-Davies, G., Becher, M.A., Osborne, J.L., 2021. BEE-STEWART: A research and decision-support software for effective land management to promote bumblebee populations. *Methods in Ecology and Evolution* 12 (10), 1809–1815. [10.1111/2041-210X.13673](https://doi.org/10.1111/2041-210X.13673).
- Umweltstiftung Michael Otto, 2022. F.R.A.N.Z.: Gemeinsam für mehr Vielfalt in der Agrarlandschaft, <https://www.franz-projekt.de/>.
- Walther-Hellwig, K., Frankl, R., 2000. Foraging habitats and foraging distances of bumblebees, *Bombus* spp. (Hym., Apidae), in an agricultural landscape. *J. Appl. Entomol.* 124 (7–8), 299–306.
- Westphal, C., Steffan-Dewenter, I., Tschardtke, T., 2006. Bumblebees experience landscapes at different spatial scales: possible implications for coexistence. *Oecologia* 149 (2), 289–300. <https://doi.org/10.1007/s00442-006-0448-6>.
- Westphal, C., Steffan-Dewenter, I., Tschardtke, T., 2009. Mass flowering oilseed rape improves early colony growth but not sexual reproduction of bumblebees. *J. Appl. Ecol.* 46 (1), 187–193. <https://doi.org/10.1111/j.1365-2664.2008.01580.x>.
- Westrich, P., 2018. Die Wildbienen Deutschlands. Verlag Eugen Ulmer, Stuttgart.
- Westrich, P., 1996. Habitat requirements of central European bees and the problems of partial habitats, in: *The Linnean Society Symposium Series and the International Bee Research Association (Ed.), The Conservation of Bees*, pp. 1–16.
- Wilensky, U., 1999. NetLogo. Center for Connected Learning and Computer-Based Modelling, Northwestern University, Evanston.