



Response of honeybee colony size to flower strips in agricultural landscapes depends on areal proportion, spatial distribution and plant composition

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Abstract

We investigated the effects of the areal proportion, spatial distribution and plant composition (quality) of flower strips in agricultural landscapes on the size of honeybee colonies using individual-based models (BEESCOUT, BEEHAVE). For this purpose, we developed 25 landscape scenarios for an intensively used landscape (3 × 3 km) in Havelland (Brandenburg, Germany). In the scenarios, we varied areal proportion (0.22–1.04%), distribution (clustered vs. even) and quality (high vs. low pollen and nectar supply) of flower strips. Then, we simulated the response of honeybee colony size to the landscape scenarios over twelve years with 100 repetitions per scenario. Colony size increased with increasing areal proportion and more even distribution of flower strips. However, this was only true for flower strips of high quality, whereas low-quality flower strips did not benefit the honeybee colonies. Our approach can help to pinpoint optimal quality, areal proportion and distribution of additional food sources for honeybees provided by flower strips in agricultural landscapes.

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Introduction

Loss of biodiversity and associated ecosystem services in agricultural landscapes is a major concern. The main cause of biodiversity loss is likely the intensification of agriculture, which has led to increased field sizes, loss of semi-natural

habitats and landscape elements, simplified crop rotations and intensified crop management (Beckmann et al., 2019; Matson, Parton, Power & Swift, 1997; Tilman, Cassman, Matson, Naylor & Polasky, 2002). Thus, intensification of agriculture has created structurally poor landscapes (Tilman et al., 2002) and caused fragmentation and loss of habitats for wild animals and plants, which contributes to overall biodiversity decline (Chase, Blowes, Knight, Gerstner & May, 2020; Díaz et al., 2019). Especially, pollinator diversity and abundance has decreased globally in recent years (Cardoso et al., 2020; Hallmann et al., 2017; Potts et al., 2010b), which is concerning as the ecosystem

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service of pollination is essential for both wild plant species in natural ecosystems and crops in agricultural production systems (Klein et al., 2007; MacLeod et al., 2020). For managed honeybees, declines in colony numbers have been reported from central Europe for decades between 1965 and 2005 (Potts et al., 2010b). Over the past decade, the number of honeybee hives in Europe has again increased (FAO 2018 in (Wood et al., 2020)).

Pollinators, such as native bees and bumble bees, and also managed honeybees (*Apis mellifera* L.), are affected by loss of natural and semi-natural habitats, resulting in a decline of availability of floral resources in space and time (Brown & Paxton, 2009; Kremen et al., 2007; Potts et al., 2010b; Williams, Regetz & Kremen, 2012). In particular, the insufficient abundance of forage resources throughout the year is one of the main reasons for the decline of honeybee colonies in agricultural landscapes (Decourtye et al., 2011). The lack of food affects the health and foraging behaviour of honeybee colonies (Decourtye, Mader & Desneux, 2010; Naug, 2009), whereby pests, pathogens and environmental stressors can exacerbate declines of honeybee colonies (Neumann & Carreck, 2010; Potts et al., 2010a, 2010b).

Agri-environment schemes (AES) have been implemented in the Common Agricultural Policy (CAP) of the European Union, promoted by Rural Development Programmes (RDP) in order to counteract the decline of biodiversity (Pe'er et al., 2019). In this framework, sown flower strips have been introduced as an agri-environmental measure in several European countries to support the conservation of insects and to ensure crop pollination (Haaland, Naisbit & Bersier, 2011; Ouvrard, Transon & Jacquemart, 2018). Flower strips appear to have augmented availability of floral resources that increase the local abundance of honeybees (Ramseier et al., 2016) and of native bees and other wild pollinators throughout the crop season (Balzan, Bocci & Moonen, 2014; Decourtye et al., 2010; Geppert et al., 2020; Potts, Vulliamy, Dafni, Ne'eman & Willmer, 2003; Scheper et al., 2015). Nevertheless, it remains unclear whether local increases in honeybee abundance on flower strips translate into colony growth.

Thus, the question arises whether flower strips might also counteract the decline in the colony sizes of managed honeybees in agricultural landscapes (Carvell, Meek, Pywell & Nowakowski, 2004; Pywell et al., 2005). While the knowledge of the general link between floral resource availability, colony growth and honey production is widely distributed among beekeepers (Sponsler & Johnson, 2015), the importance of flower strips in intensive agricultural landscapes for honeybee colonies is still an open question. Especially, because it remains unclear which quantity of flower strips of which floral composition (quality) may be required for filling the often existing gap of flower resources in agricultural landscapes between end of May and end of July (Ramseier et al., 2016), as honeybee recruitment behaviour and diet breadth is influenced by the seasonal changes of pollen resource (Park & Nieh, 2017). Effects of flower strips

on colony size may depend on the respective seed mixture and the resulting temporal nectar and pollen supply by flowers growing in the strip (Haaland et al., 2011). Furthermore, effects of flower strips may depend on landscape context, likewise influencing the abundance of honeybees and wild bees (Blaauw & Isaacs, 2014). Yet, previous studies have rarely investigated effects of flower strips on honeybees at the landscape scale (Kleijn et al., 2018).

Finally, it is not known how flower strips should be spatially arranged (clustered or evenly distributed) and how much area of flower strips is required in a landscape to achieve colony increases. The flight distance covered by honeybees is farther in spring and autumn, when less forage can be found (Couvillon, Schürch & Ratnieks, 2014a). For honeybee workers, the search for food is associated with a cost-benefit trade-off (Couvillon, Schürch & Ratnieks, 2014b). Hence, it remains unknown to what extent local and landscape-scale factors determine honeybee responses to flower strips (Scheper et al., 2015).

We used a simulation modelling approach to study effects of flower strips on honeybees in intensively-used agricultural landscapes. Simulation models have the advantage that they allow to investigate effects of flower strips at the level of colonies rather than local abundances, and to study many different landscape scenarios over multiple years providing immediate results. Therefore, the application of simulation models to study the response of honeybee colonies to different implementations of agri-environmental measures at landscape scale may be a useful complement to field studies. The published models BEESCOUT (Becher et al., 2016) and BEEHAVE (Becher et al., 2014) simulate the scouting behaviour and in-hive dynamics of honeybee colonies. They build upon the rich knowledge on the behaviour and colony dynamics of honeybees that makes them suitable as a model organism. Recent studies applied these models in order to evaluate the effect of pesticide use (Agatz, Kuhl, Miles, Schad & Preuss, 2019) or colony resilience to changes in food foraging distance, forage supply, and forage gaps (Horn et al., 2020; Horn, Becher, Kennedy, Osborne & Grimm, 2016). A forage gap is a period without pollen and nectar resources (Horn et al., 2016). In the present paper, we used the simulation models BEESCOUT and BEEHAVE to investigate how honeybee colony size would respond to i.) increasing areal proportion of flower strips in agricultural landscapes from 0.2 to 1.0%, ii.) different distribution patterns of flower strips (even vs. clustered), and iii.) different levels of availability of nectar and pollen resources per unit area ('quality' of flower strips). Further, we explored whether the honey store has an impact on the dynamics and the resilience of the colony over an observation time of 12 years. With respect to resource availability, we took the phenology of flowering plants into account based on realistic plant seed mixtures used for establishing flower strips.

Materials and methods

Study area

We used a real agricultural landscape as a basis to develop landscape scenarios with different arrangements of flower strips. The study area was located in the region Havelland in the state of Brandenburg, Germany (lat 52°37' N; long 12° 45'E) and had a size of 3 × 3 km. The Havelland is representative of intensive agricultural landscapes in Eastern Germany. The study area was dominated by arable crops (88.0%, 792 ha), such as winter cereals, oilseed rape and maize, which are grown in rotation on a four-year cycle (oilseed rape–winter cereals–maize–winter cereal). The remaining land cover was composed of permanent grassland (13.8%), forest (8.7%), hedgerows (0.3%) and remaining land use (3.0%, urban and unknown land use). In the simulation model, suitable floral resources to honeybees were provided by the fields with the

crops oilseed rape and maize next to the semi-natural habitats (see Definition of food sources). The mean size of arable fields, excluding permanent grasslands, was 11.1 ha.

Overview of the modelling approach

We used the agent-based models BEESCOUT (Becher et al., 2016) and BEEHAVE (Becher et al., 2014) to simulate the development of honeybee colonies in the landscape scenarios. BEESCOUT and BEEHAVE are freely available under <http://beehave-model.net/> and are implemented in the software platform NetLogo 5.3.1 (Wilensky, 1999). The purpose of the models is to describe the effects of availability and spatio-temporal distribution of resources (nectar, pollen) on honeybee colonies to assess the risk of multiple stressors at the landscape scale (Becher et al., 2014, 2016). To this end, we developed a workflow with six steps (Fig. 1). In the following,

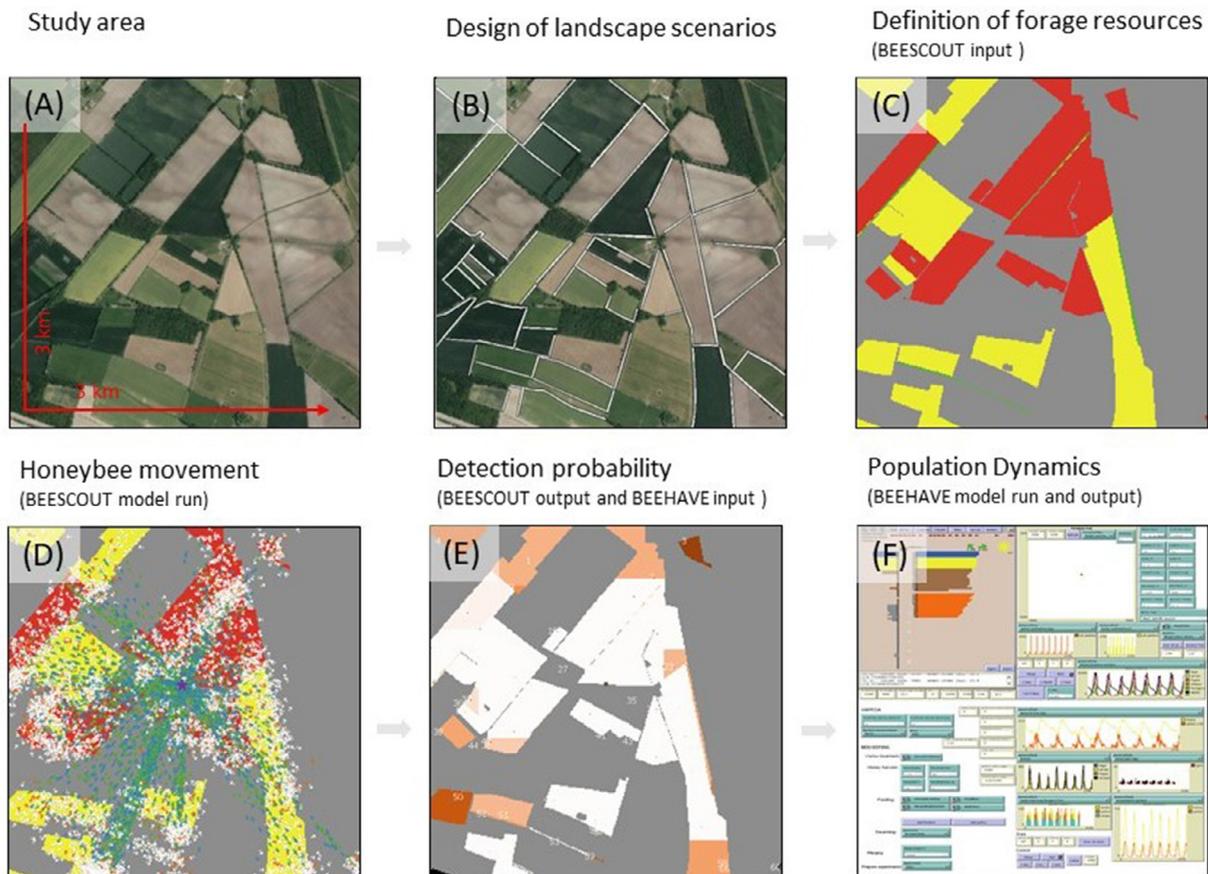


Fig. 1. (A) Land use/ land cover and crops were mapped based on fieldwork and aerial images in the study area. (B) All possible locations of flower strips meeting the criteria (see text) were digitized in GIS for designing landscape scenarios. (C) For each landscape scenario, a map of forage resources was produced as input for BEESCOUT (yellow = oilseed rape, red = maize, green = flower strips, blue = semi-natural habitats, grey = no food resource). (D) The BEESCOUT model was run to simulate the scouting of honeybees in each landscape scenario (the star shows the location of the hive and colour code is the same as in (C)). (E) Output of the model BEESCOUT: maps of detection probabilities of flower patches (brightness of patch colour indicates detection probability from black (no detection) to white (high detection probability); grey areas do not provide flowers); numbers represent the ID of flower patches; additionally, information on size, location, concentration of sugar, nectar and pollen availability of each identified flower patch for each day was stored in text files that served as input files for the model BEEHAVE (Becher et al., 2016). (F) Run and output of the model BEEHAVE: development of a honeybee colony and its population parameters over multiple years was stored in text files.

we describe shortly the models BEESCOUT and BEEHAVE, [Becher et al. \(2014\)](#), [\(2016\)](#) provide details on the definitions and techniques used for both models.

The model BEESCOUT allows us to determine the effect of landscape configuration and composition on colony size. Regarding landscape information, a digital land-use/ land-cover (LULC) map can be developed, which provides spatially-explicit input data about the flower phenology and amounts of nectar and pollen per flower for each plant species. Additionally, BEESCOUT requires information on the movement of honeybees like foraging behaviour to simulate the scouting behaviour of bees. Based on these input data, BEESCOUT categorizes the landscape into food patches ('flower patches') and non-food patches and calculates the daily nectar and pollen amount of each food patch considering the phenology of the flowering plant species. Further, it assesses the detection probability of the flower patches ([Becher et al., 2016](#)). The output of BEESCOUT is a file with the information on the flower patches as well as the detection probability of the patches, which later are used as input for the BEEHAVE model ([Becher et al., 2014](#)).

BEEHAVE simulates the development of a single honeybee colony ([Becher et al., 2014](#)) in order to investigate how landscape configuration, landscape change or stressors, such as pesticide use and viral infections transmitted by the *Varroa* mites, affect the population dynamics of the honeybees. However, effects of mites and pesticides were not considered in this study. The foraging-model of BEEHAVE simulates the foraging process of adult bees on the flower patches in the landscape and the development of a colony. The cohort-based colony model describes the in-hive processes, e.g., colony dynamics for in-hive bees, brood and drones. BEEHAVE runs in daily time steps and takes daily weather conditions into account which affect pollen and nectar collection by defining the maximal daily foraging period of the colony. Applying the models, we can only consider a single colony, therefore there is no competition with other colonies or pollinators as in reality. However, with all other settings, the model allows us to assess the effects of landscape scenarios on various colony parameters, such as total number of adult honeybees produced per year, their honey store or foraging distances without consideration of beekeeping practices and stressors as written above.

Design of landscape scenarios

We created a digital map of the study area based on digital aerial images and the digital basic landscape model 'ATKIS' ([BKG, 2018a, 2018b](#)) ([Fig. 1A](#)). The crops were recorded by field observation (Kulow, unpublished). The fields with the assigned crops oilseed rape, winter cereals and maize and remaining land use were digitized as polygons in ArcMap 10.5 ([Esri, 2018](#)). This

land use defined the Business-As-Usual (BAU) landscape scenario, which represented the control, or baseline, for exploring the effects of landscape scenarios with flower strips on honeybee colonies.

For the flower strips scenarios, we developed 25 landscape scenarios in order to investigate the effects of the areal proportion, spatial distribution and plant-species composition of flower strips in agricultural landscapes on the size of honeybee colonies. We based the design of flower strips on existing guiding information of practical implementation of flower strips focussing on (i.) area size, (ii.) connectivity, and (iii.) annual or perennial flowering aspect, species composition and origin of flower seed mixture ([Oppermann, Buhk & Pfister, 2019](#)).

For the flower strips, all potential locations along the field boundaries were digitized excluding unsuitable areas, such as along forest edges. The flower strips varied in length, but the length of the flower strips was constrained by the real field boundaries. We held the width of the flower strips constant at 18 m mimicking existing flower strips in the study area. Thus, the flower strips in the scenarios were wider than the 10–12 m recommended by [Oppermann et al. \(2019\)](#). Consequently, the area size of the flower strips was according to their length ([Table 1](#)). The total area of potential flower strips represents 6.09% of the landscape ([Fig. 1B](#)).

Regarding the placement of flower strips, the connectivity to hedgerows, forest borders or other semi-natural habitats was not a focal aspect of our investigations, but we compared the effect of even vs. clustered **spatial distribution** of flower strips in addition to their areal proportion of the landscape. In advance, the flower strips were classified according to the length. In the seven scenarios with evenly distributed flower strips, one flower strip per cardinal direction was selected. The areal proportion of evenly distributed flower strips ranged between 0.22% and 1.04%. The values of areal proportions were not smooth because the lengths of flower strips were constrained by the real boundaries of the arable fields ([Appendix A: Fig. S1B](#)). For the scenarios with clustered distribution of flower strips, two flower strips per intercardinal direction were created. The areal proportions of these four scenarios ranged between 0.24% and 0.29% ([Appendix A: Fig. S1B](#)). Additionally, we created a fifth scenario with eight flower strips that had an areal proportion of 1.04% and was the sum of the first four scenarios with clustered distribution of flower strips ([Appendix A: Fig. S1C](#)).

Under the criterion **quality**, we summarised the aspects of biennial or perennial plants and the overall plant species composition to create two fictitious seed mixtures with markedly different amounts of available nectar and pollen on the respective flower strips ([Fig. 2](#)). In doing so, we mixed crop and wild plant species as recommended in practice guides ([Oppermann et al., 2019](#)). In the following, the two species compositions are referred to as 'low' and 'high' quality scenarios.

Table 1. Overview of the landscape scenarios. The scenarios were grouped by the length of flower strips. The distance to hive is the average distance between the hive and the flower strip, calculated as weighted mean based on the distance of food patches from model BEESCOUT.

Scenario name	Location	Length [m]	Area size [ha]	Areal proportion [%]	Mean distance to hive [m]	Distribution
Evenly-0.22%	North	252	0.45	0.22	1082.83	Even
	East	238	0.43		1538.84	
	South	256	0.46		1509.50	
	West	239	0.43		1364.88	
Evenly-0.33%	North	355	0.64	0.33	1157.30	Even
	East	399	0.72		1539.10	
	South	338	0.61		380.10	
	West	376	0.68		1090.00	
Evenly-0.42%	North	417	0.75	0.42	769.00	Even
	East	470	0.85		728.00	
	South	490	0.88		1552.20	
	West	466	0.84		335.40	
Evenly-0.50%	North	485	0.87	0.50	406.10	Even
	East	542	0.98		892.70	
	South	596	1.07		222.33	
	West	578	1.04		630.70	
Evenly-0.58%	North	654	1.18	0.58	63.51	Even
	East	618	1.11		787.30	
	South	672	1.21		71.70	
	West	629	1.13		1299.03	
Evenly-0.70%	North	705	1.27	0.70	636.31	Even
	East	864	1.55		628.18	
	South	710	1.28		1187.70	
	West	795	1.43		1387.76	
Evenly-1.04%	North	1019	1.83	1.04	332.91	Even
	East	1258	2.26		833.97	
	South	728, 494	2.20		1404.71	
	West	1087	1.96		1165.00	
Clustered-0.24%	North-west	578, 472	1.89	0.24	845.43	Clustered
Clustered-0.25%	North-east	485, 618	1.99	0.25	1340.77	Clustered
Clustered-0.26%	South-west	629, 494	2.02	0.26	1428.05	Clustered
Clustered- 0.29%	South-east	700, 594	2.33	0.29	602.94	Clustered
Clustered-1.04%	North-west, north-east, south, west, south-east		8.23	1.04	1058.50	Clustered

BEESCOUT simulation

Definition of food sources

Seven LULC types were found in the study area, of which four were characterized as important food sources for the honeybees, because they provided pollen and/or nectar. These were the crops maize and rape seed, the flower strips, and semi-natural habitats comprising hedges or grasslands. In order to prevent the honeybee colony from dying over the year, we defined semi-natural habitat as a permanent food source and implemented four patches of it in each landscape scenario close to the hive on areas that were hedges, grassland or forest areas in the real landscape (Appendix A: Table S2).

We assigned nectar and pollen amounts per unit area to the LULC types based on a comprehensive literature research of the flowering time (phenology), daily amount of pollen and nectar per flower, and sugar concentration of the

nectar of the plant species and crops (Fig. 1C). For this purpose, we needed data about the average number of flowers per square metre for each plant species (Appendix A: Table S1). The pollen and nectar amount of the crops, oilseed rape and maize, and semi-natural habitats were constant over their flowering time. The pollen and nectar amount of semi-natural habitats were reduced to the required minimum for preventing the extinction of the honeybee colony in absence of other food sources.

The flower strips were composed of different plant species according to the two fictitious seed mixtures. The seed mixtures presented markedly different amounts of pollen and nectar, which we refer to as ‘high’ and ‘low’ quality. As the flowering time differed among species, the pollen and nectar amount changed on a monthly basis. The seed mixture with low quality had a flowering time from May to October, whereas the plants in the mixture with high quality flowered between April and October (Fig. 2). Regarding the handling

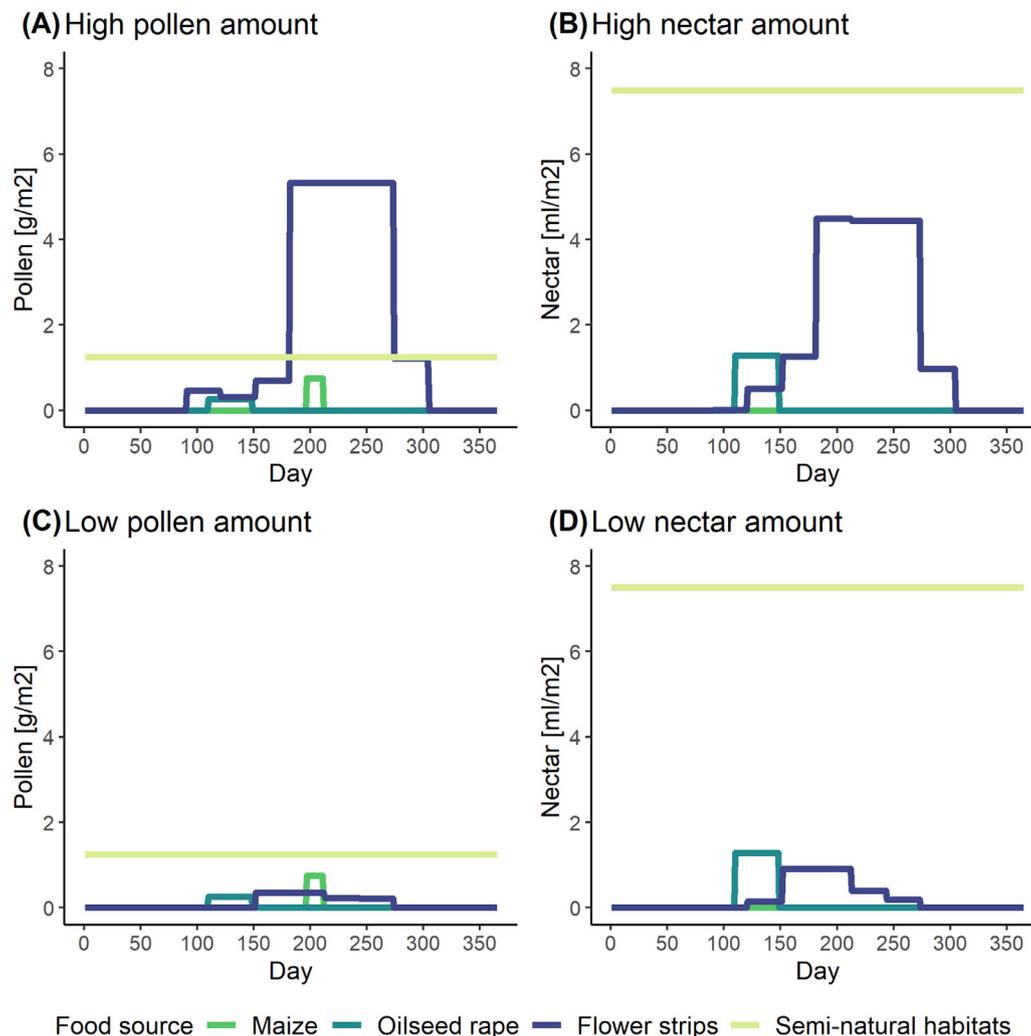


Fig. 2. (A) Pollen load (g/m^2) and (B) nectar load (ml/m^2) of the flower strips with high-quality plant species composition during the course of the year (days). (C) and (D) show the equivalent for flower strips with low quality. Maize (pollen: $0.75 \text{ g}/\text{m}^2$; no nectar), oilseed rape (pollen: $0.26 \text{ g}/\text{m}^2$, nectar: $1.28 \text{ ml}/\text{m}^2$), Flower strips high quality (pollen: $0.31\text{--}5.33 \text{ g}/\text{m}^2$, nectar multiplied by 10: $0.12\text{--}4.43 \text{ ml}/\text{m}^2$), Flower strips low quality (pollen: $0.21\text{--}0.35 \text{ g}/\text{m}^2$, nectar multiplied by 100: $0.01\text{--}0.91 \text{ ml}/\text{m}^2$), semi-natural habitats (pollen: $1.25 \text{ g}/\text{m}^2$, nectar: $7.5 \text{ ml}/\text{m}^2$).

time, i.e. the time a bee spends on the flower from landing to take-off (Becher et al., 2014), we kept BEEHAVE's default settings.

As the proportions and distribution of LULC and, consequently, food sources differed between the landscape scenarios and, additionally, between the four years of crop rotation, the simulations of nectar and pollen availability were conducted separately for each scenario and year. All LULC types regardless of crop or flower strips were divided into several food sources with point coordinates by the import procedure of BEESCOUT. Therefore, LULC types were represented by multiple point-like food sources with varying distances from the hive. For that reason, we calculated the minimum, maximum, mean and area-weighted mean distance of the food sources to the hive in order to compare travel distances among clustered and even distributions of flower strips (Fig. S3).

Detection probability

The detection probability of flower patches depends on the honeybees' search mode (Becher et al., 2016). In BEESCOUT, we selected the search mode "known flower-patch (recruitment)" in order to assess the detection probability of flower patches (Becher et al., 2016) (Fig. 1D). In this search mode, honeybees have no knowledge about the landscape before their first scouting trip, but they gather information on locations of flower patches during their trips and through waggle dances of nestmates in the hive. The detection probability was assessed on a daily basis for each scenario. The detection probabilities were higher closer to the hive than farther away (Fig. 1E).

As shown in Table 1, we tested twelve different flower-strip scenarios with different areal proportion and/or spatial distribution. Further, we tested two different quality levels of flower strips. Together with the BAU scenario, we had in

sum 25 scenarios. For the simulation of the model BEESCOUT, the difference between the quality levels of the flower strips was not considered because the scenarios should have the same detection probability independent of the quality of flower strips. Therefore, we assigned the pollen and nectar values to the flower strips in an intermediate step, before we started the simulations of population dynamics in BEEHAVE (Fig. 1F).

Settings

The rasterized landscape in BEESCOUT corresponded to the study area of 3000×3000 m and had a spatial resolution of 10 m (Appendix A: Table S2). We placed the hive in a central position in a grassland field, as area not in agricultural use in the landscape (Appendix A: Table S2). Like the default setting, we started the simulations with 10,000 worker bees in the colony at the beginning of the first year. All BEESCOUT settings not named in Appendix A: Table S2 were set to the defaults.

BEEHAVE simulation

Population dynamics

We used BEEHAVE with the default settings. All BEEHAVE simulations started on 1st January with an initial colony size of 10,000 worker bees and 25 kg honey store, which is what a colony of this size needs in order to survive until spring (Horn et al., 2020). Beekeeping practices (e.g. honey harvest or feeding) or infections due to *Varroa* mites were excluded from the simulations. Consequently, this allowed us to assess the pure effect of flower strips and the related availability of food resources on colony development. To obtain a realistic pattern, we defined local weather conditions of the years 2011 to 2016. The weather data were taken from the nearest weather station, which was located in Berge (lat $52^{\circ}62'$ N; long $12^{\circ}79'$ E, Brandenburg) (DWD, 2018). The observation time of the BEEHAVE simulations was twelve years because we wanted to test the independent effect of crop rotation and weather. In this way, the three repetitions of the four-year crop rotation cycle were combined with two repetitions of the six-year weather period. The four-year crop rotation is represented by the four text files of the model BEESCOUT. Using a python script, these text files were alternately provided to BEEHAVE as input files at the beginning of each year of the simulation repeating the crop-rotation cycle three times in order to cover the twelve years. After every year, the status of the model BEEHAVE was saved, before the new text file for the following year was loaded. BEEHAVE was repeated one hundred times in order to account for the stochasticity inherent in the model and to allow for statistical data analysis of the simulation results.

Data analysis

To investigate the effects of areal proportion, distribution and quality of flower strips on colony dynamics and resilience over an observation time of 12 years, we used the colony size at the end of each year as response variable. The colony size included the number of worker and forager bees. For the data analyses, we used the open source statistic software R (version 4.0.3 (R Core Team, 2020)). Firstly, we explored the effect of quality and distribution of flower strips pooled over all twelve years. For this purpose, we calculated mean colony size over the hundred replications of the simulation for all scenarios. We tested for significant differences between the BAU scenario and the combinations of even or clustered distribution with high or low quality using Tukey HSD test. Secondly, we analysed differences in the response of the honeybee colony among the classes of areal proportion of flower strips within each combination of distribution and quality using the Tukey HSD test. Here, we used the colony size in the last year of the simulation (year 12). Prior to the tests, we checked for Gaussian distribution and homogeneity of variance of colony size using the Shapiro and Levene tests, respectively.

In addition, we used Linear Models (LM) to analyse effects of landscape scenarios and of honey store on colony dynamics between two successive years. For this, we calculated ratios of colony size in the later year and the earlier year. We used log-transformed ratios as response variables, while honey store, flower-strip quality and 'scenario', i.e. the combination of clustered or even distribution with the class of areal proportion were used as predictor variables. We also included the interaction between quality and 'scenario'. We tested for collinearity among the predictor variables using variance inflation factors (Appendix A: Table S5). The assumptions of normal distribution of residuals and homogeneity of variance were checked graphically.

Furthermore, we built a time-series model using the data from all twelve years to analyse the effects of honey store in the previous year together with effects of the landscape scenarios and flower-strip quality on the colony size. For this purpose, we used the R package 'nlme' (Pinheiro et al., 2021) to calculate a Linear Mixed Model (LMM) which included a random effect of the simulation runs and an autoregressive correlation structure (corAR1) for the time series next to the main effects of the predictor variables.

Finally, for investigating whether the colony size was affected more by the spatial distribution or by distance of food sources from the hive, we built a multiple negative binomial generalized linear model using the function `glm.nb` from the R package MASS (Ripley et al., 2021) with subsequent variation partitioning using 'ecospat.varpart' from the package 'ecospat' (Broennimann et al., 2021). This model used mean colony size per scenario and year as dependent variable.

Results

With regard to the quality of flower strips depending on plant species composition, overall we found that honeybee colony size increased in landscape scenarios with ‘high’ nectar and pollen availability compared to BAU and ‘low’ scenarios (Fig. 3). Further, the time-series model confirmed that scenarios with high quality had a positive effect on the colony size, which was 1.15-times higher than in scenarios with low quality (Appendix A: Table S4; Fig. S4).

Regarding the spatial distribution of flower strips, honeybee colony size benefited more from evenly distributed flower strips than from clustered ones, although this only applied to high quality flower strips (Fig. 3). On average (area-weighted mean), the distance from the hive of food sources on clustered flower strips was larger (1084 m) than for evenly distributed flower strips (867 m). However, some clustered scenarios had shorter mean distances than even scenarios with comparable areal proportion of flower strips (Table 1; Appendix A: Fig. S3). We found a significant negative effect of distance of food sources on colony size for high-quality scenarios, particularly with even distribution of flower strips, whereas there was no significant effect of distance in low-quality scenarios. After taking distance of food sources into account, even distribution of flower strips still had a significant positive effect on colony size. Nevertheless, distance explained more variation of colony size (12.5%) than spatial distribution (4.1%) in the scenarios with high quality (Fig. 6, Appendix A: Table S5).

Looking at the honeybee colony size in the last year, year 12, there was an increase of colony size with the areal proportion of flower strips in the landscape only in the high-quality

scenarios (Fig. 4). When flower strips were evenly distributed in the landscape, the increase of colony size levelled off at 0.4% areal proportion (Fig. 4A), while there was a steady increase with clustered distribution (Fig. 4C). The flower strips with low quality did not show such clear patterns of increase with areal proportion (Fig. 4B,D).

In the course of the twelve years, honeybee colony size and honey store showed similar patterns in the first and the last six years, likely due to the repetition of the weather data (Fig. 5; Appendix A: Fig. S2). For the scenarios with high quality, the colony size ranged between 5.500 and 11.000 honeybee individuals and the maximum size occurred in the second and eighth year. The honey store ranged between 13 and 44 kg with high values in year 1, 5 and 10. For the flower strips with low quality, the colony size ranged between 5.000 and 9.000 and had maxima in years 6 and 12. The honey store ranged between 8.5 and 27.5 kg, with the highest values found in the BAU landscape and the Clustered-1.04% scenario. As in the scenarios with high quality, the lowest colony size was found in years 4 and 10 and the lowest honey store in years 3 and 9.

Marked declines of colony size found in years 4 and 10 were preceded by bad weather conditions and decreased honey store in the previous year. However, the magnitude of decline between the years 3-4 and 9-10, assessed as logarithms of colony size, was independent of the honey store in the later year ($p < 0.01$ and $p < -0.01$, respectively; cf. Appendix A: Table S6). Further, colony decline between these years did not differ consistently among scenarios with high quality flower strips. However, in low-quality scenarios, evenly distributed flower strips alleviated the decline compared to the BAU, whereas clustered flower strips did not (Appendix A: Table S6).

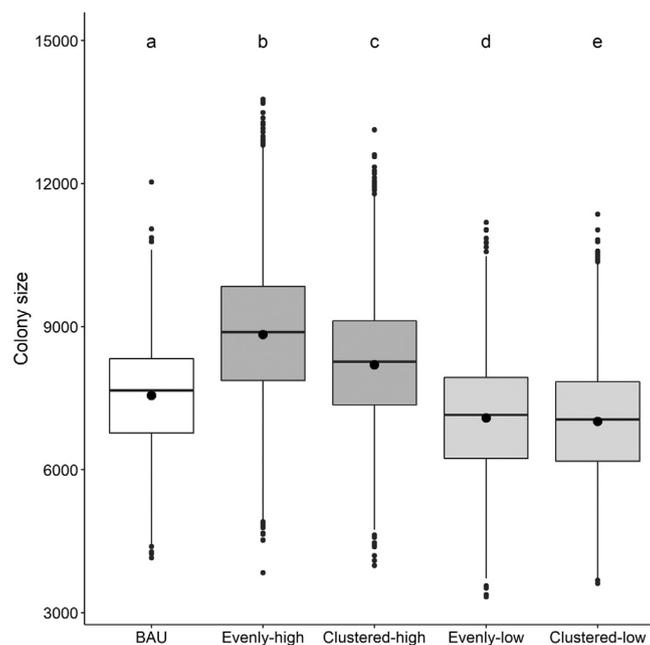


Fig. 3. Honeybee colony size in different landscape scenarios grouped by spatial distribution (evenly or clustered) and quality (high or low) of flower strips compared to the business-as-usual (BAU) scenario without flower strips over all twelve years. Different letters represent significant differences between the scenarios. Boxes show medians and inter quartile ranges. Dots indicate arithmetic means.

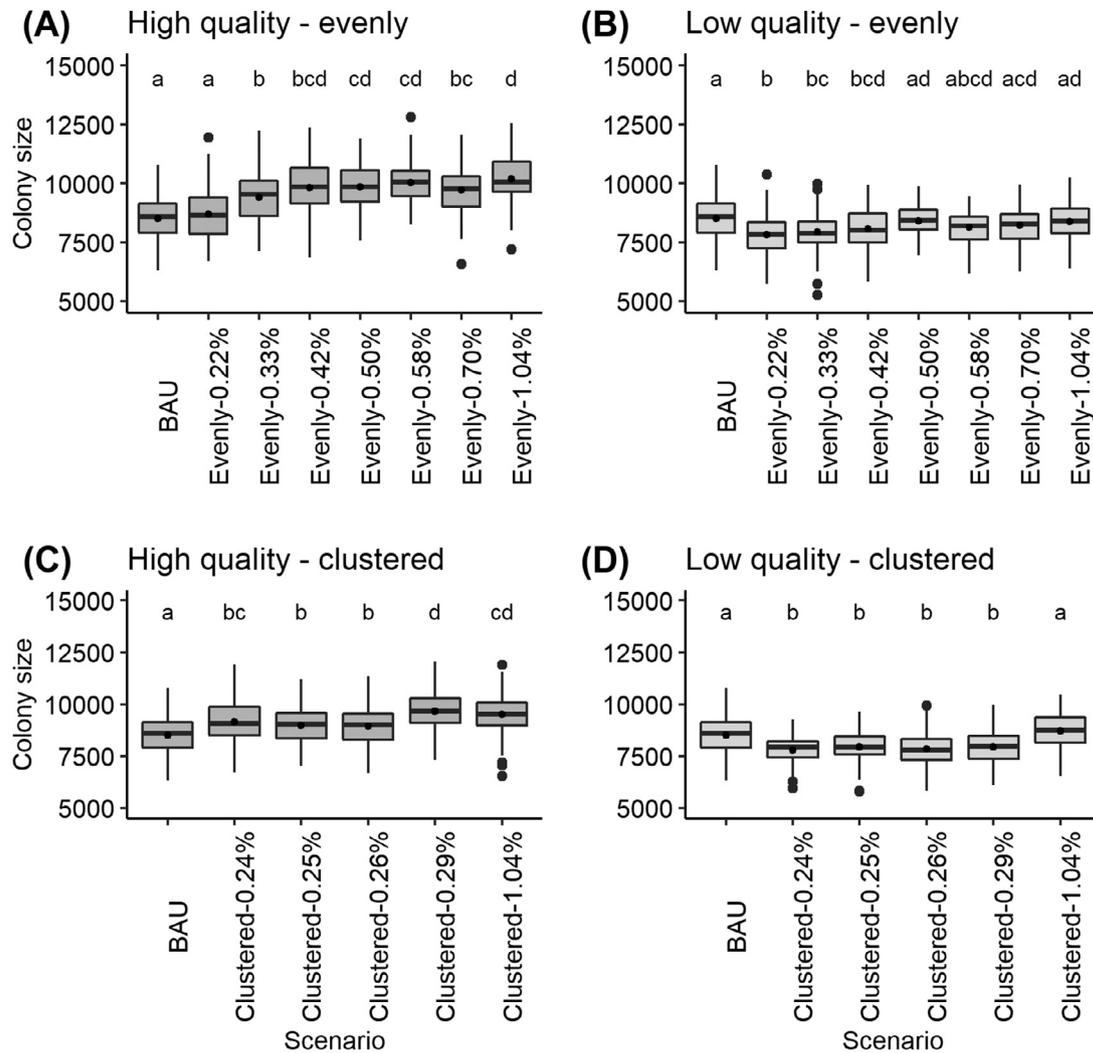


Fig. 4. Honeybee colony size (A) with high quality and evenly distributed flower strips; (B) with low quality and evenly distributed flower strips; (C) with high quality and clustered distribution of flower strips; (D) with low quality and clustered distribution of flower strips in comparison with the business-as-usual (BAU) scenario without flower strips at the end of the last year of simulations (year 12). Different letters represent significant differences between the scenarios. Boxes show medians and inter-quartile ranges. Dots indicate arithmetic means.

In the time series model, honey store from the previous year had a positive effect on colony size ($p < 0.01$). An increase of honey store by 10 kg led to an increase in colony size of 8% (Appendix A: Table S7). Further, the interaction between year and quality showed that high quality mitigated negative effects of bad weather conditions in years 3 ($p < 0.1$) and 9 ($p < 0.05$).

Discussion

Simulation results

The simulations indicate that the three investigated parameters, areal proportion, spatial distribution, and quality of the flower strips, i.e. availability of nectar and pollen determined by plant-species composition, all have

significant effects on the size of honeybee colonies in agricultural landscapes. Further, the results suggest interactions between quality and areal proportion as well as spatial distribution of flower strips. In addition, we found an interaction between areal proportion and spatial distribution. This shows that effects of flower strips on honeybee colonies and, possibly, other pollinating insects, are complex and that both local and landscape factors should be considered in research studies and planning of conservation measures.

The results of Horn et al. (2020) show that honey bee survival is less dependent on landscape structure, but rather on crop identity and diversity to fill foraging gaps in intensive agricultural landscapes. Steffan-Dewenter and Kuhn (2003) also found that seasonal patterns affect honey bee foraging and that the foraging gap in June and July is a major challenge. Enhancing the abundance and diversity of forage-rich, semi-natural habitats and measures with mid- to late-

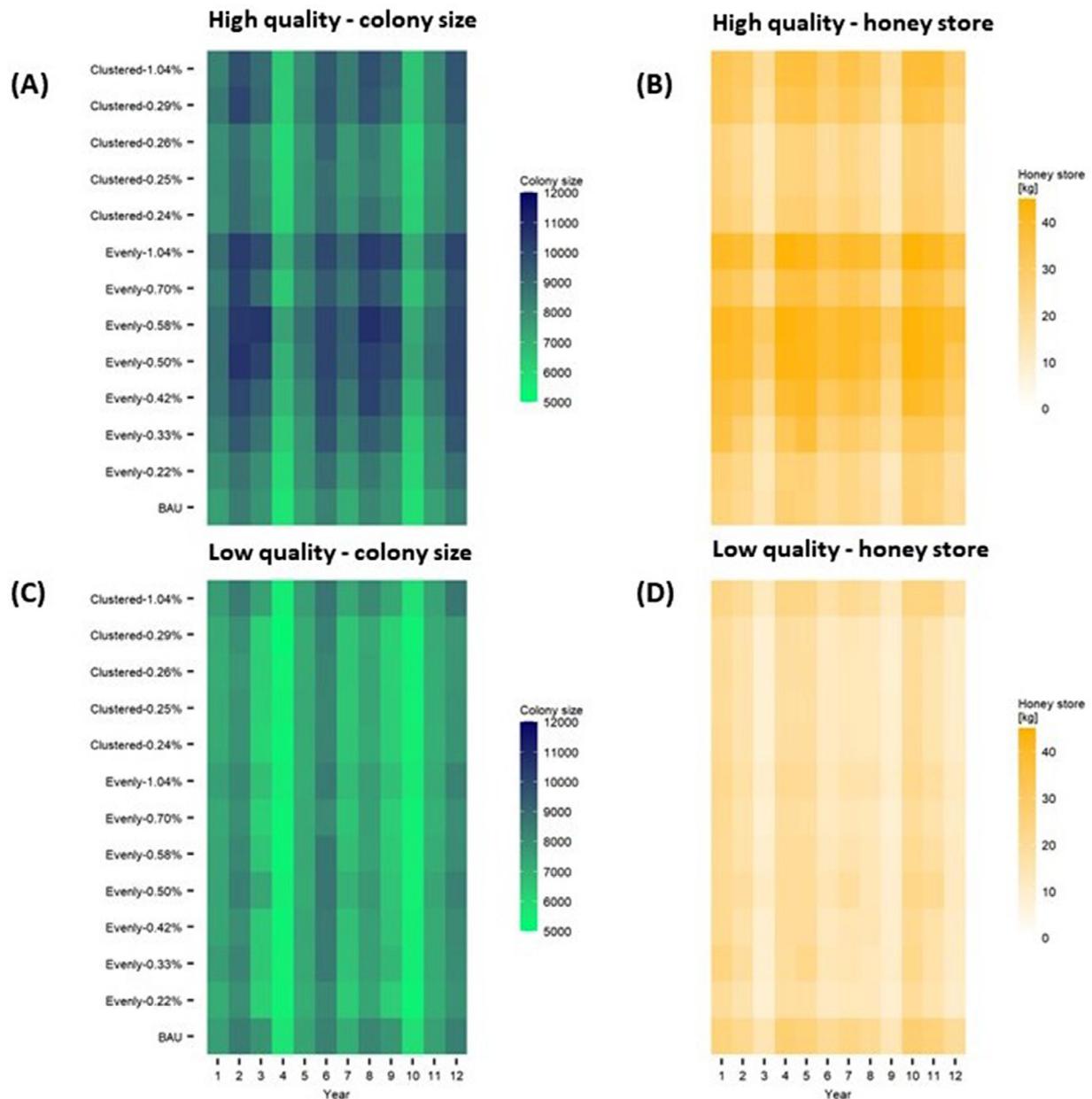


Fig. 5. Honeybee colony size (A and C) and honey store (B and D) for landscape scenarios with flower strips of high and low quality in the course of the twelve years of simulation.

flowering plants (legume-rich grass, phacelia, buckwheat) and accordingly a temporally and spatially continuous food supply is important for the viability of honey bee colonies and the life stages of the honeybee colony (Horn et al., 2020). But to find an answer to the question, how much area of measures has to be provided, is associated with much uncertainty, because it is important to know beforehand how much limiting resources are needed to support viable populations or to counteract population declines (Dicks et al., 2015).

The honeybee colony size increases with increasing areal proportion of flower strips within the studied range, up to 1% of the landscape, but only with high quality of flower

strips. The most efficient scenarios were those with even distribution where colony size levelled off at around 0.3 - 0.4% areal proportion indicating that other factors instead of choice of seed mixture became limiting for the honeybee colony. This suggests that increasing the relative availability or proportion of flower strips may not be beneficial and focus should be put on optimising resource availability on flower strips and on even spatial distribution. For some species groups other than honeybees, findings on the effects of optimised resource availability exist: A higher reproduction of bumblebees due to the shorter flight distance with increasing flowering areas (1 ha) was found by Carvell, Bourke, Osborne and Heard, (2015). The abundance and richness of

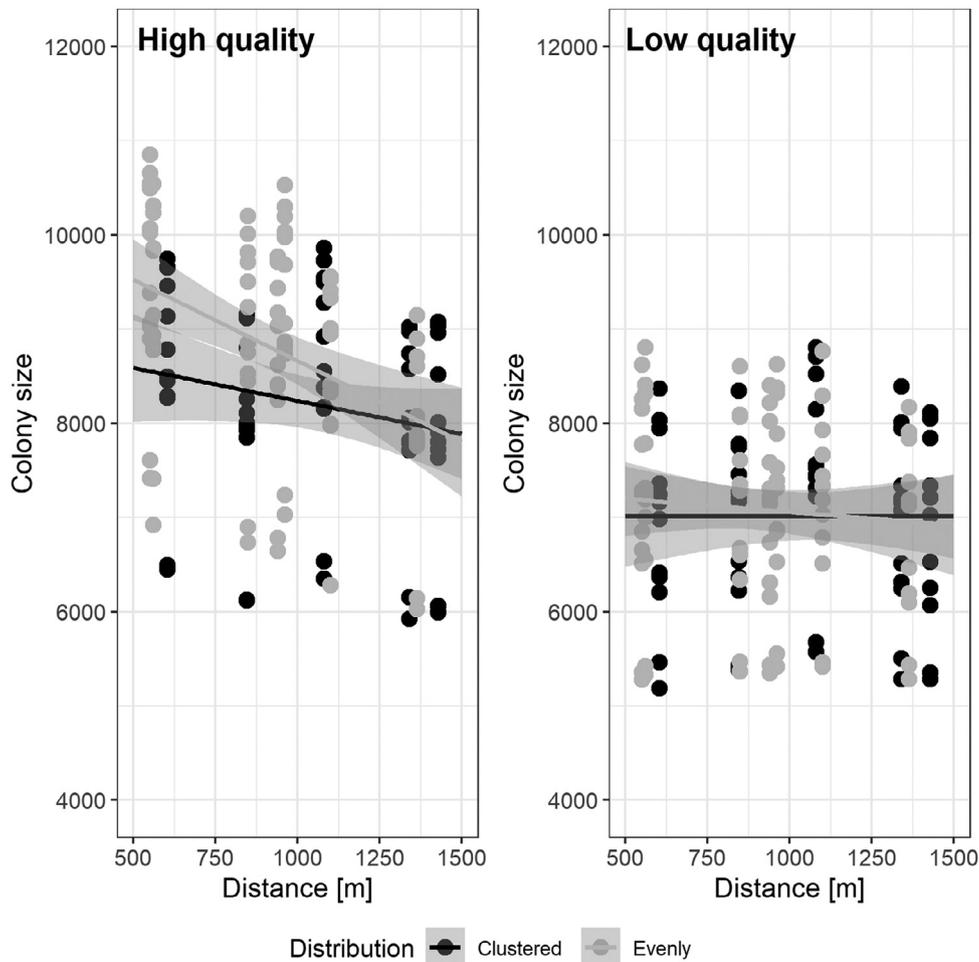


Fig 6. Correlation between the area-weighted mean distance of food sources on flower strips from the hive and colony size, for evenly distributed (grey) and clustered (black) flower strips of high and low quality.

wild bees including oligolectic species and of butterflies increased in areas (50 ha) enhanced with 10% flower strips (Buhk et al., 2018). A positive effect of increasing proportion of flower strips was observed for the species richness, but not abundance of butterflies in Switzerland (Aviron, Herzog, Klaus, Schüpbach & Jeanneret, 2011). Another study in Switzerland illustrated that the increased proportion of biodiversity promotion areas (BPA), such as extensively managed grasslands, orchards, hedges or flower strips, also increased the abundance and richness of butterflies. There were 60% more individuals of butterflies, when the proportion of BPA in the landscape increased from 5% to 15% (Zingg, Ritschard, Arlettaz & Humbert, 2019). Despite of the growth in butterfly abundance, the single effect of flower strips cannot be classified, as the mean proportion of flower strips was only 0.1% (± 0.2).

We found a significant effect of distribution on colony size, but the effect of distance explains considerably more variation. A higher energy spent during foraging can explain the smaller colony size. Therefore, we conclude that the even distribution of flower strips is more beneficial because the distances to food sources in the landscape is lower and

honeybee colonies can develop better. According to Buhk et al. (2018), the distance of food sources affected the reproduction and abundance of species. Moreover, for honeybee workers, the search for food requires balancing costs and benefits (Couvillon et al., 2014b). Field studies that took the aspects vicinity, configuration and connectivity of flower strips into account could not verify a positive effect on landscape scale (Aviron et al., 2011; Zingg et al., 2019).

The amount of available nectar and pollen played an important role in this study. The plant composition of the flower strips was based on real seed mixtures. Even though some plant species could not be considered because no information on their pollen and nectar supply was available, the species compositions appeared to be representative of realistic flower strips. Our results suggest that flower strips with low availability of nectar and pollen might even have negative effects on honeybee colonies. The development of a colony is influenced by pollen and nectar scarcity in quantity and quality (Di Pasquale et al., 2013). Hence, less pollen results in lower colony size, which in turn further decreases the number of forager bees (Keller, Fluri & Imdorf, 2005). If nectar resources are scarce, the forage search is more

difficult and the honeybees' chances of successful return to the colony decrease (Naug, 2009). The nutritional stress of individuals is a major driver of colony loss. Therefore, the spatial and temporal availability of food resources determines the colony status (Naug, 2009). Furthermore, with scarce resources, the foraging distances increase (Beekman & Ratnieks, 2000). According to Steffan-Dewenter and Kuhn (2003), in simple landscapes the foraging distance of pollen forager honeybees was higher than in complex landscapes, but this was not the case for nectar-collecting bees. We do not distinguish between nectar- or pollen-collecting bees. However, Becher et al. (2014) found out that increasing distance leads to higher foraging costs concerning energy expenditure and mortality of foragers. As a consequence, the honey store diminishes (Becher et al., 2014).

The different plant compositions had the consequence that the high-quality flower strips had longer flowering periods than the low quality one, besides generally higher availability of nectar and pollen. In early spring and summer there is a food shortage after nectar and pollen provided by mass-flowering crops (Decourtye et al., 2010). Flower strips can fill foraging gaps in this time and late season, if they contain diverse plant species (Wagner et al., 2014). In this way, temporary food dearth for wild and honeybees can be reduced or avoided (Ramseier et al., 2016; Wagner et al., 2014). Thus, flower strips can counteract the lack of floral resources that leads to a decline in bee populations (Potts et al., 2003; Wagner et al., 2014).

Comparison of our results with field studies of the effects of flower strips on species abundance is difficult because often only little information about the seed mixtures is provided. Studies about field margins with wild plant species or grass strips showed positive effects on bumblebees and wild bee populations (Carvell, Meek, Pywell, Goulson & Nowakowski, 2007; Haaland & Gyllin, 2011; Haaland et al., 2011; Heard et al., 2007; Jönsson et al., 2015; Kohler, Verhulst, van Klink & Kleijn, 2008; Pywell et al., 2005, 2006; Pywell, Meek, Carvell, Hulmes & Nowakowski, 2007) but there was no documentation about honeybees. Carvell et al. (2007) reported a high abundance of bumblebees on flower strips with pollen- and nectar-rich plant species. This was confirmed by Pywell et al. (2006). In general, agri-environment schemes can promote pollinators more in more intensively agricultural landscapes, concerning the number and species richness of bumble bees supported, than in heterogeneous landscapes where there are other foraging habitats (Carvell et al., 2011). Nevertheless, some studies indicate that generalists benefited more than rare species from flowering areas or flower strips (Haaland et al., 2011; Meek et al., 2002).

According to Warzecha, Diekötter, Wolters and Jauker (2018), the attractiveness of seed mixtures differs among pollinator species. However, attractiveness was not dependent on the number of plant species as seed mixtures with both low and high plant species richness showed high attractiveness. The high amount of key plant species in the

seed mixture with low number of plant species was accountable for the attractiveness. Thus, pollinators can be promoted with a selection of few key plant species over flowering season (Warzecha et al., 2018).

This suggests that the choice of plant species for environmental schemes should be considered carefully, particularly with respect to nectar and pollen supply (M'Gonigle, Williams, Lonsdorf & Kremen, 2017).

Independent of these three parameters (areal proportion, spatial distribution and quality), we could observe a pattern of the development of colony size and honey store in the first six years that was repeated in the second six years. The absolute food supply is not different in all years, only the spatial arrangement is different due to the four-year crop rotation. An effect of food supply can be excluded. Instead, the frequency of the observed reoccurring pattern coincides with the frequency of the implied weather regime, because weather conditions were repeated after six years. This indicates that the weather conditions - temperature and precipitation - have strong effects on the development of the honeybee colonies. Weather affected the flight time and, thus, the foraging success and the honey store. The annual flight time was lowest in the third year of each six-year sequence (Appendix A: Table S3). Accordingly, we observed the lowest level of honey store in years 3 and 9. In these years, the honeybees started foraging in the middle of April instead of middle or end of March, because the weather conditions were too wet, cold or both (Appendix A: Fig. S2). Despite poor environmental conditions, honeybees survive due to their ability to store food resources (Nürnberger, Härtel & Steffan-Dewenter, 2019). However, this depends strongly on foraging conditions during the previous year (Seeley & Kirk Visscher, 1985). Further, low temperatures in February were shown to have a negative effect on the colony and increase mortality (Switanek, Crailsheim, Truhetz & Brodschneider, 2017), although we could not see this effect at the end of years 3 and 9. Thus, the weather conditions and reduced honey stores at the end of the years 3 and 9 can explain the decline of colonies in years 4 and 10 over all scenarios (see Fig. 5). Nürnberger et al. (2019) found, that reduced foraging activity early in the year (here induced by a delay in brood onset and hence reduced worker force) led to decreased honey stores between May and August. However, there was no effect on the colony at the end of the year. In addition to food storing, the recruitment behaviour, search radius and generalist foraging behaviour of honeybees can actually buffer the risk of starvation (Nürnberger, Steffan-Dewenter & Härtel, 2017; Potts et al., 2010b), but only as long as resource environments are also sufficiently diverse (Nürnberger et al., 2019).

Methodology

Simulation modelling of honeybee colonies can be a tool for assessing how agricultural landscapes could be improved through biodiversity measures in the most efficient way in order to promote populations of honeybees and other

pollinator species. Effects of factors such as landscape configuration and composition on honeybees are difficult to investigate (Henry et al., 2017), because honeybee colonies may develop differently even under identical environmental conditions. For this the BEEHAVE model, which links two processes, the in-hive dynamics of the honey bee colony and the dynamics of foraging bees in the landscape context (Agatz et al., 2019), is a useful tool. A limitation is that in BEEHAVE we consider only one colony, whereas under real conditions competition between colonies or with other pollinators may play a role. For example, Ramseier et al. (2016) observed that foraging competition between honeybees and wild bees on remaining flowering areas is reduced when flowering strips are established. Because some interactions and stressors such as pesticide use were not included, our inferences about the effects of flower strips under real world conditions of agricultural management are limited. Nevertheless, those initial results on quality and quantity of the flower strips can help us to get a better understanding of the potential benefits they have on honeybee colony development.

While developing the landscape scenarios, we followed some guiding principles for the establishment of flower strips, e.g., area size, annual or perennial flowering aspect or location of flower strips, which influenced the connectivity and vicinity of flower strips to the hive in the landscape. Further, the number of flower strips varied in the scenarios. There were four flower strips in each ‘evenly distributed’ landscape scenario, while there were between two (*Clustered-0.24%-Clustered-0.29%*) and eight flower strips (*Clustered-1.04%*) in the ‘clustered distributed’ scenarios. The distances differed among the scenarios due to their location and possible geometric constraints. Information about the quality of food patches in the landscape and their amount of nectar and pollen was based on literature data, which is not easy to find and requires simplifying assumptions and use of approximate values. 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. Further, changes in plant species composition and richness of flowering species over the years (Frank, Aeschbacher & Zaller, 2012; Tschamtko, Batáry & Dormann, 2011) could not be considered in our study. Furthermore, the flower density is dependent on habitat type (Frank et al., 2012). However, as we did not have sufficient information on such processes, the phenology of the pollen and nectar amount was the same every year in the models, depending only on habitat size. If we had more specific information, multiple input maps, e.g., for each month could be imported in BEESCOUT. This would allow for a higher accuracy of the assessments of detection probability of the food sources, which influences the foraging behaviour of the bees in the model. Furthermore, we assumed that forage availability is either constantly high or low, i.e. nectar and pollen are replenished to their given values at the end of each day.

Conclusion

The investigations demonstrated that the quality of flower strips, represented by the plant composition of seed mixtures, influenced colony size. Colony size increased with pollen- and nectar-rich flower strips (high quality). Evenly distributed flower strips and increasing areal proportion increase honeybee colony size. In contrast, flower strips of low quality were not sufficiently rewarding for the honeybees. Thus, in the scenarios with low quality colony size tended to decrease. Furthermore, the study demonstrated that the honey store from the previous year played an important role, also regarding the resilience of a honeybee colony. Accordingly, the modelling can be a useful tool to evaluate effects of landscape composition, configuration and crop rotation on pollinating insects such as honeybees.

Declaration of Competing Interest

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

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Supplementary materials

Supplementary material associated with this article can be found in the online version at doi:[10.1016/j.baae.2022.02.005](https://doi.org/10.1016/j.baae.2022.02.005).

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