

Agri-environment schemes enhance pollinator richness and abundance but bumblebee reproduction depends on field size

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Abstract

1. Pollinators have experienced a dramatic decrease world-wide due to agricultural intensification. In many countries, agri-environment schemes (AES) have been introduced to counteract this current trend. However, until now, the relative importance of each AES for biodiversity and ecosystem services is still little understood and might change depending on landscape context. Complex landscape-experiments are required to fill this knowledge gap, enabling the implementation of sustainable intensification of food production.
2. In our study, we compared the effectiveness of the two most popular AES in Germany, organic farming and flower strips, in supporting pollinators and flower resources. We selected nine landscapes along a gradient of increasing field size, (configurational heterogeneity), each with a triplet of winter wheat fields: one organic, one conventional with flower strip and one conventional without flower strip as a control. We surveyed insect-pollinated plants and pollinators (bumblebees, solitary bees and hoverflies). Additionally, we placed bumblebee colonies in the field edges to monitor their growth (colony weight gain) and reproduction (queen production).
3. Flower strips stood out with the highest abundance and richness of pollinators. In contrast, bumblebee colony growth and plant richness benefited equally from organic and flower strip schemes. At the landscape scale, smaller fields had a positive effect on plant richness and bumblebee reproduction in flower strips. By contrast, bumblebee colonies in organic agriculture benefited most from large fields, as large organic fields provided much more flower resources than the narrow flower strips.
4. *Synthesis and applications.* Our results showed that both local and landscape management shaped pollinator communities and their reproduction. Overall, organic farming and flower strips appeared to be effective tools to mitigate flower shortage in conventional cereal fields, with organic farming supporting the highest

flowering plant cover per field. Flower strips enhanced local pollinator richness most, but increased bumblebee reproduction only when the surrounding landscapes had small fields with long field borders. Therefore, our results reveal that European Union policies need to take into account that the effectiveness of agri-environment schemes depends on the structure of the surrounding landscape.

KEYWORDS

configurational heterogeneity, edge effect, field size, flower strip, hoverfly, landscape structure, organic farming, solitary bee

1 | INTRODUCTION

Pollination is increasingly recognized as a key ecosystem service under threat. The reproduction of around 90% of flowering plant species depends on animal pollination (Ollerton, Winfree, & Tarrant, 2011), as well as about 37% of the world's food production (Klein et al., 2007). In recent years, pollinator diversity and abundance have dramatically decreased (Potts et al., 2010). The main driver of this ongoing decline is agricultural intensification leading to semi-natural habitat loss and increased use of agrochemicals (Kovács-Hostyánszki et al., 2017). Consequently, this intensification has resulted in the loss of nesting and foraging resources for pollinators.

In Europe, agri-environment schemes (AES) were introduced in the late 1980s to counteract the negative environmental effects caused by modern agricultural practices (Batáry, Dicks, Kleijn, & Sutherland, 2015). Despite their important role as conservation tools, AES implementation, monitoring and development have been limited until now (Batáry et al., 2015). Therefore, research on the effectiveness of specific AES options at delivering ecosystem service, such as pollination, is urgent. In Lower Saxony (DE), the two most popular AES concerning uptake (AES Lower Saxony, 2019), are organic farming and flower strips. Local management on the field, such as organic agriculture and flower strips, is proposed as one important driver of pollinator diversity (Kennedy et al., 2013; Kremen et al., 2007). Several studies in particular have shown local flower availability over space and time to be essential (Blaauw & Isaacs, 2014; Burkle, Delphia, & O'Neill, 2017; Carrié, Ekroos, & Smith, 2018).

Over the last two decades, evidence has been growing for the importance of the interaction between local field management and landscape effects on wild pollinators (Batáry et al., 2017; Hass et al., 2018; Rundlöf, Bengtsson, & Smith, 2008). Heterogeneous landscapes should increase pollinator diversity through higher crop and habitat diversity and higher connectivity. According to Fahrig et al. (2011), we can recognize two components of heterogeneity: compositional heterogeneity (different cover types) and configurational heterogeneity (spatial arrangement of the cover types), that can be measured by metrics such as mean patch size, edge density or patch shape. The positive effect of semi-natural areas on pollination is well known (Blaauw & Isaacs, 2014; Kremen et al., 2007; Persson & Smith, 2011; Ricketts et al., 2008), but the role of configurational

heterogeneity is less clear. Theoretically, small fields with their high amount of field boundaries should provide easy access to adjacent fields, nesting and food resources, and edges to guide the orientation of dispersing pollinators (Hass et al., 2018). In the agricultural matrix, especially when dominated by non-flowering crops, such as cereals, the role of field boundaries harbouring flowering plants becomes crucial (Alignier et al., 2020). The few studies trying to understand the effect of field size had contrasting results, sometimes highlighting the benefits of small field agriculture or high amount of field borders on pollinators (Happe et al., 2018; Hass et al., 2018; Hopfenmüller, Steffan-Dewenter, & Holzschuh, 2014; Sirami et al., 2019), sometimes finding no or weak effects (Hass et al., 2019; Holzschuh, Steffan-Dewenter, & Tschardtke, 2010; Kennedy et al., 2013; Steckel et al., 2014; Steffan-Dewenter, Münzenberg, Bürger, Thies, & Tschardtke, 2002). Due to these conflicting results, a better understanding of pollinator responses to field size and AES management is needed.

Here we evaluated the effectiveness of two AES, organic farming and flower strips, in sustaining pollinators by taking into account the effect of the mean field size in the landscape (Fahrig et al., 2015; Klimek, Lohss, & Gabriel, 2014). We sampled bees and hoverflies and surveyed the diversity of insect-pollinated plants. Moreover, we placed bumblebee colonies (*Bombus terrestris*, Linnaeus 1758, Apidae, Hymenoptera) in field edges to monitor their growth and reproduction. The relative importance of different AES for biodiversity conservation remains unclear and might change with landscape context. Hence, only complex landscape experiments may fill this knowledge gap. We conducted a study at the landscape scale under a real-world scenario by placing bumblebee colonies next to the fields. *Bombus terrestris* is a generalist eusocial bee that follows an annual colony cycle and is common throughout European agricultural landscapes (Goulson, Hughes, Derwent, & Stout, 2002). Moreover, *B. terrestris* is a central place forager with large foraging ranges and adults and larvae completely depend on pollen and nectar collected by the workers, therefore, colony fitness is mostly driven by flower resources available at the landscape scale (Goulson, 2003; Westphal, Steffan-Dewenter, & Tschardtke, 2006).

We addressed the following hypotheses: (a) flower strips support pollinators (hoverfly and bee abundance and species richness; bumblebee colony growth) and insect-pollinated plant richness better than organic farming, and organic farming better than conventional

farming; (b) effects are expected to be moderated by mean field size in the landscape with a positive effect of small-scale agriculture.

2 | MATERIALS AND METHODS

2.1 | Study sites and experimental design

We carried out this study in Southern Lower Saxony, in the counties of Göttingen, Northeim and Osterode in June and July 2017. In the study region, nine landscapes were selected. In each landscape, we selected a triplet of winter wheat fields (within triplet distance = 1.58 ± 0.20 km ($M \pm SE$); between triplet distance = 24.79 ± 1.87 km), consisting of one organic field (AES), one conventional with a flower strip (AES) and one conventional field as control (field size 1–5 ha). Overall, 27 fields were selected belonging to 18 different farmers, as the conventional field and the one with flower strip within the same triplet always belonged to the same farmer. A preselection of possible triplets was carried out using ArcGIS 10.2 (1999–2013 ESRI Inc.) and then the final site selection was done after personal interviews with farmers and site visits in April and May 2017. To standardize the comparison, all selected fields were adjacent to a grassy margin adjoining a (dirt) road (Figure 1). In the case of fields with flower strips, the strip was located between the grassy margin and the field edge. In Lower Saxony, flower strips can be 6–30 m wide (Table S1) and they must contain at least five flowering species listed in the AES rules of Lower Saxony 2014 (Appendix S1; AES Lower Saxony, 2019). All selected landscapes were situated in simple agricultural landscapes with low amounts of semi-natural habitat (semi-natural habitat percentage in 1,000 m radius buffer $M \pm SE$: 11.30 ± 1.12). The study landscapes represented a gradient of mean field size in a buffer of 1,000 m around each field (Fahrig et al., 2015; Klimek et al., 2014). This gradient of field size ranged from 1.75 to 4.24 ha and it was independent from semi-natural habitat percentage (Pearson correlation, $r = -0.147$, $p = 0.462$). As expected, the length of linear elements and mean

field size in a buffer area of 1,000 m radius were closely correlated (Pearson correlation, $r = -0.726$, $p < 0.001$). In addition, focal field size ($M \pm SE = 4.76 \pm 0.614$) and mean field size were correlated (Pearson correlation, $r = 0.549$, $p = 0.002$). In each field edge, we established one linear transect (50 × 2 m, 1 m in the grassy margin and 1 m in the field) between the grassy margin and the field (Figure 1). In fields with flower strips, the transect was located between the grassy margin and the flower strip.

2.2 | Data collection

2.2.1 | Plant survey

In each field, we recorded all plant species and cover between June and July 2017 in the transect in four plots (5 × 1 m in size and 10 m distance between them) in the grassy margin and in four plots (5 × 1 m in size and 10 m distance between them) in the field edge ($n = 216$; Figure 1). We identified all plant species in the plots and selected for later analysis only the insect-pollinated ones according to 'BioFlor' database on biological and ecological traits of the vascular flora of Germany (Klotz & Durka, 2002).

2.2.2 | Pollinator survey

Two different surveys were carried out three times between June and July 2017. First, we surveyed bees and hoverflies by a 15-min transect walk along the 50-m transect (Holzschuh et al., 2010; Rundlöf et al., 2008). Second, a sweep-net sampling standardized with 60 sweeps per transect (one sweep per footstep) was carried out along the transect. Therefore, the term 'pollinator' refers actually to flower visitors. Pollinators were killed with ethyl acetate (70%), brought to the laboratory and conserved at 4°C. We identified pollinators to species level. Surveys were carried out between 9 a.m. and 6 p.m. in weather conditions allowing the activity of the



FIGURE 1 Experimental study design: nine triplets of wheat fields consisting in a conventional field with flower strip, an organic and a conventional control field

studied insects (sunny or partly cloudy and temperature above 15°C). Temperature, weather conditions, wind (Beaufort-scale) and flower cover were registered during the survey. Flower cover was estimated by sight as the percentage cover of actual flower corollas per area ground surface.

2.2.3 | Bumblebee experiment

About 54 colonies of commercial bumblebees *B. terrestris* were bought at STB Control, Aarbergen, Germany and set up in the fields during the second week of June 2017 after the mass flowering of the oilseed rape when floral resources were available in the flower strips. Each colony consisted of the founding queen and approximately 40 workers. Two colonies were randomly assigned to every field. They were installed next to each other in the middle of the transect (Figure 1). The colonies were housed in inner plastic cages contained inside cardboard boxes, and a Plexiglas tube allowed the bees to freely forage outside. The boxes were placed on wooden pallets and were sheltered from sun and rain by a white plastic roof (Figure S1). During the first week, the bumblebees had time to familiarize with the surrounding environment while they were provided with sugar syrup (Goulson & Stout, 2001; Klein et al., 2007). In the second week, the sugar syrup was removed. The colonies were weighted weekly in the field to monitor the colony growth (Westphal, Steffan-Dewenter, & Tschardtke, 2009). This enabled us to measure the proportional colony weight gain, which we measured as the ratio between the maximum weight gained by the colony during the experiment and the initial weight (Westphal et al., 2009). Additionally, we performed colony traffic rate observations in July 2017 to study colony foraging intensity (Stanley, Russell, Morrison, Rogers, & Raine, 2016). One observer sitting 1 m from the colony entrance counted the total number of individuals flying in and out of the colony during 15 min. Observations were carried out between 9 a.m. and 6 p.m. in weather conditions allowing the activity of bumblebees (sunny or partly cloudy and temperature above 15°C). In the fifth week, the colonies were collected and frozen at -18°C to preserve the bumblebees for further investigations. Afterwards, we dissected the nests to count the number of queen brood cells. In *B. terrestris* the body size distribution of females is strongly bimodal as queens usually show much larger body sizes than workers (Rundlöf et al., 2015). In our colonies, larger cells were easily distinguishable from average ones and, therefore, we were able to select all exceptionally large cells. Moreover, the inter tegula distance of 20 random workers of every colony was measured with Vernier callipers in order to estimate colony body sizes (Persson & Smith, 2011; Stanley et al., 2016).

2.3 | Statistical analyses

To understand how landscape configuration and management type affected wild pollinators, bumblebee colonies and insect-pollinated plants, we applied linear mixed effect models by using the `LME4` package (Bates, Mächler, Bolker, & Walker, 2015) of the statistical

software R version 3.4.1 (R Core Team, 2017). Mean field size within a 1,000-m radius around the transect in each field was used as proxy to characterize the landscape configuration. Before running any model, data exploration was carried out through visual inspection of box-plots, smoothed histograms, quantile-quantile plots and scatterplots (Zuur, Ieno, & Elphick, 2010). Plots were created using the R-packages `GGPLOT2` (Wickham, 2009) and `EFFECTS` (Fox, 1987). We operated a step-wise backward selection comparing the AICc (Burnham, Anderson, & Huyvaert, 2011) of models where ML was specified as the method and refitted the best linear mixed effects models using the Restricted Maximum Likelihood to report the results. All models were validated visually by checking homoscedasticity and residual normality (Zuur, Ieno, Walker, Saveliev, & Smith, 2009).

2.3.1 | Plant richness

We tested the effects of management (one factor with three levels: flower strip, organic and conventional), mean field size, plot position (one factor with two levels: margin and field) and their interactions on the species richness of insect pollinated plants. The nested study design was taken into account in the random structure of the models, by considering field nested in farmer nested in village as random effects, as the conventional and the flower strip fields always belonged to the same farmer and as the plant survey was performed in every field once in the grassy margin and once in the field. To check all pairwise comparisons of management levels, the `relevel` function was applied. Additionally, we tested the effect of management on the percentage of flower cover using the `lmer` function (`LME4` package; Bates et al., 2015). Finally, we extrapolated flowering plant cover to field level, by multiplying local flowering plant cover per field area (ha). To consider also the differing amount of flower resources offered by the flower strip and its neighbouring conventional wheat field, in case of flower strip fields, we summed the extrapolated flowering plant cover per strip and the extrapolated flowering plant cover per conventional wheat field.

2.3.2 | Pollinator richness and abundance

We pooled together the pollinator survey data of the two survey methods and three rounds and analysed separately species richness and abundance of solitary bees, bumblebees and hoverflies, and abundance of honeybees. All full models included three fixed effects: management, mean field size and semi-natural area. The random effects were farmer nested in village. We fitted GLMMs assuming Poisson or negative binomial error distribution. We used the control parameter optimizer 'bobyqa', part of the `MINQA` package (Bates, Mullen, Nash, & Varadhan, 2014; Zuur et al., 2009) that is used by default as the optimization algorithm by the `LME4` package (Bates et al., 2015). We also fitted GLMMs assuming Poisson or negative binomial error distribution to test the effect of flower cover on species richness and abundance of solitary bees, bumblebees and

hoverflies. Finally, to investigate the effects of flower strip width and length on pollinators occurring in flower strips, we fitted a generalized linear model assuming negative binomial distribution.

2.3.3 | Bumblebee experiment

To test the effect of management, field size and semi-natural area and their interactions on proportional colony weight gains and on colony body size, we applied linear mixed-effects models (LMEs) using the function `lmer` (LME4 package; Bates et al., 2015). When analysing the number of queen cells, we fitted a GLMMs assuming negative binomial error distribution. Since in each transect two bumblebee colonies were installed, the random structure of the models was transect nested in farmer nested in village.

3 | RESULTS

3.1 | Plant richness

We recorded a total of 98 insect-pollinated plant species (Klotz & Durka, 2002), 66 species in the grassy margins and 80 species within the field edge. Fourteen species were indicated as flower strip species according to the (AES Lower Saxony, 2019; Table S2). Overall, both AES sustained higher plant species richness compared to conventional fields (Figure 2; Table S3). The interaction between transect

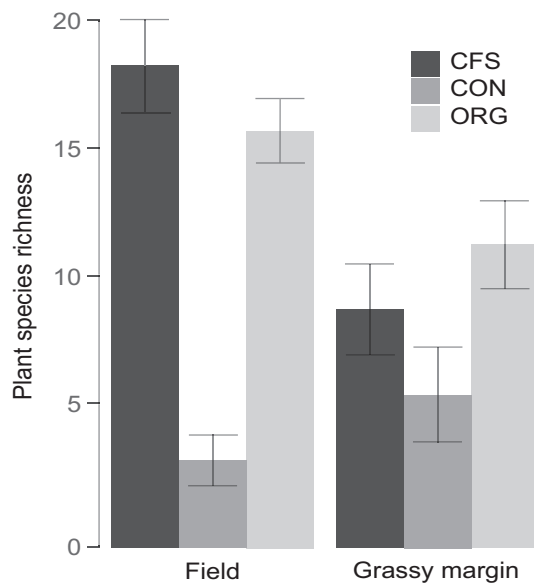


FIGURE 2 Mean of insect-pollinated plant richness in relation to management type (flower strip, conventional or organic), within the field edge and in the grassy margin ($n = 27$). Without considering the species that are officially requested to be part of flower strips, species richness in flower strips would decrease to 12.45 ± 1.42 (mean \pm SEM). Error bars represent standard error means (SEM). CFS, conventional field edge with flower strip; CON, conventional field edge; ORG, organic field edge

and management revealed that the highest plant species richness was found in the field edge in flower strips, while in the grassy margin under organic farming. Additionally, increasing field sizes had a marginal negative effect on plant species richness (Figure S2; Table S3).

3.2 | Pollinator richness and abundance

We recorded a total of 1,018 pollinators: 641 bees and 377 hoverflies. We identified 17 hoverfly species and 28 bee species. *Bombus terrestris* was the most abundant bee species (357 individuals) followed by *Bombus lapidarius* (Linnaeus, 1758, 89 individuals), *Bombus pascuorum* (Scopoli, 1763, 60 individuals) and *Lasioglossum pauxillum* (Schenck, 1853, 27 individuals). *Episyrphus balteatus* (De Geer, 1776, 72 individuals), *Melanostoma mellinum* (Linnaeus, 1758, 62 individuals), *Sphaerophoria scripta* (Linnaeus, 1758, 61 individuals) and *Platycheirus clypeatus* (Meigen, 1822, 9 individuals) were the most abundant hoverfly species (complete species list in Table S4). Most hoverflies recorded have aphidophagous larvae and may therefore use wheat fields as reproduction sites when pesticide levels are low. Management was the main driving factor in all models, having a significant effect on all response variables. Bumblebees had the highest abundance and species richness in flower strips, and the lowest abundance and species richness in conventional fields with intermediate levels in organic management (Figure 3a; Table S5). We found the same pattern for solitary bee species richness and hoverfly abundance, but solitary bee abundance was equally high under flower strip and organic management and there were no effects on hoverfly species richness (Figure 3b). Additionally, we did not find any effect of width or length of the flower strip on overall pollinator abundance or on pollinator species richness, and we found a strong positive effect of the percentage of flower cover on abundance and species richness of all considered pollinator groups (Table S6). Mean field size and semi-natural habitat (removed from final models) did not have an effect neither on abundance nor on species richness. By contrast, larger field size had a negative effect on honeybee abundance in fields with flower strips and a positive effect in organic fields (Figure S4). Finally, we tested the relationship between local flower cover and management, showing that floral availability strongly depends on management type (Table S3). Results did not change excluding insects collected by sweep-netting.

3.3 | Bumblebee experiment

Bombus terrestris colonies showed an overall better development when located in organic fields or fields with flower strips compared to fields with conventional management. The weight of the colonies increased over the course of the experiment until the third or fourth week of exposure when the colonies started to collapse. Management was the variable that most strongly explained the changes in proportional colony weight gain. Both, the colonies installed in conventional fields with flower strips and in organic fields, gained significantly more weight than the ones in conventional fields

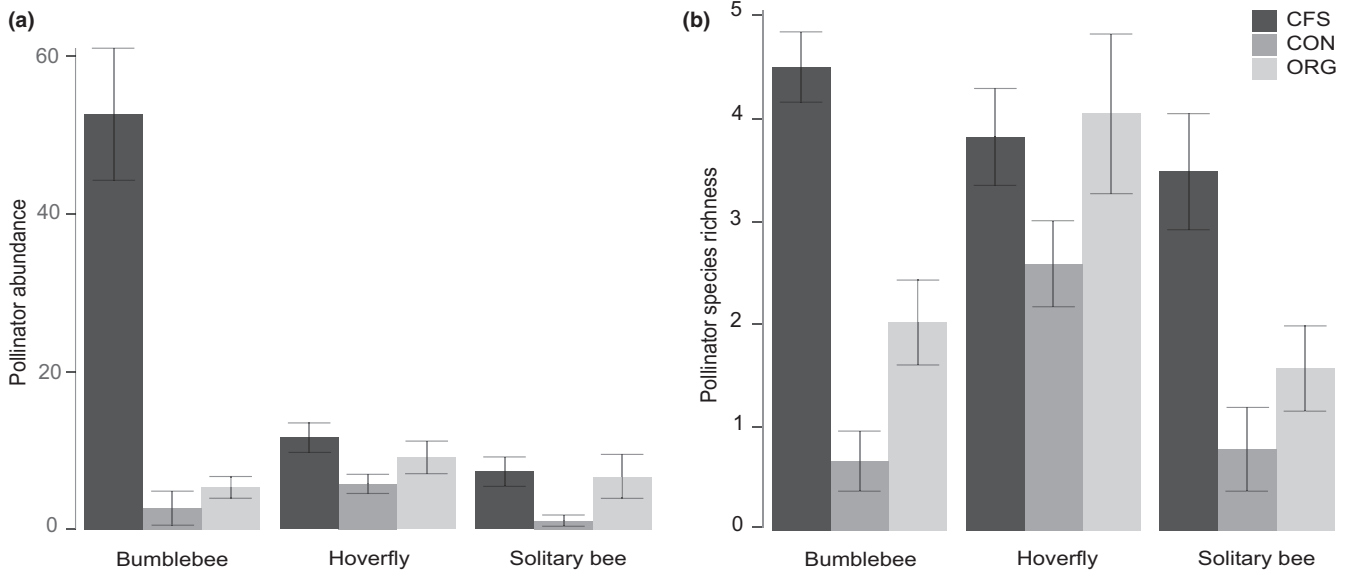


FIGURE 3 Mean of pollinator abundance (a) and species richness (b) in relation to management type (flower strip, conventional or organic; $n = 27$). Error bars represent standard error means (SEM). CFS, conventional field edge with flower strip; CON, conventional field edge; ORG, organic field edge

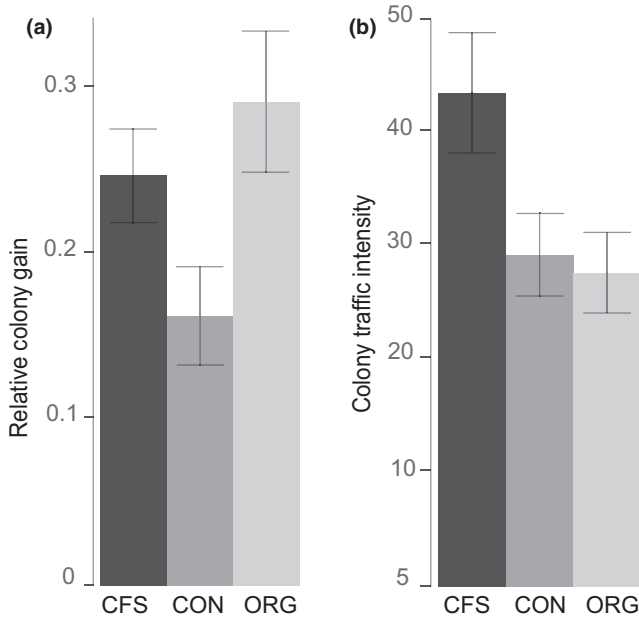


FIGURE 4 Mean of relative colony growth ratio (a) and foraging intensity (b) in relation to management type (flower strip, conventional or organic; $n = 50$). Error bars represent standard error means (SEM). CFS, conventional field edge with flower strip; CON, conventional field edge; ORG, organic field edge

(Table S7; Figure 4a). However, we did not find any significant difference between organic and flower strip management. Colonies installed in fields with flower strips had a significantly higher colony foraging rate (Figure 4b) than colonies installed in organic and conventional fields. Mean field size and semi-natural habitat (removed from final models) did not have an effect on colony weight gain nor foraging rate. The interaction between management and mean field size was the most important factor explaining the number of queen

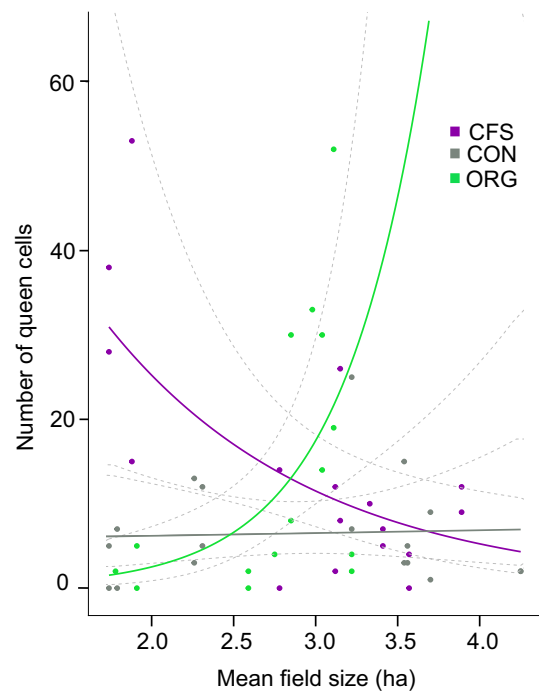


FIGURE 5 The effect of the interaction between management and mean field size in a 1,000-m radius on colony queen brood cells ($n = 50$). Different colours depict the management types, as indicated in the legend: CFS, conventional field edge with flower strip; CON, conventional field edge; ORG, organic field edge. The regression lines are based on the full model (link function: log)

brood cell (Table S7). In fields with flower strips, queen brood cell number decreased when mean field size at the landscape scale increased, in contrast to organic fields, where we found the opposite trend (Figure 5). For mean colony body size we did not find any significant effect (Table S7).

4 | DISCUSSION

Here we showed that flower strips and organic management enhanced pollinator richness and abundance, as well as bumblebee colony performance much more than conventional agriculture. Bumblebee reproductive success was moderated by field size with smaller fields having a positive effect on the colonies in flower strips, whereas colony reproduction in organic agriculture benefited from large fields.

4.1 | Plant richness

We found the lowest species richness of insect-pollinated plants in field edges with conventional management. This was probably because of the use of herbicides and inorganic fertilizers, which impact not only the field but also the grassy margin adjacent to it (Fried, Villers, & Porcher, 2018). In contrast, no herbicides are allowed in organic fields and flower strips, which is probably why we found three times higher plant species richness in both AES. Several studies already showed that organic management can strongly increase plant diversity compared to conventional management (Batáry, Sutcliffe, Dormann, & Tschardt, 2013; Ekroos, Heliölä, & Kuussaari, 2010; Romero, Chamorro, & Sans, 2008), but we are the first to directly compare organic management and flower strips in a gradient of field size, showing that flower strips sustained the highest in-field species richness of insect-pollinated plants, whereas organic fields had the highest richness in the margins. Diverse seed mixtures are sown in flower strips, and therefore, their high plant diversity is not surprising. Conversely, it is important to point out that organic management strongly increased plant richness both within the wheat field edge and in the grassy margin compared to conventional management (Batáry et al., 2013). In particular, the margins of organic fields supported a higher richness than flower strips. The reason might be that strips of conventional fields are usually turned to flowering AES for some years and the legacy of conventional management can still be visible in the grassy margin adjacent to the flower strip. Overall, both AES sustained high levels of plant diversity, but they differed in the amount and spatial distribution of the flower resources provided. In fact, in conventional fields with flower strips, flower resources were densely concentrated in the flower strips, while there were more flower per field under organic farming.

In our study, smaller fields had a positive effect on plant richness. Little is known about landscape effects on plant species richness and findings in the literature are mixed, reporting no effect of heterogeneity (Batáry et al., 2013; Krauss, Klein, Steffan-Dewenter, & Tschardt, 2004; Marini, Fontana, Scotton, & Klimek, 2008) or positive effects (Janišová, Michalcová, Bacaro, & Ghisla, 2014; Sutcliffe et al., 2015). Our results show that heterogeneous landscapes with more field margins might increase the potential pool of species available to colonize local sites because of an overall higher connectivity.

4.2 | Pollinator richness and abundance

The pollinator survey revealed that both AES supported and enhanced the presence of pollinators in contrast to conventional fields. Abundances of all considered groups (hoverfly, solitary bee and bumblebee) and bee species richness reached their peaks in fields with flower strips. Therefore, our results back up evidence of pollinator enhancement from flower strips already found in literature (Blaauw & Isaacs, 2014; Buhk et al., 2018; Jönsson et al., 2015; Scheper et al., 2013). This response is likely due to additional nesting sites and rewarding food resources, such as *Cirsium arvense* or *Phacelia tanacetifolia* (Figure S5; Ouvrard & Jacquemart, 2018). However, the outstanding performance of flower strips as a scheme enhancing pollinators should be taken with caution. First, the strong effect of short living flower strips could be a result of attracting pollinators without sustaining their populations locally (Wood, Holland, & Goulson, 2015). In fact, studies on a population level at the landscape scale are still lacking (Kleijn et al., 2018) and the observed positive effect could be due to behavioural spatio-temporal concentration or dilution of otherwise unaffected populations (Scheper et al., 2013). Second, pesticides are sprayed in conventional fields adjacent to flower strips and their side effects may act as an ecological trap. However, recently, Kleijn et al. (2018) found enhanced bee abundance at the landscape levels in response to wildflower fields. For most pollinator groups we found intermediate levels of abundance and species richness in organic fields. This might be only due to the fact that the resources in organic fields were not as densely concentrated as in flower strips, but more distributed across the fields. Consequently, organic farming showed overall higher flowering plant cover per field (Figure S3), but lower pollinator densities than in flower strips per unit area. Additionally, organic farming supplies several other benefits over the total field areas (e.g. enhancing pest control, preventing soil erosion and holding more water; Gattinger et al., 2012).

Concerning the second hypothesis, we did not find any evidence of a landscape effect, probably due to the fact that the landscapes did not differ enough in mean field size. In fact, Sirami et al. (2019) and Hass et al. (2018) found a positive effect of field size on pollinators using more than 200 agricultural landscapes and a much steeper gradient of heterogeneity (range of field mean size: 0.48–12.71 ha). In addition, also field margin quality and not only field size might play an important role in sustaining pollinators at the landscape scale.

4.3 | Bumblebee experiment

The weight gain of colonies installed in organic fields or in fields with flower strips was significantly higher compared to the control in conventional fields. Main drivers of this result are probably the abundance and diversity of floral resources that are vital for bumblebees (Crone & Williams, 2016; Westphal et al., 2009; Wood et al., 2015). As bumblebees do not store great amounts of

pollen and nectar, they are directly affected by resource shortages (Westphal et al., 2009). In our study, conventional fields provided the lowest flowering plant species richness and cover, partly explaining the poor performance of the colonies in conventional fields (Spiesman, Bennett, Isaacs, & Gratton, 2017). Bumblebees are central place foragers and their fitness strongly depends on the distance between the nest and the flower resources. In flower strips, proximity to floral resources determined short foraging distances (Figure 4b) and probably affected colony growth positively. Interestingly, colonies next to fields with organic management showed the same colony weight gain as colonies next to flower strips although the local flower cover was much lower. One reason might be that there were more flowers per field in organic rather than in fields with flower strips, where resources were spatially concentrated in the strip (Figure S3). In addition, organic fields provided higher floral diversity. Pollen of different plants differ in their nutritional contribution and the availability of high pollen diversity can be important for optimal colony growth (Hass et al., 2019; Vaudo, Tooker, Grozinger, & Patch, 2015). Besides floral resources, a second potential driver of bumblebee colony development could have been the exposure to insecticides. Insecticides can have strong lethal and sub-lethal effects on bees causing changes in foraging behaviour (Stanley et al., 2016; Whitehorn, O'Connor, Wackers, & Goulson, 2012). In our study, conventional fields were sprayed with insecticides that are not permitted in the AES areas. Moreover, in our study, colony reproduction was moderated by the interaction of management type and field size at the landscape scale. The production of queens is very important for colony fitness, because it determines the population size after hibernation (Westphal et al., 2009). We found that the mean field size in a 1,000-m buffer had a negative effect on the number of queen brood cells produced by the colonies in flower strips. This could be explained by the higher configurational heterogeneity established by smaller field sizes, which provided corridors, more food resources and nesting sites in the agricultural matrix (Fahrig et al., 2015; Persson & Smith, 2011). This indicates that the positive effect of increased colony growth in flower strips can only lead to increased reproductive output in landscapes with smaller fields and more field borders. By contrast, the effect of mean field size on queen production in organic fields was positive. Since focal field sizes and mean field sizes in this study were highly correlated, a possible explanation would be that larger organic fields had a more beneficial effect on bumblebees, as they provided larger amount of resources and pesticide free areas. Carvell et al. (2017) found that more queens survived when workers were able to forage closer to their nest. In this study, both combinations of smaller fields with flower strips or larger fields with organic farming likely provided more resources nearby the nests. This might also explain the similar effect of field size found on the abundance of honeybees, and even more mobile pollinators than large bumblebees (Figure S4). In conventionally managed fields, reproductive success remained equally low across all landscapes indicating the

detrimental effect of low resource availability and pesticide exposure in combination with bumblebee reproduction.

5 | CONCLUSIONS

Our study demonstrates that organic farming and flower strips are effective tools to support pollinators and mitigate partly conventional practice effects in agricultural landscapes. Local management had a strong effect on both pollinators and their food resources. Our colonies in conventional fields likely experienced food shortages, whereas the AES likely provided a higher amount of better quality food resources. In general, we found the highest abundance and species richness of pollinators in flower strips and intermediate levels in organic fields. However, bumblebee colonies in organic fields performed as well as those in flower strips suggesting that organic fields can equally support pollinators. The lower pollinator densities per unit area in organic fields compared to flower strips might be only due to the dilution of pollinators and their resources over a larger area across the field compared to the dense concentrations in narrow flower strips. Thus, we emphasize the importance of using different methods when studying the effectiveness of AES, as results based only on transect walks might be misleading. Finally, the effect of field size on bumblebee reproduction changed depending on local management. Therefore, our findings reveal that European Union policies need to take into account that AES effectiveness depends on the structure of the surrounding landscape.

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AUTHORS' CONTRIBUTIONS

C.G. carried out the field work, analysed the data and drafted the manuscript; A.H. identified the bees collected and helped to draft the manuscript; R.F. identified the hoverflies collected; B.D. and A.A. performed the field surveys and compiled data; T.T. helped in designing the study and developing the conceptual foundations for this manuscript; P.B. conceived, designed and coordinated the study; he also helped to analyse the data and draft the manuscript. All authors contributed substantially to revisions and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available via the Zenodo Database: <https://doi.org/10.5281/ZENODO.3823890> (Geppert et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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