RESEARCH ARTICLE

Functional groups of wild bees respond differently to faba bean *Vicia faba* L. cultivation at landscape scale

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Abstract

1. Concerns about insect declines are growing and the provisioning of ecosystem services like pollination may be threatened. To safeguard biodiversity, greening measures were introduced within the reform of the EU's Common Agricultural Policy. One measure commonly applied by farmers is the cultivation of nitrogen fixing crops. Although underlying studies are largely missing, this measure is criticized as providing no significant biodiversity benefit.

2. Using a landscape-scale approach, we selected 30 paired study landscapes (1 km × 1 km) in Germany, that is, 15 study landscapes with faba bean (FB) fields (*Vicia faba* L.) and 15 without any grain legumes. Flower-visiting wild bees were recorded with transect walks at the field margins of different crops using a stratified sampling approach. We analysed the effect of FB cultivation and landscape composition on the abundance and species richness of wild bees as well as on the functional composition of the bee communities.

3. Bumblebee densities (*Bombus* spp. Latreille) were more than twice as high in FB compared to control landscapes after the flowering of the beans. Non-*Bombus* wild bee densities, however, were not affected by FB cultivation, but were enhanced by increasing amounts of semi-natural habitats (SNH).

4. After the beans' blooming had ceased, FB landscapes had a higher proportion of wild bees collecting pollen from Fabaceae than control landscapes. The community-weighted means for bee size, measured as intertegular distance, were not affected by FB cultivation, but we found smaller species and species with shorter tongues with an increasing percentage of SNH.

5. *Synthesis and applications*. The cultivation of faba bean *Vicia faba* L. strongly increased bumblebee densities throughout the season. This indicates that also on-field greening measures can support biodiversity. Nevertheless, since only functional groups adapted to faba bean benefit, measures to promote semi-natural habitats in agricultural landscapes need to be implemented. We conclude that the combination of on- and off-field measures is essential to maintain farmland biodiversity and the Common Agricultural Policy should furthermore promote both.
1 | INTRODUCTION

The increasing intensification of agriculture and the accompanying loss of habitat heterogeneity are main drivers of global insect declines and decreasing biodiversity in agricultural areas (Benton, Vickery, & Wilson, 2003; Seibold et al., 2019). Biodiversity loss involves the disruption of ecosystem functioning with potential negative effects on the provisioning of ecosystem services, such as pollination (Tscharntke, Klein, Kruess, Steffan-Dewenter, & Thies, 2005). Pollinators are declining globally and one of the main causes is the simplification of landscapes and the associated lack of nesting sites and floral resources (Potts et al., 2016). Depending on specific species traits, like dietary specialization of oligolectic bees or body size, some pollinator species are more affected by habitat loss than others (Bommarco et al., 2010; Warzecha, Diekötter, Wolters, & Jauker, 2016). The functional composition of insect communities might be altered by anthropogenic land use through filtering of specific species traits, leading to functional homogenization of communities (Gámez-Virués et al., 2015). However, agriculture can also contribute to biodiversity conservation, depending on local farm management and landscape context. Besides low intensity agriculture, like organic farming and the promotion of semi-natural habitats (SNH), the utilization of diversified crop rotations including flowering crops, such as legumes, can support insects in agroecosystems (Gabriel et al., 2010; Tscharntke et al., 2005). Yet, the effects of diversified farming systems have largely been studied in organic and not in conventional systems, which are the most common ones in the EU and other industrialized countries (e.g. Kremen & Miles, 2012; Lichtenberg et al., 2017).

Since the introduction of the greening reform of the Common Agricultural Policy (CAP) in 2013, 30% of the direct payments in the first pillar are associated with greening measures aiming at biodiversity conservation, such as crop diversification, maintenance of permanent grassland and Ecological Focus Areas (EFA; European Commission, 2017). Yearly approx. 12 billion € are spend on them by the EU (European Court of Auditors, 2017). However, the effectiveness of the greening measures has been questioned. Most commonly implemented EFA are on-field measures, like nitrogen fixing crops and catch crops. They accounted for about 80% of the total area declared as EFA in Germany in 2019 (BMEL, 2019) but are criticized to provide no significant benefits for biodiversity (European Commission, 2017; Pe’er et al., 2019). The European Commission (2017) even assumes detrimental effects for pollinators from the cultivation of nitrogen fixing crops because they might act as ecological trap by attracting pollinators to simplified landscapes with lacking resources after the beans’ flowering has ceased and by exposing them to insecticides in conventionally managed fields. Nevertheless, the effect of conventional grain legume cultivation as part of the current greening reform on pollinating insects, particularly at the landscape scale, is understudied (Everwand, Cass, Dauber, Williams, & Stout, 2017).

The cultivation of grain legumes entails several environmental benefits, such as reduction of synthetic nitrogen fertilizer applications, increased yields of subsequent cereal crops and possible promotion of biodiversity (Everwand et al., 2017; Köpke & Nemecek, 2010). Nitrogen leaching however might increase (Köpke & Nemecek, 2010) and might affect biodiversity in adjacent field margins by improving conditions for a few competitive plant species (Bobbink et al., 2010). The cultivation of grain legumes has dropped in the last decades and the environmental benefits accompanying their cultivation are often not considered. Although the promotion of grain legumes within the greening has increased their cultivation, they cover only 1.7% of the arable land in Germany (Destatis, 2019).

Faba bean (FB) *Vicia faba* L. is an important grain legume crop. It is a partially allogamous plant species and is grown worldwide for green manure or as protein source for humans and animal feed (Bond & Poulsen, 1983). Yield increases from 16% to 185% due to insect pollination have been reported (Bartomeus et al., 2014; Bishop, Jones, Lukac, & Potts, 2016; Nayak et al., 2015). Due to long corolla tubes and the papilionaceous flower morphology (Bond & Poulsen, 1983), which requires force from pollinators to access the reward of the flowers (Bailes, Pattrick, & Glover, 2018), only big pollinators with long tongues can easily access the nectar. The most frequent and effective pollinators of FB in temperate regions are bumblebees, predominantly long-tongued species, like *Bombus hortorum* (Bond & Poulsen, 1983; Marzinzig et al., 2018). Short-tongued bumblebees often rob nectar by biting holes in the base of the corollas (Bond & Poulsen, 1983; Garratt et al., 2014; Marzinzig et al., 2018). As demonstrated for other mass-flowering crops, such as oilseed rape (OSR; Herrmann, Westphal, Moritz, & Steffan-Dewenter, 2007; Westphal, Steffan-Dewenter, & Tscharntke, 2003), the cultivation of *V. faba* might offer a potential food resource for pollinators during midsummer, when other floral resources are often lacking in simplified agricultural landscapes. While the effect of early and late mass-flowering crops on wild bees has already been studied (e.g. Kallioniemi et al., 2017; Westphal et al., 2003), we are not aware of studies investigating effects of conventionally cultivated faba beans on different taxonomic groups and functional diversity of wild bees.

Here, we assess the potential benefits of the nitrogen fixing crop *V. faba* for wild bees, which might be a relevant contribution to future evaluations of the CAP greening reform. Since most studies analyse landscape impacts on pollinators at plot level without...
scaling-up effects to landscape level (Kleijn et al., 2018), we chose a novel landscape-scale approach. We compared pollinator communities in 30 paired 1 km² landscapes, that is, 15 study landscapes with FB fields and 15 without grain legumes (Pascher et al., 2011). We hypothesize that the cultivation of FB enhances the abundance and species richness of wild bees at landscape scale. In addition to bumblebees, we expect non-Bombus wild bees to benefit from FB cultivation. They might use the nectar from the bean’s extrafloral nectaries or from bite holes in the corolla base. Due to the flower morphology of the beans, long-tongued bees and bigger bees with higher body mass and proportional longer tongues, which enables them to access the reward of the flowers, should be favoured by FB cultivation. Moreover, FB cultivation should promote bees, frequently collecting pollen from Fabaceae.

2 | MATERIALS AND METHODS

2.1 | Study design

The study was conducted within 30 paired study landscapes of 1 km² (1 km × 1 km) size each, which were situated in three regions of Germany (Figure 1). In all, 12 study landscapes were in the surroundings of Göttingen in Central Germany (51°32′N, 9°56′E). In total, 10 study landscapes were located close to the North Sea in vicinity of the city Itzehoe (53°55′N, 9°30′E) and eight in the east of Germany close to Leipzig (51°20′N, 12°22′E). One landscape of every pair was selected around a FB field belonging to a conventional farm with diversified crop rotations, including grain legumes for at least 3 years (FB landscape: FB+). For the respective paired control landscape, it was assured that no grain legumes were present and that most fields belonged to conventional farms using standard crop rotations without grain legumes (control landscape: FB−).

Landscape selection was based on ATKIS land cover data (Digitales Basis-Landschaftsmodell). The landscape composition was analysed for the entire area (1 km²). Control landscapes were matched based on a similar landscape composition with respect to major land use types using Euclidean distance as similarity measure. Due to the large foraging ranges of up to several kilometres of some bee species (Greenleaf, Williams, Winfree, & Kremen, 2007; Westphal, Steffan-Dewenter, & Tscharntke, 2006), paired study landscapes (FB+ and FB−) had a minimum distance of 5 km to each other to prevent bees from visiting both landscapes.

All crop and habitat types with a minimum area of 10 m² were mapped for each study landscape. Landscape composition was characterized by two landscape metrics, known to affect wild bees and often used to quantify foraging and nesting opportunities (e.g. Diekötter, Peter, Jauker, Wolters, & Jauker, 2014): percentage of oilseed rape (OSR) Brassica napus L. and percentage cover of semi-natural and flower-rich habitats (SNH), including sown flower strips and fields, hedgerows, groves, extensive grasslands, calcareous grasslands, fallows, orchard meadows, ruderal sites, succession sites and forest edges (4 m width based on a 2 m buffer along the forest polygons’ outer border). Forest was not included in SNH since it

FIGURE 1 Location of the study landscapes in three regions of Germany. Landscapes with faba bean cultivation (FB+) are depicted in green and controls without grain legumes (FB−) in orange. One representative landscape pair is shown in detail. Different colours indicate different land use types and crops. OSR: oilseed rape, SNH: semi-natural habitat. Black arrows show the location of the seven standardized transects per landscape, located at field margins of different crop types following a stratified sampling design [Colour figure can be viewed at wileyonlinelibrary.com]
represented a rather unsuitable foraging habitat for pollinators (Proesmans et al., 2019). Calculations were done with QGIS version 2.18 (QGIS Development Team, 2016).

2.2 | Wild bee surveys

In summer 2017, wild bees were sampled within seven standardised transect walks per study landscape (Westphal et al., 2008), located at field margins of different annual crop fields. Transect area was always 400 m², mostly 100 m × 4 m, while for some smaller field margins transect length was adjusted accordingly. The number of transects assigned to the margins of each crop type was proportionally selected to its area in the study landscape (stratified sampling design; Beduschi, Tscharnkte, & Scherber, 2015).

The bee densities, that is, the number of all foraging bees per transect area (bees/400 m²) was recorded within 10 min, excluding handling time. If species could not be identified in the field, bees were taken to the laboratory for further identification. Due to the difficulty of distinguishing Bombus terrestris and B. lucorum in the field, these two species were aggregated. We identified sampled bumblebees in the laboratory (Amiet, 1996; Mauss, 1994) and sent non-Bombus bees to an expert for identification (Frank Creutzburg, Jena). Flower cover, that is, the area covered with open flowers (m²) was estimated for every transect and did not differ between FB and control landscapes (p = 0.52; Figure S1).

Surveys were repeated three times between May and August: run 1 (22.05–19.06), run 2 (22.06−20.07) and run 3 (27.07–22.08). In run 1, almost all FB fields were in full bloom, in run 2 the bloom of most bean fields was ceasing and in run 3 FB was not flowering anymore. Transects per landscape were visited in a random order from 9 a.m. until 7 p.m. on days with suitable weather conditions for pollinators (i.e. air temperature >15°C, low wind speed, no rain). As we focus on the effects of grain legumes on wild bees, we excluded managed honeybees from the analyses.

2.3 | Functional trait composition of bee communities

To assess how V. faba cultivation and landscape composition affect the functional structure of bee communities, we focused on three functional traits: tongue length, body size and pollen collection behaviour, that is, whether bee species are known to collect or not collect pollen from Fabaceae (lecty). Cleptoparasites were excluded from the analysis due to their different life-history strategy and because certain traits, like lecty are not defined for them (12 species). As a proxy for body size, we measured the intertegular distance (ITD) of minimum one and maximum five female individuals per species (in total 68 species; Table S1). We focused trait measurements on pollen collecting female bees as main pollinators. For 10 species, only one or two single male individuals were caught and no ITD measures could be conducted. Since the tongue length of bees is difficult to measure, bee proboscis length was calculated on the basis of bee family and ITD which explain 91% of the variance in proboscis length between species (Cariveau et al., 2016). Calculations were performed with the R package BzIT (Cariveau et al., 2016; Table S1). The information on dietary preferences (lecty) was obtained from Westrich (2018).

2.4 | Statistical analyses

Analyses were conducted in R version 3.6.1 (R Core Team, 2019). For analyses of FB cultivation and landscape metrics on wild bees, data were summed up for each landscape and run. Our response variables were the density of bumblebees, non-Bombus wild bees, the species richness of all wild bees, community-weighted means (CWM) of ITD and proboscis length and proportion of bee species foraging on Fabaceae (Fabaceae foragers). Data were analysed using mixed-effects models with Poisson or negative binomial distribution for bee densities and species richness, Gaussian distribution for CWM data and binomial family for proportion Fabaceae foragers. Explanatory variables included in all models were FB cultivation (FB+/FB−), flower cover, sampling run (1–3), percentage of SNH and percentage of OSR in the study landscape, including all possible two-way interactions. Region, landscape pair and the study landscape were included as nested random effects. Following a multimodel inference approach (Burnham & Anderson, 2002), all models within delta AICc < 2 indicating a positive effect were run (Σ wi = 1), FB cultivation (Σ wi = 0.97), their interaction (Σ wi = 0.91) and flower cover (Σ wi = 0.91) as well as the interaction between run and flower cover (Σ wi = 0.32; Tables S2 and S3). Most bumblebees were observed in run 2, on average 28 individuals per

3 | RESULTS

We observed 2,198 wild bees of which 1,794 were identified to species level. In total, 80 different species were recorded (Table S1). Bumblebees made up 63% of all observed individuals. We found three threatened long-tongued bumblebee species: B. muscorum (red list category [RL] 2), B. ruderarius (RL 3) and B. subterraneus (RL 2; Table S1; Westrich et al., 2011). We recorded 980 honeybees whose densities did not differ between FB+ and FB− landscapes (Figure S2).

3.1 | Bumblebee density

There were two models with dAICc < 2 indicating a positive effect of FB cultivation and local flower cover on bumblebee densities (Table S2). Explanatory variables included in the best-fitting models were run (Σ wi = 1), FB cultivation (Σ wi = 0.97), their interaction (Σ wi = 0.91) and flower cover (Σ wi = 0.91) as well as the interaction between run and flower cover (Σ wi = 0.32; Tables S2 and S3). Most bumblebees were observed in run 2, on average 28 individuals per
study landscape (Table S5). In the second and third runs, more than twice as many bumblebees were present in FB landscapes compared to controls (Figure 2A). Densities increased with increasing local transect flower cover. This effect was slightly more pronounced in runs 2 and 3 than in run 1 (Figure S3a).

3.2 Non-**Bombus** wild bee density

The multi-model inference revealed two best fitting models explaining the effect of FB cultivation and landscape composition on non-**Bombus** densities (Table S2). Explanatory variables included in the best fitting models were run (\(\Sigma w_i = 1\)), local flower cover (\(\Sigma \omega_i = 1\)), SNH (\(\Sigma \omega_i = 1\)) and all possible interactions (\(\Sigma \omega_i\) between 0.93 and 1) as well as FB (\(\Sigma \omega_i = 0.44\); Tables S2 and S3). We found similar average densities in FB and control landscapes (Figure 2B; Table S5). There was a positive relationship between percentage of SNH and non-**Bombus** wild bee densities with strongest increase in the second run (Figure 2C). Densities increased with increasing flower cover in runs 1 and 3 but decreased in run 2 (Figure 2D). The effect of enhanced bee densities with increasing flower cover was strongest, when percentage of SNH was high (Figure S3b).

3.3 Species richness of all wild bees

There were three best fitting models indicating a positive FB cultivation and local flower cover effect on wild bee species richness (Table S2). Explanatory variables included were run (\(\Sigma w_i = 1\)), flower cover (\(\Sigma \omega_i = 1\)), their interaction (\(\Sigma \omega_i = 1\)), FB cultivation (\(\Sigma \omega_i = 0.81\)) and the interaction between FB and flower cover (\(\Sigma \omega_i = 0.35\); Tables S2 and S3). Species richness increased with enhanced flower cover. This effect was strongest in run 3 (Figure 3A) and more pronounced in control compared to FB landscapes (Figure S4). Mean species richness per study landscape was 5.5 for FB and 4.4 in control landscapes (Table S5; Figure 3B).

3.4 Functional trait composition of bee communities

The multi-model inference approach resulted in two best fitting models for the CWM ITD and in five best models for the CWM for proboscis length (Table S6). Run (\(\Sigma w_i = 0.82\)), SNH (\(\Sigma w_i = 0.90\)), flower cover (\(\Sigma \omega_i = 0.58\)) and the interaction between local flower cover and SNH (\(\Sigma \omega_i = 0.26\)) were the most important explanatory variables for CWM ITD (Tables S6 and S7). We found that average body size in bee communities was smallest in run 3 (Table S4; Figure 4A) and CWM ITD decreased with increasing percentage of SNH (Figure 4B). This effect was more pronounced when local flower cover was low (sure S5A). The cultivation of FB did not affect CWM ITD. Due to the correlation between CWM ITD and proboscis length, the respective models show the same patterns (Figure S5b,c). Additionally, compared to ITD models, mean proboscis length increased with increasing flower cover in control landscapes but decreased in FB landscapes (\(\Sigma \omega_i = 0.33\); Tables S6 and S7; Figure S5d).

For the proportion of species foraging on Fabaceae, we found a single best fitting model including FB cultivation, run and their interaction as most important explanatory variables, each with \(\Sigma w_i = 1\) (Tables S6 and S7). There was a higher percentage of species collecting pollen from Fabaceae in landscapes with FB cultivation compared to controls during the second and third runs, whereas the
opposite was true for run 1 (Figure 4C). The proportion of Fabaceae foragers was enhanced with increasing percentage of SNH in run 1, whereas it decreased in run 2 ($\Sigma w_i = 0.99$; Figure S6a). Moreover, the proportion of Fabaceae foragers was positively related with transect flower cover in run 2 and negatively in run 3 ($\Sigma w_i = 0.71$; Figure S6b).

4 | DISCUSSION

4.1 | Bumblebee density

We found a positive landscape-scale effect of the cultivation of conventionally managed V. faba on bumblebees. While no effect was observed in run 1, when most FB fields were in full bloom, bumblebee densities were higher in FB than in control landscapes in the second and third runs after the flowering of the beans. A possible reason for why we did not detect differences in run 1 is that bumblebee colonies still needed to grow after founding in spring. Throughout the season, the colonies in FB landscapes were probably able to produce more workers due to the additional resource in June. This points towards a positive carry-over effect of the presence of the mid-season mass flowering crop V. faba on bumblebees, which has already been observed for late-flowering crops (Kallioniemi et al., 2017). In comparison with wheat field margins, Hanley et al. (2011) found increased pollinator abundances in FB field margins. This positive FB effect was however restricted to the flowering period of the beans. Unlike...
Hanley et al. (2011), who investigated the local pollinator spill-over effect from a mass flowering crop into surrounding field margins, we sampled our data in the entire 1 km² landscape and can depict effects at landscape level. For bumblebees, it has been shown that there is a food gap with low-resource availability in agricultural landscapes in June, in the time period between the bloom of early mass flowering crops and the floral resources in summer (Timberlake, Vaughan, & Memmott, 2019). Our study indicates that V. faba has the potential to bridge this resource gap and act as a valuable mid-season food source for bumblebees. For the case of faba beans and bumblebees, we cannot support the assumption that grain legumes act as ecological trap (European Commission, 2017). According to our findings, the resources provided by FB seem to compensate for possible negative management effects due to pesticide applications as indicated by increased bumblebee densities in FB landscapes. Nevertheless, we cannot preclude potential negative pesticide effects of conventionally managed beans on bees.

Bumblebees can benefit from a high cover of SNH (Nayak et al., 2015; Öckinger & Smith, 2007). However, in accordance with other studies conducted in Central Germany (Herrmann et al., 2007; Westphal et al., 2003, 2006), we did not find any effect of the amount of SNH on bumblebee densities. Bumblebees, especially short-tongued species, are strongly attracted to mass resources (Walther-Hellwig & Frankl, 2000) and probably preferred those over the more sparsely distributed floral resources in SNH. However, cover of mass-flowering OSR did not have any effect on bumblebees, contrary to other investigations (Herrmann et al., 2007; Westphal et al., 2003, 2006). Bumblebee densities were only driven by mass-flowering FB and the local flower cover in our study. A positive effect between flower cover and bumblebees has already been reported in previous studies (e.g. Nayak et al., 2015; Öckinger & Smith, 2007).

4.2 | Non-Bombus wild bee density

Unlike bumblebees, non-Bombus wild bees did not benefit from FB cultivation, which might be due to the interplay of bean flower morphology and bees’ functional traits. A long tongue and force are needed to extract nectar from the front of the flowers (Bailes et al., 2018; Bond & Poulsen, 1993), making it difficult for small- and short-tongued bees, like most observed non-Bombus bees, to forage on V. faba flowers. However, we found a positive effect of the amount of SNH on non-Bombus bees, which offer a diverse and continuous nectar and pollen supply. This result is in line with previous studies (Diekötter et al., 2014; Steffan-Dewenter, Münzenberg, Bürger, Thies, & Tscharntke, 2002). The simplification of agricultural landscapes with the loss of SNH has been stated as one of the reasons for the current pollinator diversity decline (Potts et al., 2016). The strongest positive SNH effects became apparent in run 2, when we found highest densities of non-Bombus wild bees and when SNH displayed a high floral cover with grasslands and flower strips being in full bloom (F. Kirsch, unpubl. data, Figure S7). Moreover, bee densities were enhanced by an increasing local flower cover in runs 1 and 3, in accordance with other studies (Ebeling, Klein, Schumacher, Weisser, & Tscharntke, 2008; Potts, Vulliamy, Dafni, Ne’eman, & Willmer, 2003). However, in the second run, densities were not enhanced by a higher local flower cover. This might be explained by a dilution effect caused by an enhanced floral display in SNH that attracted non-Bombus bees during that period (F. Kirsch, unpubl. data). This can however not be supported by a three-way interaction between SNH, flower cover and run. When including three-way interactions in models, none of them turned out to have an effect and results stayed the same. Nevertheless, the temporal shift of non-Bombus density responses to field margin flower cover suggests that wild bees prefer rewarding SNH over field margins, if available. Holzschuh et al. (2016) showed mass-flowering crops to cause dilution effects. Temporally high rewarding SNH caused similar effects in our study, which might impair pollination services in sparsely flowering wild plant populations in field margins or other SNH (Holzschuh et al., 2016).

Highest non-Bombus densities were found when the cover of SNH and the transect flower cover were high, which emphasizes the importance of heterogeneous landscapes with diverse and continuous flower supply and suitable nesting opportunities for wild bees within and across habitats (Schellhorn, Gagic, & Bommarco, 2015; Westrich, 2018).

4.3 | Species richness of all wild bees

The cultivation of mass-flowering crops, like OSR, has been shown to increase wild bee species richness (Diekötter et al., 2014). A positive effect of FB cultivation on wild bee richness has never been shown, also not in our study. The species richness of our study landscape was generally very low, only on average five wild bee species. This indicates that agricultural landscapes in Germany are rather resource- and species poor. Species richness was mainly driven by the local flower cover of field margins. Generally, positive relationships between bee species richness and local floral resource availability are well known (e.g. Ebeling et al., 2008; Kallioniemi et al., 2017; Potts et al., 2003). Besides flower abundance, local floral diversity is known to support wild bee species richness as diverse plant communities offer food for a wider range of bee species with different flower preferences (Ebeling et al., 2008; Potts et al., 2003). Thus, the provision of sufficient and diverse floral resources is essential to conserve a high farmland bee species richness and abundance (Ebeling et al., 2008; Leidenfrost et al., 2020).

4.4 | Functional trait composition of bee communities

The cultivation of V. faba increased the proportion of bees foraging on Fabaceae after the bloom of the beans had ceased. During the flowering, Fabaceae foragers were probably attracted by bean
fields and we detected lower densities of them in field margins of FB landscapes. The proportion of Fabaceae foragers varied in relation to interacting effects between sampling time and the amount of SNH and local flower cover, respectively. These interaction effects highlight that both local- and landscape-scale resources moderate the functional composition of bee communities across the season presumably due to phenological fluctuations of flower availability (Ogilvie and Forrest, 2017).

The cultivation of FB did not affect the functional trait composition of bee communities in terms of bee size. But communities were composed of individuals with lower mean size and shorter tongues later in the season, which might be due to species-specific activity periods. Species belonging to the genera Osmia, Eucera and most of the observed Andrena species with high ITD, appear only early in the season (Westrich, 2018), whereas all observed Hylaeus, Halictus and Lasioglossum species with low ITDs were active throughout the whole season. Additionally, we found a higher proportion of smaller bees with increasing amounts of SNH in the surrounding landscape, in line with other studies (Jauker, Krauss, Jauker, & Steffan-Dewenter, 2013; Warzecha et al., 2016). Since the maximum foraging distance of bees increases with body size (Greenleaf et al., 2007), smaller bees are more susceptible to land-use change and habitat fragmentation, since large distances need to be covered to reach suitable floral resources (Jauker et al., 2013; Steffan-Dewenter et al., 2002; Warzecha et al., 2016). The effect of decreasing mean bee size with increasing percentage of SNH was mitigated by a high field margin flower cover highlighting the negative impact of low-resource availability at local and landscape scales especially for bees with small foraging ranges in agricultural landscapes.

5 | CONCLUSIONS

To our knowledge, this is the first study showing that conventionally grown faba beans enhance bumblebee densities at landscape scale. This finding helps to reduce the concern that grain legumes act as an ecological trap, at least for bumblebees (European Commission, 2017). The inclusion of faba beans in diversified conventional crop rotations could thus be a reasonable measure to counteract bumblebee declines.

However, the beneficial faba bean effects are restricted to bee species adapted to the flower morphology of V. faba. Since non-Bombus densities were mainly driven by the availability of SNH, we conclude that faba beans alone cannot conserve wild bees in agricultural landscapes. On-field greening measures, like diversified legume-based crop rotations enhance temporal and spatial nectar and pollen availability in conventional farming systems and fall within a land-sharing approach. More importantly, CAP regulations should prioritize off-field measures aiming at the promotion of SNH, which can be considered as land-sharing approach at smaller spatial scales (Ekroos et al., 2016). Considering the human demand for agricultural products and the need for farmland biodiversity and ecosystem service conservation, we suggest a combined land-sharing and land-sparing approach in predominantly conventionally managed agricultural landscapes (Balmford, Green, Onial, Phalan, & Balmford, 2019; Grass et al., 2019). While diversified crop rotations with grain legumes sustain high crop yields and benefit generalist crop pollinators, the conservation of SNH promotes diverse wild bee communities.

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AUTHORS’ CONTRIBUTIONS

C.W. and J.D. conceived the study and supervised the project; N.B., K.S.-K. and F.K. implemented the study sites; N.B. collected the data; N.B. and D.G. performed the data analysis with advice of C.W.; N.B. wrote the manuscript with advice of D.G., F.K. and C.W. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.ttdz08kvs (Beyer et al. 2020).

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