The effect of diversified crop rotations with faba beans (*Vicia faba* L.) on pollinators and pollination services

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Contents

Summary

Agricultural intensification and the loss of suitable habitats are drivers of insect declines. Besides the promotion of semi-natural habitats (SNH), the utilization of diversified crop rotations including flowering crops is an option to sustain pollinators. As flowering and nitrogen fixing crops, grain legumes provide several environmental benefits but are underrepresented in the EU. Since 2013 they are promoted within the greening reform of the Common Agricultural Policy (CAP). On-field biodiversity measures are often criticized, though their possible benefits for biodiversity are widely unknown. My PhD thesis aims at investigating the landscape-scale effect of conventional faba bean (*Vicia faba* L.) cultivation on wild bee communities, their resource utilization and their pollination services. Experiments were conducted in 1km x 1km study landscapes in Germany. For the first three chapters a paired study design was applied with one landscape of a pair comprising at least one faba bean field and the respective control landscape without grain legumes.

In the first chapter we studied effects of faba bean cultivation on functional groups of wild bees. We conducted pollinator surveys at field margins of different crops in 30 study landscapes. Bumblebee densities were more than twice as high in faba bean compared to control landscapes, while non-*Bombus* wild bees were only driven by the amount of SNH. These results indicate that a combination of on- and off-field greening measures is necessary to conserve farmland biodiversity and we recommend that the CAP should furthermore promote both. **In the second chapter** we investigated the effect of two mass-flowering crops (MFC) on the functional trait composition of bee communities in SNH. Faba bean cultivation promoted bumblebees, especially long-tongued species, social bees and bees foraging on Fabaceae. High oilseed rape (OSR) covers changed wild bee community composition in favor for solitary bees. Local flower cover of SNH was the main driver of non-*Bombus* wild bees and wild bee species richness. Thus, different MFC promote specific functional bee groups adapted to the crop`s flower morphology. Concluding, the cultivation of functionally diverse crops, combined with a high local flower cover of SNH needs to be targeted by management practices to sustain diverse pollinator communities. **In the third chapter** we studied landscape and faba bean cultivation effects on the colony development and resource utilization of bumblebees (*Bombus terrestris* L.). The colonies` reproductive success was not influenced by landscape composition but enhanced by landscape diversity. Faba bean cultivation and pollen diversity interacted and resulted in more young queens with increasing pollen diversity in landscapes without faba bean. In addition, colonies that collected a higher pollen diversity had a reduced *A. sociella* depredation. Increased parasitism had a cascading negative effect on the reproductive success of bumblebees by limiting colony growth. Our study shows that high landscape diversity and diverse pollen diets can enhance the reproductive success of bumblebees. A diverse diet even mitigated depredation by wax moths. To sustain vital bumblebee populations and their pollination services, diverse and floral rich habitat types should be conserved or restored in agricultural landscapes. **In the fourth chapter** we investigated, how bee densities in OSR fields are affected by past and current MFC cultivation and how insect pollination affects OSR yield components. Bee densities were positively affected by past MFC covers and negatively affected by current OSR covers. Pollinator exclusion decreased seed number per pod and increased seed weight. Insect pollination interacted with the plants` pod number in shaping yields, while compensating for low pod numbers. **In the fifth chapter** we analyzed the effect of landscape composition on the densities of different functional bee groups and their foraging behavior in faba bean fields in 11 different landscapes. Moreover, the effect of insect pollination and of landscape composition was tested on faba bean yield components. Landscape composition affected the bees` foraging behavior in the crop. Increasing covers of faba bean and of semi-natural habitats in a landscape had a positive effect on bee densities and on faba bean yield, while oilseed rape cover had a negative effect. Our study emphasizes the importance of considering landscape management in order to maximize flowering crop yields.

In conclusion, *Vicia faba* cultivation is an effective measure to promote wild bees, which are needed for high crop yields. Though, since benefits for pollinator groups depend on the crops` flower morphology, functional trait composition of wild bee communities can be changed in landscapes with a dominating mass-flowering crop species. Thus, landscape and local farm management should aim at increasing farmland plant diversity. The combination of a high cover and quality of semi-natural habitats as well as of diversified farming practices targeting a high spatial and temporal crop diversity is essential to conserve diverse pollinator communities and to sustain high crop yields.

General introduction

Landscape effects on pollinators and pollination services

Human induced global change impacts biodiversity and the loss of biodiversity threatens the provisioning of ecosystem services (Cardinale et al., 2012). Being a major land use type on earth, agriculture is one of the main drivers of this development (Foley et al., 2005). Since agroecosystems depend on ecosystem services, it is essential to conserve biodiversity and associated services, like pollination via a sustainable farm and landscape management (Power, 2010). The global insect decline has largely been attributed to agricultural intensification and the resulting loss of habitat heterogeneity (Benton et al., 2003; Seibold et al., 2019). Diversified farming systems and low intensity agriculture, like organic farming or the use of diversified crop rotations with flowering crops can on the other hand promote insects and lead to enhanced diversity in agroecosystems (Kennedy et al., 2013; Rosa-Schleich et al., 2019; Tscharntke et al., 2005).

Pollinators are susceptible to landscape changes (Potts et al., 2010) and the composition and the configuration of a landscape affect pollinator densities and species richness in agricultural landscapes (Kallioniemi et al., 2017; Kennedy et al., 2013; Martin et al., 2019). An increased landscape heterogeneity positively impacts pollinators (Benton et al., 2003; Hass et al., 2018; Mallinger et al., 2016) and landscape simplification has been shown to negatively affect pollinators and their pollination services (Dainese et al., 2019). Moreover, landscape simplification can lead to a functional homogenization of insect communities that will mainly be consisting of species with generalist feeding traits and large body size (Gámez-Virués et al., 2015; Perović et al., 2015). The provisioning of floral resources can however mitigate such developments (Grab et al., 2019). The availability and diversity of flowers is a major factor driving wild bee abundances and species richness (Ebeling et al., 2008; Potts et al., 2003). A high cover of semi-natural habitats has been shown to positively affect bees (Diekötter et al., 2014; Nayak et al., 2015; Steffan-Dewenter et al., 2002) and to enhance their reproductive success (Requier et al., 2020). This in turn has implications for crop pollination because enhanced pollinator densities have been observed in crop fields with increasing proportions of semi-natural habitats in the surrounding landscape (Carré et al., 2009; Nayak et al., 2015).

Pollinators depend on a continuous supply of floral resources (Schellhorn et al., 2015) and have been shown to move between non-crop habitats and crop fields according to their changing resource availability (Bänsch et al., 2020a; Mandelik et al., 2012). The cultivation of mass-flowering crops provides temporally high pollen and nectar amounts for insects and has been shown to promote solitary bees and bumblebees (Diekötter et al., 2014; Jauker et al., 2012; Riedinger et al., 2015; Westphal et al., 2003). Bumblebee colonies mainly show increases of worker numbers in the literature, but no increased reproductive success, i.e. number of young queens or number of colonies (Herrmann et al., 2007; Westphal et al., 2009). Moreover, mass-flowering crops can lead to a dilution by strongly attracting bees with negative impacts on the pollination of co-flowering crops or wild plants (Bänsch et al., 2020b; Grab et al., 2017; Holzschuh et al., 2016). Additionally, the composition of pollinator communities can be changed if certain species are predominantly promoted by a certain mass-flowering crop (Diekötter et al., 2010). Different mass-flowering crops have been shown to be visited by different pollinator communities (Garratt et al., 2014). Generally, a high pollinator functional diversity is associated with high crop yields, since morphological traits of the crop and of the pollinator need to match in order to achieve successful pollination and maximum yields (Garibaldi et al., 2015; Woodcock et al., 2019). To maintain a high pollinator functional diversity, a high functional diversity of farmland plants is essential (Sutter et al., 2017), which requires high covers of semi-natural habitats and a high crop diversity (Aguilera et al., 2020).

Diversified crop rotations with grain legumes

Diversified farming systems promote biodiversity and ecosystem service provisioning, like pest control and pollination (Lichtenberg et al., 2017; Rosa-Schleich et al., 2019). One option are diversified crop rotations, which are temporal sequences of different crops grown on the same land (Rosa-Schleich et al., 2019). The inclusion of grain legumes into crop rotations results in a temporal and spatial farmland diversification. While environmental benefits of grain legume cultivation are generally known (Kremen and Miles, 2012; Preissel et al., 2015), the specific effects on biodiversity are understudied.

Environmental benefits of grain legume cultivation

The cultivation of grain legumes provides several agronomic and ecological benefits. Via biological nitrogen fixation, legumes can fix atmospheric nitrogen in symbiosis with rhizobia bacteria, which supplies ecosystems with biologically available nitrogen (Herridge et al., 2008; Vitousek et al., 2002). Thus, the cultivation of grain legumes can lead to a reduction of synthetic nitrogen fertilizer application and associated energy savings (Köpke and Nemecek, 2010; Kremen and Miles, 2012; Preissel et al., 2015). Moreover, legumes are known to positively affect soil fertility and act as a break crop in simple cereal-based crop rotations (Böhm et al., 2020; Köpke and Nemecek, 2010; Kremen and Miles, 2012; Preissel et al., 2015). A diversification of crop rotations is known to reduce the occurrence of diseases, pests and weeds as well as the associated application of plant protection products (Kremen and Miles, 2012; Rosa-Schleich et al., 2019). The cultivation of different crop species with varying sowing times, growing periods, management and competitive abilities can prevent the spread and interrupt the life cycle of weeds or pathogens and avoid resistances (Liebman and Dyck, 1993; Nichols et al., 2015). Furthermore, the inclusion of grain legumes into diversified farming systems can potentially enhance biodiversity and associated ecosystem services (Kremen and Miles, 2012; Rosa-Schleich et al., 2019). Beneficial arthropods, such as pollinators, predatory and parasitoid species might benefit from an inclusion of grain legumes into cropping systems by supplying food resources (Böhm et al., 2020; Nuessly et al., 2004). Furthermore, the high protein content of grain legume seeds makes them a valuable domestic protein source for human and animal feed and the increased use of domestic protein plants can help to reduce the long-distance import of soy (DAFA, 2012; Zander et al., 2016). Moreover, grain legumes play a role in terms of healthy plant-biased diets (DAFA 2012; Zander et al., 2016). Dietary changes with associated reduction in meat production and consumption would lower the negative environmental impacts of agriculture (Westhoek et al., 2014). Since legumes are an important part of a sustainable agriculture, their cultivation is promoted within current agricultural programs. The cultivation of domestic grain legumes coincides with the Protein Crop Strategy, which aims at the reduction of competitive disadvantages of protein crops, to increase the production of domestic protein plants in Germany and to increase biodiversity and associated ecosystem services (BMEL, 2020). Beyond that, the diversification of crop rotations goes along with the targets of the Arable Farming Strategy (BMEL, 2019a). Since the last Greening reform of 2013 grain legumes can be declared as Ecological Focus Area (EFA) within the first pillar of the Common Agricultural Policy (CAP). This recent development has resulted in increasing interest in grain legumes, which had been largely forgotten during the last decades.

Grain legume cultivation in Germany

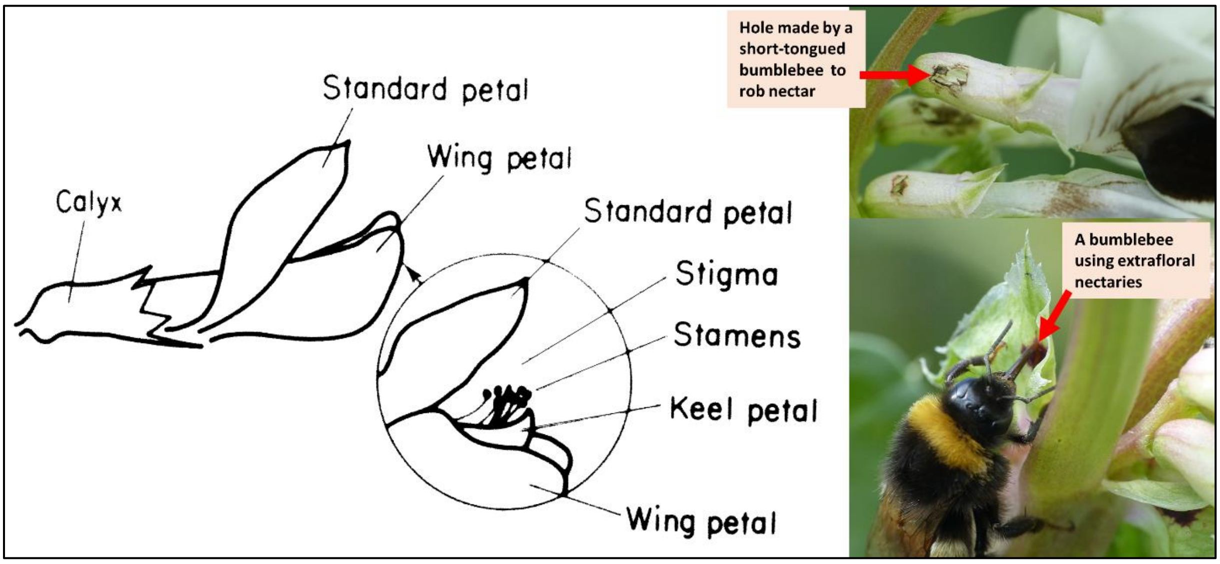
Despite providing plenty environmental benefits, grain legume cultivation in Germany and in the whole EU is underrepresented. The cultivation area of the most important grain legumes in Germany, peas, faba beans, lupins and soybeans in 2020 made up only 1.7 % of the total arable land (Destatis, 2020). There has been a drop of legume cultivation during the last decades. Several reasons have been denoted, such as low yield stability of grain legumes, the availability of cheap imported soy, the lack of marketing and processing opportunities and the increased cultivation of cereals and maize (Böhm et al., 2020; DAFA, 2012; Preissel et al., 2015; Zander et al., 2016). As a consequence, grain legumes can often not compete with crops, such as cereals. In the EU, there is a deficit in domestic protein plant production and grain legumes are even undervalued in the EU feed market considering their high protein content (Jensen et al., 2010; Köpke and Nemecek, 2010; Nemecek et al., 2008; Zander et al., 2016). When assessing the profitability of diversified crop rotations with grain legumes, the positive effects on the environment are often not considered and in terms of biodiversity largely unknown.

In response to the promotion of nitrogen fixing crops withing the CAP Greening reform, the cultivation area of grain legumes almost tripled from 2013 to 2020 (Destatis, 2020). On-field (productive) greening measures are a common choice among farmers and made up approx. 80 % of the total area declared as EFA in 2019 in Germany (BMEL, 2019b). Off-field (non-productive) measures, like field margins or hedgerows, have however been shown to be more effective for biodiversity conservations than on-field measures (Batáry et al., 2015). Thus, on-field measures are widely criticized to provide no benefit for biodiversity (European Commission, 2017, 2020; Pe’er et al., 2019). Nevertheless, there is missing knowledge about the effect of grain legume cultivation on biodiversity, especially under conventional management.

Faba bean - Relevance and pollination ecology

Relevance and plant traits

The faba bean or broad bean (*Vicia faba* L.) is an important grain legume crop originating from the Near East, which is grown world-wide for animal feed, human consumption or for green manure (Bond and Poulsen, 1983; Cubero, 2011; Jensen et al., 2012). With respect to production, faba beans are the second major pulse crop after peas in the EU and in Germany (Destatis, 2020; Eurostat, 2020). Faba beans belong to the genus *Vicia* within the family *Fabaceae* and they have a papilionaceous flower structure, which is typical for most species of the *Faboideae* subfamily (Fig. 1). The bilateral flowers consist of five petals, the standard petal or banner, the two wing petals and the two keel petals, which are fused to form a keel (Bond and Poulsen, 1983). The wing petals usually have a big dark melanin spot. Faba beans have ten stamens and nine of them form a sheath surrounding the ovary (Bond and Poulsen, 1983; Stoddard and Bond, 1987). During a pollinator` s visit, the wing and keel petals are depressed and release the stigma and the pollen, which is called “tripping”. Nectar is located at the base of the corolla tubes and short-tongued bumblebees often rob nectar by biting a hole into the calyx (Pond &Poulsen, 1983; Stoddard & Bond, 1987) (Fig. 1). Faba beans have extrafloral nectaries underneath the stipules (Fig. 1), which have been observed to be used by parasitic wasps and bees (Bond and Poulsen, 1983; Nuessly et al., 2004).



Hole made by a short-tongued bumblebee to rob nectar

A bumblebee using extrafloral nectaries

Figure 1 Left: Papilionaceous flower structure of faba bean (from Bond & Poulsen, 1983). Right: Hole in the flower calyx, made by a nectar robbing short-tongued bumblebee and a bumblebee using an extrafloral nectary of a faba bean plant (photos: Nicole Beyer).

The protein content of the faba bean seeds is quite high, between 22 and 36 % (Burstin et al., 2011). Important pest species of faba beans are the black bean aphid (*Aphis fabae* Scopoli), the broad bean weevil (Bruchus rufimanus Boheman) (Fig. 2) and the pea leaf weevil (*Sitona lineatus* L.) (Demonetz Erbse/Bohne, 2020; Karkanis et al., 2018).

Faba bean flower visitors and pollinators

Most frequent flower visitors of faba beans in temperate regions are honeybees and bumblebees, predominantly long-tongued species (Bond and Poulsen, 1983; Garratt et al., 2014b; Marzinzig et al., 2018) (Fig. 2). Next to bumblebees, also other bees have been observed to visit the plants. Bees of the genera *Eucera*, *Anthophora* and *Xylocopa* are known to be frequent visitors and pollinators of faba beans but also few Halictidae have been observed visiting and feeding on faba bean flowers (Aouar-sadli et al., 2008; Marzinzig et al., 2018; Nuessly et al., 2004; Stoddard and Bond, 1987). The morphology of the faba bean flowers allows only visitors with certain functional traits to access their rewards. Force, as well as a long tongue are prerequisites to forage on faba bean flowers (Bailes et al., 2018). Therefore, long-tongued bumblebees, like *Bombus hortorum* have been found to be most effective pollinators (Marzinzig et al., 2018). Nectar robbing is a way to circumvent the floral barrier, which is a very common behavior on flowers with tubular corollas (Irwin et al., 2010). Honeybees do not bite holes, but commonly use the holes made by bumblebees (Soper, 1952). Nectar robbing in faba beans has been observed to reduce the pod set compared to honeybee or bumblebee legitimate visitation. But still robbed flowers set more pods than flowers, which were not visited by any bees (Kendall and Smith, 1975). The authors suggest that nectar robbing might indirectly increase pollination success because robbers shake flowers and thereby facilitate self-fertilization. As partially allogamous plant species, faba beans can reproduce by self-fertilization and by cross-fertilization. Approx. one third of the plants in a faba bean field are hybrid plants, while two thirds are self-pollinated (Filippetti and Ricciardi, 1993; Kendall and Smith, 1975; Soper, 1952). The benefit from insect pollination for faba beans has been shown to vary from 16 % to 40 % yield increase in terms of seed weight per plant (Bartomeus et al., 2014; Bishop et al., 2016; Gasim and Abdelmula, 2018). Knowledge about how different pollinator communities with varying foraging behavior affect yield formation in faba beans is however scarce.

Figure 2 Different insects on *V. faba*. From left to right: *Bombus terrestris* and *B. pascuorum* foraging on faba bean flowers, foraging *B. hortorum*, *B. lapidarius* approaching a faba bean flower, foraging *B. terrestris*, a foraging non-*Bombus* wild bee and a broad bean weevil (*B. rufimanus*) on a faba bean plant. Photos: Nicole Beyer.

Conservation effects of faba bean cultivation on pollinators

The cultivation of faba beans plays a relevant role in terms of resource provisioning for beneficial insects in agricultural landscapes (Everwand et al., 2017; Köpke and Nemecek, 2010) (Fig. 3). Bees can use the pollen and the nectar from the flowers, as well as the extrafloral nectaries, whose nectar is commonly used by honeybees before the onset of the bean flowering (Bond and Poulsen, 1983; Stoddard and Bond, 1987). As mass-flowering crop, *V. faba* provides a large quantity of resources during a short time period. A beneficial effect of the mass-flowering crop oilseed rape on pollinators has been demonstrate in many studies (e.g. Diekötter et al., 2014; Jauker et al., 2012; Westphal et al., 2003). This early flowering crop is the most grown mass-flowering crop in the EU (FAOSTAT, 2020). Resources in simplified agricultural landscapes are often scarce after the flowering of oilseed rape and faba beans can provide food sources for pollinators afterwards during midsummer. A study of Timberlake et al. (2019) showed that there are especially critical times in the year and mentioned a June-gap in food resource availability for bumblebees. *V. faba* flowers in that period and could therefore bridge this gap of low resource availability. Moreover, the late harvest of the beans enables the flowering of weeds late in the season and can therefore indirectly serve as food resource for insects also after their bloom (Köpke and Nemecek, 2010). There has been a strong decline of arable weeds during the last decades (Meyer et al., 2013) and their loss contributes to the floral impoverishment and biodiversity decline in agroecosystems (Storkey et al., 2012). The cultivation of faba beans has the potential to support bees in agricultural landscapes by the provisioning of resources during, before and after its flowering period (Fig. 3) and might contribute to the halting of the ongoing pollinator decline. A positive effect of faba bean cultivation on the colony density of *Bombus pascuorum* has already been shown (Knight et al., 2009) as well as higher bumblebee densities in field margins next to bean compared to wheat fields (Hanley et al., 2011). As legume species, faba beans might play a major role as forage plants for bumblebees. The decline of bumblebees, especially long-tongued species has been associated with the decline of leguminous plants (Goulson et al., 2005). However, there is a knowledge gap regarding the effect of conventionally faba bean cultivation on different functional groups of bee pollinators, especially studies at landscape scale are widely lacking.

Figure 3 Role of *V. faba* as floral resource for pollinators in agricultural landscapes. Pollinating insects can use the pollen and the nectar from the flower, as well as from the extrafloral nectaries. Faba beans provide resources in June, which are often scarce in simplified agricultural landscapes after oilseed rape has ceased flowering. Moreover, faba beans are harvested quite late, which enables the flowering of weeds, like thistles. Therefore, faba beans play an important role regarding the seasonal availability of flowers for pollinators. Photos: Nicole Beyer.

Research aims and hypotheses

The aim of my PhD thesis is to investigate the effect of the cultivation of faba beans (*Vicia faba* L.) within diversified crop rotations on bee pollinator densities, species richness and the functional trait composition of pollinator communities (Chapter 1 & 2), as well as on the colony development of bumblebees (Chapter 3). Moreover, I focus on the effects of landscape composition on bee pollinator communities in mass-flowering crops and the combined effects of landscape composition and insect pollination on crop yields, for two important entomophilous crops, oilseed rape (*Brassica napus* L.) (Chapter 4) and *V. faba* (Chapter 5). I tested following hypotheses:

- The cultivation of faba beans enhances the density and species richness of bees at landscape scale and the reproductive success of bumblebee colonies.

- Faba bean cultivation predominantly promotes functional bee groups adapted to the morphology of its flowers, i.e. bumblebees, especially long-tongued species and bees with a foraging preference for Fabaceae.
- Landscape composition, i.e. the cover of oilseed rape and of semi-natural habitats positively affects bees at landscape scale and influences bee densities in faba bean fields as well as the foraging behavior of different functional bee groups.
- Mass-flowering crop cultivation in the past and in the current year shapes bee densities in oilseed rape fields.
- Insect pollination enhances the crop yield of oilseed rape and of faba bean and interacts with landscape composition in shaping yield components and yield.

In Chapter 1 I focus on the landscape scale effect of faba bean cultivation and landscape composition on pollinators. For this I recorded bees in field margins in 30 different landscapes with and without faba bean cultivation and discuss the effectivity of faba bean cultivation as biodiversity measure withing the CAP greening reform. For Chapter 2 bees were recorded within the same landscapes in the semi-natural habitats and I aim at investigating, whether different mass-flowering crops (oilseed rape and *V. faba*) differently affect the functional composition of pollinator communities. In Chapter 3, the focus is on the development and resource utilization of bumblebee colonies (*Bombus terrestris* L.) and whether faba bean cultivation and other landscape composition metrics can enhance the colonies` reproductive success. In Chapter 4 I address the influence of past and present mass-flowering crop cultivation on bee densities in oilseed rape fields and the effect of insect pollination on the crops` yield formation. For this, I conducted a pollinator exclusion experiment in 17 landscapes along a mass-flowering crop gradient. Likewise, I conducted a pollinator exclusion experiment in faba bean fields in 11 different landscapes, which is addressed in Chapter 5. Here, I study how the cover of oilseed rape, faba bean and semi-natural habitats influences the density of different bee functional groups and their foraging behavior with resulting effects on faba bean yield.

Research approach

All field studies took place in agricultural landscapes in Germany. For the field studies of Chapter 1-3 a paired study design was chosen. Landscape pairs consisted of a landscape with at least one faba bean field and one control landscape without any grain legumes (Fig. 4). Individual landscapes had a size of 1 km x 1 km. Landscapes of a pair were at least 5 km apart to prevent pollinators from visiting both sites, because bees are known to forage up to several km away from their nests (Greenleaf et al., 2007; Westphal et al., 2006). Landscapes of a pair had similar landscape composition with regard to major land-use types.

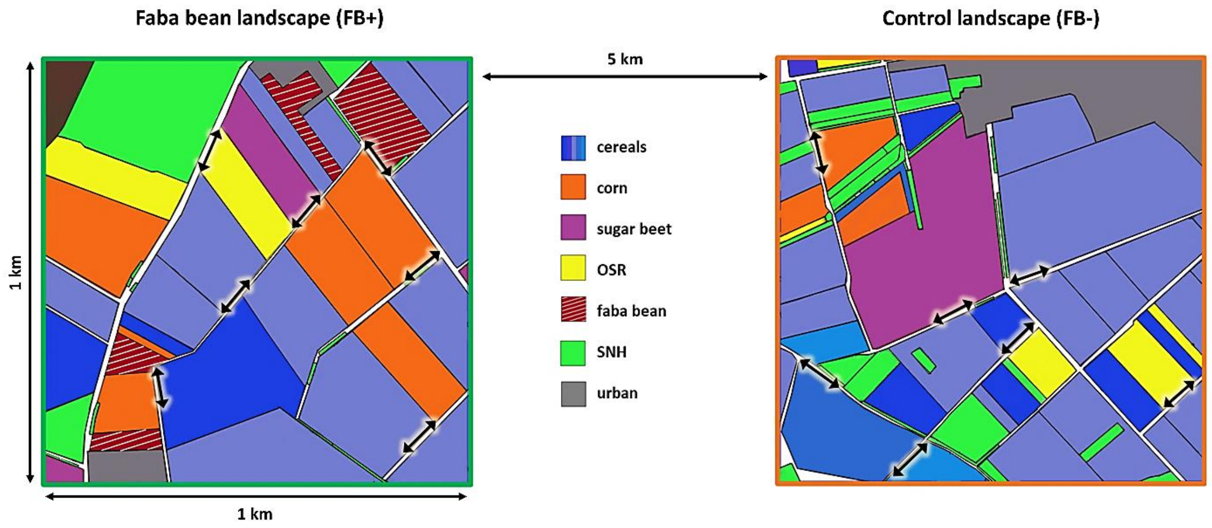


Figure 4 Example of a landscape pair in which pollinator surveys took place. A landscape of a pair (FB+) contained at least one faba bean field, while the respective control landscape did not contain any grain legumes. Stratified sampling design with transects located at field margins of different crops (depicted as arrows) according to the area coverage of the respective crop types is shown.

For Chapter 1 a stratified sampling design was used (Beduschi et al., 2015) and the number of standardized transects at different crop types was assigned according to the area coverage of the respective crop type (Fig. 4). For Chapter 2 variable transects in semi-natural habitats were chosen, which varied according to the flowering phenology of the semi-natural habitats to cover all suitable foraging habitats for wild bees at landscape scale (Westphal et al., 2008). For Chapter 3, two bumblebee colonies were placed in the center of each study landscape (Fig. 5). Their colony development was recorded, and pollen samples of foraging workers were taken at different time periods during the season. The approach for the last two chapters differed from the paired design described before. Landscapes along a mass-flowering crop and semi-natural habitat gradient were chosen and pollinator exclusion experiments took place in one oilseed rape or one faba bean field per landscape. Pollinators were excluded using bags made of fine mesh, which were put around the whole plants (Fig. 5). It is important to take the whole plant into account for yield analyses to account for plant compensation effects (Ouvrard and Jacquemart, 2019). Each bag was stabilized by four reed poles to prevent the bags from damaging the plants and bags were removed after plants had ceased flowering. After plants had matured, the yield components of bagged and open pollinated plants were assessed.

Figure 5 From left to right: Two bumblebee colonies, which were set up in the center of the study landscapes of Chapter 3, pollinator exclusion experiment in oilseed rape (Chapter 4) and in faba bean fields (Chapter 5). Photos: Nicole Beyer.

All studies of this PhD project were conducted within the framework of the RELEVANT project (Regulating ecosystem services in crop rotations with field bean (*Vicia faba*) and pea (*Pisum sativum*): quantification, assessment and realization) (https://www.thuenen.de/en/bd/projects/relevant/).

References

Aguilera, G., Roslin, T., Miller, K., Tamburini, G., Birkhofer, K., Caballero-Lopez, B., Lindström, S.A.M. et al., 2020. Crop diversity benefits carabid and pollinator communities in landscapes with semi-natural habitats. J. Appl. Ecol. 1–10. https://doi.org/10.1111/1365-2664.13712

Aouar-sadli, M., Louadi, K., Doumandji, S., 2008. Pollination of the broad bean (Vicia faba L.var. major) (Fabaceae) by wild bees and honey bees (Hymenoptera: Apoidea) and its impact on the seed production in the Tizi-Ouzou area (Algeria). African J. Agric. Res. 3, 266–272.

Bailes, E.J., Pattrick, J.G., Glover, B.J., 2018. An analysis of the energetic reward offered by field bean (Vicia faba) flowers: Nectar, pollen, and operative force. Ecol. Evol. 8, 3161–3171. https://doi.org/10.1002/ece3.3851

Bänsch, S., Tscharntke, T., Gabriel, D., Westphal, C., 2020a. Crop pollination services: complementary resource use by social vs solitary bees facing crops with contrasting flower supply. J. Appl. Ecol. 0–1. https://doi.org/10.1111/1365-2664.13777

Bänsch, S., Tscharntke, T., Ratnieks, F.L.W., Härtel, S., Westphal, C., 2020b. Foraging of honey bees in agricultural landscapes with changing patterns of flower resources. Agric. Ecosyst. Environ. 291, 106792. https://doi.org/10.1016/j.agee.2019.106792

Bartomeus, I., Potts, S.G., Steffan-Dewenter, I., Vaissière, B.E., Woyciechowski, M., Krewenka, K.M., Tscheulin, et al. , 2014. Contribution of insect pollinators to crop yield and quality varies with agricultural intensification. PeerJ 2014, 1–20. https://doi.org/10.7717/peerj.328

Batáry, P., Dicks, L. V., Kleijn, D., Sutherland, W.J., 2015. The role of agri-environment schemes in conservation and environmental management. Conserv. Biol. 29, 1006–1016. https://doi.org/10.1111/cobi.12536

Beduschi, T., Tscharntke, T., Scherber, C., 2015. Using multi-level generalized path analysis to understand herbivore and parasitoid dynamics in changing landscapes. Landsc. Ecol. 30, 1975–1986. https://doi.org/10.1007/s10980-015-0224-2

Benton, T.G., Vickery, J.A., Wilson, J.D., 2003. Farmland biodiversity: Is habitat heterogeneity the key? Trends Ecol. Evol. 18, 182–188. https://doi.org/10.1016/S0169-5347(03)00011-9

Bishop, J., Jones, H.E., Lukac, M., Potts, S.G., 2016. Insect pollination reduces yield loss following heat stress in faba bean (Vicia faba L.). Agric. Ecosyst. Environ. 220, 89–96. https://doi.org/10.1016/j.agee.2015.12.007

BMEL, 2020. Ackerbohne, Erbse & Co. Die Eiweißpflanzenstrategie des Bundesministerium für Ernährung und Landwirtschaft zur Förderung des Leguminosenanbaus in Deutschland.

BMEL, 2019a. Discussion Paper. 2035 Arable Farming Strategy. Prospects for Productive and Diverse Crop Farming.

BMEL 2019b. Beantragte Ökologische Vorrangflächen im Jahr 2019, Federal Ministry for Food and Agriculture (BMEL), Berlin, url: https://www.bmel.de/SharedDocs/Downloads/Landwirtschaft/Foerderung/OekologischeVorrangflaechen2019.html

Böhm, H., Dauber, J., Dehler, M., Gallardo, D.A.A., Witte, T. De, Fuß, R., 2020. Übersichtsarbeit Fruchtfolgen mit und ohne Leguminosen : ein Review 72. https://doi.org/10.5073/JfK.2020.10-11.01

Bond, D.A., Poulsen, M.H., 1983. Pollination. In: Hebblethwaite, P. D., Ed., The Faba Bean (Vicia faba L.). Butterworths, London, 77-101.

Burstin, J., Gallardo, K., Mir, R. R., Varshney, R. K., Duc, G., Burstin, J., Gallardo, K., Duc, G., 2011. Chapter 20: Improving protein content and nutrition quality. In: A Pratap, J Kumar (eds) Biology and Breeding of Food Legumes, Biology and Breeding of Food Legumes.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., et al., 2012. Biodiversity loss and its impact on humanity. Nature 486, 59–67. https://doi.org/10.1038/nature11148

Carré, G., Roche, P., Chifflet, R., Morison, N., Bommarco, R., Harrison-Cripps, J., Krewenka, K.,et al., 2009. Landscape context and habitat type as drivers of bee diversity in European annual crops. Agric. Ecosyst. Environ. 133, 40–47. https://doi.org/10.1016/j.agee.2009.05.001

Cubero, J.I., 2011. The faba bean: a historic perspective. In: Grain Legumes. The magazine of the European Association for Grain Legume Research.

DAFA, 2012. The Legumes Expert Forum. Science, economy and society - making ecosystem services from legumes competitive. A research strategy of the German Agricultural Research Alliance. Braunschweig: German Agricultural Research Alliance.

Dainese, M., Martin, E.A., Aizen, M.A., Albrecht, M., Bartomeus, I., Bommarco, R., Carvalheiro, L.G., et al., 2019. A global synthesis reveals biodiversity-mediated benefits for crop production. Sci. Adv. 5, eaax0121.

Demonetz Erbse/Bohne, 2020. Schädlinge an Ackerbohnen [WWW Document]. URL https://www.demoneterbo.agrarpraxisforschung.de/index.php?id=100 (accessed 11.3.20).

Destatis, 2020. Ackerland nach Hauptnutzungsarten und Kulturarten. Accessed: 03 November 2020 [WWW Document]. URL https://www.destatis.de/DE/Themen/Branchen-

Unternehmen/Landwirtschaft-Forstwirtschaft-Fischerei/Feldfruechte-Gruenland/Tabellen/ackerland-hauptnutzungsarten-kulturarten.html

Diekötter, T., Kadoya, T., Peter, F., Wolters, V., Jauker, F., 2010. Oilseed rape crops distort plant-pollinator interactions. J. Appl. Ecol. 47, 209–214. https://doi.org/10.1111/j.1365-2664.2009.01759.x

Diekötter, T., Peter, F., Jauker, B., Wolters, V., Jauker, F., 2014. Mass-flowering crops increase richness of cavity-nesting bees and wasps in modern agro-ecosystems. GCB Bioenergy 6, 219–226. https://doi.org/10.1111/gcbb.12080

Ebeling, A., Klein, A.M., Schumacher, J., Weisser, W.W., Tscharntke, T., 2008. How does plant richness affect pollinator richness and temporal stability of flower visits? Oikos 117, 1808–1815. https://doi.org/10.1111/j.1600-0706.2008.16819.x

European Commission, 2017. Evaluation study of the payment for agricultural practices beneficial for the climate and the environment - Final Report, European Commission, Brussels.

European Commission, 2020. Evaluation of the impacts of the CAP on habitats, landscape, biodiversity. Final Report. Publications Office of the European Union. Luxembourg.

Eurostat, 2020. Dry pulses in EU agriculture - statistics on cultivation, production and economic value. Accessed: 03 November 2020. [WWW Document]. URL https://ec.europa.eu/eurostat/statistics-explained/index.php/Dry_pulses_in_EU_agriculture_-_statistics_on_cultivation,_production_and_economic_value

Everwand, G., Cass, S., Dauber, J., Williams, M., Stout, J., 2017. Legume Crops and Biodiversity, in: Murphy-Bokern, D., Stoddard, F.L., Watson, C.A. (Eds.), Legumes in Cropping Systems. Wallingford, CAB International.

FAOSTAT, 2020. (Food and Agriculture Organisation of the United States) [WWW Document]. URL http://www.fao.org/faostat/en/#data/QC (accessed 9.10.20).

Filippetti, A., Ricciardi, L., 1993. Faba bean (Vicia faba L.). In:G. Kalloo & B.O. Berg (Eds.), Genetic Improvement of Vegetable Crops, pp. 355–385. Pergamon Press, Oxford.

Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S.,et al., 2005. Global consequences of land use. Science (80-.). 309, 570–574. https://doi.org/10.1126/science.1111772

Gámez-Virués, S., Perović, D.J., Gossner, M.M., Börschig, C., Blüthgen, N., De Jong, H., Simons, N.K., et al., 2015. Landscape simplification filters species traits and drives biotic homogenization. Nat. Commun. 6. https://doi.org/10.1038/ncomms9568

Garibaldi, L.A., Bartomeus, I., Bommarco, R., Klein, A.M., Cunningham, S.A., Aizen, M.A., Boreux, V., et al., 2015. Trait matching of flower visitors and crops predicts fruit set better than trait diversity. J. Appl. Ecol. 52, 1436–1444. https://doi.org/10.1111/1365-2664.12530

Garratt, M.P.D., Coston, D.J., Truslove, C.L., Lappage, M.G., Polce, C., Dean, R., Biesmeijer, J.C., Potts, S.G., 2014. The identity of crop pollinators helps target conservation for improved ecosystem services. Biol. Conserv. 169, 128–135. https://doi.org/10.1016/j.biocon.2013.11.001

Gasim, S.M., Abdelmula, A.A., 2018. Impact of Bee Pollination on Yield of Faba Bean (<i>Vicia faba</i> L.) Grown under Semi-Arid Conditions. Agric. Sci. 09, 729–740. https://doi.org/10.4236/as.2018.96051

Goulson, D., Hanley, M.E., Darvill, B., Ellis, J.S., Knight, M.E., 2005. Causes of rarity in bumblebees. Biol. Conserv. 122, 1–8. https://doi.org/10.1016/j.biocon.2004.06.017

Grab, H., Blitzer, E.J., Danforth, B., Loeb, G., Poveda, K., 2017. Temporally dependent pollinator competition and facilitation with mass flowering crops affects yield in co-blooming crops. Sci. Rep. 7, 1–9. https://doi.org/10.1038/srep45296

Grab, H., Brokaw, J., Anderson, E., Gedlinske, L., Gibbs, J., Wilson, J., Loeb, G.,et al., 2019. Habitat enhancements rescue bee body size from the negative effects of landscape simplification. J. Appl. Ecol. 56, 2144–2154. https://doi.org/10.1111/1365-2664.13456

Greenleaf, S.S., Williams, N.M., Winfree, R., Kremen, C., 2007. Bee foraging ranges and their relationship to body size. Oecologia 153, 589–596. https://doi.org/10.1007/s00442-007-0752-9

Hanley, M.E., Franco, M., Dean, C.E., Franklin, E.L., Harris, H.R., Haynes, A.G., Rapson, S.R., et al., 2011. Increased bumblebee abundance along the margins of a mass flowering crop: Evidence for pollinator spill-over. Oikos 120, 1618–1624. https://doi.org/10.1111/j.1600-0706.2011.19233.x

Hass, A.L., Kormann, U.G., Tscharntke, T., Clough, Y., Baillod, A.B., Sirami, C., Fahrig, L., et ak., 2018. Landscape configurational heterogeneity by small-scale agriculture, not crop diversity, maintains pollinators and plant reproduction in western Europe. Proc. R. Soc. B Biol. Sci. 285. https://doi.org/10.1098/rspb.2017.2242

Herridge, D.F., Peoples, M.B., Boddey, R.M., 2008. Global inputs of biological nitrogen fixation in agricultural systems. Plant Soil 311, 1–18. https://doi.org/10.1007/s11104-008-9668-3

Herrmann, F., Westphal, C., Moritz, R.F.A., Steffan-Dewenter, I., 2007. Genetic diversity and mass resources promote colony size and forager densities of a social bee (Bombus pascuorum) in agricultural landscapes. Mol. Ecol. 16, 1167–1178. https://doi.org/10.1111/j.1365-294X.2007.03226.x

Holzschuh, A., Dainese, M., González-Varo, J.P., Mudri-Stojnić, S., Riedinger, V., Rundlöf, M., Scheper, et al., 2016. Mass-flowering crops dilute pollinator abundance in agricultural landscapes across Europe. Ecol. Lett. 19, 1228–1236. https://doi.org/10.1111/ele.12657

Irwin, R.E., Bronstein, J.L., Manson, J.S., Richardson, L., 2010. Nectar Robbing: Ecological and Evolutionary Perspectives. Annu. Rev. Ecol. Evol. Syst. 41, 271–292. https://doi.org/10.1146/annurev.ecolsys.110308.120330

Jauker, F., Peter, F., Wolters, V., Diekötter, T., 2012. Early reproductive benefits of mass-flowering crops to the solitary bee Osmia rufa outbalance post-flowering disadvantages. Basic Appl. Ecol. 13, 268–276. https://doi.org/10.1016/j.baae.2012.03.010

Jensen, E.S., Peoples, M.B., Boddey, R.M., Gresshoff, P.M., Henrik, H.N., Alves, B.J.R., Morrison, M.J., 2012. Legumes for mitigation of climate change and the provision of feedstock for biofuels and biorefineries. A review, Agronomy for Sustainable Development. https://doi.org/10.1007/s13593-011-0056-7

Jensen, E.S., Peoples, M.B., Hauggaard-Nielsen, H., 2010. Faba bean in cropping systems. F. Crop. Res.

115, 203–216. https://doi.org/10.1016/j.fcr.2009.10.008

Kallioniemi, E., Åström, J., Rusch, G.M., Dahle, S., Åström, S., Gjershaug, J.O., 2017. Local resources, linear elements and mass-flowering crops determine bumblebee occurrences in moderately intensified farmlands. Agric. Ecosyst. Environ. 239, 90–100. https://doi.org/10.1016/j.agee.2016.12.039

Karkanis, A., Ntatsi, G., Lepse, L., Fernández, J.A., Vågen, I.M., Rewald, B., Alsiņa, I., et al., 2018. Faba bean cultivation – revealing novel managing practices for more sustainable and competitive European cropping systems. Front. Plant Sci. 9, 1–14. https://doi.org/10.3389/fpls.2018.01115

Kendall, A.D.A., Smith, B.D., 1975. The Pollinating Efficiency of Honeybee and Bumblebee Visits to Field Bean Flowers (Vicia faba L.) 12, 709–717.

Kennedy, C.M., Lonsdorf, E., Neel, M.C., Williams, N.M., Ricketts, T.H., Winfree, R., Bommarco, R., et al., 2013. A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. Ecol. Lett. 16, 584–599. https://doi.org/10.1111/ele.12082

Knight, M.E., Osborne, J.L., Sanderson, R.A., Hale, R.J., Martin, A.P., Goulson, D., 2009. Bumblebee nest density and the scale of available forage in arable landscapes. Insect Conserv. Divers. 2, 116–124. https://doi.org/10.1111/j.1752-4598.2009.00049.x

Köpke, U., Nemecek, T., 2010. Ecological services of faba bean. F. Crop. Res. 115, 217–233. https://doi.org/10.1016/j.fcr.2009.10.012

Kremen, C., Miles, A., 2012. Ecosystem Services in Biologically Diversified versus Conventional Farming Systems: Benefits, Externalitites, and Trade-Offs. Ecol. Soc. 17, 1–23. https://doi.org/10.5751/ES-05035-170440

Lichtenberg, E.M., Kennedy, C.M., Kremen, C., Batáry, P., Berendse, F., Bommarco, R., Bosque-Pérez, et al., 2017. A global synthesis of the effects of diversified farming systems on arthropod diversity within fields and across agricultural landscapes. Glob. Chang. Biol. 23, 4946–4957. https://doi.org/10.1111/gcb.13714

Liebman, M., Dyck, E., 1993. Crop Rotation and Intercropping Strategies for Weed Management. Ecol. Appl. 3, 92–122.

Mallinger, R.E., Gibbs, J., Gratton, C., 2016. Diverse landscapes have a higher abundance and species richness of spring wild bees by providing complementary floral resources over bees' foraging periods. Landsc. Ecol. 31, 1523–1535. https://doi.org/10.1007/s10980-015-0332-z

Mandelik, Y., Winfree, R., Neeson, T., Kremen, C., 2012. Complementary habitat use by wild bees in agro-natural landscapes. Ecol. Appl. 22, 1535–1546. https://doi.org/10.1890/11-1299.1

Martin, E.A., Dainese, M., Clough, Y., Báldi, A., Bommarco, R., Gagic, V., Garratt, et al., 2019. The interplay of landscape composition and configuration: new pathways to manage functional biodiversity and agroecosystem services across Europe. Ecol. Lett. 22, 1083–1094. https://doi.org/10.1111/ele.13265

Marzinzig, B., Brünjes, L., Biagioni, S., Behling, H., Link, W., Westphal, C., 2018. Bee pollinators of faba bean (Vicia faba L.) differ in their foraging behaviour and pollination efficiency. Agric. Ecosyst. Environ. 264, 24–33. https://doi.org/10.1016/j.agee.2018.05.003

Meyer, S., Wesche, K., Krause, B., Leuschner, C., 2013. Dramatic losses of specialist arable plants in Central Germany since the 1950s/60s - a cross-regional analysis. Divers. Distrib. 19, 1175–1187. https://doi.org/10.1111/ddi.12102

Nayak, G.K., Roberts, S.P.M., Garratt, M., Breeze, T.D., Tscheulin, T., Harrison-Cripps, J., Vogiatzakis, I.N., et al., 2015. Interactive effect of floral abundance and semi-natural habitats on pollinators in field beans (Vicia faba). Agric. Ecosyst. Environ. 199, 58–66. https://doi.org/10.1016/j.agee.2014.08.016

Nemecek, T., von Richthofen, J.S., Dubois, G., Casta, P., Charles, R., Pahl, H., 2008. Environmental impacts of introducing grain legumes into European crop rotations. Eur. J. Agron. 28, 380–393. https://doi.org/10.1016/j.eja.2007.11.004

Nichols, V., Verhulst, N., Cox, R., Govaerts, B., 2015. Weed dynamics and conservation agriculture principles: A review. F. Crop. Res. 183, 56–68. https://doi.org/10.1016/j.fcr.2015.07.012

Nuessly, G.S., Hentz, M.G., Beiriger, R., Scully, B.T., 2004. Insects Associated With Faba Bean, Vicia Faba (Fabales: Fabaceae), in Southern Florida. Florida Entomol. 87, 204–211. https://doi.org/10.1653/0015-4040(2004)087[0204:iawfbv]2.0.co;2

Ouvrard, P., Jacquemart, A.L., 2019. Review of methods to investigate pollinator dependency in oilseed rape (Brassica napus). F. Crop. Res. 231, 18–29. https://doi.org/10.1016/j.fcr.2018.11.006

Pe'er, G., Zinngrebe, Y., Moreira, F., Sirami, C., Schindler, S., Müller, R., Bontzorlos, V., et al., 2019. A greener path for the EU Common Agricultural Policy. Science (80-.). 365, 449–451.

Perović, D., Gámez-Virués, S., Börschig, C., Klein, A.M., Krauss, J., Steckel, J., Rothenwöhrer, C., et al., 2015. Configurational landscape heterogeneity shapes functional community composition of grassland butterflies. J. Appl. Ecol. 52, 505–513. https://doi.org/10.1111/1365-2664.12394

Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O., Kunin, W.E., 2010. Global pollinator declines: Trends, impacts and drivers. Trends Ecol. Evol. 25, 345–353. https://doi.org/10.1016/j.tree.2010.01.007

Potts, S.G., Vulliamy, B., Dafni, A., Ne'eman, G., Willmer, P., 2003. Linking bees and flowers: How do floral communities structure pollinator communities? Ecology 84, 2628–2642. https://doi.org/10.1890/02-0136

Power, A.G., 2010. Ecosystem services and agriculture: Tradeoffs and synergies. Philos. Trans. R. Soc. B Biol. Sci. 365, 2959–2971. https://doi.org/10.1098/rstb.2010.0143

Preissel, S., Reckling, M., Schläfke, N., Zander, P., 2015. Magnitude and farm-economic value of grain legume pre-crop benefits in Europe: A review. F. Crop. Res. 175, 64–79. https://doi.org/10.1016/j.fcr.2015.01.012

Requier, F., Jowanowitsch, K.K., Kallnik, K., Steffan-Dewenter, I., 2020. Limitation of complementary resources affects colony growth, foraging behavior, and reproduction in bumble bees. Ecology 101, 0–3. https://doi.org/10.1002/ecy.2946

Riedinger, V., Mitesser, O., Hovestadt, T., Steffan-Dewenter, I., Holzschuh, A., Rosenheim, J.A., 2015. Annual dynamics of wild bee densities: Attractiveness and productivity effects of oilseed rape. Ecology 96, 1351–1360. https://doi.org/10.1890/14-1124.1

Rosa-Schleich, J., Loos, J., Mußhoff, O., Tscharntke, T., 2019. Ecological-economic trade-offs of Diversified Farming Systems – A review. Ecol. Econ. 160, 251–263. https://doi.org/10.1016/j.ecolecon.2019.03.002

Schellhorn, N.A., Gagic, V., Bommarco, R., 2015. Time will tell: Resource continuity bolsters ecosystem services. Trends Ecol. Evol. 30, 524–530. https://doi.org/10.1016/j.tree.2015.06.007

Seibold, S., Gossner, M.M., Simons, N.K., Blüthgen, N., Ambarl, D., Ammer, C., Bauhus, J., et al., 2019. Arthropod decline in grasslands and forests is associated with drivers at landscape level. Nature 574, 1–34. https://doi.org/10.1038/s41586-019-1684-3

Soper, M.M.H., 1952. A study of the principal factors affecting the establishment and development of the field bean (vicia faba). J. Agric. Sci. 42, 335–346. https://doi.org/10.1017/S0021859600057233

Steffan-Dewenter, I., Münzenberg, U., Bürger, C., Thies, C., Tscharntke, T., 2002. Scale-dependent effects of landscape context on three pollinator guilds. Ecology 83, 1421–1432. https://doi.org/10.1890/0012-9658(2002)083[1421:SDEOLC]2.0.CO;2

Stoddard, F.L., Bond, D.A., 1987. The pollination requirements of the Faba Bean. Bee World 68, 144–152. https://doi.org/10.1080/0005772X.1987.11098923

Storkey, J., Meyer, S., Still, K.S., Leuschner, C., 2012. The impact of agricultural intensification and land-use change on the European arable flora. Proc. R. Soc. B Biol. Sci. 279, 1421–1429. https://doi.org/10.1098/rspb.2011.1686

Sutter, L., Jeanneret, P., Bartual, A.M., Bocci, G., Albrecht, M., 2017. Enhancing plant diversity in agricultural landscapes promotes both rare bees and dominant crop-pollinating bees through complementary increase in key floral resources. J. Appl. Ecol. 54, 1856–1864. https://doi.org/10.1111/1365-2664.12907

Timberlake, T.P., Vaughan, I.P., Memmott, J., 2019. Phenology of farmland floral resources reveals seasonal gaps in nectar availability for bumblebees. J. Appl. Ecol. 56, 1585–1596. https://doi.org/10.1111/1365-2664.13403

Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I., Thies, C., 2005. Landscape perspectives on agricultural intensification and biodiversity - Ecosystem service management. Ecol. Lett. 8, 857–874. https://doi.org/10.1111/j.1461-0248.2005.00782.x

Vitousek, P.M., Cassman, K., Cleveland, C., Crews, T., Field, C.B., Grimm, N.B., Howarth, R.W., et al., 2002. Towards an ecological understanding of biological nitrogen fixation. Biogeochemistry 57–58, 1–45. https://doi.org/10.1023/A:1015798428743

Westhoek, H., Lesschen, J.P., Rood, T., Wagner, S., De Marco, A., Murphy-Bokern, D., Leip, A., et al., 2014. Food choices, health and environment: Effects of cutting Europe’s meat and dairy intake. Glob. Environ. Chang. 26, 196–205. https://doi.org/10.1016/j.gloenvcha.2014.02.004

Westphal, C., Bommarco, R., Carré, G., Lamborn, E., Morison, N., Petanidou, T., Potts, S.G., et al., 2008. Measuring bee diversity in different European habitats and biogeographical regions. Ecol. Monogr. 78, 653–671. https://doi.org/10.1890/07-1292.1

Westphal, C., Steffan-Dewenter, I., Tscharntke, T., 2009. Mass flowering oilseed rape improves early colony growth but not sexual reproduction of bumblebees. J. Appl. Ecol. 46, 187–193. https://doi.org/10.1111/j.1365-2664.2008.01580.x

Westphal, C., Steffan-Dewenter, I., Tscharntke, T., 2006. Bumblebees experience landscapes at different spatial scales: Possible implications for coexistence. Oecologia 149, 289–300. https://doi.org/10.1007/s00442-006-0448-6

Westphal, C., Steffan-Dewenter, I., Tscharntke, T., 2003. Mass flowering crops enhance pollinator densities at a landscape scale. Ecol. Lett. 6, 961–965. https://doi.org/10.1046/j.1461-0248.2003.00523.x

Woodcock, B.A., Garratt, M.P.D., Powney, G.D., Shaw, R.F., Osborne, J.L., Soroka, J., Lindström, et al., 2019. Meta-analysis reveals that pollinator functional diversity and abundance enhance crop pollination and yield. Nat. Commun. 10, 1–10. https://doi.org/10.1038/s41467-019-09393-6

Zander, P., Amjath-Babu, T.S., Preissel, S., Reckling, M., Bues, A., Schläfke, N., Kuhlman, T., et al., 2016. Grain legume decline and potential recovery in European agriculture: a review. Agron. Sustain. Dev. 36. https://doi.org/10.1007/s13593-016-0365-y

Chapter 1

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

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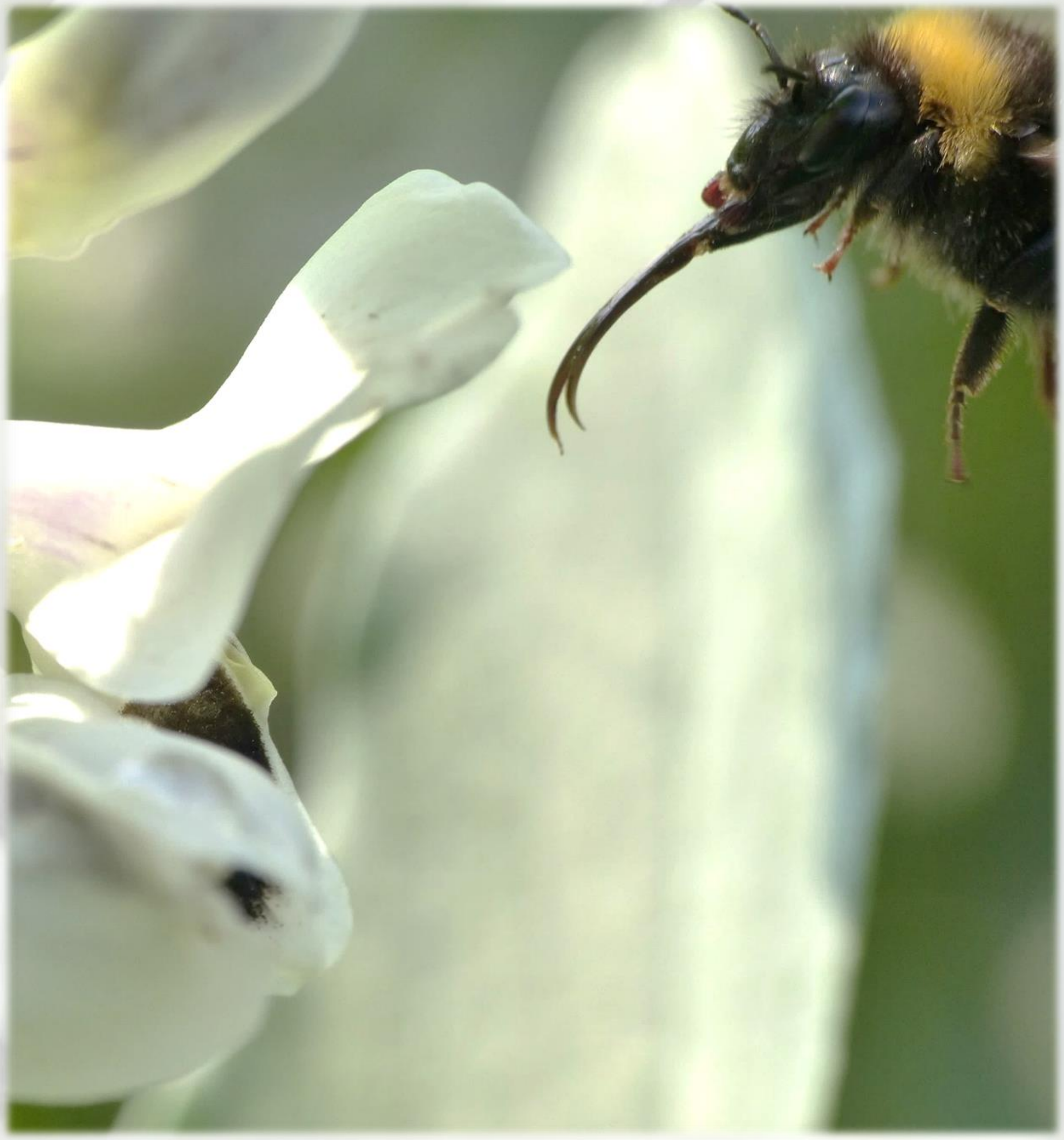

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Abstract

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. 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. 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). 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.

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 seminatural 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.

Keywords

bumblebee, ecosystem services, functional traits, grain legumes, greening, mass-flowering crops, oilseed rape, pollinators

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 et al., 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 et al. 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 EFAs 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 EU 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 et al., 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 world-wide 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 et al., 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 et al., 2007; Westphal et al., 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 analyze 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 km^2 landscapes, i.e. 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 favored by FB cultivation. Moreover, FB cultivation should promote bees, frequently collecting pollen from Fabaceae.

Materials and Methods

Study design

The study was conducted within 30 paired study landscapes of 1 km^2 (1km x 1km) size each, which were situated in three regions of Germany (Fig. 1). Twelve study landscapes were in the surroundings of Göttingen in Central Germany (51°32´N, 9°56´E). Ten 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 three 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-).

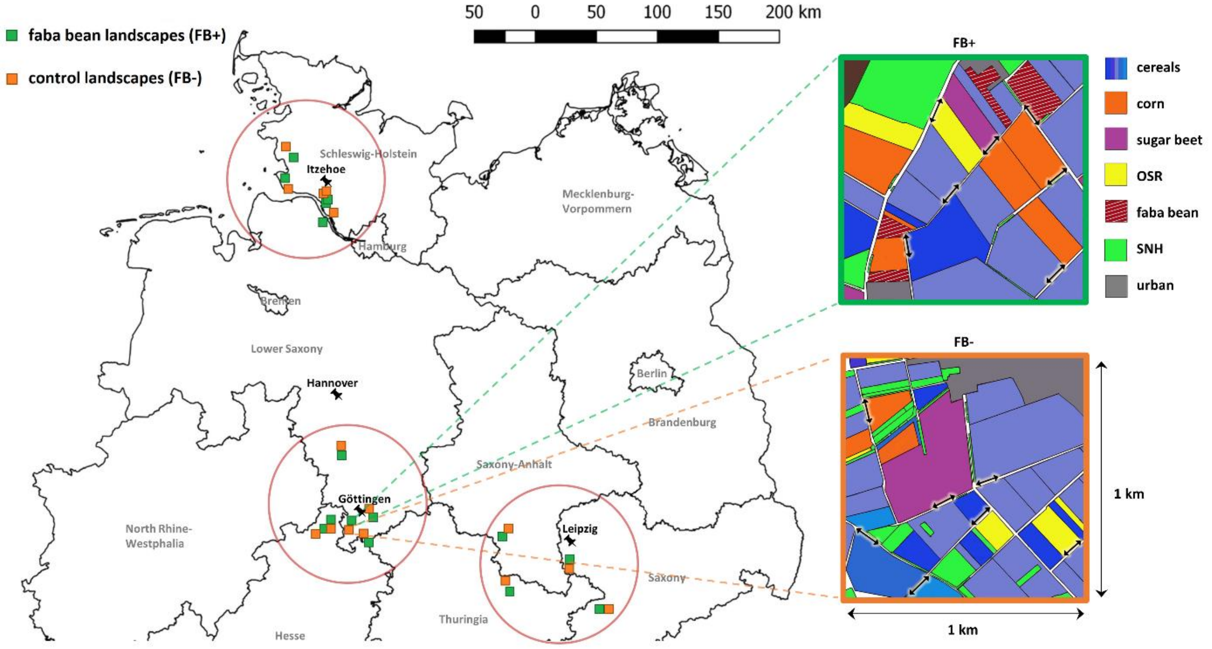

Figure 1 Location of the study landscapes in three regions of Germany. Landscapes with faba bean cultivation (FB+) are depicted in green and controls without grain legumes (FB−) in orange. One representative landscape pair is shown in detail. Different colours indicate different land use types and crops. 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.

Landscape selection was based on ATKIS land cover data (Digitales Basis-Landschaftsmodell). The landscape composition was analysed for the entire area (1 km^2). 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 et al., 2007; Westphal et al., 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 m^2 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 et al., 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) (SNH). Forest was not included in SNH since it represented a rather unsuitable foraging habitat for pollinators (Proesmans et al., 2019). Calculations were done with QGIS version 2.18 (QGIS Development Team, 2016).

Wild bee surveys

In summer 2017, wild bees were sampled within seven standardized transect walks per study landscape (Westphal et al., 2008), located at field margins of different annual crop fields. Transect area was always 400 m^2, mostly 100 m x 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, Tscharntke & Scherber, 2015).

The bee densities, i.e. the number of all foraging bees per transect area (bees/400m^2) was recorded within 10 min, excluding handling time. If species could not be identified in the field, bees were taken to the lab 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 lab (Mauss 1992; Amiet 1996) and sent non-*Bombus* bees to an expert for identification (Frank Creutzburg, Jena). Flower cover, i.e. the area covered with open flowers (m^2) was estimated for every transect and did not differ between FB and control landscapes (p=0.52) (Fig. 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.

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, i.e. 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 ten 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 *BeeIT* (Cariveau et al., 2016; Table S1). The information on dietary preferences (lecty) was obtained from Westrich (2018).

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 was 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 in comparison with the best fitting model were considered for interpretation. Akaike weights (w_i) as measure of the relative likelihood of individual models and the sum of Akaike weights (Σw_i) as measure of the relative importance of explanatory variables were used for interpretation (Burnham & Anderson, 2002). For detailed information about statistical analyses, see supplementary material.

Results

We observed 2198 wild bees of which 1794 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 which densities did not differ between FB+ and FB- landscapes (Fig. S2).

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 ($\Sigma w_i = 1$), FB cultivation ($\Sigma w_i = 0.97$), their interaction ($\Sigma w_i = 0.91$) and flower cover ($\Sigma w_i = 0.91$) as well as the interaction between run and flower cover ($\Sigma w_i = 0.32$) (Table S2 & S3). Most bumblebees were observed in run 2, on average 28 individuals per study landscape (Table S4). In the second and third run more than twice as many bumblebees were present in FB landscapes compared to controls (Fig. 2A). Densities increased with increasing local transect flower cover. This effect was slightly more pronounced in run 2 and 3 than in run 1 (Fig. S3a).

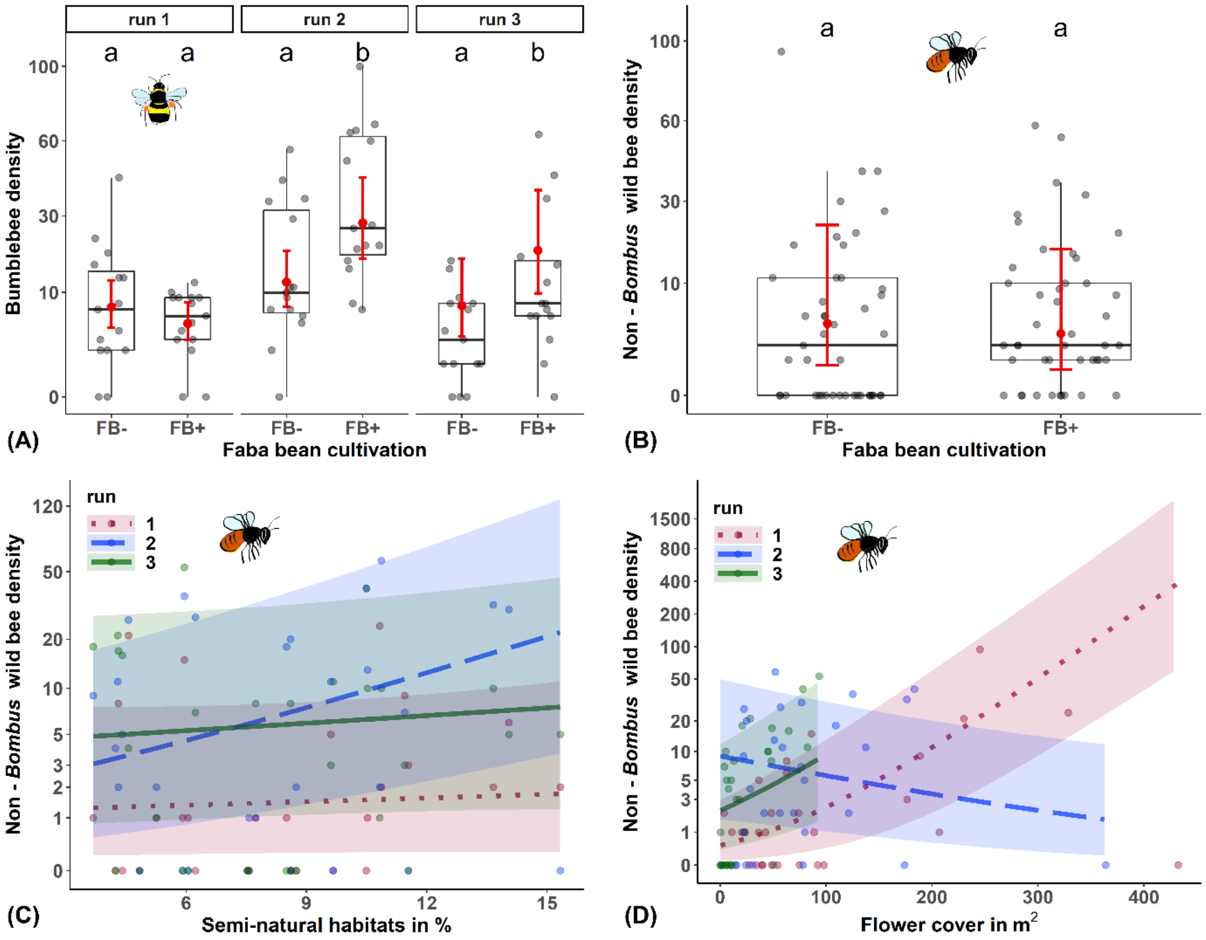

Figure 2 Effects of faba bean cultivation on **(A)** bumblebee densities per landscape for the three sampling runs and on **(B)** non-*Bombus* densities. Different letters above groups indicate significant differences between landscapes with (FB+) and without faba bean cultivation (FB−; within each run for [A]). Effects of **(C)** proportion of semi-natural habitats (%) and **(D)** local flower cover (m^2) on non-*Bombus* bee densities for the three sampling runs. Predicted mean values and 95% confidence intervals are displayed in red for boxplots and in different colours (according to different runs) for line graphs. All predictions are based on the second-best fitting model *bb2* for (A) and *nb2* for (B) and (C) (Table S2). Y-axes in (A) and (B) are sqrt- and in (C) and (D) log transformed for graphical reasons.

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 ($\Sigma w_i = 1$), SNH ($\Sigma w_i = 1$) and all possible interactions (Σw_i between 0.93 and 1) as well as FB ($\Sigma w_i = 0.44$) (Table S2 & S3). We found similar average densities in FB and control landscapes (Fig. 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 (Fig. 2C). Densities increased with increasing flower cover in run 1 and 3 but decreased in run 2 (Fig. 2D). The effect of enhanced bee densities with increasing flower cover was strongest, when percentage of SNH was high (Fig. S3b).

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 ($\Sigma w_i = 1$), their interaction ($\Sigma w_i = 1$), FB cultivation ($\Sigma w_i = 0.81$) and the interaction between FB and flower cover ($\Sigma w_i = 0.35$) (Table S2 & S3). Species richness increased with enhanced flower cover. This effect was strongest in run 3 (Fig. 3A) and more pronounced in control compared to FB landscapes (Fig. S4). Mean species richness per study landscape was 5.5 for FB and 4.4 in control landscapes (Table S5; Fig. 3B).

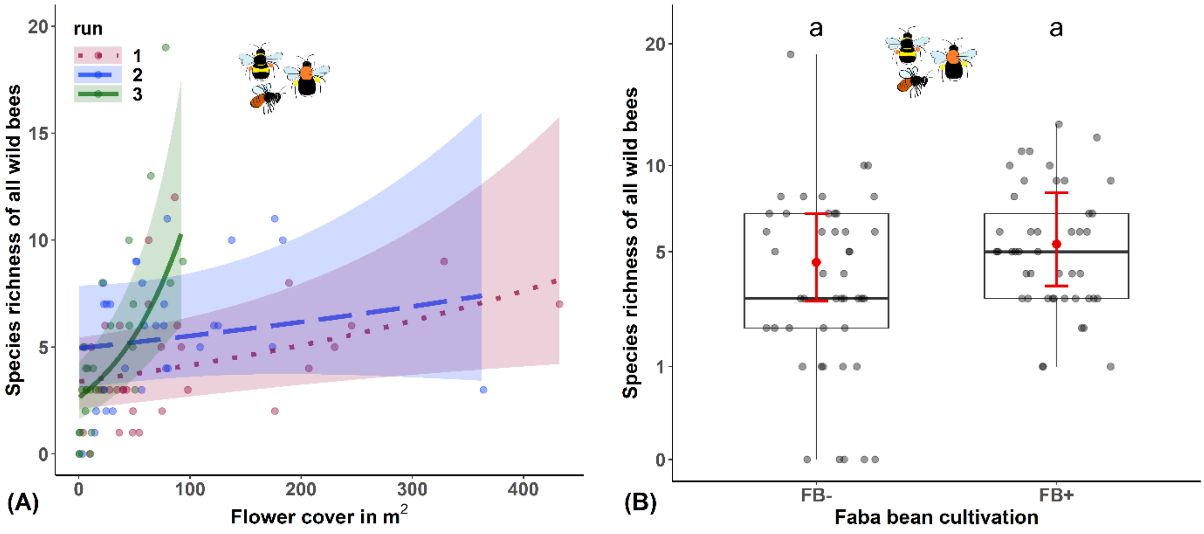

Figure 3 Effects of **(A)** local flower cover (m^2) on wild bee species richness for the three sampling runs. Effects of **(B)** faba bean cultivation on wild bee species richness. Predicted mean values and 95% confidence intervals are displayed in red for boxplots and in different colours (according to different runs) for line graphs. Same letters above groups indicate non-significant differences between landscapes with (FB+) and without (FB−) faba bean cultivation. All predictions are based on the best fitting model *sri1* (Table S2). Y-axis in (B) is sqrt-transformed for graphical reasons.

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 ($\Sigma w_i = 0.58$) and the interaction between local flower cover and SNH ($\Sigma w_i = 0.26$) were the most important explanatory variables for CWM ITD (Table S6 & S7). We found that average body size in bee communities was smallest in run 3 (Table S4; Fig. 4A) and CWM ITD decreased with increasing percentage of SNH (Fig. 4B). This effect was more pronounced when local flower cover was low (Fig. 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 (Fig. S5b & c). Additionally, compared to ITD models, mean proboscis length increased with increasing flower cover in control landscapes but decreased in FB landscapes ($\Sigma w_i = 0.33$) (Table S6 & 7) (Fig. 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 $\Sigma w_i=1$ (Table S6 & 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 run, whereas the opposite was true for run 1 (Fig. 4C). The proportion of Fabaceae foragers was enhanced with increasing percentage of SNH in run 1, whereas it decreased in run 2 ($\Sigma w_i = 0.99$) (Fig. S6a). Moreover, the proportion of Fabaceae foragers was positively related with transect flower cover in run 2 and negatively in run 3 ($\Sigma w_i = 0.71$) (Fig. S6b).

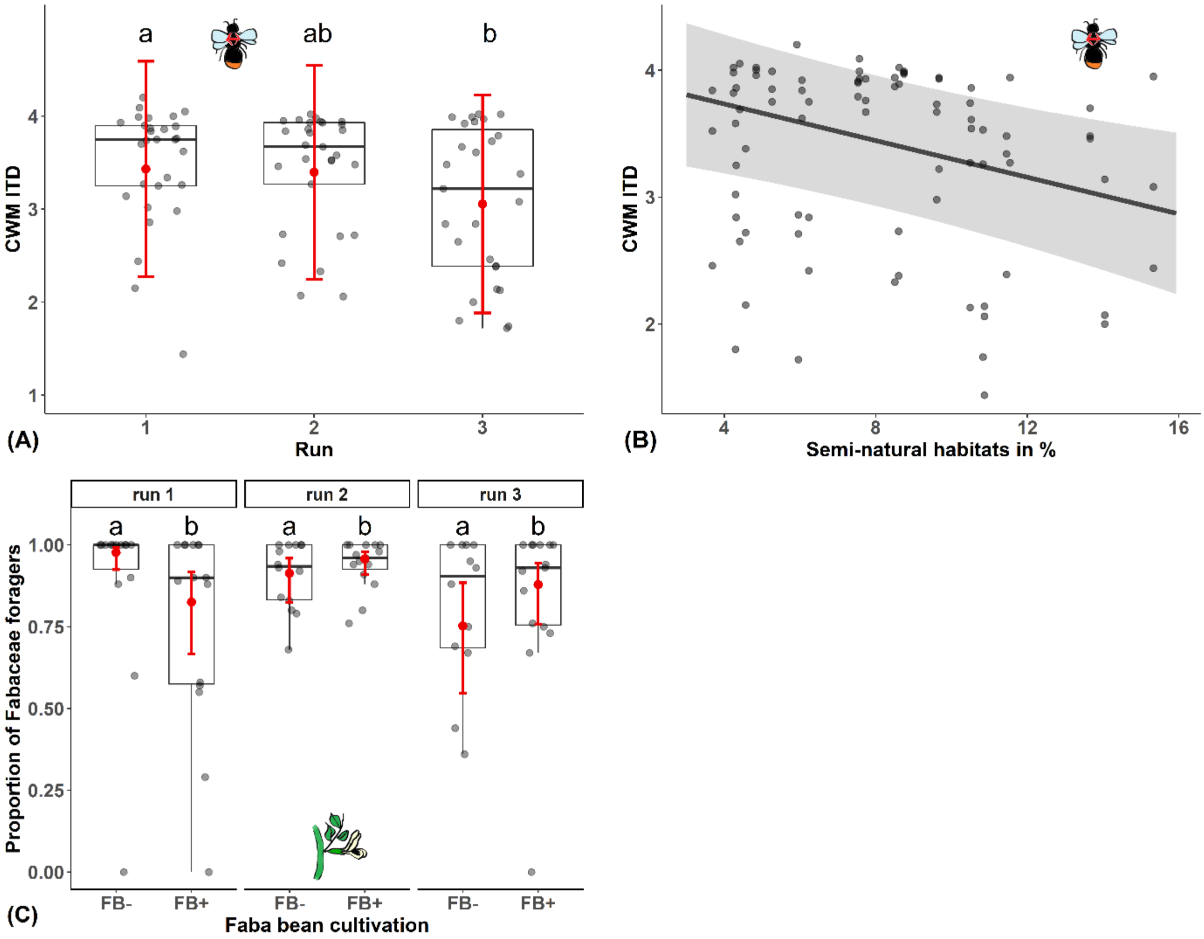

Figure 4 Effects of **(A)** sampling run and of **(B)** semi-natural habitats (%) on community-weighted means (CWM) for intertegular distance (ITD; mm). Effects of **(C)** faba bean cultivation on the proportion of bee species foraging on Fabaceae for the different sampling runs. Predicted mean values and 95% confidence intervals are displayed in red. Predictions for (A) are obtained from the second-best model *cmITD2* and for (C) from the best fitting model *mL1* (Table S6). Different letters above groups indicate significant differences between runs in (A) and between landscapes with (FB+) and without faba bean cultivation (FB−) within each run in (C).

Discussion

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 run 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 km^2 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 et al., 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).

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, 1983), 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 et al., 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, unpublished data, Fig. S7). Moreover, bee densities were enhanced by an increasing local flower cover in run 1 and 3, in accordance with other studies (Ebeling et al., 2008; Potts et al., 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, unpublished 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 SHN 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 et al., 2015; Westrich, 2018).

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).

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 & 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 et al., 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 scale especially for bees with small foraging ranges in agricultural landscapes.

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-sparing 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 (Grass et al., 2019; Balmford 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

CW and JD conceived the study and supervised the project; NB, KS-K and FK implemented the study sites; NB collected the data; NB and DG performed the data analysis with advice of CW; NB wrote the manuscript with advice of DG, FK and CW. 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).

References

Amiet, F. (1996) *Hymenoptera Apidae: 1. Teil, Allgemeiner Teil, Gattungsschlüssel, die Gattungen Apis, Bombus und Psithyrus*. Insecta Helvetica Fauna 12

Bailes, E. J., Pattrick, J. G., & Glover, B. J. (2018). An analysis of the energetic reward offered by field bean (Vicia faba) flowers: Nectar, pollen, and operative force. *Ecology and Evolution*, *8*(6), 3161–3171. doi: 10.1002/ece3.3851

Balmford, B., Green, R.E., Onial, M., Phalan, B. & Balmford, A. (2019). How imperfect can land sparing be before land sharing is more favourable for wild species? *Journal of Applied Ecology, 56,* 73-84

Bartomeus, I., Potts, S. G., Steffan-Dewenter, I., Vaissière, B. E., Woyciechowski, M., Krewenka, K. M. *et al.* (2014). Contribution of insect pollinators to crop yield and quality varies with agricultural intensification. *PeerJ*, *2014*(1), 1–20. doi: 10.7717/peerj.328

Beduschi, T., Tscharntke, T., & Scherber, C. (2015). Using multi-level generalized path analysis to understand herbivore and parasitoid dynamics in changing landscapes. *Landscape Ecology*, *30*(10), 1975–1986. doi: 10.1007/s10980-015-0224-2

Benton, T. G., Vickery, J. A., & Wilson, J. D. (2003). Farmland biodiversity: Is habitat heterogeneity the key? *Trends in Ecology and Evolution*, *18*(4), 182–188. doi: 10.1016/S0169-5347(03)00011-9

Beyer, N., Gabriel, D., Kirsch, F., Schulz-Kesting, K., Dauber, J. & Westphal, C. (2020) Data from: Functional groups of wild bees respond differently to faba bean (*Vicia faba* L.) cultivation at landscape scale. *Dryad Digital Repository*. https://doi.org/10.5061/dryad.ttdz08kvs

Bishop, J., Jones, H. E., Lukac, M., & Potts, S. G. (2016). Insect pollination reduces yield loss following heat stress in faba bean (Vicia faba L.). *Agriculture, Ecosystems and Environment*, *220*, 89–96. doi: 10.1016/j.agee.2015.12.007

BMEL (2019). Beantragte Ökologische Vorrangflächen im Jahr 2019, Federal Ministry for Food and Agriculture (BMEL), Berlin, url: https://www.bmel.de/SharedDocs/Downloads/Landwirtschaft/Foerderung/OekologischeVorrangflaechen2019.html

Bobbink, R., Hicks, K., Galloway, J., Spranger, T., Alkemade, R., Ashmore, M. et al. (2010). Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis. *Ecological Applications, 20(1)*, 30-59. doi: 10.1890/08-1140.1

Bommarco, R., Biesmeijer, J. C., Meyer, B., Potts, S. G., Pöyry, J., Roberts, S. P. M. *et al.* (2010). Dispersal capacity and diet breadth modify the response of wild bees to habitat loss. *Proceedings of the Royal Society B: Biological Sciences*, *277*(1690), 2075–2082. doi: 10.1098/rspb.2009.2221

Bond, D. A., & Poulsen, M. H. (1983). *Pollination. In: Hebblethwaite, P. D., Ed., The Faba Bean (Vicia faba L.)*. Butterworths, London, 77-101.

Burnham, K. P., & Anderson, D. R. (2002). *Model Selection and Multimodel Inference. A Pracitcal Information-Theoretic Approach* (2nd ed.). Springer-Verlag.

Cariveau, D. P., Nayak, G. K., Bartomeus, I., Zientek, J., Ascher, J. S., Gibbs, J., & Winfree, R. (2016). The allometry of bee proboscis length and its uses in ecology. *PLoS ONE*, *11*(3), 1–13. doi: 10.1371/journal.pone.0151482

Destatis (2019). Acreage after main crop groups and crops in a time comparison. Federal Statistical Office (Destatis), Wiesbaden, url: https://www.destatis.de/EN/Themes/Economic-Sectors-Enterprises/Agriculture-Forestry-Fisheries/Field-Crops-Grassland/Tables/acreage-of-main-crops-in-a-time-comparison-neu.html

Diekötter, T., Peter, F., Jauker, B., Wolters, V., & Jauker, F. (2014). Mass-flowering crops increase richness of cavity-nesting bees and wasps in modern agro-ecosystems. *GCB Bioenergy*, *6*(3), 219–226. doi: 10.1111/gcbb.12080

Digitales Basis-Landschaftsmodell (Basis-DLM). URL: https://gdz.bkg.bund.de/index.php/default/digitale-geodaten/digitale-landschaftsmodelle/digitales-basis-landschaftsmodell-ebenen-basis-dlm-ebenen.html

Ebeling, A., Klein, A. M., Schumacher, J., Weisser, W. W., & Tscharntke, T. (2008). How does plant richness affect pollinator richness and temporal stability of flower visits? *Oikos*, *117*(12), 1808–1815. doi: 10.1111/j.1600-0706.2008.16819.x

Ekroos, J., Ödman, A. M., Andersson, G. K. S., Birkhofer, K., Herbertsson, L., Klatt, B. K., et al. (2016). Sparing land for biodiversity at multiple spatial scales. F*rontiers in Ecology and Evolution, 3*, 1-11. doi: 10.3389/fevo.2015.00145

European Commission. (2017). Evaluation study of the payment for agricultural practices beneficial for the climate and the environment - Final Report. In *European Commission, Brussels*.

European Court of Auditors. (2017). *Greening: a more complex income support scheme, not yet environmentally effective. Special Report No. 21/2017*.

Everwand, G., Cass, S., Dauber, J., Williams, M., & Stout, J. (2017). Legume Crops and Biodiversity. In *Murphy-Bokern, D., Stoddard, F.L., Watson, C.A. (Eds.), Legumes in Cropping Systems*. Wallingford, CAB International.

Gabriel, D., Sait, S. M., Hodgson, A., Schmutz, U., Kunin, W. E., & Benton, T. G. (2010). Scale matters: the impact of organic farmin on biodiversit at different spatial scales. Ecology Letters, 13, 858-869. doi: 10.1111/j.1461-0248.2010.01481.x

Gámez-Virués, S., Perović, D. J., Gossner, M. M., Börschig, C., Blüthgen, N., De Jong, H. *et al.* (2015). Landscape simplification filters species traits and drives biotic homogenization. *Nature Communications*, *6*. doi: 10.1038/ncomms9568

Garratt, M. P. D., Coston, D. J., Truslove, C. L., Lappage, M. G., Polce, C., Dean, R. *et al.* (2014). The identity of crop pollinators helps target conservation for improved ecosystem services. *Biological Conservation*, *169*, 128–135. doi: 10.1016/j.biocon.2013.11.001

Grass, I., Loos, J., Baensch, S., Batáry, P., Librán-Embid, F., Ficiciyan, A. *et al.* (2019). Land-sharing/-sparing connectivity landscapes for ecosystem services and biodiversity conservation. *People and Nature, 1*, 262-272.

Greenleaf, S. S., Williams, N. M., Winfree, R., & Kremen, C. (2007). Bee foraging ranges and their relationship to body size. *Oecologia*, *153*(3), 589–596. doi: 10.1007/s00442-007-0752-9

Hanley, M. E., Franco, M., Dean, C. E., Franklin, E. L., Harris, H. R., Haynes, A. G. *et al.* (2011). Increased bumblebee abundance along the margins of a mass flowering crop: Evidence for pollinator spill-over. *Oikos*, *120*(11), 1618–1624. doi: 10.1111/j.1600-0706.2011.19233.x

Herrmann, F., Westphal, C., Moritz, R. F. A., & Steffan-Dewenter, I. (2007). Genetic diversity and mass resources promote colony size and forager densities of a social bee (Bombus pascuorum) in agricultural landscapes. *Molecular Ecology*, *16*(6), 1167–1178. doi: 10.1111/j.1365-294X.2007.03226.x

Holzschuh, A., Dainese, M., González-Varo, J. P., Mudri-Stoinic, S., Riedinger, V., Rundlöf, M. et al. (2016) Mass-flowering crops dilute pollinator abundance in agricultural landscapes across Europe. *Ecology Letters, 19*, 1228-1236. doi: 10.1111/ele.12657

Jauker, B., Krauss, J., Jauker, F., & Steffan-Dewenter, I. (2013). Linking life history traits to pollinator loss in fragmented calcareous grasslands. *Landscape Ecology*, *28*(1), 107–120. doi: 10.1007/s10980-012-9820-6

Kallioniemi, E., Åström, J., Rusch, G. M., Dahle, S., Åström, S., & Gjershaug, J. O. (2017). Local resources, linear elements and mass-flowering crops determine bumblebee occurrences in moderately intensified farmlands. *Agriculture, Ecosystems and Environment*, *239*, 90–100. doi: 10.1016/j.agee.2016.12.039

Kleijn, D., Linders, T. E. W., Stip, A., Biesmeijer, J. C., Wäckers, F. L., Bukovinszky, T. (2018). Scaling up effects of measures mitigating pollinator loss from local- to landscape-level population responses. *Methods in Ecology and Evolution, 9,* 1727-1738. doi: 10.1111/2041-210X.13017

Köpke, U., & Nemecek, T. (2010). Ecological services of faba bean. *Field Crops Research*, *115*(3), 217–233. doi: 10.1016/j.fcr.2009.10.012

Kremen, C., & Miles, A. (2012). Ecosystem Services in Biologically Diversified versus Conventional Farming Systems: Benefits, Externalities, and Trade-Offs. Ecology and Society 17 (4), 40. doi: 10.5751/ES-05035-170440

Leidenfrost, R.M., Bänsch, S., Prudnikow, L., Brenig, B., Westphal, C. & Wünschiers, R. (2020). Analyzing the Dietary Diary of Bumble Bee. *Frontiers in Plant Science*, 11.

Lichtenberg, E.M., Kennedy, C.M., Kremen, C., Batáry, P., Berendse, F., Bommarco, R. *et al.* (2017). A global synthesis of the effects of diversified farming systems on arthropod diversity within fields and across agricultural landscapes. *Global Change Biology*, 1-12.

Marzinzig, B., Brünjes, L., Biagioni, S., Behling, H., Link, W., & Westphal, C. (2018). Bee pollinators of faba bean (Vicia faba L.) differ in their foraging behaviour and pollination efficiency. *Agriculture, Ecosystems and Environment*, *264*(May), 24–33. doi: 10.1016/j.agee.2018.05.003

Mauss, V. (1994) *Bestimmungsschlüssel für HUMMELN* (5th ed.). Deutscher Jugendbund für Naturbeobachtung, Hamburg

Nayak, G. K., Roberts, S. P. M., Garratt, M., Breeze, T. D., Tscheulin, T., Harrison-Cripps, J. *et al.* (2015). Interactive effect of floral abundance and semi-natural habitats on pollinators in field beans (Vicia faba). *Agriculture, Ecosystems and Environment*, *199*, 58–66. doi: 10.1016/j.agee.2014.08.016

Öckinger, E, & Smith, H. G. (2007). Semi-natural grasslands as population sources for pollinating insects in agricultural landscapes. *Journal of Applied Ecology*, *44*(1), 50–59. doi: 10.1111/j.1365-2664.2006.01250.x

Ogilvie, J. E., Forrest, RK. (2010) Interacitions between bee foraging and floral resource phenology shape bee populations and communities. *Current Opinion in Insect Science, 21*, 75-82. doi: 10.1016/j.cois.2017.05.015

Pascher, K., Moser, D., Dullinger, S., Sachslehner, L., Gros, P., Sauberer, N. et al. (2011). Setup, efforts and practical experiences of a monitoring program for genetically modified plants - an Austrian case study for oilseed rape and maize. *Environmental Sciences Europe*, *23*, 12. doi: 10.1186/2190-4715-23-12

Pe'er, G., Zinngrebe, Y., Moreira, F., Sirami, C., Schindler, S., Müller, R. *et al.* (2019). A greener path for the EU Common Agricultural Policy. *Science*, *365*(6452), 449–451. Retrieved from https://science.sciencemag.org/content/365/6452/449.summary

Potts, S. G., Imperatriz-Fonseca, V., Ngo, H. T., Aizen, M. A., Biesmeijer, J. C., Breeze, T. D. *et al.* (2016). Safeguarding pollinators and their values to human well-being. *Nature*, *540*(7632), 220–229. doi: 10.1038/nature20588

Potts, S. G., Vulliamy, B., Dafni, A., Ne'eman, G., & Willmer, P. (2003). Linking bees and flowers: How do floral communities structure pollinator communities? *Ecology*, *84*(10), 2628–2642. doi: 10.1890/02-0136

Proesmans, W., Bonte, D., Smagghe, G., Meeus, I., Decocq, G., Spicher, F. et al. (2019). Small forest patches as pollinator habitat: oases in an agricultural desert? *Landscape Ecology, 34,* 487-501. doi: 10.1007/s10980-019-00782-2

R Core Team. (2019). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Schellhorn, N. A., Gagic, V., & Bommarco, R. (2015). Time will tell: Resource continuity bolsters ecosystem services. *Trends in Ecology and Evolution*, *30*(9), 524–530. doi: 10.1016/j.tree.2015.06.007

Seibold, S., Gossner, M. M., Simons, N. K., Blüthgen, N., Ambarl, D., Ammer, C. *et al.* (2019). Arthropod decline in grasslands and forests is associated with drivers at landscape level. *Nature*, *574*(February), 1–34. doi: 10.1038/s41586-019-1684-3

Steffan-Dewenter, Ingolf, Münzenberg, U., Bürger, C., Thies, C., & Tscharntke, T. (2002). Scale-dependent effects of landscape context on three pollinator guilds. *Ecology*, *83*(5), 1421–1432. doi: 10.1890/0012-9658(2002)083[1421:SDEOLC]2.0.CO;2

Timberlake, T. P., Vaughan, I. P., & Memmott, J. (2019). Phenology of farmland floral resources reveals seasonal gaps in nectar availability for bumblebees. *Journal of Applied Ecology*, *56*(7), 1585–1596. doi: 10.1111/1365-2664.13403

Tscharntke, T., Klein, A. M., Kruess, A., Steffan-Dewenter, I., & Thies, C. (2005). Landscape perspectives on agricultural intensification and biodiversity - Ecosystem service management. *Ecology Letters*, *8*(8), 857–874. doi: 10.1111/j.1461-0248.2005.00782.x

Walther-Hellwig, K., & Frankl, R. (2000). Foraging habitats and foraging distances of bumblebees, Bombus spp. (Hym., Apidae), in an agricultural landscape. *Journal of Applied Entomology*, *124*(7–8), 299–306. doi: 10.1046/j.1439-0418.2000.00484.x

Warzecha, D., Diekötter, T., Wolters, V., & Jauker, F. (2016). Intraspecific body size increases with habitat fragmentation in wild bee pollinators. *Landscape Ecology*, *31*(7), 1449–1455. doi: 10.1007/s10980-016-0349-y

Westphal, C., Bommarco, R., Carré, G., Lamborn, E., Morison, N., Petanidou, T. *et al.* (2008). Measuring bee diversity in different European habitats and biogeographical regions. *Ecological Monographs*, *78*(4), 653–671. doi: 10.1890/07-1292.1

Westphal, C., Steffan-Dewenter, I., & Tscharntke, T. (2003). Mass flowering crops enhance pollinator densities at a landscape scale. *Ecology Letters*, *6*(11), 961–965. doi: 10.1046/j.1461-0248.2003.00523.x

Westphal, C., Steffan-Dewenter, I., & Tscharntke, T. (2006). Bumblebees experience landscapes at different spatial scales: Possible implications for coexistence. *Oecologia*, *149*(2), 289–300. doi: 10.1007/s00442-006-0448-6

Westrich, P. (2018). *Die Wildbienen Deutschlands* (1st ed.). Eugen Ulmer Verlag, Stuttgart.

Westrich, P., Frommer, U., Mandery, K., Riemann, H., Ruhnke, H., Saure, C., & Voith, J. (2011). Rote Liste und Gesamtartenliste der Bienen (Hymenoptera, Apidae) Deutschlands. In *Binot-Hafke et al. (Red.): Rote Liste gefährdeter Tiere, Pflanzen und Pilze Deutschlands. Band 3: Wirbellose Tiere (Teil 1).* Münster (Landwirtschaftsverag): Naturschutz und Biologische Vielfalt 70(3), 373-416.

Supplementary material

Statistical analyses

To test the effect of FB cultivation and different landscape metrics on the number and species richness of wild bees we fitted generalized linear mixed models with the *glmmTMB* package (Brooks et al., 2017). To depict effects at landscape level, the number of all wild bees and the flower cover were summed up across all transects for each landscape and run, leading to observations per 2800 m^2 and 70 min. One transect turned out to be a flower strip and was excluded in further analyses. To account for different sampling effort at landscape scale (in three out of 90 cases we had only six transects), we included the log of the number of transects as offset into the models for bee densities and species richness. Our response variables were the density of bumblebees, the density of non-*Bombus* wild bees and the species richness of all wild bees. Bee densities included all observed bees, while for species richness of wild bees only identified individuals were used. The explanatory variables included in the models were FB cultivation (FB+/ FB-), flower cover, sampling run (1-3), percentage of SNH and the percentage of OSR in the study landscape, including all possible two-way interactions. To improve the convergence of the models, continuous explanatory variables (flower cover, SNH, OSR) were standardized to a mean of zero and a standard deviation of 1. Region, landscape pair and the study landscape were included as nested random effects (region/landscape pair/landscape).

Model selection was based on second order Akaike Information Criterion (AICc). Global models containing all explanatory variables were fitted with Poisson and negative binomial distribution and when sensible with and without zero inflation terms to account for an excess of zeros. The model with lowest AICc was chosen as global model for each analysis (Bolker 2008; 2020). For the density of bumblebees this was the model with negative binomial distribution, for the species richness the model with Poisson distribution and for the density of non-*Bombus* wild bees the model with Poisson distribution and general zero inflation term.

To assess the functional structure of bee traits in a community, we aggregated data at landscape level (i.e. the sum over all transects and runs) and calculated community weighted means (CWM) for ITD and proboscis length using the *FD* package (Laliberté & Legendre, 2010). CWM were analysed using linear mixed effects models and the *nlme* package (Pinheiro et al., 2019). To analyse lecty, bees were grouped into species collecting and not collecting pollen from Fabaceae. We used a generalized linear mixed model with binomial family and logit link to test the effect of FB cultivation and landscape metrics on the proportion of bee species foraging on Fabaceae (proportion of Fabaceae foragers). The global models for the trait data contained the same explanatory variables and random effects as described above for the abundance and species richness. Since we calculated proboscis length on the basis of ITD measurements and because bigger bees generally have longer tongues than smaller ones, the CWM of ITD and proboscis length are highly correlated (r Pearson correlation = 0.98, $p < 0.001$).

Based on the global models and following a multimodel inference approach (Burnham & Anderson, 2002) candidate models containing all possible combinations of explanatory variables and their interactions were fitted using the *dredge* function of the *MuMIn* package (Barton, 2019). We restricted the number of parameters in the model comparison procedure to a maximum of seven variables. Candidate models were ranked by AICc and Akaike weights (w_i) were used to estimate the relative support of individual models to have the best fit across all models (Burnham & Anderson, 2002). All models with a delta AICc < 2 in comparison with the best fitting model were considered to have substantial empirical support. The relative importance of each explanatory variable was assessed using the sum of Akaike weights (Σw_i) over all models that include the respective explanatory variable. The larger the value, the more important is the variable. $\Sigma w_i > 0.2$ were considered for interpretation and are reported. Model assumptions were validated by inspecting residual plots. To evaluate the goodness of fit of our models we calculated the marginal (R_m^2) and conditional (R_c^2) R^2 values (Nakagawa et al., 2017) with the *performance* package (Lüdecke et al., 2020). Post hoc tests were applied to test for differences in bee abundances, species richness and proportion of Fabaceae foragers between FB and control landscapes and for differences in the CWM between different sampling runs using the *emmeans* package (Lenth, 2019) and alpha level of 0.05. Predictions and confidence intervals in scatter plots were obtained from the *effects* package (Fox & Weisberg, 2019) and in the boxplots from the emmeans package. All graphics were generated with the *ggplot2* package (Wickham, 2016).

References

Barton, K. (2019). *MuMIn: Multi-Model Inference. R package version 1.43.6*. URL: *https://cran.r-project.org/package=MuMIn*

Bolker, B. (2008). Ecological models and data in R. Princeton University Press, Princeton, New Jersey, USA.

Bolker, B. (2020). Getting started with the glmmTMB package. Available online: https://cran.r-project.org/web/packages/glmmTMB/vignettes/glmmTMB.pdf assessed May 2020

Brooks, M. E., Kristensen, K., Benthem, K. J. van, Magnusson, A., Berg, C. W., Nielsen, A. *et al.* (2017). glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. *The R Journal*, *9*(2), 378–400.

Burnham, K. P., & Anderson, D. R. (2002). *Model Selection and Multimodel Inference. A Pracitcal Information-Theoretic Approach* (2nd ed.). Springer-Verlag.

Fox, J. and Weisberg, S. 2019. An R Companion to Applied Regression, 3rd Edition. Thousand Oaks, CA. URL: *http://tinyurl.com/carbook*

Laliberté, E., & Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, *91*, 299–305.

Lenth, R. (2019). *emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.4.1.* URL*: https://CRAN.R-project.org/package=emmeans*

Lüdecke, D., Makowski, D., Waggoner, P., Patil, I. (2020). *performance: Assessment of Regression Models Performance. R package version 0.4.5*. URL: *https://CRAN.R-project.org/package=performance*

Nakagawa, S., Johnson, P. C. D., Schielzeth, H. (2017) The coefficient of determination R^2 and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. *J. R. Soc. Interface, 14*, 20170213. doi: 10.1098/rsif.2017.0213

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., & R Core Team. (2019). *nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-140.* URL: *https://CRAN.R-project.org/package=nlme*

Wickham, H. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York, 2016.

Figures

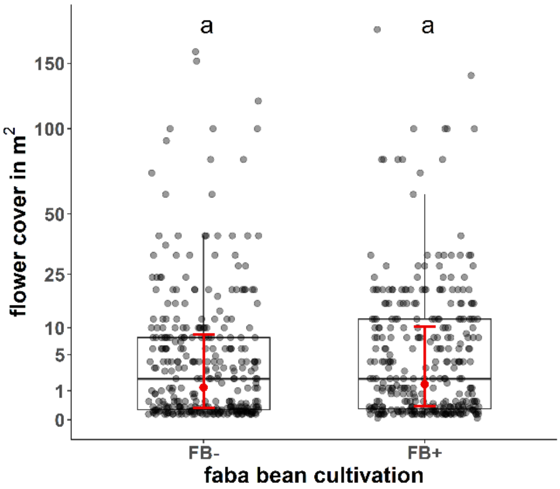

Figure S1 Local flower cover of all field margins for landscapes with (FB+) and without (FB-) faba bean cultivation. A linear mixed effects model with log- transformed flower cover as response, FB cultivation as predictor variable and region, landscape pair, landscape and run as nested random effects was conducted. Predicted mean values and 95% confidence intervals are displayed in red. Letters above groups indicate non-significant differences between FB+ and FB- landscapes (t=0.66; p=0.52) (n=627). Y axis is sqrt-transformed for graphical reasons.

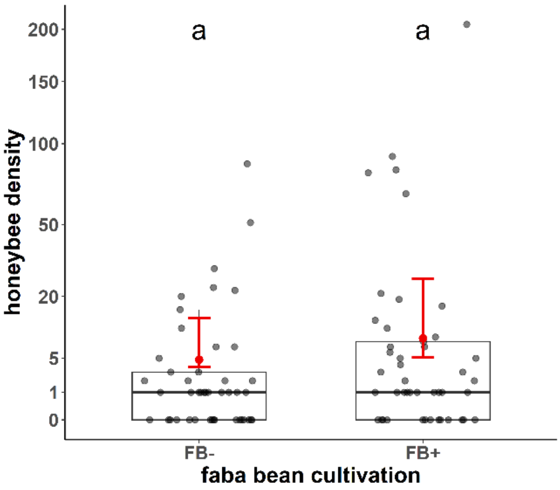

Figure S2 Honeybee density for landscapes with (FB+) and without (FB-) faba bean cultivation. A generalized linear mixed effects model with honeybee density as response, FB cultivation as predictor variable and region, landscape pair and landscape as nested random effects was conducted. Predicted mean values and 95% confidence intervals are displayed in red. Letters above groups indicate non-significant differences between FB+ and FB- landscapes (z=1.40; p=0.16) (n=90). Y axis is sqrt-transformed for graphical reasons.

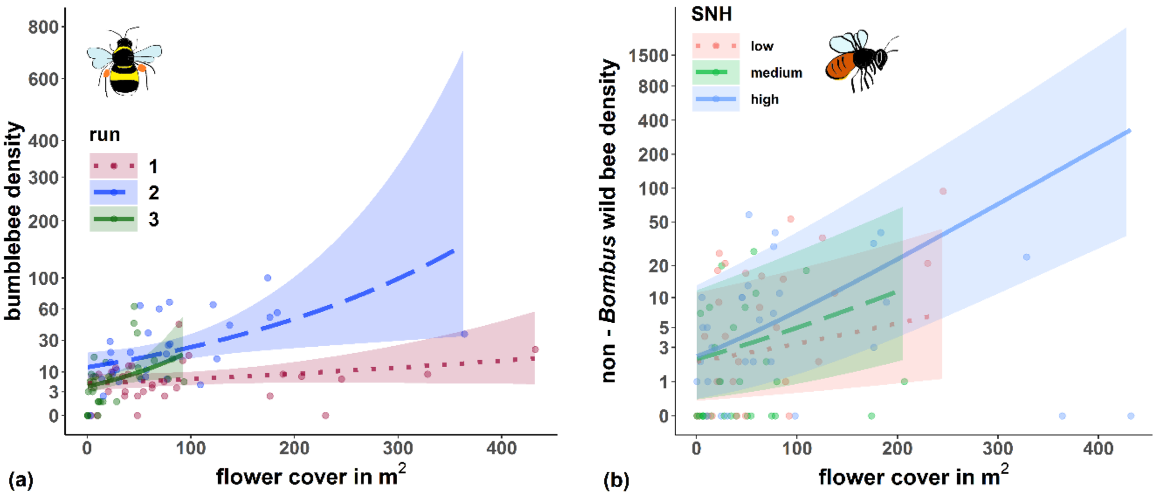

Figure S3 Effect of local flower cover (m²) on **(a)** the bumblebee density per landscape for the three sampling runs. Effect of local flower cover (m²) on **(b)** bee densities for different levels of % semi-natural habitats (SNH). Dotted (low), dashed (medium) and solid (high) line represent 4.31, 8.12 and 11.76 % SNH, i.e. the vaules of the 10th, 50th and 90th percentiles respectively. Observed values are colored according to the SNH group (lower 33%, medium, upper 66%), to which they belong to. Predicted mean values and 95 % confidence intervals are displayed in different colours (according to different runs and different levels of SNH respectively). Predictions are based on the second-best fitting model *bb2* for (a) and *nb2* for (b) (Table S2). Y-axis in (a) is sqrt- and in (b) log-transformed for graphical reasons.

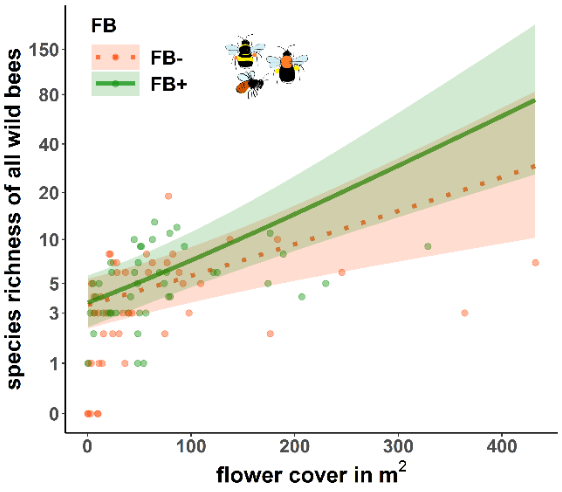

Figure S4 Effects of local flower cover (m²) on wild bees species richness for landscapes with (FB+) and without (FB-) faba bean cultivation. Predicted mean values and 95 % confidence intervals are displayed in different colors according to FB. Predictions are based on the best fitting model *sri1* (Table S2). Y-axis is log-transformed for graphical reasons.

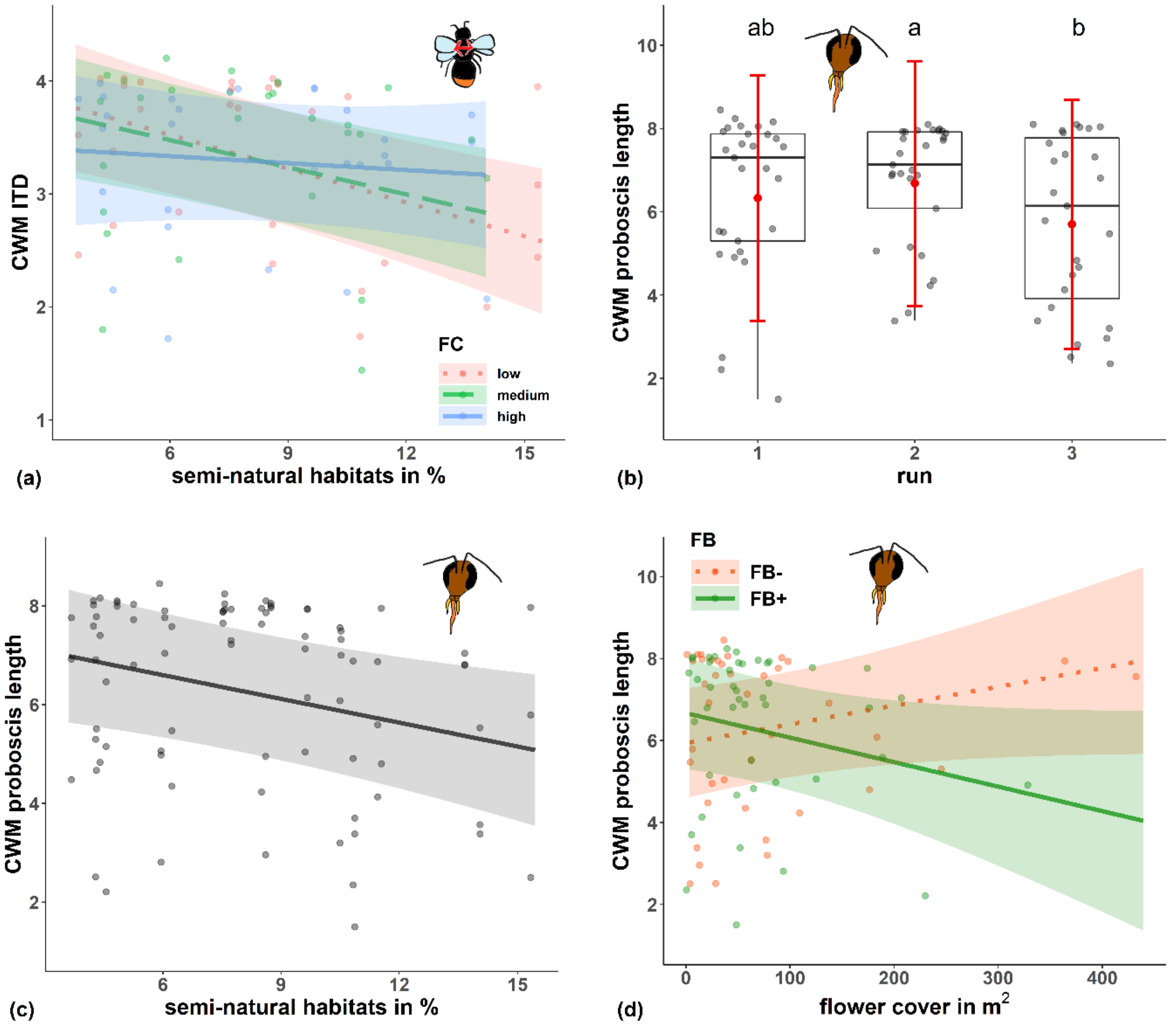

Figure S5 Effect of **(a)** percentage of semi-natural habitats (%) on community weighted means (CWM) for ITD for different levels of flower cover (FC). Dotted (low), dashed (medium) and solid (high) line represent 6.62, 48.44 and 176.34 % fc, i.e. the 10th, 50th and 90th percentiles respectively. Effects of **(b)** sampling run and **(c)** the percentage of semi-natural habitats (%) on the community weighted means for proboscis length (mm). **(d)** Effect of flower cover (m^2) on the CWM for proboscis length for the different landscapes with and without faba bean cultivation (FB+: landscapes with faba bean cultivation (depicted in green); FB-: landscapes without faba bean cultivation (depicted in orange). Predictions for (a) are obtained from the second-best model *cmITD2* for (a) and *cmto2* for (b)-(d) (Table S6). Predicted mean values and 95% confidence intervals are displayed in red in boxplots and in different colours (according to FB and different levels of fc respectively) in scatter plots. Different letters above groups indicate significant differences between runs.

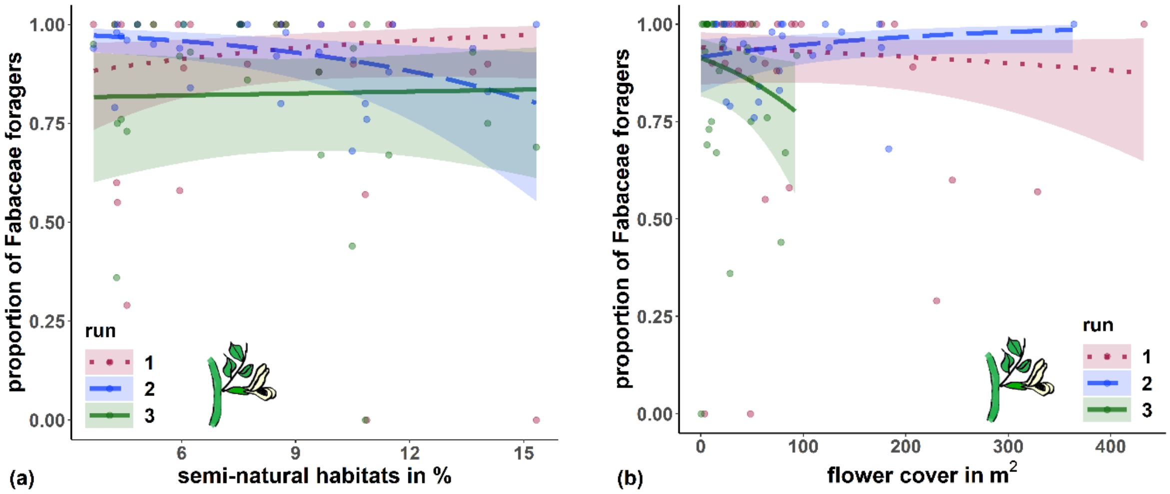

Figure S6 Effect of **(a)** the percentage of semi-natural habitats (%) and **(b)** flower cover (m^2) on the proportion of Fabaceae foragers in the three different sampling runs. Predicted mean values and 95 % confidence intervals are displayed in different colours (according to different runs). Predictions are obtained from the best fitting model *mL1* (Table S6). A possible explanation for our results might be the temporal distribution of resources in the different semi-natural habitat structures. In our landscapes the woodland structures, like hedges had the highest floral display in the first sampling run, whereas the extensive grasslands had the highest flower cover during the second sampling run (F. Kirsch, unpublished data, Fig. S7). It might be that the bee species not foraging on Fabaceae were strongly attracted to the flower of semi-natural woodland structures early in the season, whereas Fabaceae foragers might have been strongly attracted to extensive grasslands, which often constitute of many Fabaceae plants, flowering later in the season. When flower cover was high, we found highest proportions of Fabaceae foragers in run 2 and lowest in run 3. Faba beans were in full bloom in the first sampling run and probably attracted the Fabaceae foragers into the bean fields, which led to lower proportions in the field margins in run 1 compared to run 2. The decreased numbers in the last run probably mirror the phenology of the bee species. While in the first run our bee communities consisted of about 1.5 times as many bee species not using compared to bee species using Fabaceae, this number increased to almost twice as many in the last run. Therefore, the unproportional lower numbers of bee species using Fabaceae in the latest run may have driven the lower proportion of bee individuals using Fabaceae.

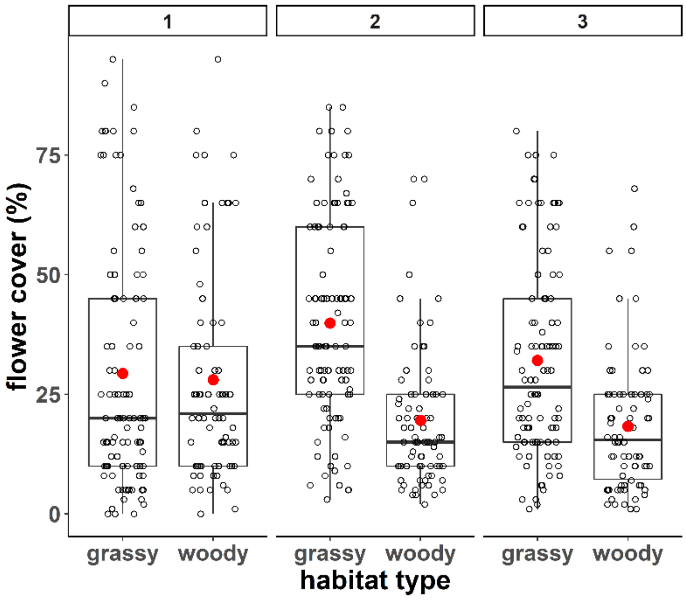

Figure S7 Boxplot showing percentage of local flower cover of semi-natural habitats (SNH) within the 30 1 km^2 study landscapes for the three different sampling runs and different habitat types. Flower cover within SNH was recorded in a parallel study, conducting pollinator surveys in different grassy and woody SNH structures. *grassy* includes extensive grasslands, calcareous grasslands, flower strips, clover leys, orchards, succession sites with mainly grassy habitat; *woody* comprises hedges, forest edges, groves, succession sites with mainly woody habitat structures. Observations are shown as jittered points and arithmetic means are displayed in red. Data from F. Kirsch (unpublished data).

Tables

Table S1 Number of individuals, mean ITD (intertegular distance), calculated proboscis length, lecty Fabaceae (species collecting pollen from Fabaceae = 1, species not collecting pollen from Fabaceae = 0) and red list status for all 80 identified species of the transect walks. Cleptoparasites were excluded from analyses of functional traits and therefore no trait values are given for them. ITD was measured for maximum five female individuals per species. If only males of a species were caught (10 cases), ITD was not measured and tongue length not calculated. Red list information follow Westrich et al., 2011. * least concern, NT near threatened, 3 vulnerable, 2 endangered, 3 critically endangered. Note that the abundance of in total 2198 wild bees got recorded, while 1794 wild bees were identified and used for species richness and trait analyses. We always recorded the abundance of all bees. However, sometimes wild bees escaped from the net but could still be recorded as wild bee or Bombus/non-Bombus observation (as specific as possible). Occasionally, when there were several bees present in the transect which could not be determined in the field, it was only possible to catch one of them and the others escaped because of the disturbance.

species	number of individuals	ITD	tongue	lecty Fabaceae	red list status
Andrena chrysosceles (Kirby 1802)	1	2.04	2.10	0	*
Andrena cineraria (Linnaeus 1758)	6	2.94	2.98	0	*
Andrena dorsata (Kirby 1802)	1	1.90	1.96	1	*
Andrena flavipes Panzer 1799	29	2.50	2.55	1	*
Andrena fulva (Müller 1766)	1	2.95	2.99	0	*
Andrena gravida Imhoff 1832	1	2.90	2.95	0	*
Andrena haemorrhoa (Fabricius 1781)	5	2.44	2.50	0	*
Andrena labialis (Kirby 1802)	1	2.80	2.85	1	NT
Andrena labiata Fabricius 1781	1	NA	NA	0	*
Andrena lathyri Alfken 1899	6	2.44	2.50	1	*
Andrena minutula (Kirby 1802)	12	1.38	1.44	0	*
Andrena minutuloides Perkins 1914	1	1.40	1.46	0	*
Andrena nigroaenea (Kirby 1802)	13	2.98	3.02	1	*
Andrena nitida (Müller 1776)	5	2.90	2.95	0	*
Andrena ovatula (Kirby 1802)	2	2.20	2.26	1	*
Andrena proxima (Kirby 1802)	3	1.90	1.96	0	*
Andrena scotica Perkins 1916	1	2.90	2.95	0	*
Andrena subopaca Nylander 1848	5	1.44	1.50	0	*
Anthophora aestivalis (Panzer 1801)	2	NA	NA	1	3
Bombus barbutellus (Kirby 1802)	1	NA	NA	NA	*
Bombus bohemicus (Seidl 1837)	4	NA	NA	NA	*
Bombus hortorum (Linnaeus 1761)	46	4.20	8.45	1	*
Bombus hypnorum (Linnaeus 1758)	3	3.64	7.36	1	*

Bombus lapidarius (Linnaeus 1758)	216	3.70	7.48	1	*
Bombus muscorum (Linnaeus 1758)	5	3.84	7.75	1	2
Bombus pascuorum (Scopoli 1763)	423	4.02	8.10	1	*
Bombus pratorum (Linnaeus 1761)	21	3.60	7.29	1	*
Bombus ruderarius (Müller 1765)	9	3.42	6.93	1	3
Bombus rupestris (Fabricius 1793)	13	NA	NA	NA	*
Bombus subterraneus (Linnaeus 1758)	2	4.00	8.06	1	2
Bombus sylvarum (Linnaeus 1761)	21	3.20	6.51	1	NT
Bombus terrestris (Linnaeus 1758) / *Bombus lucorum* (Linnaeus 1761)	590	3.90	7.87	1	*
Bombus vestalis (Geoffroy 1785)	7	NA	NA	NA	*
Colletes similis Schenck 1853	1	NA	NA	0	NT
Dasypoda hirtipes (Fabricius 1793)	2	2.90	NA	0	NT
Eucera longicornis Linnaeus 1758	2	3.60	7.29	1	NT
Eucera nigrescens Perez 1879	2	3.45	6.99	1	*
Halictus eurygnathus Blüthgen 1931	2	NA	NA	NA	*
Halictus maculatus Smith 1848	2	1.50	2.04	1	*
Halictus quadricinctus (Fabricius 1776)	1	2.90	3.84	0	3
Halictus rubicundus (Christ 1791)	11	2.12	2.84	1	*
Halictus scabiosae (Rossi 1790)	14	2.52	3.35	0	*
Halictus simplex Blüthgen 1923	15	1.94	2.61	0	*
Halictus subauratus (Rossi 1792)	4	1.60	2.17	0	*
Halictus tumulorum (Linnaeus 1758)	23	1.42	1.93	1	*
Hylaeus communis Nylander 1852	5	1.28	1.09	0	*
Hylaeus confusus Nylander 1853	2	1.47	1.24	1	*
Hylaeus gredleri Förster 1871	1	0.95	0.82	0	*
Lasioglossum albipes (Fabricius 1781)	3	1.60	2.17	0	*
Lasioglossum calceatum (Scopoli 1763)	52	1.74	2.35	0	*
Lasioglossum fulvicorne (Kirby 1802)	1	1.35	1.84	0	*
Lasioglossum laticeps (Schenck 1868)	4	1.50	2.04	0	*
Lasioglossum lativentre (Schenck 1853)	2	1.50	2.04	1	NT
Lasioglossum leucopus (Kirby 1802)	1	NA	NA	0	*
Lasioglossum leucozonium (Schrank 1781)	16	1.98	2.66	0	*
Lasioglossum lineare (Schenck 1868)	1	NA	NA	0	*
Lasioglossum malachurum (Kirby 1802)	3	NA	NA	1	*
Lasioglossum minutissimum (Kirby 1802)	1	NA	NA	0	*
Lasioglossum morio (Fabricius 1793)	2	1.03	1.42	0	*
Lasioglossum nitidiusculum (Kirby 1802)	2	1.25	1.71	0	NT
Lasioglossum pauxillum (Schenck 1853)	120	1.12	1.54	1	*
Lasioglossum villosulum (Kirby 1802)	8	1.38	1.88	0	*
Lasioglossum xanthopus (Kirby 1802)	1	2.30	3.07	0	*
Megachile ericetorum Lepeletier 1841	1	3.00	5.37	1	*
Megachile versicolor Smith 1844	3	3.10	5.54	1	*
Melitta nigricans Alfken 1905	3	2.70	NA	0	*
Nomada flavoguttata (Kirby 1802)	2	NA	NA	NA	*
Nomada fucata Panzer 1798	1	NA	NA	NA	*
Nomada ruficornis (Linnaeus 1758)	1	NA	NA	NA	*

Osmia bicolor (Schrank 1781)	1	2.80	5.02	1	*
Osmia bicornis (Linnaeus 1758)	3	3.20	5.71	1	*
Osmia cantabrica (Benoist 1935)	1	NA	NA	0	*
Osmia rapunculi (Lepeletier 1841)	1	1.65	3.02	0	*
Osmia truncorum (Linnaeus 1758)	1	NA	NA	0	*
Panurgus calcaratus (Scopoli 1763)	4	1.84	1.90	0	*
Sphecodes albilabris (Fabricius 1793)	1	NA	NA	NA	*
Sphecodes crassus Thomson 1870	1	NA	NA	NA	*
Sphecodes ephippius (Linnaeus 1767)	7	NA	NA	NA	*
Sphecodes gibbus (Linnaeus 1758)	1	NA	NA	NA	*
Sphecodes monilicornis (Kirby 1802)	1	NA	NA	NA	*

Table S2 Summary of the best fitting candidate (dAICc<2) and null-models for the effects of faba bean cultivation and landscape metrics on the number of bumblebees, number of non-*Bombus* wild bees and species richness of all wild bees. Marginal (R_m^2) and conditional (R_c^2) R^2 values are given as a measure of the model´s goodness of fit. Data is summed up across all transects per landscape; FB: faba bean cultivation (FB+/FB-), run: sampling round (1-3), FC: local flower cover of transect area, OSR: percentage of oilseed rape, SNH: percentage of semi-natural habitats.

Response variable	Model	DF	AICc	dAICc	Akaike weight (w_i)	Explanatory variables	R_m^2	R_c^2
Number of bumblebees (n=90)	bb1	11	646.64	0.00	0.17	FB + run + FC + FB:run	0.36	0.57
	bb2	13	647.16	0.52	0.13	FB + run + FC + FB:run + run:FC	0.41	0.57
	bb0	5	682.74	36.11	0.00	1	-	-
Number of non-*Bombus* wild bees (n=90)	nb1	14	485.44	0.00	0.42	Run + FC + SNH + run:FC + run:SNH + FC:SNH	0.09	0.26
	nb2	15	485.51	0.97	0.41	FB + run + FC + SNH + run:FC + run:SNH + FC:SNH	0.09	0.25
	nb0	5	832.14	346.70	0.00	1	-	-
Species richness of all wild bees (n=90)	sri1	11	424.13	0.00	0.10	FB + run + FC + FB:FC + run:FC	0.10	0.20
	sri2	10	424.26	0.13	0.10	FB + run + FC + run:FC	0.10	0.20
	sri3	9	425.29	1.16	0.06	Run + FC + run:FC	0.09	0.18
	sri0	4	445.23	21.11	0.00	1	-	-

Table S3 The relative importance of explanatory variables expressed by Σw_i (sum of Akaike weights) for models to explain the effects of the different landscape metrics on the number of bumblebees, non-*Bombus* wild bees and the species richness of all wild bees (best fitting models are shown in Table S2). Only model parameters having $\Sigma w_i > 0.2$ are shown. FB: faba bean cultivation (FB+/FB-), run: sampling round (1-3), FC: local flower cover of transect area, OSR: percentage of oilseed rape, SNH: percentage of semi-natural habitats.

Models	**Response variable**	**FB**	**run**	**FC**	**OSR**	**SNH**	**FB: run**	**run: FC**	**FB: FC**	**run: SNH**	**FC: SNH**
bb	no. of bumblebees	0.98	1.00	0.97	0.32	0.32	0.91	0.32	-	-	-
nb	No. of non-*Bombus* wild bees	0.44	1.00	1.00	-	1.00	-	1.00	-	1.00	0.93
sri	Species richness of all wild bees	0.81	1.00	1.00	0.37	0.35	-	1.00	0.35	-	-

Table S4 Mean values, median, standard deviation (sd), minimum (min), maximum (max) and sample size (n) of observed pollinator numbers, species richness and of functional traits for each sampling run.

response variable	**run**	**mean**	**median**	**sd**	**min**	**max**	**n**
number of bumblebees	1	8.2	6.5	8.9	0.0	44.0	30
	2	27.9	20.5	24.9	0.0	100.0	30
	3	10.3	6.5	17.3	0.0	63.0	30
number of non-*Bombus* wild bees	1	6.6	1.0	17.6	0.0	94.0	30
	2	11.9	4.5	15.2	0.0	58.0	30
	3	8.4	4.5	12.2	0.0	53.0	30
species richness of all wild bees	1	4.4	3.5	2.9	0.0	12.0	30
	2	5.7	6.0	3.0	0.0	11.0	30
	3	4.7	3.5	4.1	0.0	19.0	30
CMW ITD	1	3.5	3.8	0.6	1.4	4.2	29
	2	3.4	3.7	0.6	2.1	4.0	29
	3	3.1	3.2	0.8	1.7	4.0	27
CMW proboscis length	1	6.4	7.3	1.9	1.5	8.5	29
	2	6.7	7.1	1.5	3.4	8.1	29
	3	5.8	6.1	2.1	2.4	8.1	27
lecty Fabaceae	1	0.8	1.0	0.3	0.0	1.0	29
	2	0.9	1.0	0.1	0.7	1.0	29
	3	0.8	0.9	0.2	0.0	1.0	27

Table S5 Mean values, median, standard deviation (sd), minimum (min), maximum (max) and sample size (n) of observed pollinator numbers, species richness and of functional traits depending on faba bean cultivation (FB). FB+: Landscapes with faba bean cultivation; FB-: control landscapes without faba beans.

response variable	**FB**	**mean**	**median**	**sd**	**min**	**max**	**n**
number of bumblebees	FB+	19.9	9.0	23.2	0.0	100.0	45
	FB-	11.1	7.0	13.3	0.0	56.0	45
number of non-Bombus wild bees	FB+	9.0	2.0	13.6	0.0	58.0	45
	FB-	8.9	2.0	16.7	0.0	94.0	45
species richness of all wild bees	FB+	5.5	5.0	3.1	1.0	13.0	45
	FB-	4.4	3.0	3.6	0.0	19.0	45
CMW ITD	FB+	3.4	3.6	0.7	1.4	4.1	45
	FB-	3.3	3.6	0.7	1.8	4.2	40
CMW proboscis length	FB+	6.4	7.0	1.9	1.5	8.2	45
	FB-	6.3	7.0	1.9	2.5	8.5	40
lecty Fabaceae	FB+	0.8	0.9	0.2	0.0	1.0	45
	FB-	0.9	1.0	0.2	0.0	1.0	40

Table S6 Summary of the best fitting candidate (dAICc<2) and null-models for the effects of faba bean cultivation and landscape metrics on the community weighted means (CWM) for ITD and proboscis length as well as for the proportion of bee species collecting pollen from Fabaceae (lecty Fabaceae). Marginal (R_m^2) and conditional (R_c^2) R^2 values are given as a measure of the models goodness of fit. Data is summed up across all transects and runs per landscape. FB: faba bean cultivation (FB+/FB-), run: sampling round (1-3), FC: local flower cover of transect area, OSR: percentage of oilseed rape, SNH: percentage of semi-natural habitats.

Response variable	Model	DF	AICc	dAICc	Akaike weight (w_i)	Explanatory variables	R_m^2	R_c^2
CWM ITD (n= 85)	cmITD1	8	163.26	0.00	0.13	Run + SNH	0.15	0.56
	cmITD2	10	165.13	1.87	0.05	Run + FC + SNH + FC:SNH	0.17	0.56
	cmITD0	5	170.58	7.32	0.00	1	-	-
CWM proboscis length (n=85)	cmto1	8	332.73	0.00	0.08	Run + snh	0.13	0.50
	cmto2	11	334.01	1.28	0.04	FB + run + fc + snh + FB:fc	0.16	0.52
	cmto3	6	334.25	1.52	0.04	Snh	0.09	0.44
	cmto4	7	334.53	1.80	0.03	Run	0.04	0.46
	cmto5	12	334.68	1.95	0.03	FB + run + fc + snh + FB:fc + fc:snh	0.17	0.51
	cmto0	5	336.17	3.44	0.02	1	-	-
Lecty Fabaceae (n=85)	mL1	15	328.74	0.00	0.70	FB + run + fc + snh + FB:run + run:fc + run:snh	0.18	0.32
	mL0	4	396.31	67.57	0.00	1		

Table S7 The relative importance of explanatory variables expressed by Σw_i (sum of Akaike weights) for models to explain the effects of faba bean cultivation and the landscape metrics on the community weighted means for ITD and proboscis length as well as for the proportion of bee species collecting pollen from Fabaceae (lecty Fabaceae) (best fitting models are shown in Table S6). Only model parameters having $\Sigma w_i > 0.2$ are shown. FB: faba bean cultivation (FB+/FB-), run: sampling round (1-3), FC: local flower cover of transect area, OSR: percentage of oilseed rape, SNH: percentage of semi-natural habitats.

Models	**Response variable**	**FB**	**run**	**FC**	**OSR**	**SNH**	**FB: run**	**FB:FC**	**FC: SNH**	**run: SNH**	**run: FC**
cmITD	CWM ITD	0.39	0.82	0.58	0.37	0.90	-	-	0.26	-	-
cmto	CWM proboscis length	0.53	0.69	0.61	0.33	0.81	-	0.33	0.21	-	-
mL	Lecty Fabaceae	1	1	0.82	-	0.99	1	-	-	0.99	0.71

Chapter 2

Identity of mass-flowering crops moderates functional trait composition of pollinator communities

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Abstract

Pollinator declines and functional homogenization of farmland insect communities have been reported. Mass-flowering crops (MFC) can support pollinators by providing floral resources. Knowledge about how MFC with dissimilar flower morphology affect functional groups and functional trait compositions of wild bee communities is scarce. We investigated how two morphologically different MFC, land cover and local flower cover of semi-natural habitats (SNH) and landscape diversity affect wild bees and their functional traits (body size, tongue length, sociality, foraging preferences). We conducted landscape-level wild bee surveys in SNH of 30 paired study landscapes covering an oilseed rape (OSR) (*Brassica napus* L.) gradient. In 15 study landscapes faba beans (*Vicia faba* L.) were grown, paired with respective control landscapes without grain legumes. Faba bean cultivation promoted bumblebees (*Bombus* spp. Latreille), whereas non-*Bombus* densities were only driven by the local flower cover of SNH. High landscape diversity enhanced wild bee species richness. Faba bean cultivation enhanced the proportions of social wild bees, bees foraging on Fabaceae and slightly of long-tongued bumblebees. Solitary bee proportions increased with high covers of OSR. High local SNH flower covers mitigated changes of mean bee sizes caused by faba bean cultivation. Our results show that MFC support specific functional bee groups adapted to their flower morphology and can alter pollinators` functional trait composition. We conclude that management practices need to target the cultivation of functionally diverse crops, combined with high local flower covers of diverse SNH to create heterogeneous landscapes, which sustain diverse pollinator communities.

Keywords

wild bees, ecosystem services, floral resources, legumes, greening, functional traits

Introduction

Insects are declining worldwide (IPBES 2019) and the loss of insects acting as pollinators, such as wild bees, poses a threat to ecosystem services in natural and agricultural systems (Potts et al. 2010). In Germany alone, 53 % of all native bee species are red listed (Westrich et al. 2011). Agricultural intensification through increased use of pesticides, the simplification of landscapes and the vanishing of nesting sites and food resources poses a big challenge to most pollinators (Potts et al. 2010; Vanbergen and Insect Pollinators Initiative 2013). The loss of suitable habitats can lead to a functional homogenization of insect communities through filtering for specific species traits but local effects can be mitigated by increasing landscape heterogeneity (Gámez-Virués et al. 2015; Perović et al. 2015).

The availability of floral resources is the main driver of wild bee abundances (Potts et al. 2003) and the loss of floral host species in the past century is a major reason for wild bee declines (Scheper et al.

2014). Heterogeneous landscapes with a high diversity of different habitats harbor diverse pollinator communities (Steckel et al. 2014; Shackelford et al. 2013) and increasing the amount of SNH in a landscape enhances wild bee abundance and species richness (e.g. Nayak et al. 2015; Steffan-Dewenter et al. 2002). In addition to the amount of SNH in a landscape, the quality of SNH, in terms of flower cover of important forage plants might be an essential factor shaping pollinator responses (Bartual et al. 2019) since both a high local flower cover and plant species richness are positively correlated with wild bee abundances and species richness (Ebeling et al. 2008; Kallioniemi et al. 2017; Potts et al. 2003).

Also, the cultivation of mass-flowering crops (MFC) can benefit wild bees by temporary providing high pollen and nectar amounts (Diekötter et al. 2014; Rundlöf et al. 2014; Westphal et al. 2003). The most commonly grown MFC in Europe is oilseed rape (OSR) (*Brassica napus* L.). But due to extreme drought during summer, cultivation area dropped by 28 % from 2018 to 2019, accounting for 7.4% of the total German cropland (Destatis 2020). Other MFC, like grain legumes, are rarely cultivated (1.7 % of cropland in Germany), although their cultivation area increased due to their promotion as ecological focus area (EFA) within the CAP greening reform of 2013 (Destatis 2020).

Successful crop pollination depends on the availability of suitable pollinators, whose morphological traits match those of the crops` flowers (Garibaldi et al. 2015). Vice versa, flower visiting pollinator communities of different MFC vary (Garratt et al. 2014). While OSR is visited by a diverse pollinator community (Garratt et al. 2014), only a few pollinator species, mainly honeybees and bumblebees, forage on faba beans (*Vicia faba* L.) (Garratt et al. 2014; Marzinzig et al. 2018). This is due to the complex flower morphology of faba beans and nectar located deep in the corolla tubes (Bond and Poulsen 1983). Force and a long tongue are necessary to access the flowers` reward (Bailes et al. 2018). Long-tongued bumblebees are therefore most effective pollinators of faba beans (Marzinzig et al. 2018), while solitary wild bees have been shown to be most effective pollinators for oilseed rape (Woodcock et al. 2013).

Regarding biodiversity benefits of MFC, the identity of the flowering crop might determine, which pollinator species are promoted with possible implications for functional trait compositions of pollinator communities (Diekötter et al. 2010). Beneficial effects of early flowering OSR on bumblebees and solitary wild bees are widely known (e.g. Diekötter et al. 2014; Jauker et al. 2012; Westphal et al. 2003, 2009), whereas there are only few studies, showing a positive effect of faba bean cultivation on bumblebees (Hanley et al. 2011; Knight et al. 2009). There is limited understanding of how MFC with differing flower morphologies, interactively affect wild bee communities in SNH of agricultural landscapes. Especially possible landscape-scale effects on the functional trait composition of wild bee communities are understudied.

In this study, we aim to investigate how crop identity of two MFC species affects wild bee densities, species richness and their functional traits in SNH at landscape-scale. Moreover, we focus on the relative importance of local flower cover of SNH, the amount of SNH and landscape diversity for wild bees. We established 30 paired 1 km^2 study landscapes, i.e. 15 study landscapes with *V. faba* fields and 15 without grain legumes.. We expect that faba bean cultivation increases mainly numbers of bumblebees, the main pollinators of *V. faba*, by offering mid-seasonal resources. Further, we hypothesize that all wild bees benefit from an enhanced coverage of OSR, from an enhanced amount and local flower cover of SNH in the study landscapes and high landscape diversity. We expect local and landscape resource availability to modify the functional trait composition of wild bee communities, regarding bee size, foraging preferences, sociality and bumblebee tongue length. With respect to faba bean flower morphology, bigger pollinators, which are heavier and have proportional longer tongues and bees known to forage on Fabaceae should be favored by its cultivation. In contrast, OSR with nectar being easily accessible from flowers might promote predominantly small bees with proportional shorter tongues and bee species with no preference for Fabaceae. We expect social bees to be attracted by and to benefit from both MFC stronger than solitary bees. In addition, we hypothesize, that especially long tongued and big bumblebees, might be favored by faba bean cultivation because their morphology facilitates access to the reward of the flowers.

Material and Methods

Study design

We selected 30 paired 1 km x 1 km study landscapes in three different regions in Germany (see Beyer et al., 2020) (Fig. 1). Twelve landscapes were situated close to Göttingen in Central Germany (51°32´N, 9°56´E), ten landscapes close to the North Sea in vicinity of the city Itzehoe (53°55´N, 9°30´E) and eight in eastern Germany close to Leipzig (51°20´N, 12°22´E). 15 landscapes were surrounding a conventionally managed faba bean field (faba bean landscapes: FB+). We ensured that the respective farmers applied diversified crop rotations, i.e. conventional crop sequences that included grain legumes as an additional component for at least three years. Respecting control landscapes (FB-) did not include any grain legumes. Landscape selection was based on a similar landscape composition of the study landscapes within a pair. For further details see Beyer et al., 2020.

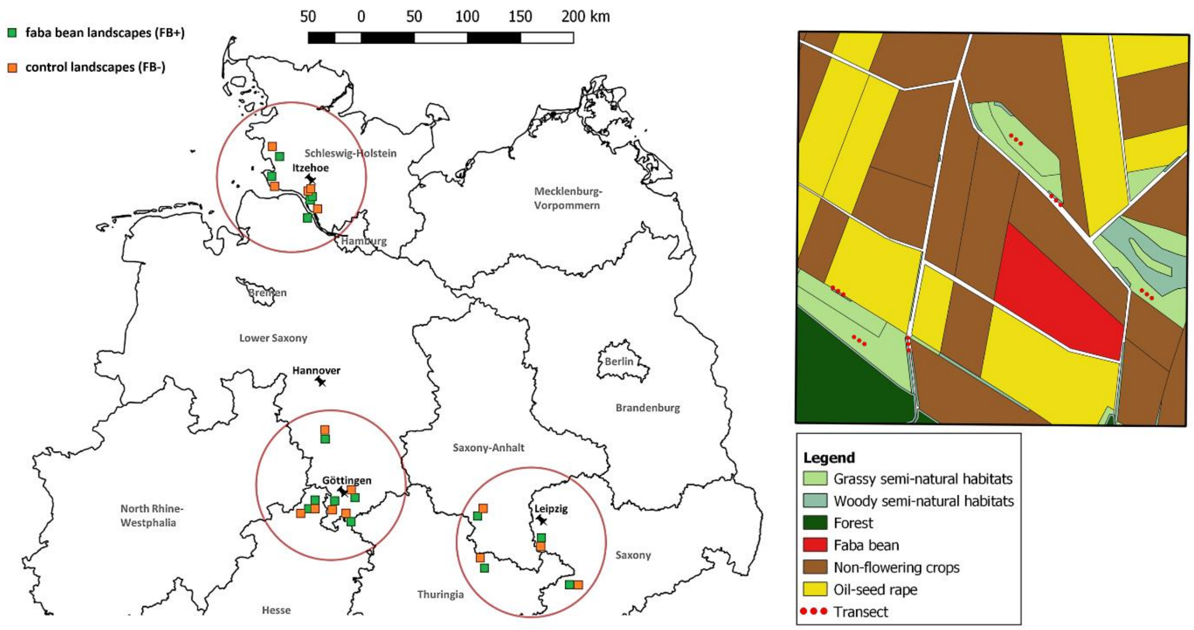

Figure 1 Map showing the location of the study landscapes in the three regions of Germany. Landscapes with faba bean cultivation (FB+) are depicted in green and control landscapes (FB-) in orange. On the right, an example of a study landscape is shown with six transects located in grassy and woody semi-natural habitats.

All landscape elements with a minimum size of 10 m^2 were mapped within the study landscapes by site inspections. As landscape composition measures, we calculated the percentage cover of semi-natural and flower-rich habitats (SNH, Table S1), landscape diversity (Shannon index of 14 land-use types; see appendix for further information) and percentage cover of mass-flowering OSR with QGIS version 2.18 (QGIS Development Team 2016). Our study landscapes covered an independent gradient of SNH and OSR (Fig. S1).

Wild bee sampling

The study was conducted during the summer of 2017 and wild bee sampling was repeated three times between May and August (early summer: 22.05. - 19.06., mid-summer: 22.06. - 20.07., late summer: 27.07. - 22.08.). Oilseed rape full bloom was over when sampling started. Faba beans were in full bloom during the first sampling run in early summer and did not flower during the last two sampling runs for most of the study landscapes. During every sampling run six variable transect walks (50 m x 5 m, 5 min. excluding handling time) were conducted within the most attractive flower rich SNH in each study landscape to cover the entire spectrum of suitable foraging patches for wild bees at landscape scale (Westphal et al. 2008) (Fig. 1). Due to the high spatial and temporal floral variability in SNH, we think that varying the transect location according to floral availability is a good approach to capture the entire pollinator community in each study landscape across the season. To cover different structural SNH types, we distributed the transect walks, if possible, equally within both, woody and grassy SNH types (for details see Table S1&S2).

Transect walks were conducted between 9 a.m. and 7 p.m. on days with suitable weather conditions (no rain, low wind speed, temperatures > 15°C). Walking slowly through the transect in one direction, the number of flower-visiting bees was counted. Species, that could not be identified in the field, were caught and taken to the lab for further identification. To avoid excessive killing, we collected only the first five bumblebee individuals of every species/morphospecies per transect for confirmatory identification. Based on similar coloration, we defined three morphospecies: (1) *Bombus terrestris*, *B. lucorum*, *B. hortorum*, *B. bohemicus* and *B. sylvestris,* (2) *B. lapidarius*, *B. ruderarius* and *B. rupestris,* (3) *B. pascuorum* and *B. muscorum*. All other bumblebee species could be distinguished as separate species. We identified all bumblebees (Mauss 1994) and all non-Bombus wild bees (Amiet et al. 2001, 2007, 2014) in the lab. Because *Bombus terrestris*, *B. lucorum, B. cryptarum* and *B. magnus* are difficult to distinguish, we aggregated them. The percentage of local flower cover within the transect area was estimated during each transect walk (mean: 28.7 %, range: 0 - 95 %). Flowering plants, on which we observed pollinator visits were recorded on family level (Fig. S2).

Functional trait composition of pollinator communities

To study the effects of faba bean cultivation and landscape metrics on the functional trait composition of wild bee communities, we chose three functional traits, likely to be affected by local and landscape resource availability: body size, foraging preferences and sociality. Trait analyses were conducted for all sampled wild bees. Since we collected only the first five individuals of every *Bombus* color group per transect, the sampled bumblebee individuals do not mirror the actual structure of the bumblebee community in a certain study landscape. To account for the community structure, we only considered the first five collected bumblebee individuals per transect for the trait analyses. We consider this sub-sample to be representative as the mean density of recorded bumblebees per transect was 3.8 and in approx. 80 % of the cases we only caught five or less bumblebee individuals per transect. We excluded cleptoparasites from the trait analyses (six species) because of their different life-history strategy and undefined foraging preferences. We measured the intertegular distance (ITD) of at least one and maximum five worker individuals per species (57 species in total) as a measure of body size (Table S3). For four species we caught only one single male individual and thus were not able to measure ITD. For the foraging preferences, wild bees were categorized into species collecting pollen from Fabaceae (any species, known to forage on Fabaceae, not specifically Fabaceae specialists) and species not known to exploit Fabaceae (specialists of a different plant family or generalists, not known to visit Fabaceae). For sociality, wild bees were grouped into social and solitary bees. Foraging preference and sociality information were extracted from the literature (Westrich, 2018) (Table S3).

Since bumblebees are the main pollinators of faba beans, we additionally tested whether MFC affect the functional trait composition of bumblebee communities concerning bumblebee body size and tongue length. The tongue length of maximum 12 bumblebee workers per species was measured and the tongue length relative to the bees` body sizes were calculated. According to the mean relative tongue length, bumblebee species were assigned to the long- or short-tongued category (Table S4).

Statistical analyses

All analyses were conducted in R version 3.6.1 (R Core Team 2019) using generalized linear mixed models with the *glmmTMB* package (Brooks et al. 2017) and linear mixed effect models with the *nlme* package (Pinheiro et al., 2019). We followed a multimodel inference approach (Burnham and Anderson 2002). Based on global models (see details below), we fitted candidate models containing all possible combinations of explanatory variables and their interactions with the help of the *dredge* function of the *MuMIn* package (Barton 2019). The number of variables in the single candidate models was restricted to a maximum of seven. Candidate models were ranked by Bayesian Information Criterion (BIC), which is an information criterion similar to the more commonly used Akaike information criterion (AIC), but with a penalty term that also considers the number of samples. BIC thus tends to select less complex models in comparison to AIC (Burnham and Anderson 2002; Link and Barker 2006). We considered all models with a delta BIC < 2 compared to the best fitting model to have important empirical support (Raftery 1995). We used BIC model weights (w_i), to assess the posterior probability of each model (Link and Barker 2006) and derived the sum of BIC model weights (Σw_i) across all models to rank the importance of explanatory variables.

We used residual plots to validate model assumptions. As a measure of the model´s goodness of fit we calculated marginal (R_m^2) and conditional (R_c^2) R^2 values with the *MuMIn* package. To test for collinearity, we used the variance inflation factor (VIF), which was below 3 for all cases (Zuur et al., 2010). To test for differences between faba bean and control landscapes or between different runs we performed post hoc tests with the *emmeans* package (Lenth 2019) at alpha level of 0.05. All graphics were generated with *ggplot2* package (Wickham 2016) and predictions and confidence intervals in scatter plots were obtained from the *effects* package (Fox and Weisberg 2019) and in the boxplots from the *emmeans* package.

Wild bee densities and species richness

To analyze the effect of local and landscape resource availability on pollinator densities, we performed two separate models for bumblebees and all other wild bees (non-*Bombus* wild bees). While all observed wild bees (excluding honeybees) were included in the wild bee densities, only identified individuals were used for the wild bee species richness. Overall species richness (see Fig. S3 for species accumulation curve) was analyzed at landscape scale (due to very low species numbers per transect), i.e. richness was calculated across all six transects per study landscape and run and SNH flower cover was averaged across all transects per study landscape and run. Our response variables were: density of bumblebees, density of non-*Bombus* wild bees (per 250 m^2 transect area and 5 min), species richness of all wild bees per study landscape (per 1500 m^2 transect area and 30 min), and additionally, density of the long-tongued *B. pascuorum*/ *B. muscorum* color group (hereinafter referred to as *B. pascuorum* densities, since *B. muscorum* made up only a small proportion of that group). We included faba bean cultivation (FB+/ FB-), local flower cover of the SNH transect area (FC), sampling run (early/mid/late summer), percentage of SNH and of OSR per study landscape and landscape diversity as explanatory variables in the global models. Moreover, we added all possible two-way interactions, as we consider each of them as ecologically relevant. All continuous explanatory variables were standardized to a mean of zero and a standard deviation of 1 to improve model convergence. As nested random effects, we included study region, landscape pair, study landscape and sampling run (region/landscape pair/landscape/run) into the pollinator density models and region, landscape pair and study landscape (region/landscape pair/landscape) into the species richness model.

Global generalized linear mixed models with all independent variables and two-way interactions were fitted with Poisson and in case of overdispersion with negative binomial distribution. For pollinator densities, models with and without zero inflation terms were compared and the model with lowest BIC was selected for multimodel inference. The zero inflation was either assumed to be constant across the data or to be related to the local flower cover (Brooks et al. 2017). The model with negative binomial distribution and without zero inflation term was selected for the bumblebee densities and for non-*Bombus* densities we chose the model with negative binomial distribution and zero inflation related to the local flower cover. For the species richness, we chose the model with Poisson distribution. To test for competition effects of honeybees on wild bee densities, we repeated density analyses as described above, with honeybee densities as additional predictor.

Functional trait composition of wild bee communities

To analyze the effects of faba bean cultivation and landscape metrics on the functional traits of wild bees at landscape level, we aggregated data across transects for each run. Using the *FD* package (Laliberté and Legendre 2010), we calculated the community weighted means (CWM) for ITD for the entire pollinator community and for bumblebees seperately. We applied linear mixed effect models with Gamma distribution and log link for the entire wild bee community and with normal distribution for the analysis of CWM ITD of bumblebees. Moreover, we used generalized linear mixed models with binomial familiy and logit link to test the effect of local and landscape wide floral resources on the following response variables: the proportion of wild bees collecting pollen from Fabaceae (Fabaceae foragers) and the proportion of social wild bees relative to all bees as well as the proportion of long-tongued bumblebees relative to all bumblebees. The explanatory variables, random effects and multimodel inference procedure were the same as described above for the species richness.

Results

In total we observed 2620 wild bees of which 78.0 % were bumblebees. 1342 wild bees were caught and used for species identification, resulting in 66 recorded species (Table S3). The most frequently caught wild bee was *Bombus terrestris/lucorum* accounting for about 29.7 % of all sampled bees, making up 64.6 % of all short-tongued bumblebees. *B. pascuorum* accounted for 24.4 % of all wild bees and represented 82.8 % of all long-tongued bumblebees. 12.2 % of all collected bees were *Bombus lapidarius*. *Lasioglossum pauxillum* was the most commonly found non-*Bombus* bee and accounted for 5.2 % of all wild bees. Most visited families of all visited plants in early summer were Fabaceae, Boranginaceae and Rosaceae, while in mid and late summer Fabaceae, Boranginaceae and Asteraceae were most visited (Fig. S2). 44.3 % of all non-cuckoo species were categorized as Fabaceae foragers, which corresponded to 87.8 % of all caught individuals.

Wild bee densities and species richness

The multimodel inference revealed two models within dBIC < 2 explaining the effect of faba bean cultivation ($\Sigma w_i = 0.96$), local flower cover ($\Sigma w_i = 1.00$) and run ($\Sigma w_i = 1.00$) on bumblebee densities (Table 1, S5, S6). We found on average 1.6 times more bumblebees in faba bean compared to control landscapes (Fig. 2a).

Table 1 Summary of the best fitting candidate models (dBIC<2) and null models for the effects of faba bean cultivation and landscape metrics on bee densities, species richness and functional traits of all wild bees and bumblebees. Marginal (R_m^2) and conditional (R_c^2) R^2 values are given as a measure of the model´s goodness of fit. Data for species richness and for functional traits is summed up across all transects per study landscape. n: number of observations, FB: faba bean cultivation (FB+/FB-), run: sampling run (early/mid/late summer), FC: local flower cover, LD: landscape diversity, OSR: percentage of oilseed rape, SNH: percentage of semi-natural habitats.

Response variable	model	df	BIC	deltaBIC	BIC weight	Explanatory variables	R_m^2	R_c^2
Pollinator densities and species richness								
Bumblebee density (n=540)	m.bb1	11	2287.43	0.00	0.49	FB + FC + run + FB:FC	0.53	-
	m.bb2	10	2289.01	1.58	0.22	FB + FC + run	0.52	-
	m.bb0	7	-	-	-	1	-	-
Non-*Bombus* density (n=540)	m.nb1	9	1268.77	0.00	0.59	FC	0.06	0.42
	m.nb0	7	1341.80	73.03	0.00	1	0	0.46
Species richness of all wild bees (n=90)	m.spr1	6	408.82	0.00	0.26	FC + LD	0.20	0.37
	m.spr2	5	409.69	0.88	0.17	FC	0.19	0.38
	m.spr0	4	421.61	12.79	0.00	1	0.00	0.33
Functional traits of all wild bees								
CWM ITD (n=90)	m.itd1	5	174.46	0.00	0.32	1	0.00	0.43
Foraging preferences (n=90)	m.l1	9	312.62	0.00	0.30	FB + run + FB:run	0.08	0.22
	m.l0	4	333.93	21.30	0.00	1	0.00	0.14
Sociality (n=90)	m.s1	9	326.64	0.00	0.16	FB + run + FB:run	0.16	0.31
	m.s2	10	327.76	1.12	0.09	FB + run + OSR + FB:run	0.17	0.30
	m.s3	12	328.25	1.61	0.07	FB + run + SNH + FB:run + run:SNH	0.18	0.33
	m.s0	4	413.84	87.21	0.00	1	0.00	0.14
Functional traits of Bombus								
Proportion long-tongued bumblebees (n=90)	m.ltb1	7	361.28	0.00	0.33	FC + run	0.19	0.27
	m.ltb2	8	362.99	1.71	0.14	FC + FB + run	0.20	0.27
	m.ltb0	4	431.28	70.00	0.00	1	0.00	0.18
CWM ITD Bombus (n=90)	m.itdb1	8	-223.76	0.00	0.44	FB + FC + FB:FC	0.18	0.18
	m.itdb0	5	-219.62	4.15	0.06	1	0.00	0.00

The highest bumblebee densities were observed in run 2 and lowest in run 3 (Fig. S4). Moreover, bumblebee densities increased with increasing local flower cover and this effect was stronger in control compared to bean landscapes ($\Sigma w_i = 0.66$) (Fig. 2b). There was a single model within dBIC < 2, showing positive effects of local SNH flower cover ($\Sigma w_i = 1.00$), on the density of non-*Bombus* wild bees (Table 1, S5, S6, Fig. 2c). There were two best-fitting models, showing a positive effect of local SNH flower cover ($\Sigma w_i = 1.00$) and of landscape diversity ($\Sigma w_i = 0.67$) on the species richness of all wild bees (Table 1, S5, S6, Fig. 2d, e).

Honeybees did not affect wild bee densities (see Table S7 & S8).

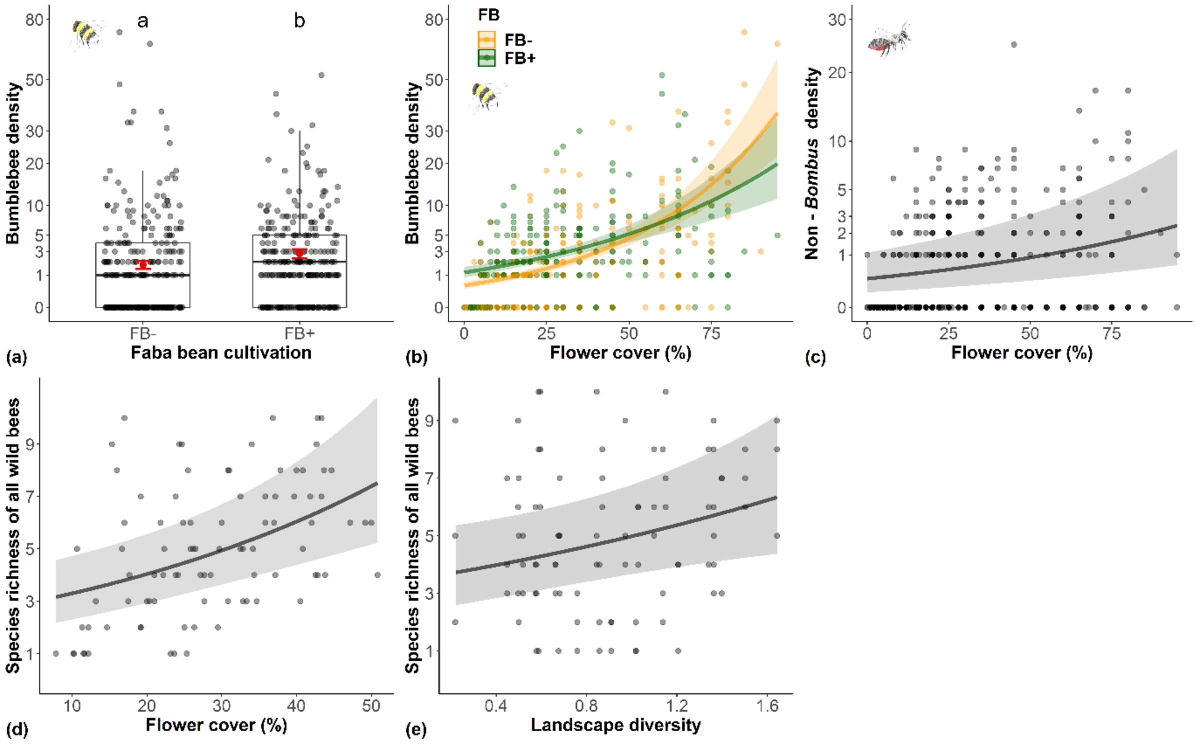

Figure 2 Effect of faba bean cultivation on bumblebee densities in landscapes with (FB+) and without (FB-) faba bean cultivation (p<0.001) (**a**). Effect of local flower cover (%) on bumblebee densities in FB+ and FB- landscapes (**b**). Effect of local flower cover (%) on non-*Bombus* wild bee densities (**c**) and on species richness of all wild bees (**d**). Effect of landscape diversity on wild bee species richness (**e**). Predicted mean values and 95% confidence intervals are displayed (in red for (a)). Different letters above boxplots indicate significant differences between FB+ and FB- landscapes. Predictions are based on the respective best fitting models m.bb1, m.nb1 and m.spr1 (Table 1). Y-axes are sqrt-transformed in (a-c) for graphical reasons.

Functional trait composition of wild bee communities

All wild bees

Functional composition of bee communities with respect to the bees' body sizes (CWM of ITD) were not affected by local or landscape resource availability. No fitted model was superior to the null model (Table 1).

Three models with dBIC < 2 explained faba bean cultivation ($\Sigma w_i = 0.99$), run ($\Sigma w_i = 1.00$), OSR ($\Sigma w_i = 0.32$) and SNH cover ($\Sigma w_i = 0.40$) effects on the proportion of social wild bees within the communities. (Table 1, S5, S6). We found a higher proportion of social bees in control compared to faba bean landscapes in run 1, whereas a higher proportion of social bees was recorded in bean landscapes in comparison with controls in the second and third run (Fig. 3a). The proportion of social bees decreased with increasing amounts of OSR in the surrounding study landscape (Fig. 3b). We found proportions of social bees to increase with increasing percentage of SNH in run 1 and to decrease in run 2 and 3 (Fig. S5).

The multimodel inference resulted in one best model explaining faba bean cultivation ($\Sigma w_i = 0.83$) and run ($\Sigma w_i = 1.00$) effects on the proportion of Fabaceae foragers (Table 1, S5, S6). Patterns were similar as for the proportion of social bees, which might be due to the correlation of the two response variables (spearman r=0.74, p<0.001). Proportions of Fabaceae foragers were higher in faba bean landscapes compared to controls in run 2 and 3, whereas the opposite was true for run 1 (Fig. S6). Besides, composition of the bee communities was unaffected by faba bean cultivation but changed by OSR cover, mainly due to common bumblebee species (for further details see supplementary material Table S9 & Fig. S7).

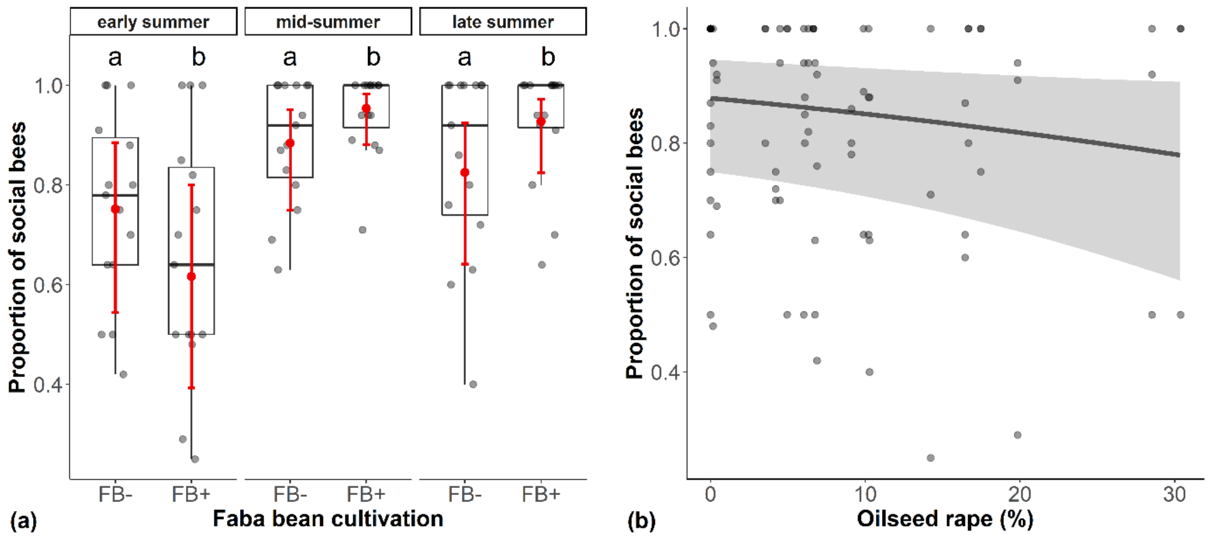

Figure 3 Effect of (**a**) faba bean cultivation and of (**b**) oilseed rape cover on the proportion of social bees (for the three different sampling runs in (a)). Different letters above boxplots indicate significant differences between faba bean (FB+) and control (FB-) landscapes within each run. Predicted mean values and 95% confidence intervals are displayed (in red for (a)). Predictions are based on the second-best fitting model m.s2 (Table 1).

Bumblebees

There were two models within dBIC < 2 explaining the effect of faba bean cultivation ($\Sigma w_i = 0.40$), sampling run ($\Sigma w_i = 1.00$) and local flower cover ($\Sigma w_i = 1.00$) on the proportion of long-tongued bumblebees (Table 1, S5, S6). We found 51 % of the bumblebee community to be long-tongued in faba bean landscapes and 42 % in control landscapes (p=0.07) (Fig. 4a). Highest proportions of long-tongued bumblebees were present in the last sampling run (Fig. S8) and the proportions decreased with increasing local flower cover (Fig. 4b). Focusing on the most dominant long-tongued species, we found higher *B. pascuorum* densities in faba bean compared to control landscapes (p<0.01) (Fig. S9). Densities were highest in run 2 and lowest in 1.

The CWM for ITD of bumblebees was fitted by a single best model including faba bean cultivation (Σw_i = 0.90), local flower cover (Σw_i = 0.88) and their interaction (Σw_i = 0.86) as predictors (Table 1, S5, S6). Mean size of bumblebees did not differ between faba bean and control landscapes (Fig. 4c). CWM ITD increased with increasing flower cover in control landscapes, whereas it decreased in faba bean landscapes (Fig. 4d). CWM ITD was higher in faba bean compared to control landscapes when local flower cover of SNH was low (p < 0.01), while at high local flower cover of SNH CWM ITD did not differ significantly (p=0.07).

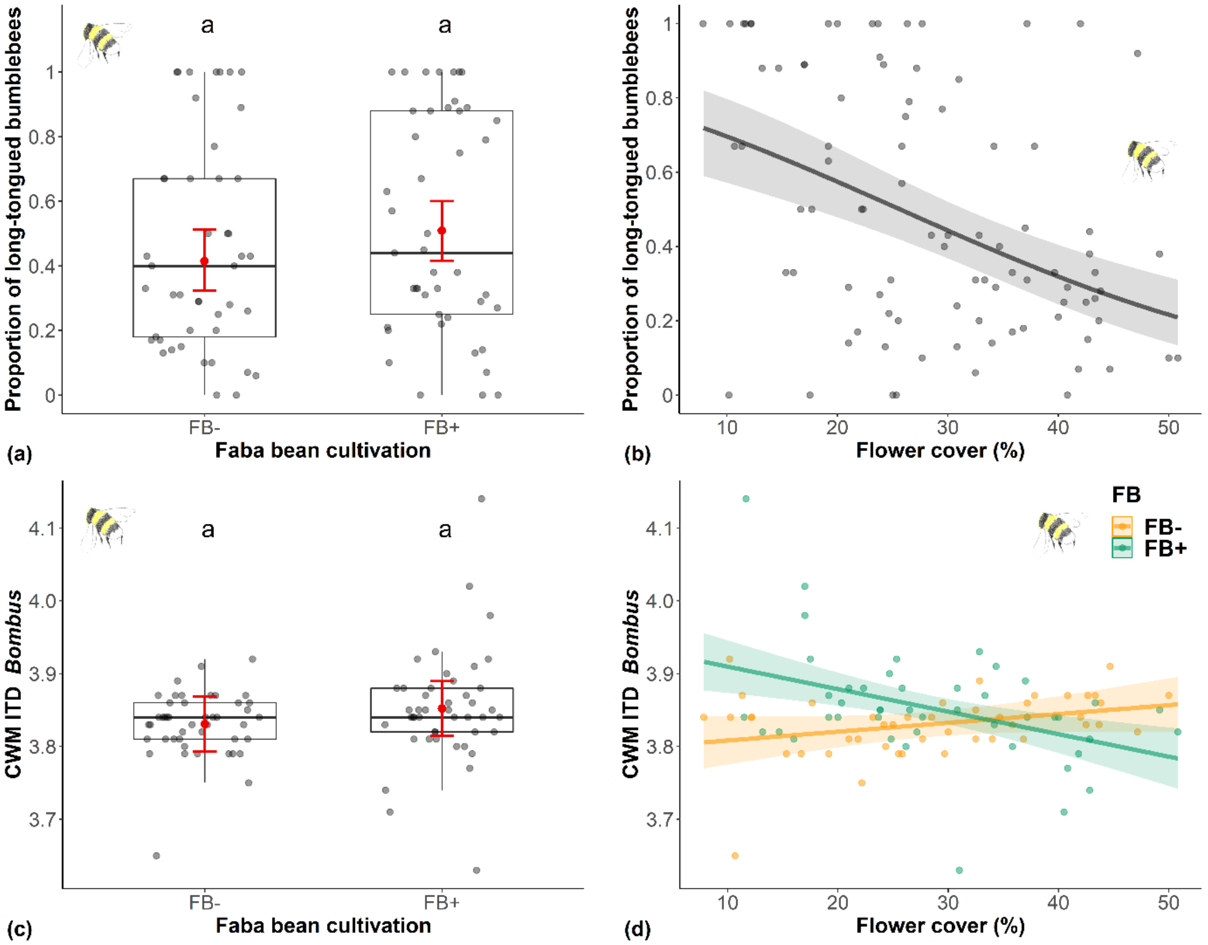

Figure 4 Effect of faba bean cultivation (p=0.07) (**a**) and of local flower cover (%) (**b**) on the proportions of long-tongued bumblebees. Effect of faba bean cultivation (p=0.12) (**c**) and of local flower cover (%) (**d**) for faba bean (FB+) and control (FB-) landscapes on the community weighted means (CWM) for intertegular distance (ITD) of bumblebees. Same letters above boxplots indicate non-significant differences between FB+ and FB- landscapes. Predicted mean values and 95% confidence

intervals are displayed (in red for (a&c)). Predictions are based on the second-best model m.ltb2 for the proportion of long-tongued bumblebees and on the best fitting model m.itdb1 for CWM ITD of *Bombus* (Table 1).

Discussion

Wild bee densities and species richness

We showed that faba bean cultivation enhances bumblebee densities in SNH, which is in accordance with our hypothesis. Accordingly, bumblebee densities were enhanced in faba bean landscapes, when sampling within field margins (Beyer et al., 2020). Bumblebees are known to preferentially forage on flowers, that offer high quality, protein-rich pollen, like Fabaceae (Somme et al. 2015) and are, next to honeybees, the most common flower visitors to faba beans in temperate regions (Bond and Poulsen 1983; Garratt et al. 2014; Marzinzig et al. 2018). Due to their tongue length and body size, bumblebees` morphology fits the morphology of faba beans with its very long corolla-tubes. Force and a long tongue is necessary to easily access nectar of faba bean flowers (Bailes et al. 2018). An increased colony density of long-tongued *Bombus pascuorum* in the vicinity of faba bean fields (Knight et al. 2009) and a higher density of bumblebees in field margins adjacent to bean compared to wheat fields (Hanley et al. 2011) has already been shown. However, the effect of faba bean cultivation on biodiversity at landscape-scale is widely unknown. Our study provides evidence that conventionally managed faba beans increase bumblebee densities at landscape-scale by providing resources during mid-summer after the flowering of OSR. Resource continuity is of major importance for pollinators to persist in simplified agricultural landscapes (Schellhorn et al. 2015; Westphal et al. 2009) and March, June and August/September have been identified as critical times of nectar scarcity for bumblebees (Timberlake et al. 2019). Thus, faba beans might provide essential resources for wild bees in times of food scarcity during June. Resource continuity throughout the season might be especially important for colonial species, while most solitary bees have shorter life cycles and depend on resource availability at the time of their activity period. This might be one reason for why non-*Bombus* wild bees did not benefit from faba bean cultivation. Another reason is the beans` flower morphology with rewards not easily accessible for small bees with short tongues. Non-*Bombus* wild bees and bumblebees were closely linked to the quantity of floral resources within the SNH of our study landscapes. Bumblebee densities increased more strongly with increasing local flower cover in control compared to bean landscapes. Faba bean cultivation might have mitigated the concentration of bumblebees on highly attractive SNH through the provisioning of an alternative resource. In addition to common grassland species, woody plant species were frequently used by our wild bees (Rosaceae in run 1), emphasizing their importance as wild bee forage plants (Leidenfrost et al. 2020, Kämper et al. 2016). While SNH flower cover was the most important determinant for non-Bombus wild bee densities recorded in the respective SNH, the cover of SNH had no effect on wild bees. However, when investigating wild bees outside SNH, such as field margins or crop fields, SNH cover has been shown to be an important driver of wild bee densities (Beyer et al. 2020; Nayak et al. 2015). Wild bees have been shown to shift between different crop and non-crop habitats in agricultural landscapes according to their flowering phenology and changing resource availability (Mandelik et al. 2012). Similarly, local floral resource availability drove wild bees in our study. However, only bumblebees but not non-*Bombus* wild bees were additionally affected by landscape metrics, which might be explained by the larger foraging ranges of bumblebees compared to smaller and less mobile solitary bees (Greenleaf et al. 2007).

In addition to the local flower cover within SNH, landscape diversity enhanced wild bee species richness. More complex landscapes might offer more diverse nesting and foraging habitats supporting diverse pollinator communities with different resource requirements (Perović et al., 2015; Shackelford et al., 2013). Our study provides important evidence that diverse and flower-rich landscapes are prerequisites to promote and conserve species-rich pollinator communities in often species-poor agricultural landscapes.

Contrary to our expectations, the cover of OSR did neither affect bumblebee, non-*Bombus* wild bee densities, nor wild bee species richness. OSR has been shown to be beneficial for wild bees (Diekötter et al. 2014; Westphal et al. 2003). Nevertheless, Westphal et al. (2009) showed that early positive effects on bumblebee colonies do not translate into a higher colony reproductive success later in the season. Similarly, the early resources provided by OSR in our study did not affect wild bees in SNH. Our sampling started after most OSR fields had ceased blooming in mid-May. Thus, a possible boost through an early resource pulse in April did not translate into persistent effects in our wild bee communities.

Functional trait composition of wild bee communities

All wild bees

Faba bean cultivation affected the proportion of social bees and of faba bean foragers in SNH, depending on the sampling time. While we observed higher proportions in control than in bean landscapes when faba beans were in full bloom, the effect was reversed afterwards as also shown in Beyer et al. (2020). While a higher proportion of social bees might result from an increase of social bees or a decrease of solitary bees or both, those effects were probably driven by bumblebees, the most dominant group of social bees in our study landscapes. They are known to frequently forage on Fabaceae (Somme et al. 2015) and are attracted by mass-flowers (Walther-Hellwig and Frankl 2000). Most of them were likely to forage in faba bean fields instead of SNH, where we sampled, when beans were blooming. Such dilution effects driven by MFC have been already shown for OSR and might lead to diminishing pollination services for less attractive wild plant populations (Holzschuh et al. 2016). Similar effects are conceivable concerning faba bean flowering, pulling social bees away from SNH during their blooming period with possible negative implications for wild Fabaceae populations that are adapted and dependent on bumblebee pollinators. After the flowering of *V. faba*, we observed a higher proportion of social bees and Fabaceae foragers in bean than in control landscapes. This indicates that faba bean cultivation generally promotes social bees and bees foraging on Fabaceae. Again, this effect might be driven by the bumblebees through an enhanced colony growth facilitated by the additional resources provided by beans in June, as already shown for later flowering crops (Rundlöf et al. 2014).

High amounts of OSR in the surrounding landscape had a slightly negative effect on the proportion of social bees in wild bee communities found in SNH. OSR is visited by a variety of different pollinator groups, with solitary wild bees as most effective pollinators (Woodcock et al. 2013). Solitary bees, which are known to be promoted by OSR (Diekötter et al. 2014; Jauker et al. 2012) might have benefited more than social bees, like bumblebees, which are associated with Fabaceae (Goulson et al. 2005). Our results indicate that high covers of OSR can modify the functional trait composition of wild bee communities in terms of sociality with resulting effects on the community composition.

In contrast to faba beans that enhanced the proportion of social bees and Fabaceae foragers, oilseed rape promoted solitary wild bees. Consequently, a single species of MFC cannot conserve functionally diverse wild bee communities in agricultural landscapes. Biodiversity conservation measures should therefore aim at increasing crop diversity, which is already one of the three CAP greening practices, farmers receive payments for. The introduction of the crop diversification measure in fact might have led to a decreased cultivation of common cereals in favor of an increased cultivation area of rape, sunflower and leguminous crops in 2015 (European Commission 2017). Nevertheless, agricultural management should also target the cultivation of morphologically different MFC to increase functional farmland plant diversity, which enhances pollinator diversity (Sutter et al. 2017).

Bumblebees

In addition to higher bumblebee densities, there was a slight tendency of enhanced proportions of long-tongued bumblebees in faba bean compared to control landscapes. Additionally, we found enhanced densities of *B. pascuorum* in bean landscapes, which was the most dominant species of the long-tongued bumblebees (more than 80 %) in our study sites. Thus, faba bean cultivation promotes particularly long-tongued bumblebee species. Long-tongued bumblebees have been shown to be most effective faba bean pollinators, while short-tongued species often rob nectar by biting holes into the corolla base (Bond and Poulsen 1983; Marzinzig et al. 2018). Many long-tongued bumblebee species are threatened and the decrease of bumblebee forage plants, especially legumes, during the last decades has been postulated as a reason for their decline (Goulson et al. 2005). Most long-tongued bumblebee species emerge late (May/June) in contrast to the early emerging short-tongued bumblebees (Goulson et al. 2005). Likewise, we found highest proportions of long-tongued bumblebees in the latest run from mid-July to mid-August. Dietary specialization, a long tongue and a late emergence time have been related to rarity in bumblebees (Goulson et al. 2005). Hence, the cultivation of faba beans could help to promote rare long-tongued bumblebee species, for which the faba bean provides valuable resources for colony establishment.

An increasing local flower cover led to higher proportions of short-tongued bumblebees. Short-tongued bumblebee species are known to be particularly attracted by mass-flowers (Walther-Hellwig and Frankl 2000) which explains their dominance in bumblebee communities when flower cover of SNH was high. The cover of OSR did not affect the functional composition of the bumblebee communities. Contrary, Diekötter et al. (2010) found decreased densities of long-tongued bumblebees with increasing amounts of OSR in the landscape. This pattern probably arose from competition effects through short-tongued bumblebees, which strongly profited from OSR, leading to higher rates of nectar robbing on red clover (Diekötter et al. 2010).

We found bumblebees to have higher mean sizes in faba bean compared to control landscapes when local flower cover of SNH was low. Faba beans provided additional resources in simplified agricultural landscapes, from which bumblebee colonies were likely to benefit (Knight et al. 2009). Bumblebees in complex landscapes with more floral resources have been shown to be larger than in simple landscapes (Persson and Smith 2011) since fewer resources result in smaller offspring (Oliveira et al. 2016; Radmacher and Strohm 2010). Another explanation might be that bigger bumblebees have proportional longer tongues and can apply more force, which is required to access the *V. faba* flower rewards (Bailes et al. 2018). The improved resource exploitation of big bumblebees is likely to have driven their dominance of the community. However, when local flower cover of SNH increased, the difference between bean and control landscapes regarding mean bee size disappeared. If bumblebees were resource limited in our study landscapes, more flower-rich SNH were likely to enable a bigger worker size through increased nectar and pollen supply, explaining increasing ITD of bumblebees in control landscapes. Accordingly, Grab et al. (2019) showed that the provisioning of floral resources can buffer against a decrease of bee body sizes due to the simplification of landscapes. Contrary, mean bumblebee size in faba bean landscapes decreased with increasing SNH flower cover. Increased alternative resource availability probably compensated for the dominance of big bumblebees, benefiting from faba beans and exerting competitive pressure on smaller bees. Potential wild bee functional trait composition changes driven by faba beans are therefore likely to be mitigated by a high floral resource supply of SNH, i.e. heterogenous, resource-rich landscapes.

Conclusions

Our study shows that the identity of MFC moderates functional trait compositions of pollinator communities. Different MFC promote different functional groups of wild bees and the dominance of one MFC cannot conserve diverse pollinator communities. High OSR covers shifted bee communities towards a higher proportion of solitary wild bees. Faba bean cultivation enhanced bumblebee densities at landscape-scale and filtered for functional traits associated with Fabaceae. Social wild bees, bees foraging on Fabaceae and long-tongued bumblebee species were promoted. Increased floral resource availability can buffer against changes of the functional trait composition regarding bumblebee size, caused by a dominance of faba beans in resource-poor landscapes. It is already known that the loss of suitable foraging and nesting habitats in simplified agricultural landscapes results in a functional homogenization of insect communities (Gámez-Virués et al. 2015; Perović et al. 2015). Since crop yields are positively correlated with functional pollinator diversity (Garibaldi et al 2015; Woodcock et al. 2019), it is desirable to conserve diverse pollinator communities, which requires a high landscape heterogeneity (Perović et al. 2015; Steckel et al. 2014) and a high functional diversity of farmland plants (Sutter et al. 2017). Farmland floral resources can be provided by either promoting SNH or by the cultivation of MFC and both approaches have already been shown to benefit pollinators (e.g. Diekötter et al. 2014; Westphal et al. 2003). Biodiversity conservation measures should therefore include both, off-field practices targeting SNH as well as on-field practices aiming at crop diversification, especially with respect to flowering crops with various flower morphologies. A high crop and landscape diversity, combined with a high quantity and quality of SNH can help to promote common crop pollinators, to conserve functional diverse pollinator communities and to ultimately secure crop yields.

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Autor contributions

CW conceived the study and supervised the project; NB and FK implemented the study sites; FK collected the data; NB performed data analyses with support of FK and advice of DG and CW; NB wrote the first manuscript draft. All authors contributed critically and gave final approval for publication.

References

Amiet F, Herrmann M, Müller A, Neumeyer R (2007) Apidae 5. *Ammobates, Ammobatoides, Anthophora, Biastes, Ceratina, Dasypoda, Epeoloides, Epeolus, Eucera, Macropis, Melecta, Melitta, Nomada, Pasites, Tetralonia, Thyreus, Xylocopa*. Fauna Helvetica 20. CSCF and SEG, Neuchâtel.

Amiet F, Müller A, Neumeyer R (2014) Apidae 2. *Colletes, Dufourea, Hylaeus, Nomia, Nomioides, Rhophitoides, Rophites, Sphecodes, Systropha.* Fauna Helvetica 4. CSCF and SEG, Neuchâtel.

Amiet F, Müller A, Neumeyer R (2001) Apidae 3. *Halictus, Lasioglossum*. Fauna Helvetica 6. CSCF and SEG, Neuchâtel.

Bailes EJ, Pattrick JG, Glover BJ (2018) An analysis of the energetic reward offered by field bean (Vicia faba) flowers: Nectar, pollen, and operative force. Ecology and Evolution 8: 3161–3171. https://doi.org/10.1002/ece3.3851

Barton K (2019) MuMIn: Multi-Model Inference. R package version 1.43.6

Bartual AM, Sutter L, Bocci G, Moonen AC, Cresswell ME, Giffard B, Jacot K, Jeanneret P, Holland J, Pfister S, Pintér O, Veromann E, Winkler K, Albrecht M (2019) The potential of different semi-natural habitats to sustain pollinatiors and natural enemies in European agricultural landscapes. Agric Ecosyst Environ 279: 43-52. https://doi.org/10.1016/j.agee.2019.04.009

Beyer N, Gabriel D, Kirsch F, Schulz-Kesting K, Dauber J, Westphal C (2020) Functional groups of wild bees respond differently to faba bean *Vicia faba* L. cultivation at landscape scale. J. Appl. Ecol. 57: 2499-2508. https://doi.org/10.1111/1365-2664.13745Bond DA, Poulsen MH (1983) Pollination. In: Hebblethwaite PD (ed) The Faba Bean (*Vicia faba* L.). Butterworths, London, pp 77-101

Brooks ME, Kristensen K, van Benthem K, Koen J, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Machler M, Bolker BM (2017) glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. The R Journal 9: 378–400. https://doi.org/10.3929/ethz-b-000240890

Burnham KP, Anderson DR (2002) Model Selection and Multimodel Inference. A Practical Information-Theoretic Approach, 2nd edn. Springer-Verlag

Dainese M, Martin EA, Aizen MA et al (2019) A global synthesis reveals biodiversity-mediated benefits for crop production. Science Advances 5: eaax0121

Destatis. Statistisches Bundesamt. https://www.destatis.de/DE/Themen/Branchen-Unternehmen/Landwirtschaft-Forstwirtschaft-Fischerei/Flaechennutzung/_inhalt.html. Accessed 14 May 2020

Diekötter T, Kadoya T, Peter F, Wolters V, Jauker F (2010) Oilseed rape crops distort plant-pollinator interactions. J Appl Ecol 47: 209–214. https://doi.org/10.1111/j.1365-2664.2009.01759.x

Diekötter T, Peter F, Jauker B, Wolters V, Jauker F (2014) Mass-flowering crops increase richness of cavity-nesting bees and wasps in modern agro-ecosystems. GCB Bioenergy 6: 219–226. https://doi.org/10.1111/gcbb.12080

European Commission (2017) Evaluation study of the payment for agricultural practices beneficial for the climate and the environment - Final Report. European Commission, Brussels.

Fox J, Weisberg S (2019) An R Companion to Applied Regression, 3rd edn. Sage, Thousand Oaks CA. http://tinyurl.com/carbook.

Gámez-Virués S, Perović DJ, Gossner MM, Börschig C, Blüthgen N, de Jong H, Simons NK, Klein AM, Krauss J, Maier G, Scherber C, Steckel J, Rothenwöhrer C, Steffan-Dewenter J, Weiner CN, Weisser W, Werner M, Tscharntke T, Westphal C (2015) Landscape simplification filters species traits and drives biotic homogenization. Nature Communications: 6. https://doi.org/10.1038/ncomms9568

Garibaldi LA, Bartomeus I, Bommarco R et al (2015) Trait matching of flower visitors and crops predicts fruit set better than trait diversity. J Appl Ecol 52: 1436–1444. https://doi.org/10.1111/1365-2664.12530

Garratt MPD, Coston DJ, Truslove CL, Lappage MG, Polce C, Dean R, Potts SG (2014) The identity of crop pollinators helps target conservation for improved ecosystem services. Biological Conservation 169: 128–135. https://doi.org/10.1016/j.biocon.2013.11.001

Goulson D, Hanley ME, Darvill B, Ellis JS, Knight ME (2005) Causes of rarity in bumblebees. Biological Conservation 122: 1–8. https://doi.org/10.1016/j.biocon.2004.06.017

Grab H, Brokaw J, Anderson E, Gedlinske L, Gibbs J, Wilson J, Loeb G, Isaacs R, Poveda K (2019) Habitat enhancements rescue bee body size from the negative effects of landscape simplification. J Appl Ecol 56: 2144–2154. https://doi.org/10.1111/1365-2664.13456

Greenleaf SS, Williams NM, Winfree R, Kremen C (2007) Bee foraging ranges and their relationship to body size. Oecologia 153: 589–596. https://doi.org/10.1007/s00442-007-0752-9

Hanley ME, Franco M, Dean CE, Franklin EL, Harris HR, Haynes AG, Rapson SR, Rowse G, Thomas C, Waterhouse BR, Knight ME (2011) Increased bumblebee abundance along the margins of a mass flowering crop: Evidence for pollinator spill-over. Oikos 120: 1618–1624. https://doi.org/10.1111/j.1600-0706.2011.19233.x

Holzschuh A, Dainese M, González-Varo JP, Mudri-Stojnić S, Riedinger V, Rundlöf M, Scheper J, Wickens JB, Wickens VJ, Bommarco R, Kleijn D, Potts SG, Roberts SPM, Smith HG, Vilà M, Vujić A, Steffan-Dewenter I (2016) Mass-flowering crops dilute pollinator abundance in agricultural landscapes across Europe. Ecol Lett 19: 1228–1236. https://doi.org/10.1111/ele.12657

IPBES (2019) Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. Díaz S, Settele ES, Ngo HT (eds) IPBES Secretariat Bonn, Germany

Jauker F, Bondarenko B, Becker HC, Steffan-Dewenter I (2012) Pollination efficiency of wild bees and hoverflies provided to oilseed rape. Agric For Entomol 14: 81–87. https://doi.org/10.1111/j.1461-9563.2011.00541.x

Kallioniemi E, Åström J, Rusch GM, Dahle S, Åström S, Gjershaug JO (2017) Local resources, linear elements and mass-flowering crops determine bumblebee occurrences in moderately intensified farmlands. Agric Ecosyst Environ 239: 90–100. https://doi.org/10.1016/j.agee.2016.12.039

Kämper W, Werner PK, Hilpert A, Westphal C, Blüthgen N, Eltz T, Leonhardt SD (2016) How landscape, pollen intake and pollen quality affect colony growth in Bombus terrestris. Landscape Ecol 31: 2245-2258. https://doi.org/10.1007/s10980-016-0395-5

Knight ME, Osborne JL, Sanderson RA, Hale RJ, Martin AP, Goulson D (2009) Bumblebee nest density and the scale of available forage in arable landscapes. Insect Conserv Divers 2: 116–124. https://doi.org/10.1111/j.1752-4598.2009.00049.x

Kremen C, Williams NM, Aizen MA et al (2007) Pollination and other ecosystem services produced by mobile organisms: A conceptual framework for the effects of land-use change. Ecol Lett 10: 299–314. https://doi.org/10.1111/j.1461-0248.2007.01018.x

Laliberté E, Legendre P (2010) A distance-based framework for measuring functional diversity from multiple traits. Ecology 91: 299–305.

Leidenfrost RM, Bänsch S, Prudnikow L, Brenig B, Westphal C, Wünschiers R (2020) Analyzing the Dietary Diary of Bumble Bee. Frontiers in Plant Science 11: 1–9. https://doi.org/10.3389/fpls.2020.00287

Lenth R (2019) emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.4.1. https://CRAN.R-project.org/package=emmeans

Link WA, Barker RJ (2006) Model weights and the foundations of multimodel inference. Ecology 87: 2626–2635. https://doi.org/10.1890/0012-9658(2006)87[2626:MWATFO]2.0.CO;2

Mauss V (1994) Bestimmungsschlüssel für HUMMELN, 5th edn. Deutscher Jugendbund für Naturbeobachtung, Hamburg

Mandelik Y, Winfree R, Neeson T, Kremen C (2012) Complementary habitat use by wild bees in agro-natural landscapes. Ecol Appl 22: 1535–1546. https://doi.org/10.1890/11-1299.1

Marzinzig B, Brünjes L, Biagioni S, Behling H, Link W, Westphal C (2018) Bee pollinators of faba bean (Vicia faba L.) differ in their foraging behaviour and pollination efficiency. Agric Ecosyst Environ 264: 24–33. https://doi.org/10.1016/j.agee.2018.05.003

Nayak GK, Roberts SPM, Garratt M, Breeze TD, Tscheulin T, Harrison-Cripps J, Vogiatzakis IN, Stirpe MT, Potts SG (2015). Interactive effect of floral abundance and semi-natural habitats on pollinators in field beans (*Vicia faba*). Agric Ecosyst Environ 199: 58–66. https://doi.org/10.1016/j.agee.2014.08.016

Oliveira MO, Freitas BM, Scheper J, Kleijn D (2016) Size and sex-dependent shrinkage of Dutch bees during one-and-a-half centuries of land-use change. PLoS ONE 11: 1–8. https://doi.org/10.1371/journal.pone.0148983

Perović D, Gámez-Virués S, Börschig C, Klein AM, Krauss J, Steckel J, Rothenwöhrer C, Erasmi S, Tscharntke T, Westphal C (2015) Configurational landscape heterogeneity shapes functional community composition of grassland butterflies. J Appl Ecol 52: 505–513. https://doi.org/10.1111/1365-2664.12394

Persson AS, Smith HG (2011) Bumblebee colonies produce larger foragers in complex landscapes. Basic Appl Ecol 12: 695–702. https://doi.org/10.1016/j.baae.2011.10.002

Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team (2019) nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-140. https://CRAN.R-project.org/package=nlme

Potts SG, Biesmeijer JC, Kremen C, Neumann P, Schweiger O, Kunin WE (2010) Global pollinator declines: Trends, impacts and drivers. Trends Ecol Evol 25: 345–353. https://doi.org/10.1016/j.tree.2010.01.007

Potts SG, Vulliamy B, Dafni A, Ne'eman G, Willmer P (2003) Linking bees and flowers: How do floral communities structure pollinator communities? Ecology 84: 2628–2642. https://doi.org/10.1890/02-0136

R Core Team (2019) R: A language and environment for statistical computing. Vienna, Austria, R Foundation for Statistical Computing

Radmacher S, Strohm E (2010) Factors affecting offspring body size in the solitary bee *Osmia bicornis* (Hymenoptera, Megachilidae). Apidologie 41: 169–177. https://doi.org/10.1051/apido/2009064

Raftery AE (1992) Bayesian Model Selection in Social Research. Sociological Methodology 25: 111-163.

Rundlöf M, Persson AS, Smith HG, Bommarc R (2014) Late-season mass-flowering red clover increases bumble bee queen and male densities. Biological Conservation 172: 138– 145. http://dx.doi.org/10.1016/j.biocon.2014.02.027

Schellhorn NA, Gagic V, Bommarco R (2015) Time will tell: Resource continuity bolsters ecosystem services. Trends Ecol Evol 30: 524–530. https://doi.org/10.1016/j.tree.2015.06.007

Scheper J, Reemer M, van Kats R, Ozinga WA, van der Linden GTJ, Schaminée JHJ, Siepel H, Kleijn D (2014) Museum specimens reveal loss of pollen host plants as key factor driving wild bee decline in The Netherlands. PNAS 111: 17552-17557. https://doi.org/10.1073/pnas.1412973111

Shackelford G, Steward PR, Benton TG, Kunin WE, Potts SG, Biesmeijer JC, Sait SM 2013) Comparison of pollinators and natural enemies: a meta-analysis of landscape and local effects on abundance and richness in crops. Biol. Rev. 88: 1002-1021. https://doi.org/10.1111/brv.12040

Somme L, Vanderplanck M, Michez D, Lombaerde I, Moerman R, Wathelet B, Wattiez R, Lognay G, Jacquemart AL (2015) Pollen and nectar quality drive the major and minor floral choices of bumble bees. Apidologie 46: 92–106. https://doi.org/10.1007/s13592-014-0307-0

Steffan-Dewenter I, Münzenberg U, Bürger C, Thies C, Tscharntke T (2002) Scale-dependent effects of landscape context on three pollinator guilds. Ecology 83: 1421–1432. https://doi.org/10.1890/0012-9658(2002)083[1421:SDEOLC]2.0.CO;2

Steckel J, Westphal C, Peters MK, Bellach M, Rothenwoehrer C, Erasmi S, Scherber C, Tscharntke T & Steffan-Dewenter I (2014) Landscape composition and configuration differently affect trap-nesting bees, wasps and their antagonists. Biological Conservation 172: 56-64.

Sutter L, Jeanneret P, Bartual AM, Bocci G, Albrecht M (2017) Enhancing plant diversity in agricultural landscapes promotes both rare bees and dominant crop-pollinating bees through complementary increase in key floral resources. J Appl Ecol 54: 1856–1864. https://doi.org/10.1111/1365-2664.12907

Timberlake TP, Vaughan IP, Memmott J (2019) Phenology of farmland floral resources reveals seasonal gaps in nectar availability for bumblebees. J Appl Ecol 56: 1585–1596. https://doi.org/10.1111/1365-2664.13403

Vanbergen AJ, The Insect Pollinators Initiative (2013). Threats to an ecosystem service: pressures on pollinators. Front Ecol Environ 11: 251-259

Wagenmakers EJ, Farrell S (2004) AIC model selection using Akaike weights. Psychonomic Bulletin and Review 11: 192–196. https://doi.org/10.3758/BF03206482

Walther-Hellwig K, Frankl R (2000) Foraging habitats and foraging distances of bumblebees, *Bombus* spp. (Hym., Apidae), in an agricultural landscape. J Appl Entomol 124: 299–306. https://doi.org/10.1046/j.1439-0418.2000.00484.x

Westphal C, Bommarco R, Carré G, Lamborn E, Morison N, Petanidou T, Potts SG, Roberts SPM, Szentgyörgyi H, Tscheulin T, Vaissière BE, Woyciechowski M, Biesmeijer JC, Kunin WE, Settele J, Steffan-Dewenter I (2008) Measuring bee diversity in different European habitats and biogeographical regions. Ecological Monographs 78: 653–671. https://doi.org/10.1890/07-1292.1

Westphal C, Steffan-Dewenter I, Tscharntke T (2003) Mass flowering crops enhance pollinator densities at a landscape scale. Ecol Lett 6: 961–965. https://doi.org/10.1046/j.1461-0248.2003.00523.x

Westphal C, Steffan-Dewenter I, Tscharntke T (2009) Mass flowering oilseed rape improves early colony growth but not sexual reproduction of bumblebees. J Appl Ecol 46: 187–193.

https://doi.org/10.1111/j.1365-2664.2008.01580.x

Westrich P (2018) Die Wildbienen Deutschlands, 1st edn. Eugen Ulmer Verlag, Stuttgart

Westrich P, Frommer U, Mandery K, Riemann H, Ruhnke H, Saure C, Voith J (2011) Rote Liste und Gesamtartenliste der Bienen (Hymenoptera, Apidae) Deutschlands. Naturschutz und Biologische Vielfalt 70: 373-416

Wickham H (2016) ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York. https://ggplot2.tidyverse.org.

Woodcock BA, Edwards M, Redhead J, Meek WR, Nuttall P, Falk, S, Nowakowski M, Pywell RF (2013) Crop flower visitation by honeybees, bumblebees and solitary bees: Behavioural differences and diversity responses to landscape. Agric Ecosyst Environ 171: 1–8. https://doi.org/10.1016/j.agee.2013.03.005

Woodcock BA, Garratt MPD, Powney GD et al (2019) Meta-analysis reveals that pollinator functional diversity and abundance enhance crop pollination and yield. Nature Communications 10: 1–10. https://doi.org/10.1038/s41467-019-09393-6

Supplementary material

Figures

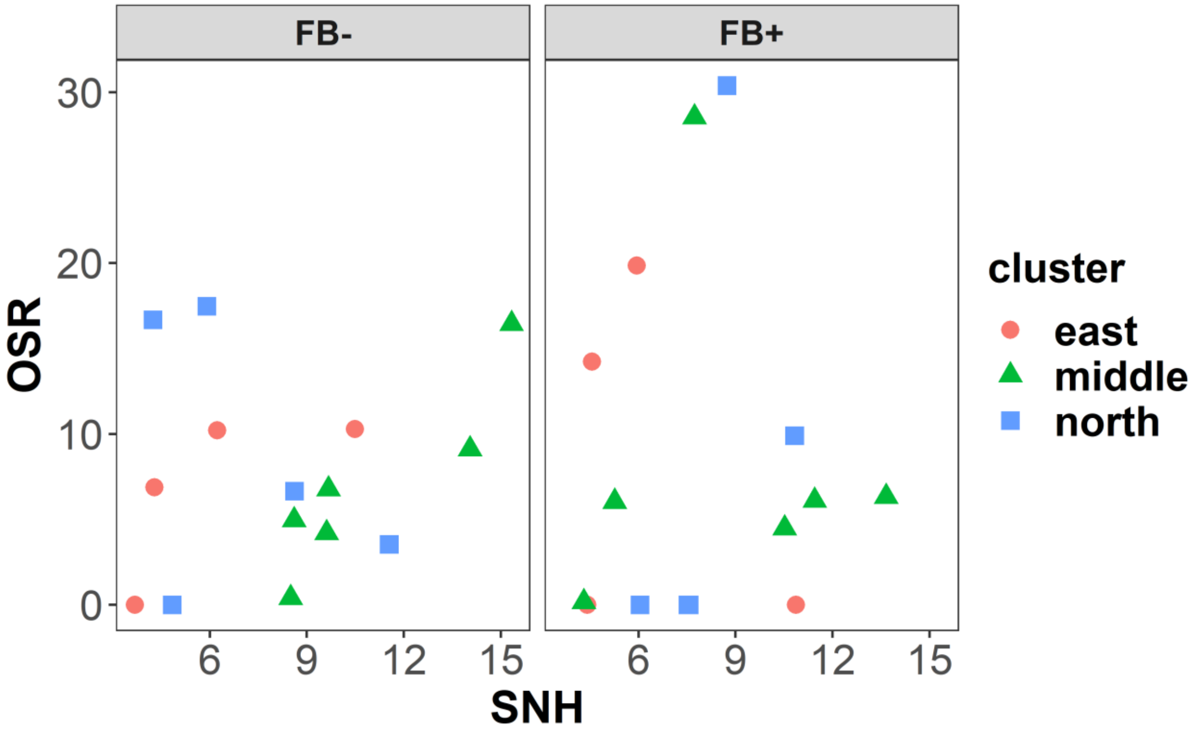

Figure S1 Scatterplot of explanatory variables: percentage cover of semi-natural habitats (SNH) and of oilseed rape (OSR) in our 30 paired study landscapes: 15 landscapes with faba bean cultivation (FB+) and 15 without (FB-). Landscapes were situated in three different regions of Germany: east (red circles), middle (green triangles) and north (blue squares) of Germany. Mean area of OSR of our study landscapes was 7.99 m^2 (min: 0.00 m^2, max: 30.38 m^2). Mean area of SNH was 8.17 m^2 (min: 3.68 m^2; max: 15.34 m^2).

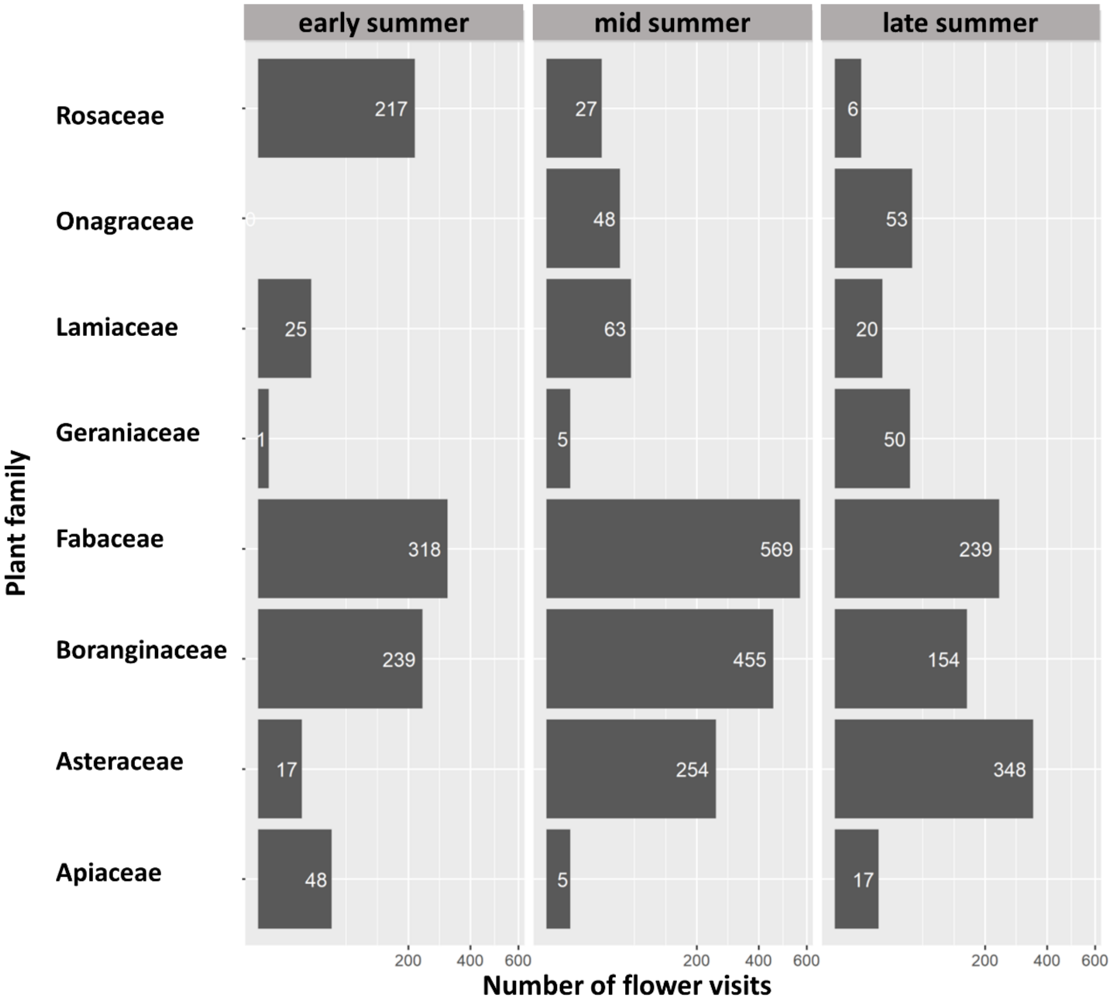

Figure S2 Number of observed flower visits on the eight most visited plant families for the three different sampling runs in early summer (22.05.-19.06.), mid-summer (22.06.-20.07.) and late summer (27.07.-22.08.). Note that x-axes are sqrt-transformed for graphical reasons. Common plant species / genus in the eight most visited plant families were for example: Fabaceae: *Cytisus scoparius, Lupinus polyphyllus, Medicago sativa, Trifolium incarnatum, Trifolium hybridum, Trifolium pratense, Trifolium repens*. Boraginaceae: *Borago officinalis, Echium vulgare, Phacelia tanacetifolia, Symphytum officinale, Myosotis spp.* Asteraceae: *Taraxacum officinale agg., Arctium tomentosum, Bellis perennis, Cichorium intybus, Helianthus annuus, Matricaria recutita, Tanacetum vulgare, Achillea spp., Cirsium spp.* Rosaceae: *Rubus idaeus, Rubus sect. Rubus, Rosa spp.* Lamiaceae: *Lamium album, Salvia pratensis, Stachys sylvatica*. Onagraceae: *Epilobium angustifolium*. Apiaceae: *Daucus carota, Heracleum sphondylium* . Geraniaceae: *Geranium spp.*

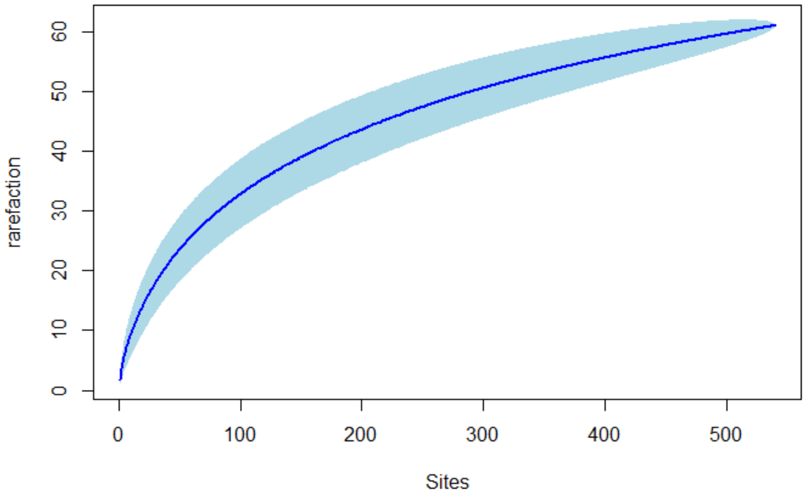

Figure S3 Rarefaction curve across all transects and study landscapes using the *specaccum* command of the vegan package (Oksanen et al. 2019).

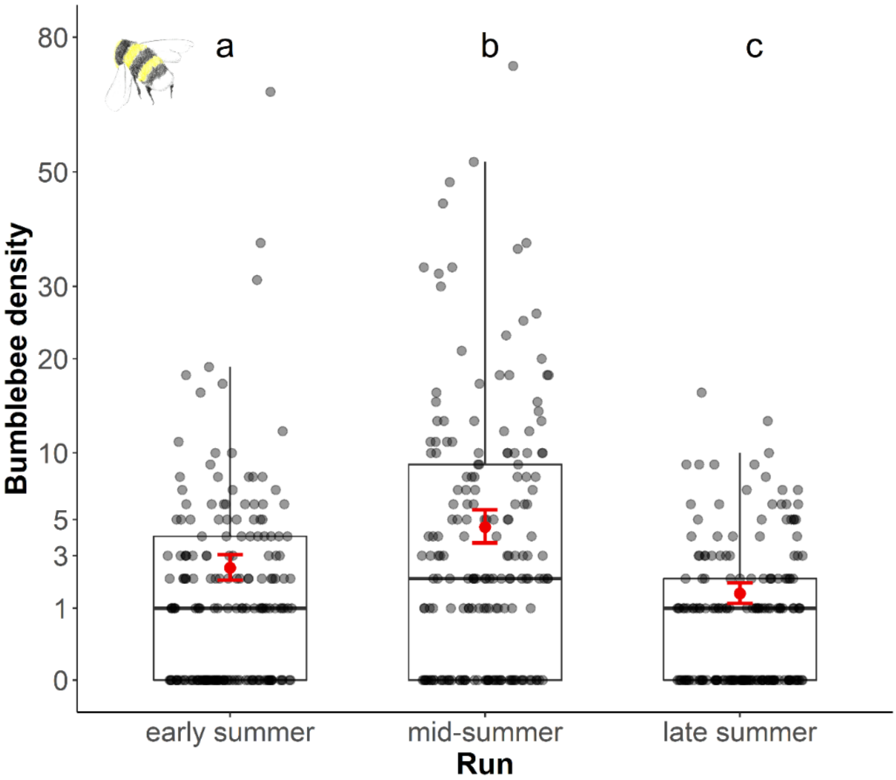

Figure S4 Effect of sampling run on the density of bumblebees. Predicted mean values and 95% confidence intervals are displayed in red. Different letters above boxplots indicate significant differences between runs. Predictions are based on the best model m.bb1 (Table 1). Y-axis is sqrt-transformed for graphical reasons.

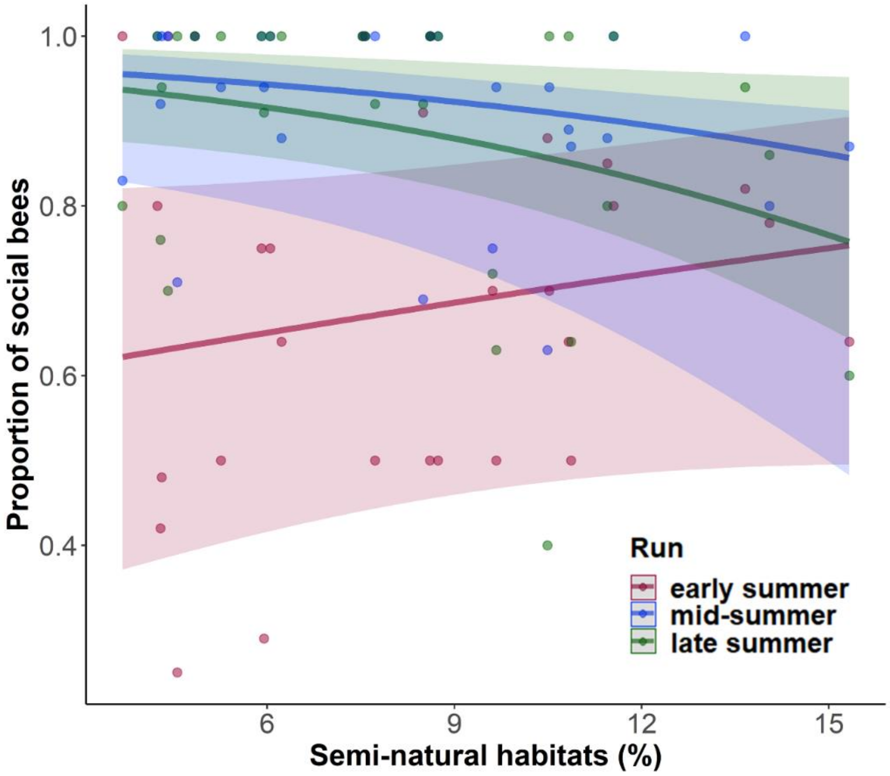

Figure S5 Effect of percentage semi-natural habitats on the proportion of social bees for the different sampling runs in early, mid and late summer. Predicted mean values and 95% confidence intervals are displayed. Predictions are based on the third-best fitting model m.s3 (Table 1).

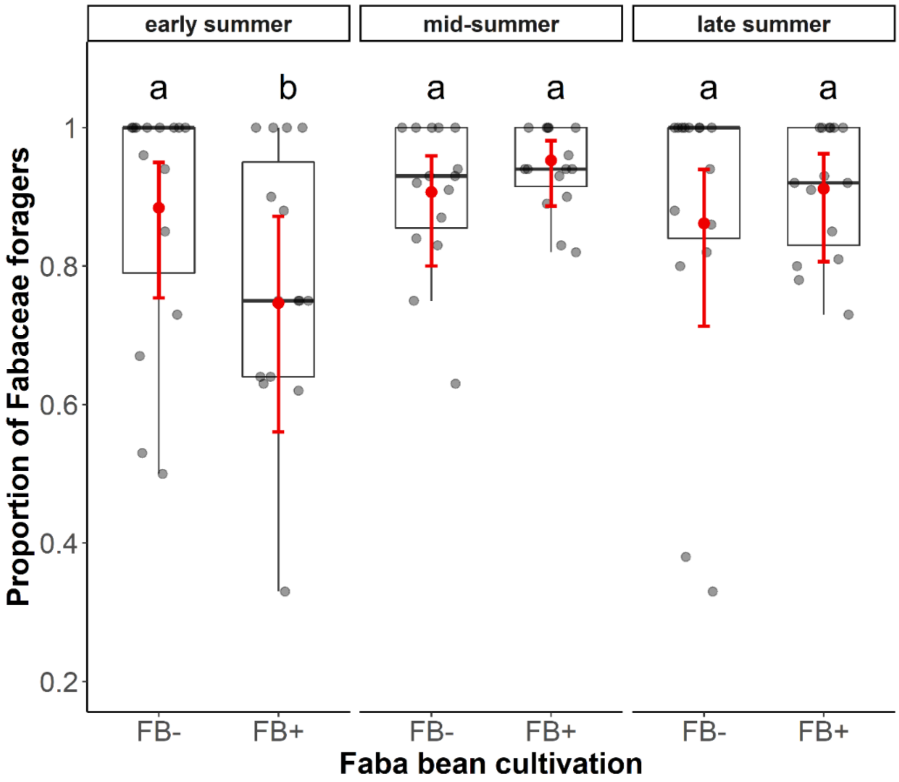

Figure S6 Effect of faba bean cultivation on the proportion of Fabaceae foragers for the three different sampling runs in early, mid and late summer. Different letters above boxplots indicate significant differences between faba bean (FB+) and control

(FB-) landscapes within each run. Predicted mean values and 95% confidence intervals are displayed in red. Predictions are based on the best fitting model m.l1 (Table 1).

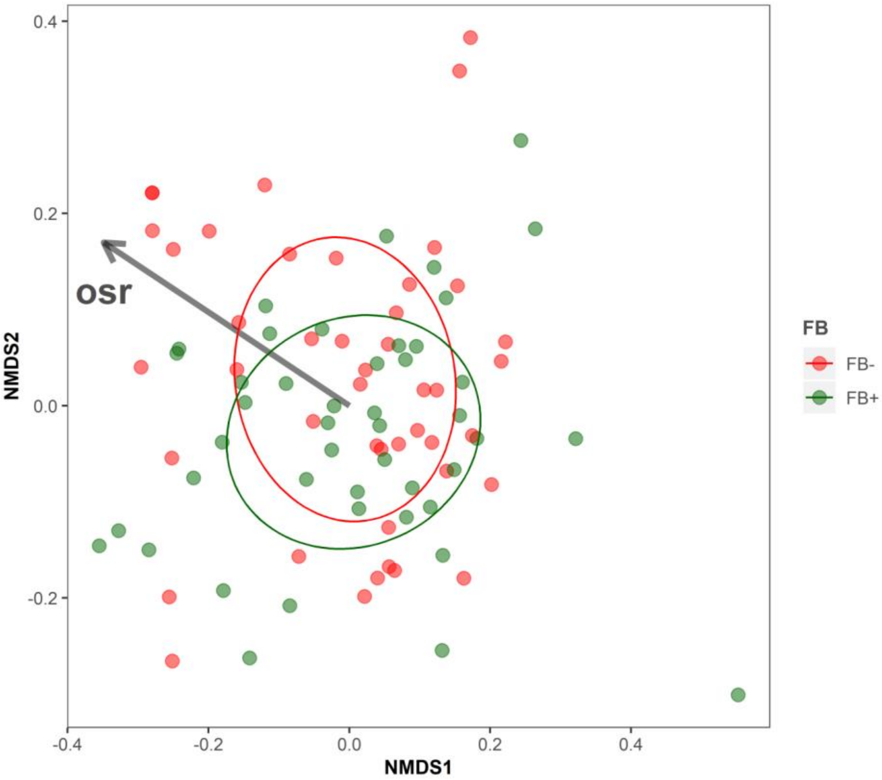

Figure S7 Changes of bee communities due to mass-flowering crop cultivation. Non-metric multidimensional scaling (NMDS) using the *metaMDS* and *envfit* functions of the vegan package (Oksanen et al. 2019) and Bray-Curtis distance was used to visualize the results of the PERMANOVA (see Table S9). Red points and ellipse show communities of landscapes without faba bean cultivation (FB-) and green points and ellipse communities of landscapes with faba bean cultivation (FB+). Each point represents one study landscape per sampling run. The vector shows direction of the landscape metrics oilseed rape (osr) cover.

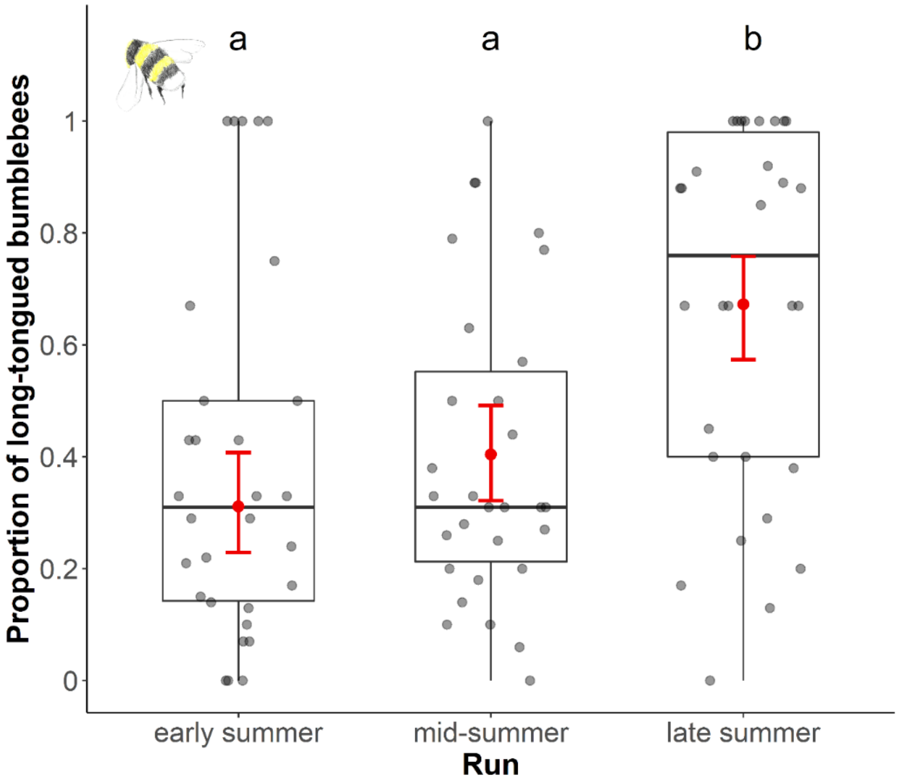

Figure S8 Effect of sampling run on the proportion of long-tongued bumblebees. Predicted mean values and 95% confidence intervals are displayed in red. Different letters above boxplots indicate significant differences between runs. Predictions are based on the second-best model m.ltb2 (Table 1). Y-axis is sqrt-transformed for graphical reasons.

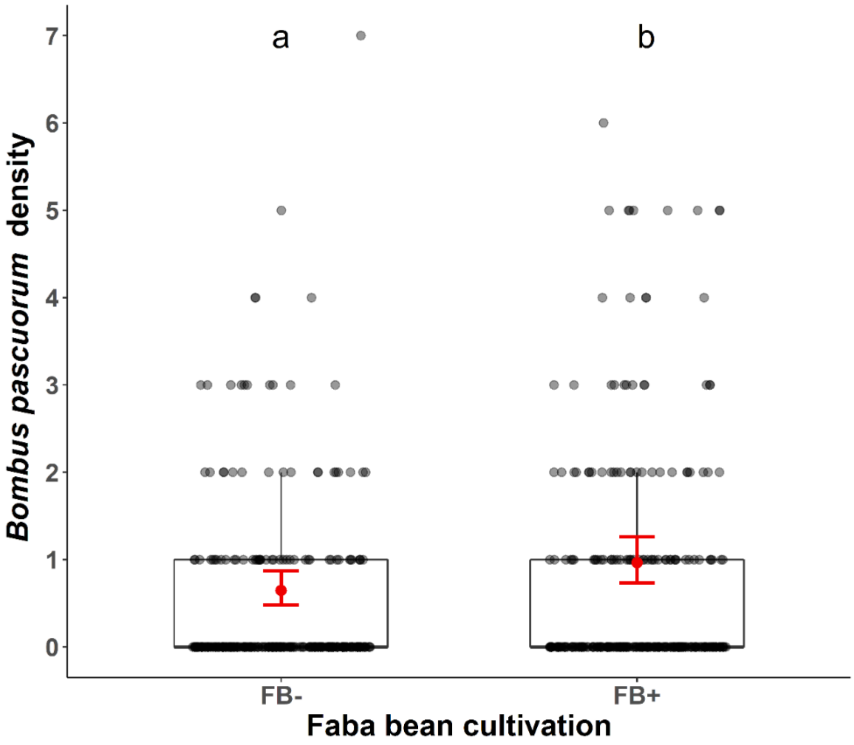

Figure S9 Effect of faba bean cultivation on *Bombus pascuorum* densities. Predicted mean values and 95% confidence intervals are displayed in red. Different letters above boxplots indicate significant differences between runs. Predictions are based on the first-best model.

Tables

Table S1 Definitions of all grassy and woody habitat types considered as semi-natural habitat (SNH) in our study.

Habitat type	**Habitat category**	**Definition**
Hedge	woody	Linear woody structure; mainly shrubs; longer than wide; width ≤ 10 m
Grove	woody	Areal woody structure; mainly trees; width > 10 m; not part of a larger forest patch but isolated in the arable matrix
Forest edges	woody	5 m wide strip; extends 2.5 m into and covers 2.5 m in front of a larger forest patch
Succession site	woody	Areal habitat in a progressed state of succession; emerging shrubs covers most of the area
Flower strip	grassy	Linear or areal habitat with flowering plants sown as an agri-environmental measurement
Extensive grassland / calcareous grassland	grassy	Areal habitat; diverse, flower-rich and extensively managed grassland; no shrubs present
Orchard meadows	grassy	Grass-dominated areal habitat with a stand of old fruit trees; extensively managed or abandoned
Fallows	grassy	Areal fallow land; dominated by naturally occurring pioneer vegetation (e.g. *Cirium spp.; Arctium spp.; Urtica dioica; Atriplex spp.)*
Succession site	grassy	Areal habitat in an initial state of succession; emerging shrubs are present but grassy vegetation still dominating most of the area
Grass-clover leys	grassy	Areal habitat cultivated with a flower-rich grass-legume mix; mostly *Trifolium spp.* but also other legumes like *Medicago sativa*

Table S2 Number of transects per semi-natural habitat category (grassy/woody) for every landscape and sampling run (early/mid/late summer). Woody habitat category includes hedges, groves, forest edges, woody succession sites. The grassy habitat category includes flower strips, extensive and calcareous grasslands, orchard meadows, fallows, grassy succession sites, grass/clover leys. Two landscape pairs lacked woody habitat structures and all transects had to be assigned to grassy habitats. For the first run, the number of transects per habitat category for certain landscapes was not balanced (numbers in bold). l. pair = landscape pair ID; FB = faba bean cultivation

			early summer			mid summer			late summer		
region	**l. pair**	**FB**	**grassy**	**woody**	**total**	**grassy**	**woody**	**total**	**grassy**	**woody**	**total**
east	3	FB-	3	3	6	3	3	6	3	3	6
east	3	FB+	3	3	6	3	3	6	3	3	6
east	4	FB-	**4**	**2**	6	3	3	6	3	3	6
east	4	FB+	**4**	**2**	6	3	3	6	3	3	6
east	15	FB-	**2**	**4**	6	3	3	6	3	3	6
east	15	FB+	**2**	**4**	6	3	3	6	3	3	6
east	16	FB-	**2**	**4**	6	3	3	6	3	3	6
east	16	FB+	3	3	6	3	3	6	3	3	6
middle	9	FB-	**4**	**2**	6	3	3	6	3	3	6
middle	9	FB+	**4**	**2**	6	3	3	6	3	3	6
middle	10	FB-	**4**	**2**	6	3	3	6	3	3	6
middle	10	FB+	**2**	**4**	6	3	3	6	3	3	6
middle	11	FB-	**2**	**4**	6	3	3	6	3	3	6
middle	11	FB+	**4**	**2**	6	3	3	6	3	3	6
middle	12	FB-	**2**	**4**	6	3	3	6	3	3	6
middle	12	FB+	3	3	6	3	3	6	3	3	6
middle	13	FB-	3	3	6	3	3	6	3	3	6
middle	13	FB+	3	3	6	3	3	6	3	3	6
middle	14	FB-	**4**	**2**	6	3	3	6	3	3	6
middle	14	FB+	**4**	**2**	6	3	3	6	3	3	6

north	1	FB-	3	3	6	3	3	6	3	3	6
north	1	FB+	3	3	6	3	3	6	3	3	6
north	2	FB-	**6**	**0**	6	**6**	**0**	6	**6**	**0**	6
north	2	FB+	**6**	**0**	6	**6**	**0**	6	**6**	**0**	6
north	7	FB-	3	3	6	3	3	6	3	3	6
north	7	FB+	3	3	6	3	3	6	3	3	6
north	23	FB-	3	3	6	**6**	**0**	6	**6**	**0**	6
north	23	FB+	**6**	**0**	6	**6**	**0**	6	**6**	**0**	6
north	24	FB-	3	3	6	3	3	6	3	3	6
north	24	FB+	3	3	6	3	3	6	3	3	6

Table S3 Density and functional traits of all 66 collected wild bee species. ITD: measured mean intertegular distance; foraging preference: species known to collect pollen from Fabaceae (1) or not known to do so (0). Sociality: Social species (1) or solitary species (0). Foraging preference and Sociality data is from Westrich (2018). Note that *Bombus terrestris* complex includes the following species: *Bombus terrestris*, B*. lucorum, B. cryptarum* and *B. magnus*.

species	density	ITD	foraging preference	sociality
Andrena bicolor Fabricius 1775	1	2.10	0	0
Andrena carantonica Pérez 1902	4	2.98	0	0
Andrena chrysosceles (Kirby 1802)	10	2.04	0	0
Andrena cineraria (Linnaeus 1758)	8	2.94	0	0
Andrena coitana (Kirby 1802)	1	1.70	0	0
Andrena flavipes Panzer 1799	22	2.50	1	0
Andrena fucata Smith 1847	1	2.60	0	0
Andrena fulva (Müller 1766)	1	2.95	0	0
Andrena fulvida Schenck 1983	2	2.55	1	0
Andrena haemorrhoa (Fabricius 1781)	15	2.44	0	0
Andrena helvola (Linnaeus 1758)	2	2.30	0	0
Andrena labiata Fabricius 1781	2	2.30	0	0
Andrena lathyri Alfken 1899	5	2.44	1	0
Andrena minutula (Kirby 1802)	13	1.38	0	0
Andrena nigroaenea (Kirby 1802)	28	2.98	1	0
Andrena nitida (Müller 1776)	7	2.90	0	0
Andrena nitidiuscula Schenck 1853	2	NA	1	0
Andrena ovatula (Kirby 1802)	7	2.20	1	0
Andrena proxima (Kirby 1802)	5	1.90	0	0
Andrena viridescens Viereck 1916	2	1.55	0	0
Anthidium manicatum (Linnaeus 1758)	1	3.50	1	0
Anthophora furcata (Panzer 1798)	1	3.40	0	0
Anthophora plumipes (Pallas 1772)	1	3.70	1	0
Bombus bohemicus (Seidl 1837)	10	NA	NA	NA
Bombus hortorum (Linnaeus 1761)	29	4.20	1	1
Bombus hypnorum (Linnaeus 1758)	10	3.64	1	1
Bombus lapidarius (Linnaeus 1758)	164	3.70	1	1
Bombus muscorum (Linnaeus 1758)	18	3.84	1	1
Bombus pascuorum (Scopoli 1763)	328	4.02	1	1
Bombus pratorum (Linnaeus 1761)	36	3.60	1	1
Bombus ruderarius (Müller 1765)	1	3.42	1	1
Bombus rupestris (Fabricius 1793)	8	NA	NA	NA
Bombus sylvarum (Linnaeus 1761)	10	3.20	1	1
Bombus sylvestris (Lepeletier 1832)	1	NA	NA	NA
Bombus terrestris (Linnaeus 1758) complex	399	3.90	1	1
Chelostoma campanularum (Kirby 1802)	4	NA	0	0
Chelostoma florisomne (Linnaeus 1758)	4	2.05	0	0
Chelostoma rapunculi (Lepeletier 1841)	2	1.65	0	0
Colletes daviesanus Smith 1846	2	2.30	0	0
Dasypoda hirtipes (Fabricius 1793)	1	2.90	0	0

Eucera longicornis Linnaeus 1758	1	3.60	1	0
Eucera nigrescens Perez 1879	2	3.45	1	0
Halictus quadricinctus (Fabricius 1776)	1	2.85	0	0
Halictus rubicundus (Christ 1791)	4	2.12	1	1
Halictus scabiosae (Rossi 1790)	15	2.52	0	0
Halictus simplex Blüthgen 1923	4	1.94	0	0
Halictus tumulorum (Linnaeus 1758)	11	1.42	1	1
Hylaeus communis Nylander 1852	4	1.28	0	0
Hylaeus confusus Nylander 1853	3	1.46	1	0
Hylaeus gredleri Förster 1871	3	0.97	0	0
Hylaeus styriacus Förster 1871	1	NA	0	0
Lasioglossum calceatum (Scopoli 1763)	25	1.74	0	1
Lasioglossum fulvicorne (Kirby 1802)	1	1.35	0	0
Lasioglossum leucozonium (Schrank 1781)	4	1.98	0	0
Lasioglossum morio (Fabricius 1793)	3	1.03	0	1
Lasioglossum pauxillum (Schenck 1853)	70	1.12	1	1
Lasioglossum villosulum (Kirby 1802)	9	1.40	0	0
Megachile centuncularis (Linnaeus 1758)	2	3.60	1	0
Melitta haemorrhoidalis (Fabricius 1775)	1	NA	0	0
Melitta nigricans Alfken 1905	1	2.70	0	0
Nomada flavoguttata (Kirby 1802)	1	NA	NA	NA
Nomada furva Panzer 1798	2	NA	NA	NA
Osmia adunca (Panzer 1798)	3	2.80	0	0
Osmia bicolor (Schrank 1781)	1	2.80	1	0
Osmia bicornis (Linnaeus 1758)	1	3.20	1	0
Osmia parietina Curtis 1828	1	2.00	1	0

Table S4 Tongue length of bumblebee species. The length of the glossa was measured, starting from the end of the paraglossa. The number of measured bumblebee individuals per species is given, as well as their mean tongue length (TL), their mean intertegular distance (ITD) and their mean relative TL (tongue length divided by ITD) (to account for body size dependent tongue length variations). According to the mean relative TL, bumblebee species were categorized into short- and long-tongued. Species with a mean relative TL equal or higher 1.43 (the mean of all values) were assigned to the long-tongued category and species with a lower value to the short-tongued group. For all ITD and tongue measurements, we used a connected microscope and the Labscope Imaging Software (ZEISS).

species	number of bumblebees	mean TL	mean ITD	mean relative TL	TL category
B. hortorum	12	8.87	4.14	2.15	long
B. hypnorum	9	4.30	3.58	1.20	short
B. lapidarius	12	4.39	3.68	1.20	short
B. muscorum	7	5.66	3.79	1.49	long
B. pascuorum	12	5.58	3.84	1.47	long
B. pratorum	12	4.53	3.73	1.22	short
B. ruderarius	9	5.08	3.41	1.49	long
B. sylvarum	12	4.56	3.18	1.43	long
B. terrestris/lucorum	12	4.80	3.92	1.23	short

Table S5 The relative importance of explanatory variables expressed by Σw_i (sum of BIC weights) for models to explain the effects of the different landscape metrics on bee densities and species richness and functional traits of all wild bees and for bumblebees (best fitting models are shown in Table 1). Model parameters having $\Sigma w_i < 0.2$ for all response variables are not shown. FB: faba bean cultivation (FB+/FB-), run: sampling run (early/mid/late summer), FC: local flower cover of transect area, LD: landscape diversity, OSR: percentage of oilseed rape, SNH: percentage of semi-natural habitats, CWM ITD: community weighted means for bee size (intertegular distance).

Models	Response variable	FB	run	FC	LD	OSR	SNH	FB:run	run: SNH	FB:FC
	Pollinator densities and species richness									
m.bb	Bumblebee density	0.96	1.00	1.00	-	-	-	-	-	0.66
m.nb	Non-*Bombus* density	-	-	1.00	0.25	-	-	-	-	-
m.spr	Species richness of all wild bees	-	0.21	1.00	0.67	-	-	-	-	-
	Functional traits of all wild bees									
m.itd	CWM ITD	-	-	-	0.27	0.27	-	-	-	-
m.l	lecty	0.83	1.00	0.25	-	0.30	0.24	0.81	-	-
m.s	Sociality	0.99	1.00	0.34	0.27	0.32	0.40	0.98	0.24	
	Functional traits of Bombus									
m.ltb	Prop. long-tongued bb	0.40	1.00	1.00	-	0.25	-	-	-	-
m.itdb	CWM ITD Bombus	0.90	-	0.88	-	-	0.24	-	-	0.86

Table S6 Results of the best-fitting models (generalized linear mixed models and linear mixed effect models for the case of CWM ITD) explaining landscape (FB: faba bean cultivation; SNH: semi-natural habitat cover; OSR: oilseed rape cover), local flower cover (FC) and sampling time (run) effects on wild bee densities, wild bee species richness and functional trait composition of all wild bees and of bumblebees only. Estimates, Standard Error (Std.Error), lower and upper 95 % confidence intervals (lower CI/upper CI), z and p values are displayed. Note that for CWM ITD t-values instead of z-values are displayed. FB_FB+: landscapes with faba bean cultivation. run_mid.summer: second sampling run. run_late.summer: last sampling run. CWM ITD: community weighted means for bee size (intertegular distance). Information on BIC and BIC weights of best-fitting models are given in Table 1.

Response variable	Model	Explanatory variable	Estimate	Std.Error	lower CI	upper CI	z-value	P
Bumblebee density	*m.bb1*	FB_FB+	0.47	0.13	0.22	0.72	3.67	< 0.001
		FC	0.99	0.08	0.83	1.16	11.79	< 0.001
		run_mid.summer	0.60	0.15	0.31	0.90	4.08	< 0.001
		run_late.summer	-0.52	0.16	-0.83	-0.20	-3.24	< 0.001
		FB_FB+ x FC	-0.35	0.12	-0.60	-0.11	-2.82	< 0.01
		Intercept	0.52	0.13	0.26	0.77	3.98	< 0.01
	m.bb1	FB_FB+	0.41	0.12	0.17	0.66	3.32	< 0.001
		FC	0.84	0.06	0.72	0.96	13.68	< 0.001
		run_mid.summer	0.57	0.14	0.28	0.85	3.92	< 0.001
		run_late.summer	-0.55	0.16	-0.85	-0.24	-3.50	< 0.001
		Intercept	0.59	0.12	0.35	0.84	4.74	< 0.001
Non-Bombus density	*m.nb1*	FC	0.47	0.09	0.29	0.65	5.18	< 0.001
		Intercept	-0.58	0.64	-1.83	0.67	-0.91	0.36
Species richness of all wild bees	*m.spr1*	FC	0.22	0.05	0.12	0.32	4.20	< 0.001
		FD	0.13	0.05	0.03	0.24	2.55	0.011
		Intercept	1.57	0.16	1.26	1.87	10.05	< 0.001
	m.spr2	FC	0.23	0.06	0.12	0.34	4.09	< 0.001
		Intercept	1.56	0.13	1.30	1.82	11.66	< 0.001
CWM ITD all wild bees	*m.itd1*	-	-	-	-	-	-	-
Foraging preferences all wild bees	*m.l1*	FB_FB+	-0.95	0.33	-1.59	-0.31	-2.90	< 0.01
		run_mid.summer	0.24	0.32	-0.38	0.86	0.77	0.44
		run_late.summer	-0.20	0.33	-0.85	0.44	-0.61	0.54
		FB_FB+ x run_mid.summer	1.68	0.46	0.78	2.58	3.66	< 0.001

		FB_FB+ x run_late.summer	1.45	0.45	0.57	2.34	3.23	< 0.01
		Intercept	2.03	0.46	1.13	2.93	4.44	< 0.001
Sociality all wild bees	*m.s1*	FB_FB+	-0.72	0.25	-1.21	-0.23	-2.90	< 0.01
		run_mid.summer	0.93	0.27	0.40	1.45	3.44	< 0.001
		run_late.summer	0.45	0.29	-0.12	1.01	1.55	0.12
		FB_FB+ x run_mid.summer	1.68	0.42	0.86	2.50	4.01	< 0.001
		FB_FB+ x run_late.summer	1.68	0.42	0.85	2.51	3.98	< 0.001
		Intercept	1.14	0.48	0.21	2.08	2.40	0.02
	m.s2	FB_FB+	-0.63	0.25	-1.13	-0.14	-2.51	0.01
		run_mid.summer	0.93	0.27	0.40	1.45	3.44	< 0.001
		run_late.summer	0.44	0.29	-0.13	1.01	1.53	0.13
		OSR	-0.19	0.10	-0.40	0.01	-1.89	0.06
		FB_FB+ x run_mid.summer	1.63	0.42	0.80	2.45	3.88	< 0.001
		FB_FB+ x run_late.summer	1.63	0.42	0.80	2.46	3.87	< 0.001
		Intercept	1.11	0.47	0.19	2.03	2.36	0.02
	m.s3	FB_FB+	-0.70	0.26	-1.20	-0.20	-2.72	< 0.01
		run_mid.summer	1.06	0.28	0.51	1.60	3.80	< 0.001
		run_late.summer	0.60	0.30	0.02	1.19	2.02	0.04
		SNH	0.17	0.15	-0.12	0.45	1.16	0.25
		FB_FB+ x run_mid.summer	1.55	0.43	72.00	2.39	3.64	< 0.001
		FB_FB+ x run_late.summer	1.52	0.43	0.67	2.36	3.53	< 0.001
		run_mid.summer x SNH	-0.52	0.20	-0.91	-0.12	-2.57	0.01
		run_late.summer x SNH	-0.60	0.21	-1.00	-0.19	-2.90	< 0.01
		Intercept	1.09	0.50	0.10	2.07	2.16	0.03
Proportion long-tongued bumblebees	*m.ltb1*	FC	-0.59	0.12	-0.83	-0.35	-4.79	< 0.001
		run_mid.summer	0.4	0.2	0.01	0.8	2.01	0.04
		run_late.summer	1.53	0.23	1.08	1.98	6.65	< 0.001
		Intercept	-0.78	0.21	-1.2	-0.37	-3.73	< 0.001
	m.ltb2	FC	-0.58	0.12	-0.81	-0.34	-4.84	< 0.001
		FB_FB+	0.38	0.21	-0.04	0.79	1.79	0.07
		run_mid.summer	0.41	0.2	0.01	0.8	2.03	0.04
		run_late.summer	1.51	0.23	1.06	1.97	6.58	< 0.001
		Intercept	-0.98	0.24	-1.45	-0.52	-4.12	< 0.001
CWM ITD Bombus	*m.itdb1*	FB_FB+	0.02	0.01	0.00	0.05	1.74	0.10
		FC	0.01	0.01	0.00	0.03	1.59	0.12
		FB_FB+ x FC	-0.05	0.01	-0.07	-0.02	-3.76	< 0.001
		Intercept	3.83	0.01	3.81	3.85	439.52	< 0.001

Table S7 Summary of the best fitting candidate models (dBIC<2) and null models for the effects of faba bean cultivation, landscape metrics **and honeybee densities** on wild bee densities. Marginal (R_m^2) and conditional (R_c^2) R^2 values are given as a measure of the model´s goodness of fit. n: number of observations, FB: faba bean cultivation (FB+/FB-), run: sampling run (early/mid/late summer), FC: local flower cover of transect area.

Response variable	**model**	**df**	**BIC**	**deltaBIC**	**BIC weight**	**Explanatory variables**	**R_m^2**	**R_c^2**
Pollinator densities and species richness								
Bumblebee density (n=540)	m.bb1	13	2268.60	0.00	0.76	FB + FC + run + FB:FC	0.38	-
	m.bb0	7	2483.42	214.82	0.00	1	0.00	0.16
	m.nb1	9	1268.77	0.00	0.56	FC	0.06	0.42

Non-*Bombus* density (n=540)	m.nb0	7	1341.80	73.03	0.00	1	0.00	0.46

Table S8: The relative importance of explanatory variables expressed by Σw_i (sum of BIC weights) for models to explain the effects of of faba bean cultivation, landscape metrics **and honeybee densities** on wild bee densities (best fitting models are shown in Table S7). Model parameters having $\Sigma w_i < 0.2$ for all response variables are not shown. FB: faba bean cultivation (FB+/FB-), run: sampling run (early/mid/late summer), FC: local flower cover of transect area, OSR: percentage of oilseed rape, SNH: percentage of semi-natural habitats, LD: landscape diversity.

Models	Response variable	**FB**	**run**	**FC**	**OSR**	**SNH**	**LD**	**FB:FC**
m.bb	Bumblebee density	0.88	1.00	1.00	-	-	-	0.86
m.nb	Non-*Bombus* density	-	-	1.00	-	-	0.26	-

Table S9 Results of permutational multivariate analysis of variance (PERMANOVA), testing the effect of mass-flowering crop cultivation on bee community composition. To test effects of mass-flowering crop cultivation on community composition, we performed a PERMANOVA using the *adonis* function of the *vegan* package (Oksanen et al., 2019) with Bray-Curtis dissimilarity and 999 permutations. Bee communities did not differ significantly between landscapes with and without faba bean cultivation. Contrastingly, oilseed rape cover of the study landscapes impacted composition of bee communities. Simper analysis (function *simper* of *vegan* package, Bray-Curtis dissimilarities) revealed that compositional differences between landscapes with a high (> 8 %) and a low cover (< 8 %) of oilseed rape were mainly caused by the common species (landscapes were split into two groups for the purpose of simper analysis based on the mean oilseed rape cover of all study landscapes*).* *Bombus terrestris, B. pascuorum* and B. *lapidarius* together accounted for approx. 26.9 % of the total dissimilarity between landscapes with a high and a low oilseed rape cover. For NMDS, visualizing the effects, see Fig. S7.

Mass-flowering crop	Df	Pseudo-F	R^2	P
Faba bean cultivation	1	1.767	0.019	0.063
Oilseed rape cover (%)	1	2.015	0.022	0.029

Calculation of landscape diversity

Landscape diversity was calculated as the Shannon index (Krauss et al., 2003; Steffan-Dewenter et al., 2002) of 14 different land-use types using the *vegan* package (Oksanen et al., 2019). Following land-use types were utilized: arable land, settlement, water bodies, forest, forest edges, groves, hedgerows, intensive grasslands, extensive/calcareous grasslands, orchard meadows, succession sites, fallows/ ruderal sites, sown flower strips or fields, others.

References

Krauss J, Steffan-Dewenter I, Tscharntke T (2003) How does landscape context contribute to effects of habitat fragmentation on diversity and population density of butterflies? Journal of Biogeography 30: 889-900.

Steffan-Dewenter I, Münzenberg U, Bürger C, Thies C, Tscharntke T (2002) Scale-dependent effects of landscape context on three pollinator guilds. Ecology 83: 1421–1432. https://doi.org/10.1890/0012-9658(2002)083[1421:SDEOLC]2.0.CO;2

Oksanaen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn M, Minchin R, O´Hara RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E, Wagner H (2019) vegan: Community Ecology Package. R package version 2.5-5. https://CRAN.R-project.org/package=vegan

Westrich P (2018) Die Wildbienen Deutschlands, 1st edn. Eugen Ulmer Verlag, Stuttgart.

Chapter 3

Pollen and landscape diversity as well as wax moth depredation determine reproductive success of bumblebees in agricultural landscapes

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Abstract

Bumblebees are important pollinators in agricultural landscapes that are facing global declines. Main pressures include food scarcity mainly due to the reduction of semi-natural habitats (SNH) and parasite-induced vulnerability. Even though intensive agricultural landscapes are poor habitats for bumblebees, the cultivation of mass-flowering crops (MFC) can provide a high amount of floral resources and therefore can promote pollinators. In contrary to SNH, which provide a high diversity of floral resources, MFC provide only monofloral, short-term and unbalanced resources for bees. We explored the direct and indirect effects of landscape composition (proportions of MFC, SNH, urban areas), landscape diversity, diversity of pollen diets and wax moth depredation on the growth and reproductive success of bumblebee colonies. We placed 44 experimental *Bombus terrestris* L. colonies in 22 agricultural landscapes. The study landscapes represented gradients of the cover of SNH, urban areas and oilseed rape (OSR) and differed in the availability of the mid-season flowering MFC faba bean (*Vicia faba* L.). We recorded colony growth and reproductive success of the bumblebee colonies, diversity of collected pollen types and depredation by the specialized wax moth *Aphomia sociella* L.. We found no effects of landscape composition or landscape diversity on the diversity of pollen collected by the bees. However, we found a positive effect of landscape diversity on the reproductive success of bumblebees. Moreover, pollen diversity and the availability of faba bean interacted and resulted in higher numbers of young queens in landscapes without faba bean. In addition, colonies that collected a higher pollen diversity had a reduced *A. sociella* depredation. Increased parasitism had a cascading negative effect on the reproductive success of bumblebees by limiting colony growth. Our study showed that high landscape diversity and diverse pollen diets can enhance the reproductive success of bumblebees. A diverse diet even mitigated depredation by wax moths. To sustain vital bumblebee populations and their pollination services, diverse and floral rich habitat types should be conserved or restored in agricultural landscapes.

Keywords

bee decline, pollen diet, mass-flowering crops, colony performance, landscape composition, semi-natural habitats

Introduction

Bumblebees are one of the most abundant native pollinators in the temperate regions of the northern hemisphere (Goulson 2010). Not only in terms of their ecological service in maintaining plant communities and thereby ecosystems, but also in the context of food security and their role in crop pollination, they are a critically important functional group (Corbet et al. 1991, Delaplane and Mayer

2000). However, bumblebees are facing declining species richness and abundance all over the world with potentially detrimental effects on the ecosystem services they provide (Williams and Osborne 2009, Cameron et al. 2011, Nieto et al. 2014). The main drivers of this declines are a lack of suitable food and nesting sources through the loss of natural habitats (Biesmeijer et al. 2006, Carvell et al.2006), changes in habitat quality due to climate change (Rasmont et al. 2015), exposure to pesticides (Banks et al. 2020, Baron et al. 2017), novel introduced parasites (Schmid-Hempel et al. 2014), or combinations of several of stressors (Goulson et al. 2015, Schweiger et al. 2010). Therefore, studies to understand the combined pressures on bumblebees are urgently needed, especially in agricultural landscapes where most pressures accumulate and which cover most land surface of the EU (39.1% in 2018; Eurostat 2021).

Bumblebee diets are composed exclusively of floral resources and need, in comparison to other wild bee species, a relatively high amount of pollen for successful colony development (Rotheray et al. 2017). Hence, they need access to pollen and nectar during their whole colony development phase, usually from early spring to late summer (Alford 1975, Westrich 2018). Protein rich pollen is required by the developing larvae, freshly emerged workers and the queen, while nectar is the main source of carbohydrates and used for individual energy supply but also nest provisioning (Bohart and Nye 1956, Goulson 2010). Usually, most common bumblebee species are generalists and able to collect their floral resources from a wide range of different plant taxa (Kirk and Howes 2012, Leidenfrost et al. 2020). However, for pollen collection they are generally more selective aiming for high-quality pollen (Leonhardt and Blüthgen 2012, Ruedenauer et al. 2016). The nutritive and chemical properties of pollen can considerably influence the colonies' growth and reproductive success (Eckhardt et al. 2014, Génissel et al. 2002, Moerman et al. 2017, Tasei and Aupinel 2008). A high pollen diversity can enhance colony growth of bumblebees (Hass et al. 2018, Kämper et al. 2016), probably because foragers optimize the nutritional composition of the diets (Ruedenauer et al. 2016). Therefore, the analysis of bumblebees' pollen diets can give important insight into crucial food resources for conservation management recommendations (Kämper et al. 2016, Bertrand et al. 2019).

However, the amount and diversity of floral resources may strongly depend on the availability of different habitats at the landscape-scale. Semi-natural habitats (SNH) do not only enhance pollinator abundance and diversity (Kremen et al. 2002), but may also promote colony growth and reproductive success of wild bees through the provision of a continuous and diverse floral resource supply as well as nesting sites (Carvell et al. 2017, Williams et al. 2012). High covers of SNH can also help to reduce the energy investment for pollen collection of bumblebees and may explain the observed enhancement in queen production (Crone and Williams 2016, Requier et al. 2020). Likewise, villages embedded in agricultural landscapes can provide important floral resources that can be exploited by bumblebees (Udy et al. 2020). However, the cascading effects of landscape-scale habitat availability on colony growth and reproductive success of bumblebees mediated by pollen diversity remain poorly understood.

Agricultural intensification led to a substantial reduction of semi-natural habitats – one of the reasons why it is considered the major driver for pollinator losses (Williams and Osborne 2009). With respect to floral resources, intensively farmed areas often lack diverse and sufficient food supply for pollinators (Carvell et al. 2006). However, this undersupply can be mitigated through flowering monocultures, so called mass-flowering crops (MFC) such as oilseed rape or faba bean. MFC can enhance bumblebee colony performance as they provide short-term pulse of floral resources (Westphal et al. 2003, 2009). Bumblebees were shown to be highly attracted by large resource patches, such as MFC fields (Westphal et al. 2006^{b}), but rely on alternative foraging resources after mass-blooming to guarantee continuous pollen availability (Proesmans et al. 2019). The timing of the mass-blooming event in relation to the seasonal colony cycle seems to be of major importance to predict the diverging influence of MFC on the colony performance (Hemberger et al. 2020, Hovestadt et al. 2019, Westphal et al. 2009). Early-flowering MFC have only been shown to influence the number of produced workers, but not the reproductive success (Westphal et al. 2009, Williams et al. 2012), while late-flowering crops could directly be linked to reproductive success (Rundlöf et al. 2014).

In comparison to the early flowering MFC oilseed rape (*Brassica napus* L.), the effects of other MFC are much less studied. Legumes like faba beans (*Vicia faba* L.) can fix nitrogen allowing for a reduction of fertilizer input and are therefore politically promoted by the Common Agricultural Policy (CAP) (European Commission 2017). Legumes are known to efficiently increase the abundance and diversity of bees, especially bumblebees (Carvell et al. 2007), and *V. faba* fields were shown to have a positive effect on the density of bumblebees at the landscape-scale (Beyer et al. 2020). Besides nectar and pollen, *V. faba* provides extrafloral nectaries that provide an additional feeding source for pollinators (Veloso et al. 2016). Since *V. faba* fields provide a massive resource surplus during mid-season when other resources are scarce and bumblebees already invest in sexual reproductives (Hovestadt et al. 2019), they could have an essential impact on the population growth of bumblebees.

Besides resource limitations, parasites can severely impact bumblebee colonies (Carvell et al. 2008, Schmid-Hempel et al. 2014), regarding a reduction of colony growth and reproductive success (Brown et al. 2003). One specialized parasite is the wax moth *Aphomia sociella* L. (Lepidoptera: Pyralidae), also known as bumblebee moth, which can severely damage a bumblebee nest. The geographical origin of the Lepidoptera is not clear but it is widely distributed in Europe (Pouvreau 1967). Fertilized females can lay batches of eggs (between 50 and 500 eggs) in the bumblebees' nests. There, the larvae hatch after some hours or days, infiltrate the nests and feed on the comb, and consume bee larvae and pupae. The polyphagous larvae are able to destroy a whole bumblebee colony in only a few weeks (Alford 1975, Goulson 2010). They spin silken tunnels that probably protect them from the bumblebees. Infestation rates up to 80% were found in *B. terrestris* colonies in gardens in Southern England (Goulson 2010). In comparison, lower infestation of 20% (Goulson et al. 2002), 26% (Goulson et al. 2017) and 36% (Gervais et al. 2020) were detected in nests located in agricultural landscapes. So far, little is known about the effects of landscape composition on the depredation by wax moths and how these drivers interact and affect the colony development of bumblebees. A recent study could not find a relation between certain land-use types and infestation (Gervais et al. 2020).

In our study, we placed commercial *Bombus terrestris* colonies in agricultural landscapes with and without mid-season flowering MFC faba bean fields (*Vicia faba* L.) along land cover gradients of oilseed rape (OSR), SNH and of urban areas. In a landscape-scale experiment, we investigated direct and indirect effects of landscape composition (availability of *V. faba*, cover of OSR, urban area and SNH) and landscape diversity on the growth and reproductive success of the bumblebee colonies. We also included two main drivers of bee declines, i.e. the bees' diet and parasite infestation (Goulson et al. 2015) and the interaction of both in our analysis to test relationships between landscape, pollen diversity, depredation by the parasite *A. sociella* and the performance of *Bombus terrestris* L. colonies. We expected that (1) the extended provision of floral resources provided by the mid-season MFC *V. faba*, flowering after OSR enhances colony performance (colony growth and reproductive success) due to enhanced resource continuity. Moreover, we hypothesized that (2) increasing cover of SNH and urban area providing diverse and continuous floral resources to have a positive impact on the colony performance of bumblebees. We also hypothesised that (3) higher landscape diversity, providing higher floral diversity, benefits colony performance. Furthermore, we expected (4) landscape metrics to impact the colonies' parasite infestation due to a higher susceptibility to depredation under resource-poor conditions (e.g. low SNH cover) and (5) a negative impact of the parasitic wax moth *A. sociella* on colony performance.

Material and Methods

Study landscapes

The study was carried out in 22 study landscapes (11 landscape pairs) in Central Germany (Fig. 1) and included agricultural fields of collaborating conventional farmers. The study landscapes were located in Lower Saxony (17), Hesse (3), Saxony-Anhalt (1) and Thuringia (1) and covered an area of 1km x 1km each, i.e. the foragers could exploit resources within the entire landscapes considering a mean foraging range of 551m (Redhead et al. 2016). All study landscapes had a minimum distance of 3 km to each other in order to avoid overlapping foraging ranges of bumblebees from different landscapes (Westphal et al. 2006[a]). We selected eleven landscapes pairs using ATKIS land cover data (Federal Agency for Cartography and Geodesy, 2018). All study landscapes comprised at least one OSR field along a cover gradient (Table 1). Only one study landscape of each pair included at least one faba bean field (FB+), while the other study landscape did not include any grain legumes (FB-). In addition to MFC, our study landscapes comprised land cover gradients of flower-rich habitats, i.e. urban areas and semi-natural habitats (Table 1). Study landscapes of a pair had a similar landscape composition regarding major land use categories (i.e. agricultural production area, forest, groves, grassland, settlement/traffic infrastructure, water bodies, heathland/moorland/swamp, remaining vegetation). Similarity was assessed based on Euclidian distances (Beyer et al. 2020).

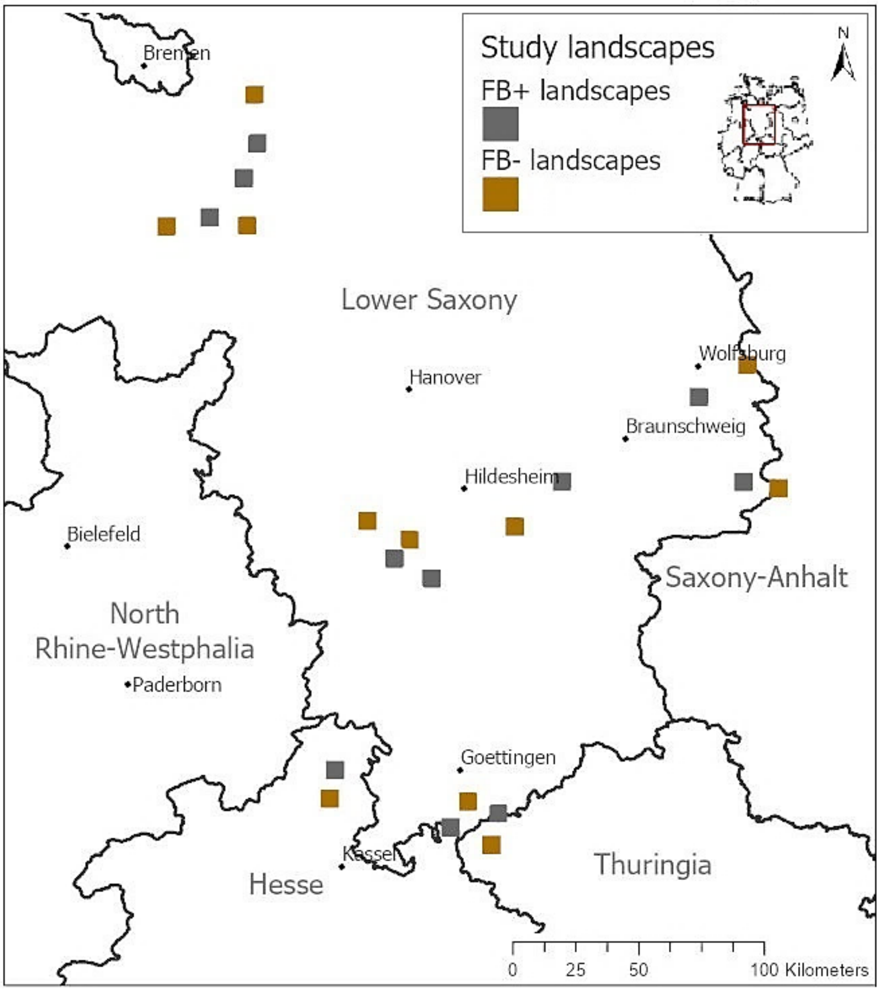

Figure 1 Map of the study landscapes located in central Germany. The landscape pairs that were located close to each other comprised either only *B. napus* (FB-) or both mass-flowering crops, *B. napus* and *V. faba* (FB+).

During the field season, the study landscapes were mapped and all land cover types with a minimum size of 10m^2 were recorded (Fig. A.1). The percentage of flower-rich land cover types (i.e. cover of OSR, urban area or SNH) within a study landscape was calculated using QGIS version 3.10 (QGIS Development Team 2019) (Table 1). SNH included flower-rich habitats with extensive land use that provide nesting and foraging habitats for bumblebees (Holland et al. 2017) (for details see Table A.1). Urban area consisted mainly of settlements that provide floral resources for bees in private gardens and parks. Moreover, landscape diversity (i.e. Shannon index) of twelve land-use types that present potential nesting or foraging habitats for bees was calculated for each study landscape (see Appendix for further information).

Table 1 Mean, standard deviation (SD), minimum (Min) and maximum (Max) of all explanatory and response variables used in the structural equation model (SEM) with distances of the landscape metrics FB, OSR, urban area and SNH to the bumblebee colonies. FB+: landscape with faba beans; FB-: landscape without faba bean cultivation.

variable	measure	mean	SD	min	max
landscape composition					
availability of *V. faba* (FB)	factor FB+ / FB-				
	distance to bumblebee colonies [m]	100.37	159.58	14.13	579.19
oilseed rape (OSR)	landscape cover [%]	13.77	9.96	1.86	37.08
	distance to bumblebee colonies [m]	186.61	156.64	10.1	575.8
urban area	landscape cover [%]	8.39	10.35	1.28	37.54
	distance to bumblebee colonies [m]	103.65	110.01	0.00	347.15
semi-natural habitats (SNH)	landscape cover [%]	4.98	3.42	0.82	12.42
	distance to bumblebee colonies [m]	35.55	63.09	0.00	205.14
landscape diversity	Shannon diversity index of the study landscapes of 12 different land-use types	0.82	0.33	0.31	1.46
pollen diversity	Shannon diversity index of the study landscapes of 55 pollen types collected by bumblebee workers	1.73	0.28	1.04	2.18
weight of wax moth larvae	weight [g]	89.76	122.39	0	408
number of brood cells	counted number	724.12	268.29	137	1412
number of young queens	counted number	9.47	12.75	0	43

Bumblebee colonies

44 colonies of the buff-tailed bumblebee (*B. terrestris*) were purchased from STB control (Aarbergen, Germany) and two colonies were placed next to each other in the centre of each squared 1km² study landscape in grassy field margins or margins of hedgerows on 3 and 4 May 2018. As bumblebees forage within a mean foraging range of 551m (Redhead et al. 2016), we expected that the workers were able to exploit all rewarding floral resources within our study landscapes despite variations in the distances to the faba bean and OSR fields as well as to SNH and urban areas (Table 1).

At the start of the field experiment, all colonies had the same age (4-5 weeks) and a mean weight of 616.8 ± 63.5 (SD) g (including the plastic box). The bumblebees were housed in ventilated plastic boxes with adjustable valves within cardboard boxes (Fig. A.2). In order to keep the colonies protected and dry, they were placed on stones and covered with water-resistant wooden roofs. Where applicable, the artificial nests were placed next to shrubs or hedges as they naturally nest in previous burrows of rodents or other belowground cavities in shady places (Alford 1975, Goulson 2010). Multiple factors determine the nutritional needs of bumblebee colonies that cannot be standardised within a landscape-scale experiment (Carnell et al. 2020). To minimize potential confounding effects due to variability between the colonies, we standardized the origin, age and size of the colonies and placed them in one location to have the same abiotic and biotic conditions for both colonies per landscape.

Pollen resources collected by the workers

During sampling round 1-3 we caught ten bumblebee workers returning to the two neighbouring hives within a study landscape with an insect net (following Bertrand et al. 2019, Hass et al. 2018) and transferred them into honeybee queen marking tubes. The corbicular pollen pellets were removed from their hind tibia using spring steel tweezers. After this procedure, bumblebees were released again. We froze pollen samples until further examination. Pollen samples were taken when either oilseed rape (round 1) or *V. faba* (round 2, partly round 3) was in its mass-flowering stage. In the lab, we mixed pellets of the ten workers per round and landscape in an Eppendorf tube filled with 4ml of a 70% ethanol. Pollen type identification of the homogeneously mixed pollen solutions per round and landscape was conducted by Melissopal – Pollenanalytik (Hammoor, Germany). The first 500 pollen grains of three subsamples of each pollen mixture (overall 4500 pollen grains per landscape) were identified using a light microscope and following the guidelines of pollen identification in honey samples (Dustmann 2006). Identified pollen types indicate the lowest taxonomic level that could be assigned to the sampled pollen grains. Hence, pollen types represent different plant taxonomic levels (family, genus, species) or groups which may contain several plant species as it was not always possible to determine the pollen grains to species level or distinguish between species with very similar pollen morphology (Beug 2015). For example, the *Brassica* type contains *B. napus* and *Sinapis spec.* To minimize potential effects of pollen that has not been actively collected by the bees, pollen types had to be counted at least five times in a sample to be included in our further analysis (Hass et al. 2018). For each identified pollen type, mean grain number of the three pollen samples was calculated for each round and landscape. Pollen diversity was calculated as Shannon index of the pooled pollen grain counting over the three sampling rounds within each landscape. In addition, we assigned pollen types with the highest counted number (pollen types that were recorded with more than 500 pollen grains across all landscapes and all sampling rounds) and also the most frequently collected ones (collected in more than 30% of our landscapes) either herbaceous or woody character.

Colony growth, reproductive success and parasite infestation

In the following, we recorded the development of the colonies (including the plastic box) four times. After 1.5 weeks, 3.5 weeks, 5 weeks and 6.5 weeks, corresponding to sampling round 1-4 (Table A.2), the colonies were visited, the plastic boxes housing the colonies were taken out of the cardboard box and weighed. The colonies were sampled in the same order to have comparable intervals between sampling round. However, due to long travelling times and bad weather conditions the time of the day and also time intervals varied. To include most of the foraging workers, the flight hole was closed and the valve that allowed the bees only to enter but not to leave the box was opened for 30 to 40 minutes.

The field experiment was terminated after 7.5 weeks, between 22 June and 25 June 2018, when the colonies were weighed for the last time. At this time, with approximately three months, colonies started to produce reproductives. Thereafter, the colonies were killed and preserved in a freezer at -20°C for further examination. During examination, the number of workers, queens, males, brood cells, pollen and nectar pots were counted and weighed. Since the number of workers and males correlated with the number of young queens, we only included the number of young queens as measure of successful reproduction in the analysis. As measure of parasite infestation, the weight of the wax moth larvae *A. sociella* was recorded. Due to a high infestation by *A. sociella* larvae with a maximum larvae weight of up to 408g which accounted for more than 50% of the colony's weight, we decided not to include this measure in our analysis as colony weight was expected to be correlated with the weight of the wax moth larvae. Instead, we used the number of brood cells at the end of the experiment as a measure of colony growth.

In our study, reproductive success refers only to the number of produced young queens as they are the founders of new colonies after hibernation in the following year and hence the main factor for reproductive fitness of bumblebee colonies (Alford 1975). As rearing young queens is energetically most demanding – for the development of young queens the food requirement is three times higher than to produce males (Williams et al. 2012) - only proper developing colonies with sufficient food resources in the landscape usually produce first males and then young queens (Duchateau and Velthuis 1988, Pelletier and McNeil 2003).

Statistical analysis

All statistical analyses were performed using R version 3.6.3 (R Core Team 2020). When colony data were missing due to destruction, we excluded these colonies from the analysis (concerning two colonies). When both neighbouring colonies in a landscape were destroyed, we excluded the entire landscape pair. This was the case for two pairs (concerning additional eight colonies). Finally, this led to an exclusion of ten colonies and statistical analyses of 34 colonies in 18 different study landscapes (Schweiger et al. 2021). Piecewise SEM (package piecewiseSEM, Lefcheck 2016) was used to analyse the effects of pollen diversity and wax moth infestation on colony growth (number of brood cells) and reproductive success (number of young queens), as well as the effects of landscape metrics such as landscape composition (availability of *V. faba*, cover of SNH, OSR and urban area) and landscape diversity on colony performance (Table 1, Table A.4). These models allow to take also potential indirect effects (e.g. the effect of the landscape on reproductive success via the pollen diversity collected by the workers) into account. The theoretical SEM (Fig. 2a) shows all potential relationships tested in our global models (Table A.4). Following the d-rule (the total number of samples to the number of variables (d) should not fall below five) (Grace et al. 2015) the models were examined in pre-analyses with linear mixed effects models (package nmle, Pinheiro et al. 2020) with landscape pairs as random effect. As our study design targets the influence of *V. faba* availability (FB+/FB-), all possible two-way interactions with other landscape metrics and pollen diversity were included in the pre-analysis. Furthermore, the two-way interactions between pollen diversity and landscape metrics as well as between pollen diversity and wax moth infestation were included in the global models (Table A.4). Differences between the amount of collected *Vicia faba* pollen between landscapes with and without faba bean cultivation (FB+/FB-) were tested using Kruskal-Wallis test. Number of queens and weight of *A. sociella* were log-transformed to achieve normality. Continuous explanatory variables were scaled to a mean of zero and a standard deviation of one to improve convergence of the models using the scale function (R Core Team 2020). The variance inflation factor (VIF) was calculated to test for potential multicollinearity between explanatory variables and showed a low correlation (VIF < 3) in all cases (Zuur et al. 2010) The best-fitting models (Table 2) were chosen using the dredge function (package MuMIn, Barton 2019) which performs an automated model selection with subsets of the supplied global models. We selected the respective best models ranked according to second order Akaike Information Criterion (AICc). This process resulted in the simplified SEM (Fig. 2b).

Table 2 Significant models resulting from the model selection step and kept in the simplified structural equation model. (a) Model explaining the effect of wax moth larvae weight on number of brood cells. (b) Model explaining the effect of number of brood cells, pollen type richness, faba bean cultivation (FB+: landscape with faba beans; FB-: landscape without faba beans) and their two-way interactions on number of young queens. (c) Model explaining the effect of semi-natural habitat cover on weight of wax moth larvae. Estimates, lower and upper 95 % confidence intervals (CI) and p-values are presented.

	Estimate	Lower 95% CI	Upper 95% CI	p-value
(a) Model 1: Response number of brood cells				
Intercept	0.00	-0.37	0.37	0.983
weight of wax moth larvae	-0.50	-0.84	-0.15	0.008
(b) Model 2: Response number of young queens				
Intercept	1.42	0.99	1.86	0.000
number of brood cells	0.43	0.10	0.75	0.013
pollen diversity	0.90	0.35	1.45	0.008
FB+ / FB-	0.02	-0.75	0.80	0.938
pollen diversity: FB+/FB-	-1.33	-2.13	-0.53	0.008
landscape diversity	0.52	0.13	0.91	0.018
(c) Model 3: Response weight of wax moth larvae				
Intercept	-0.01	-0.43	0.40	0.942
pollen diversity	-0.55	-0.97	-0.12	0.019
semi-natural habitat (SNH)	-0.33	-0.72	0.06	0.088

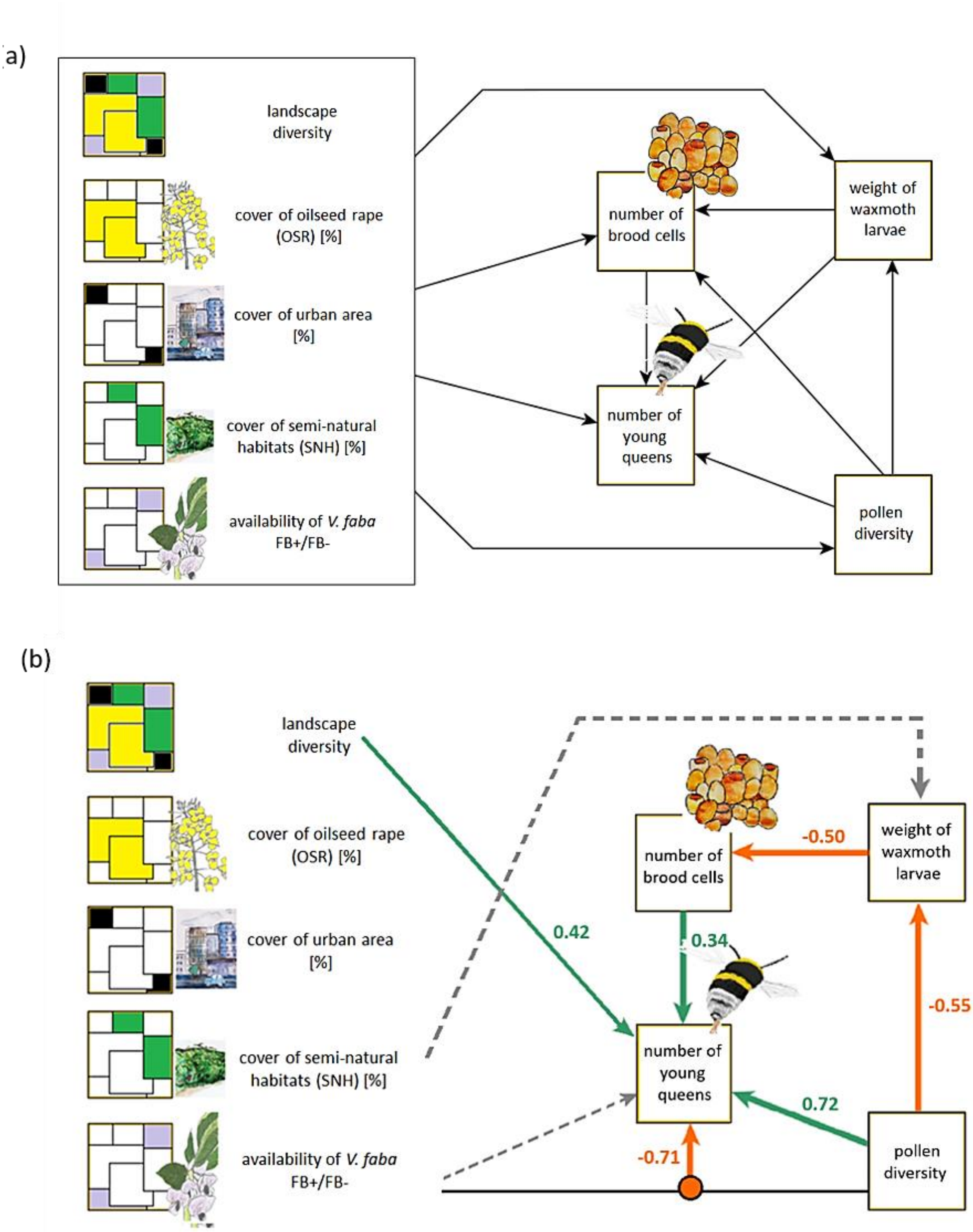

Figure 2 Structural equation models showing the relationships between landscape metrics (availability of *V. faba*, cover of oilseed rape, urban area and semi-natural habitats and landscape diversity), diversity of pollen types collected by bumblebee workers, depredation of bumblebee colonies by parasitic wax moth larvae, colony growth (number of brood cells) and colony reproductive success (number of young queens). (**a**) Theoretical SEM showing potential interaction pathways by the explanatory variables. For simplification, we show only one arrow for all landscape metrics (all metrics as one box) pointing to colony parameters, wax moth infestation and pollen diversity each, instead of one arrow for each of the five landscape metrics. The same accounts for all interactions (faba bean availability (FB+/FB-) with the remaining landscape metrics and for pollen diversity with depredation as well as for pollen diversity and landscape metrics). All global models are shown in Table A.4. (**b**) Final SEM including all pathways after model simplification based on lowest AICc. Numbers next to arrows show standardized regression coefficients.

Results

Pollen resources

In total, we identified 55 pollen types in our pollen samples over all three sampling rounds which could be assigned to 32 different plant families (Table A.3). We found 27 herbaceous forbs and 26 woody plant taxa as well as graminoid *Poaceae* and *Smilax* (prickly ivy) a plant genus containing both woody and herbaceous species. Within the three sampling rounds the overall amount of woody pollen grains was higher (66.5%) than the amount from herbaceous plants (31.6%) (Fig. A.3a). This also accounted for the most frequently collected pollen (Fig. A.3b).

Across all study landscapes, the most abundant pollen types (> 500 pollen grains across all samples) were *Tilia* accounting for 24.14%, *Pyrus* type (17.29 %), *Rubus* type (9.93%), *Ranunculus acris* (8.35 %), *Brassica* type (6.64%), *Robinia pseudoacacia* (5.52 %), *Hydrangea* (5.20 %), *V. faba* (3.65 %), *Phacelia* (2.43 %), *Prunus* type (2.00 %) and *Poaceae* (1.92%) (Fig. A.3a). Surprisingly, the collected amount of *V. faba* pollen in FB+ landscapes with 2.29% (620 ± 149 pollen grains) was relatively low and there was no significant difference found between FB+ and FB- landscapes in the amount of collected faba bean pollen (Kruskal-Wallis, p=0.150).

Colony development and depredation by the wax moth A. sociella

All analysed *B. terrestris* colonies gained weight during the experimental period of 7.5 weeks. Of the mean final colony weight (444.1 ± 186.5g) (mean ± SD), brood cells accounted for 53.2% (236.4 ± 118.3g) and pots filled with pollen and nectar for 14.1% (62.4 ± 61.5g), followed by 1.9% (8.4 ± 7.1g) weight of males, 1.8% (8.1 ± 12.3 g) weight of young queens and 1.7% (7.4 ± 6.2 g) weight of workers. All colonies produced sexual reproductives, either males and young queens (n=27), or only males (n=7). The maximum number of young queens produced in a colony was 43. Half of the colonies (17 of 34 colonies) were infested by the larvae of the wax moth (89.8 ± 122.4 g). Though, 14 of the infested colonies still produced young queens.

Direct and indirect effects of landscape composition and landscape diversity on colony growth and reproductive success

The best fitting SEM (Fisher's C= 15.74, p=0.47) showed no independence claims, suggesting that no significantly important path was missing by our variables in the SEM. Neither the cover of flower-rich land-use types, nor landscape diversity influenced the diversity of collected pollen, with the null model showing the lowest AICc. Nevertheless, landscape diversity had a positive effect on the number of young queens (p=0.018) (Fig. 3a, Table 2). Moreover, faba bean cultivation was found to modulate the effect of pollen diversity on the number of young queens (p= 0.008) (Fig. 3b). Higher pollen diversity resulted in a higher number of young queens (p=0.008) but this effect was only present in landscapes without faba beans (p=0.008). We found a negative correlation of pollen diversity and depredation (p=0.019) (Fig. 3c). Bumblebee colonies that collected higher pollen diversity were less infested by the parasite *A. sociella*. SNH cover also negatively influenced depredation, however this effect was not significant (p=0.088). In addition, wax moth depredation was found to have an indirect negative effect on the number of young queens (Fig. 3d, 3e). The number of brood cells was negatively affected by a higher infestation by *A. sociella* (p=0.008) (Fig. 3d), and the number of young queens increased with the number of brood cells (p=0.013) (Fig. 3e).

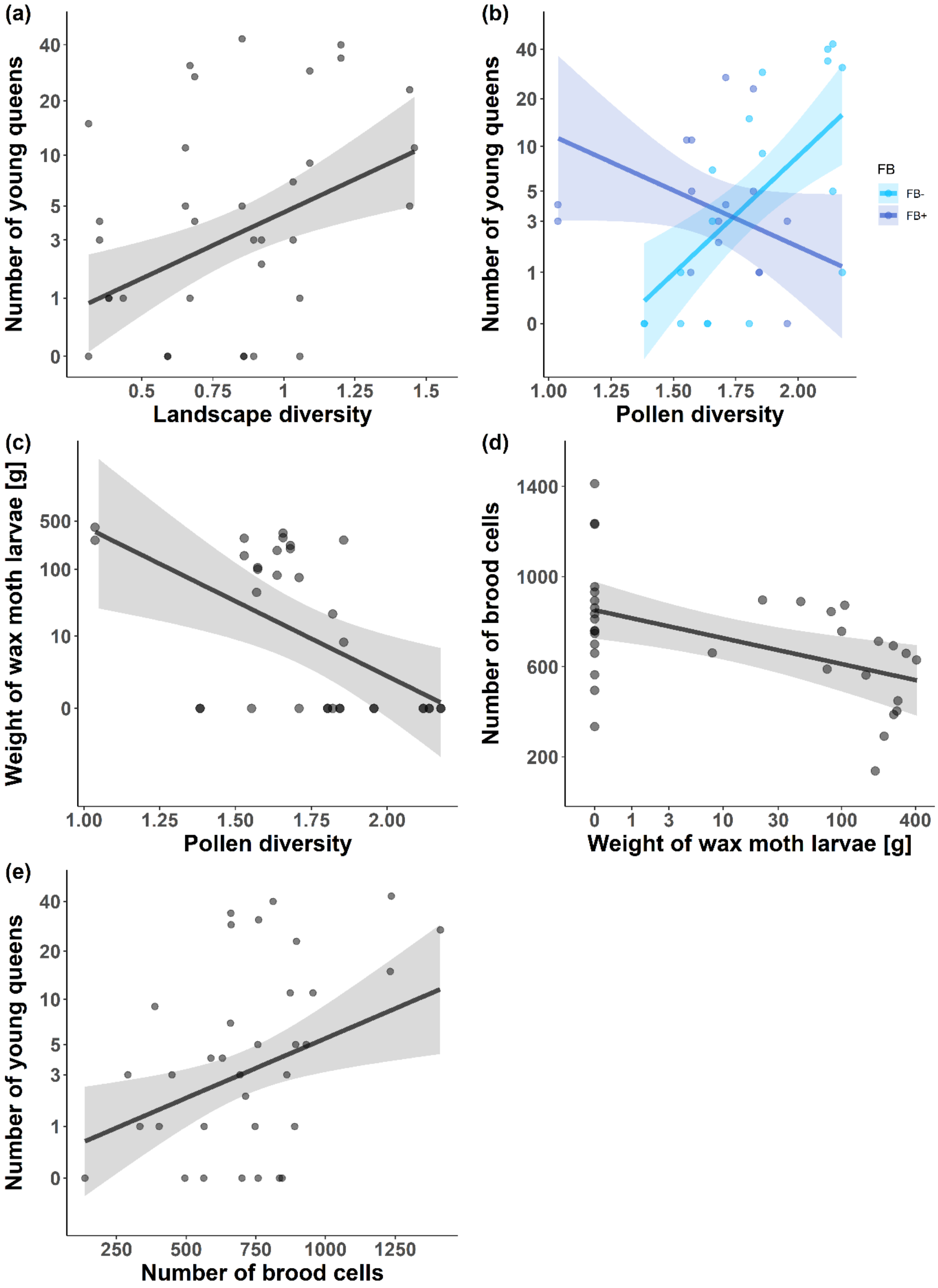

Figure 3 Effects of the (**a**) landscape diversity on the number of young queens, (**b**) pollen diversity on the number of young queens for landscapes with faba bean cultivation (FB+) and without (FB-), (**c**) pollen diversity on the weight of wax moth larvae, (**d**) weight of wax moth larvae on the number of brood cells and (**e**) number of brood cells on the number of young queens. Please note: In (d) x-axis and in (a), (b), (c) and (e) y-axes are on log-scale.

Discussion

Our study gives important insights into different drivers of bumblebee colony growth and reproduction in agricultural landscapes. We identified woody plants as important pollen sources for bumblebees. We found that pollen diversity was not affected by any of the metrics characterising the composition or diversity of agricultural landscapes with potential foraging habitats for bumblebees. Nevertheless, we demonstrated that landscape and pollen diversity are important predictors for queen production and therefore reproductive success. Moreover, we demonstrated that wax moth depredation had a harmful effect on reproductive success through their negative impact on colony growth but that infestation was mitigated by a higher diversity of collected pollen.

Pollen from woody plants is more frequently collected than pollen from MFC

The high amount of woody pollen across our different landscapes which considerably contributed to pollen diversity led us to the assumption that these plant taxa play a major role for the sufficient food provision and therefore also for reproductive success of bumblebees. These findings are in accordance with other studies who found *B. terrestris* collecting mainly woody pollen (Bailey et al. 2014, Kämper et al. 2016, Bertrand et al. 2019). Therefore, semi-natural and urban habitats that can offer pollen resources from woody plants might be crucial for bumblebees.

Even though both MFC are regularly visited plants by bumblebees (Kirk and Howes 2012), they played only subordinate role as pollen resources in our landscapes. In comparison with pollen from woody plants, lower amounts of MFC pollen types were collected in a smaller fraction of study landscapes. As it was pointed out by Kämper et al. (2016), OSR might be rather visited by *B. terrestris* for nectar than for pollen. Our findings suggest that this might also account for *V.* faba. Short-tongued bumblebees such *as B. terrestris* are morphologically not adapted to the long corolla tubes of *V. faba* (Bond & Poulsen 1983). Therefore, they usually bite little holes through the corolla close to the base of the flowers to obtain the nectar through the back rather than the front of the flower. As they might not legitimately pollinate the flower through this act, they are considered as nectar “robbers” (Bond & Poulsen 1983, Garratt et al. 2014, Marzinzig et al. 2018). Nevertheless, results might be different for long-tongued bumblebees, which are morphologically adapted to forage on flowers with very long corollas and mainly conduct regular visits on faba beans (Marzinzig et al. 2018, Beyer et al. 2020).

Pollen diversity is not affected by landscape metrics

In contrast to our expectations, we found that landscape metrics do not influence the diversity of the pollen collected by *B. terrestris* workers. Neither cover of flower-rich and diverse land-use types such as SNH or urban area contributed to pollen diversity, nor did landscape diversity. Therefore, a more precise characterization of the landscape, for example finer habitat classes or the separation of woody and herbaceous semi-natural elements (Eckerter et al. 2020) might be needed to detect potential links between landscape and pollen diversity. We did not find correlations between landscape and pollen on landscape-scale but we might have missed effects on local scale between pollen and plant diversity as this relationship was already shown by Matthias et al. (2015). The flowering period of single plant species is limited to a certain period and therefore bumblebees rely on a sequence of resource plants during their flight season (Bertrand et al. 2019). One land-use type might offer sufficient resources only at a certain time but resource continuity is needed to sustain insects and their services in agricultural landscapes (Schellhorn et al. 2015).

Landscape and pollen diversity influence reproductive success of bumblebees

Against our expectations, the number of young queens was not affected by the landscape cover of SNH, OSR and of urban area. This is in accordance with other studies which also found no direct effect of SNH and oilseed rape (Hass et al. 2018) or urban area cover on bumblebees (Vaidya et al. 2018). Even though, contradictory findings with higher bumblebee reproductive success in urban areas compared to agricultural landscapes were shown by Samuelson et al. (2018).

Though, reproductive success of *B. terrestris* was related to landscape diversity, indicating that not the habitat quantity but quality with regard to floral resource diversity seems to be of major importance for the reproductive success of bumblebees (Carvell et al. 2017). Diverse landscapes can provide a higher diversity of floral resources and therefore a more diverse food supply at different times of the season for bumblebees (Bertrand et al. 2019). Nevertheless, as we found no direct link between landscape and pollen diversity, we assume that bumblebees might also benefit from other advantages provided by a diverse landscape structure such as nectar supply.

There are other studies that already showed the importance of diverse habitats in providing a steady food supply for pollinators, indicating their benefit on the reproductive success of bumblebee colonies. Since diverse SNH provide a steady food supply, our study as others (e.g. Alford 1975, Williams et al.2012) indicate that it has beneficial influence on the colonies' reproductive success.

Colonies that collected and provisioned their larvae with a higher diversity of pollen types as protein source produced more queens. This is in accordance with previous findings of laboratory studies which showed a positive influence of diverse pollen diets on larval performance (Eckardt et al. 2014, Tasei and Aupinel 2008). Higher pollen diversity presumably increases the nutritional value of the bumblebees' diets and thus represents a prerequisite to fulfil their nutritional requirements (Eckardt et al. 2014) as pollen from different taxa vary in their micro-nutritional components (Roulston and Cane 2000). Therefore, it is likely that the nutritional composition expressed by the collected pollen diversity drives the enhanced reproductive success (Moerman et al. 2017). Additionally, a higher pollen diversity collected throughout the season as in our experiment might indicate the continuous availability of different floral resources with different times of flowering peaks in the year, which might be essential for queen production (Alford 1975). Previous field studies already found a positive effect of a diverse pollen diet on the colony weight gain of bumblebees (Hass et al. 2018, Kämper et al. 2016) and assumed that this would translate into higher reproductive success as larger colonies are thought to produce more queens (Pelletier and McNeil 2003, Vaidya et al. 2018).

The observed interacting effects between pollen diversity and faba bean cultivation on reproductive success were unexpected. Increasing pollen diversity only had a positive effect on queen production in landscapes without *V. faba* cultivation. One plausible explanation for the contrary effect of pollen diversity in the landscape pairs is deduced from modelling results showing that mass-flowering events at different times can result in different colony dynamics (Hovestadt et al. 2019). It was predicted that early MFC result in an energetic overinvestment in workers that weakens the worker efficiency and finally results in a limited reproductive success. Although these predictions were made for early flowering MFC. Similar mechanisms might be responsible for the negative effect of the mid-season MFC *V. faba* when high pollen diversity was collected. The energetic overinvestment might mainly be driven by nectar and not pollen resources since MFC pollen grains were not recorded in all study landscapes (Table A.3). Besides, the lower number of queens in landscapes with *V. faba* cultivation was mainly due to two colonies in one landscape. Therefore, more data is needed to confirm this result and to understand the potential additive effects of such mass-flowering events in connection with other, temporally available plant sources in the landscape.

Keeping in mind that more than one nutrient can simultaneously influence reproductive success (Sperfeld et al. 2012), further information about the chemical composition (e.g. lipid content, Ruedenauer et al. 2020) complementarity of the collected pollen and their nutrients is needed to detect the nutritional differences of pollen diets in landscapes with and without *V. faba* cultivation (Ruedenauer et al. 2016, Leonhardt and Blüthgen 2012).

Depredation is not affected by landscape metrics but pollen diversity

Bumblebee colonies are exposed to a high diversity of predators and parasites in nature but relations between infestation susceptibility and landscape context remains not entirely understood (Goulson et al. 2018). Higher infestation rates in urban areas than rural ones have been reported for *B. terrestris* by Goulson et al. (2002 and 2012) probably due to higher bumblebee colony densities in this land-use type (Goulson et al. 2002). In our study, we found no significant effect of urban area cover on depredation. As we do not know how dense natural bumblebee colonies occurred in the surrounding we cannot make a statement about this. No other landscape metrics had an influence on the infestation by *A. sociella*. Only SNH cover showed a non-significant tendency to decrease depredation. A plausible explanation is that natural enemies of *A. sociella* benefit from increasing amounts of SNH (Holland et al. 2017), leading to the observed negative trend of infestation rate with higher amount of SNH in the landscape. As depredation was lower in colonies which collected a higher diversity of pollen, we can emphasize the relationship between a diverse food supply and bumblebees' health. Other studies already showed a connection between the content of bees' food and reduced susceptibility to pathogens or parasites of bumblebees (Manson et al. 2010, Spear et al. 2016). Our findings thus emphasize the importance of heterogeneous landscapes, providing a diverse diet in mitigating the negative effect of parasitism on bumblebee colonies. Multiple interacting stressors, such as parasitism and unbalanced diets in simplified agricultural landscapes might in contrast severely threaten pollinator survival (Vanbergen et al. 2013).

Cascading negative effect of A. sociella on bumblebees´ reproductive success

In our study, the number of queens increased with colony growth (number of brood cells) which is in accordance with other studies (Pelletier and McNeil 2003, Vaidya et al. 2018). When a bumblebee colony reaches a sufficient size, they usually switch to the rearing of sexuals (males and young queens) and generally no more workers are reared (Goulson 2010). As we determined our experiment at the end of the bees' life cycles when already sexuals were produced, the number of queens correlated with the brood cell number, as expected. As the parasite *A. sociella* diminished colony growth (number of broodcells), we can infer a cascading negative effect of the parasite on the reproductive success of *B. terrestris*. Nevertheless, the insertion of the switching point itself, from producing workers to the production of sexual reproductives (males and young queens), did not seem to be influenced, because all infested colonies produced males and 79% of them produced queens.

Conclusions

We found different drivers of bumblebee colony growth and queen production in agricultural landscapes. Our study demonstrates that the surrounding landscape and pollen diversity collected by *B. terrestris* colonies directly affected their reproductive success. However, we found no clear links between the landscape metrics and collected pollen diversity indicating that various habitat types have the potential to offer diverse floral resources and habitat quality is more important than habitat quantity. These findings underline the importance of preserving a high amount of different plant taxa and habitat types in our agricultural landscapes to guarantee a balanced intake of essential nutrients through complementary feeding (Requier et al. 2020). Considering that individual bumblebee species differ in their response to the availability of plant taxa (Fussell and Corbet 1992), it is even more important to conserve flower diverse habitats to preserve a diverse wild bee fauna in our landscapes. Especially woody plant species should be considered in the future as they made up most of the pollen types collected in our study and are an important pollen resource for bumblebees (Bertrand et al. 2019, Kämper et al. 2016). Successively flowering MFC did not improve the reproductive success of *B. terrestris*. As higher collected pollen diversity was correlated with a lower wax moth depredation, we can assume that a more diverse food provision strengthens bumblebees' health and make them more robust against parasites such as *A. sociella*.

Overall, our study demonstrates the complexity of the relationship between predictors, shaping bumblebees' reproductive success, and that more studies are needed to fully understand the interplay of major drivers for their reproductive success. Future conservation schemes and agri-environment measures should consider landscape composition and habitat quality, targeting floral resource availability and pest control services as we found that diverse diets and parasite infestation are major factors driving the reproductive success of generalist bumblebees that are important crop pollinators in agricultural landscapes.

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Author contributions

CW and NB conceived the study. NB and SES implemented the field experiment. SES collected the data. SES, NB and ALH performed the data analysis with advice of CW. SES wrote the manuscript, the other authors provided editorial advice. All authors contributed critically to the drafts and gave final approval for publication.

References

Alford, D.V., 1975. Bumblebees. Davis-Poynter, London

Bailey, S., Requier, F., Nusillard, B., Roberts, S.P.M., Potts, S.G., Bouget, C., 2014. Distance from forest edge affects bee pollinators in oilseed rape fields. Ecol. Evol. 4, 370–380. https://doi.org/10.1002/ece3.924

Banks, J.E., Banks, H.T., Myers, N., Laubmeier, A.N., Bommarco, R., 2020. Lethal and sublethal effects of toxicants on bumble bee populations: a modelling approach. Ecotoxicology 29, 237–245. https://doi.org/10.1007/s10646-020-02162-y

Baron, G.L., Jansen, V.A.A., Brown, M.J.F., Raine, N.E., 2017. Pesticide reduces bumblebee colony initiation and increases probability of population extinction. Nat. Ecol. Evol. 1, 1308–1316. https://doi.org/10.1038/s41559-017-0260-1

Barton, K., 2019. MuMIn: Multi-Model Inference. R package version 1.43.15. https://CRAN.R-project.org/package=MuMIn

Bertrand, C., Eckerter, P.W., Ammann, L., Entling, M.H., Gobet, E., Herzog, F., Mestre, L., Tinner, W., Albrecht, M., 2019. Seasonal shifts and complementary use of pollen sources by two bees, a lacewing and a ladybeetle species in European agricultural landscapes. J. Appl. Ecol. 56, 2431–2442. https://doi.org/10.1111/1365-2664.13483

Beug, H.J., 2015. Leitfaden der Pollenbestimmung für Mitteleuropa und angrenzende Gebiete, second ed. Publishing House Dr. Friedrich Pfeil, Munich

Beyer, N., Gabriel, D., Kirsch, F., Schulz-Kesting, K., Dauber, J., Westphal, C., 2020. Functional groups of wild bees respond differently to faba bean Vicia faba L. cultivation at landscape scale. J. Appl. Ecol. 1–10. https://doi.org/10.1111/1365-2664.13745

Biesmeijer, J.C., Roberts, S.P.M., Reemer, M., Ohlemüller, R., Edwards, M., Peeters, T., Schaffers, A.P., Potts, S.G., Kleukers, R., Thomas, C.D., Settele, J., Kunin, W.E., 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. Science 313, 351–354. https://doi.org/10.1126/science.1127863

Bohart, G.E., Nye, W.P., 1956. Bees. Foraging for nectar and pollen. Gleanings Bee Cult. 84 (10): 602–606

Bond, D.A. & Poulson, M.H., 1983. Pollination. In P. D. Hebblethwaite (Ed.), The faba bean (Vicia faba L.) (pp. 77–101). London, UK: Butterworths.

Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Maechler, M., Bolker, B.M., 2017. GlmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R Journal 9(2): 378-400

Brown, M.J.F., Schmid-Hempel, R., Schmid-Hempel, P., 2003. Strong context-dependent virulence in a host-parasite system: Reconciling genetic evidence with theory. J. Anim. Ecol. 72, 994–1002. https://doi.org/10.1046/j.1365-2656.2003.00770.x

Cameron, S.A., Lozier, J.D., Strange, J.P., Koch, J.B., Cordes, N., Solter, L.F., Griswold, T.L., 2011. Patterns of widespread decline in North American bumble bees. Proc. Natl. Acad. Sci. 108, 662–667. https://doi.org/10.1073/pnas.1014743108

Carnell, J.D., Hulse, R.A., Hughes, W.O.H., 2020. A review of nutrition in bumblebees: The effect of caste, life-stage and life history traits. Adv. In Insect Phys. 59, 71–129. https://doi.org/10.1016/bs.aiip.2020.09.003

Carvell, C., Bourke, A.F.G., Dreier, S., Freeman, S.N., Hulmes, S., Jordan, W.C., Redhead, J.W., Sumner, S., Wang, J., Heard, M.S., 2017. Bumblebee family lineage survival is enhanced in high-quality landscapes. Nature 543, 547–549. https://doi.org/10.1038/nature21709

Carvell, C., Rothery, P., Pywell, R.F., Heard, M.S., 2008. Effects of resource availability and social parasite invasion on field colonies of Bombus terrestris. Ecol. Entomol. 33, 321–327. https://doi.org/10.1111/j.1365-2311.2007.00961.x

Carvell, C., Meek, W.R., Pywell, R.F., Goulson, D., Nowakowski, M., 2007. Comparing the efficacy of agri-environment schemes to enhance bumble bee abundance and diversity on arable field margins. J. Appl. Ecol. 44, 29–40. https://doi.org/10.1111/j.1365-2664.2006.01249.x

Carvell, C., Roy, D.B., Smart, S.M., Pywell, R.F., Preston, C.D., Goulson, D., 2006. Declines in forage availability for bumblebees at a national scale. Biol. Conserv. 132, 481–489. https://doi.org/10.1016/j.biocon.2006.05.008

Corbet, S.A., Williams, I.H., Osborne, J.L., 1991. Bees and the pollination of crops and wild flowers in the European community. Bee World 72, 47–59. https://doi.org/10.1080/0005772X.1991.11099079

Crone, E.E., Williams, N.M., 2016. Bumble bee colony dynamics: Quantifying the importance of land use and floral resources for colony growth and queen production. Ecol. Lett. 19, 460–468. https://doi.org/10.1111/ele.12581

Delaplane, K.S., Mayer, D.F., 2000. Crop pollination by bees. CABI Publishing. https://doi.org/10.1079/9780851994482.0000

Duchateau, M.J., Velthuis, H.H.W., 1988. Development and reproductive strategies in Bombus terrestris colonies. Behaviour 107(3/4): 186–207. https://doi.org/10.1163/156853988X00340

Dustmann, J., 2006. Honiguntersuchung - Richtlinien zur Untersuchung/ Beurteilung von Honig unter dem Warenzeichen des Deutschen Imkerbundes e.V. pp. 1–8.

Eckerter, P.W., Albus, L., Natarajan, S., Albrecht, M., Ammann, L., Gobet, E., Herzog, F., Tinner, W., Entling, M.H., 2020. Using temporally resolved floral resource maps to explain bumblebee colony performance in agricultural landscapes. Agronomy 10. https://doi.org/10.3390/agronomy10121993

Eckhardt, M., Haider, M., Dorn, S., Müller, A., 2014. Pollen mixing in pollen generalist solitary bees: A possible strategy to complement or mitigate unfavourable pollen properties? J. Anim. Ecol. 83, 588–597. https://doi.org/10.1111/1365-2656.12168

European Commission, 2017. Evaluation study of the payment for agricultural practices beneficial for the climate and the environment – Final report. European Commission. https://doi.org/10.2762/71725

Eurostat, 2021. Land use statistics. https://ec.europa.eu/eurostat/statistics-explained/index.php?title=Land_use_statistics#Land_use (accessed 01 September 2021)

Federal Agency for Cartography and Geodesy, 2018. Authoritative Topographic-Cartographic Information System/ Digitales Basis-Landschaftsmodell (Basis-DLM). Retrieved from https://gdz.bkg.bund.de/index.php/default/digitale-geodaten/digitale-landschaftsmodelle/digitales-basis-landschaftsmodell-ebenen-basis-dlm-ebenen.html

Fussell, M., Corbet, S.A., 1992. Flower usage by bumble-bees: A basis for forage plant management. J. Appl. Ecol. 29, 451-465. https://doi.org/10.2307/2404513

Garrat, M., Coston, D.J., Truslove, C.L., Lappage, M.G., Polce, C., Dean, R., Potts, S.G., 2014. The identity of crop pollinators helps target conservation for improved ecosystem services. Biol. Conserv., 169, 128–135. https://doi.org/10.1016/j.biocon.2013

Génissel, A., Aupinel, P., Bressac, C., Tasei, J.-N., Chevrier, C., 2002. Influence of pollen origin on performance of Bombus terrestris micro-colonies. Entomol. Exp. Appl. 104, 329–336. https://doi.org/10.1046/j.1570-7458.2002.01019.x

Gervais, A., Fournier, V., Bélisle, M., 2020. Agricultural landscape composition affects the development and life expectancy of colonies of Bombus impatiens. Ecosphere 11. https://doi.org/10.1002/ecs2.3142

Goulson, D., Connor, S.O., Park, K.J., 2018. Causes of colony mortality in bumblebees 21, 45–53. https://doi.org/10.1111/acv.12363

Goulson, D., Nicholls, E., Botías, C., Rotheray, E.L., 2015. Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. Science 347 (6229), 1-9. https://doi.org/10.1126/science.1255957

Goulson, D., Whitehorn, P., Fowley, M., 2012. Influence of urbanisation on the prevalence. Ecol Entmol 37, 83–89. https://doi.org/10.1111/j.1365-2311.2011.01334.x

Goulson, D., 2010. Bumblebees: Behaviour, ecology, and conservation. Second ed. Oxford University Press, New York

Goulson, D., Hughes, W.O.H., Derwent, L.C., Stout, J.C., 2002. Colony growth of the bumblebee, Bombus terrestris, in improved and conventional agricultural and suburban habitats. Oecologia 130, 267–273. https://doi.org/10.1007/s004420100803

Grace, J.B., Schreiner, S.M., Schoolmaster, D.R., 2015. Structural equation modeling: Building and evaluating causal models. In G.A. Fox, S. Negrete-Yanlelevich, V.J. Sosa (Eds.), Ecological statistics: Contemporary theory and application. Oxford University Press. https://doi.org/10.1093/acprof:oso/9780199672547.003.0009

Hass, A.L., Brachmann, L., Batáry, P., Clough, Y., Behling, H., Tscharntke, T., 2018. Maize-dominated landscapes reduce bumblebee colony growth through pollen diversity loss. J. Appl. Ecol. 56, 294–304. https://doi.org/10.1111/1365-2664.13296

Hemberger, J., Frappa, A., Witynski, G., Gratton, C., 2020. Saved by the pulse? Separating the effects of total and temporal food abundance on the growth and reproduction of bumble bee microcolonies. Basic Appl. Ecol. 45, 1–11. https://doi.org/10.1016/j.baae.2020.04.004

Holland, J.M., Douma, J.C., Crowley, L., James, L., Kor, L., Stevenson, D.R.W., Smith, B.M., 2017. Semi-natural habitats support biological control, pollination and soil conservation in Europe. A review. Agron. Sustain. Dev. 37. https://doi.org/10.1007/s13593-017-0434-x

Hovestadt, T., Mitesser, O., Poethke, A., Holzschuh, A., 2019. Explaining the variability in the response of annual eusocial insects to mass-flowering events. J. Anim. Ecol. 88, 178–188. https://doi.org/10.1111/1365-2656.12908

Kämper, W., Werner, P.K., Hilpert, A., Westphal, C., Blüthgen, N., Eltz, T., Leonhardt, S.D., 2016. How landscape, pollen intake and pollen quality affect colony growth in Bombus terrestris. Landsc. Ecol. 31, 2245–2258. https://doi.org/10.1007/s10980-016-0395-5

Kirk, W.D.J., Howes, F.N. 2012. Plants for bees. A guide to the plants that benefit the bees of the British Isles. International Bee Research Association, Cardiff, UK

Kremen, C., Williams, N.M., Thorp, R.W. 2002. Crop pollination from native bees at risk from agricultural intensification. PNAS 99 (26) 16812-16816. https://doi.org/10.1073/pnas.262413599

Lefcheck JS, 2016. PiecewiseSEM: Piecewise structural equation modelling in R for ecology, evolution, and systematics. Methods Ecol Evol 7(5): 573-579. https://doi.org/10.1111/2041-210X.12512

Leidenfrost, R.M., Bänsch, S., Prudnikow, L., Brenig, B., Westphal, C., Wünschiers, R., 2020. Analyzing the dietary diary of bumble bee. Front. Plant Sci. 11, 1–9. https://doi.org/10.3389/fpls.2020.00287

Leonhardt, S.D., Blüthgen, N., 2012. The same, but different: Pollen foraging in honeybee and bumblebee colonies. Apidologie 43, 449–464. https://doi.org/10.1007/s13592-011-0112-y

Manson, J.S., Otterstatter, M.C., Thomson, J.D., 2010. Consumption of a nectar alkaloid reduces pathogen load in bumble bees 81–89. https://doi.org/10.1007/s00442-009-1431-9

Marzinzig, B., Brünjes, L., Biagioni, S., Behling, H., Link, W., Westphal, C., 2018. Bee pollinators of faba bean (Vicia faba L.) differ in their foraging behaviour and pollination efficiency. Agric. Ecosyst. Environ. 264, 24–33. https://doi.org/10.1016/j.agee.2018.05.003

Matthias, I., Semmler, M.S.S., Giesecke, T., 2015. Pollen diversity captures landscape structure and diversity. J. Ecol. 103, 880–890. https://doi.org/10.1111/1365-2745.12404

Moerman, R., Vanderplanck, M., Fournier, D., Jacquemart, A., Michez, D., 2017. Pollen nutrients better explain bumblebee colony development than pollen diversity. Insect Conserv. Divers. 10, 171–179. https://doi.org/10.1111/icad.12213

Nieto, A., Roberts, S.P.M., Kemp, J., Rasmont, P., Kuhlmann, M., García Criado, M., Biesmeijer, J.C., Bogusch, P., Dathe, H.H., De la Rúa, P., De Meulemeester, T., Dehon, M., Dewulf, A., Ortiz-Sánchez, F.J., Lhomme, P., Pauly, A., Potts, S.G., Praz, C., Q., Window, J., Michez, D., 2014. European red list of bees, IUCN global species programm. https://doi.org/10.2779/77003

Pelletier, L., Mcneil, J.N., 2003. The effect of food supplementation on reproductive success in bumblebee field colonies. OIKOS 103(3): 688–694. https://doi.org/10.1034/j.1600-0706.2003.12592.x

Pinheiro J.C., Bates D.M., DebRoy S.S., Sarkar D., R Core Team, 2020. Nlme: Linear and nonlinear mixed effects models. R package version 3.1-144, URL: https://CRAN.R-project.org/package=nlme

Proesmans, W., Smagghe, G., Meeus, I., Bonte, D., Verheyen, K., 2019. The effect of mass-flowering orchards and semi-natural habitat on bumblebee colony performance. Landsc. Ecol. 34, 1033–1044. https://doi.org/10.1007/s10980-019-00836-5

Pouvreau, A., 1967. Contribution a l'étude morphologique et biologique d'Aphomia sociella L. (Lepidoptera, Heteroneura, Pyralidoidea, Pyralididæ), parasite des nids de bourdons (Hymenoptera, Apoidea, Bombus Latr.) Insectes Sociaux, Paris. 57-72

QGIS Development Team, 2019. QGIS geographic information system. Open source geospatial foundation. URL: http://qgis.org

R Core Team, 2020. R: A language and environment for statistical computing. R foundation for statistical computing, Vienna, Austria. URL: https://www.R-project.org/

Rasmont, P., Franzén, M., Lecocq, T., Harpke, A., Roberts, S.P.M., Biesmeijer, J.C., Castro, L., Cederberg, B., Dvorák, L., Fitzpatrick, Ú., Gonseth, Y., Haubruge, E., Mahé, G., Manino, A., Michez, D. Neumayer, J., Ødegaard, F., Paukkunen, J., Pawlikowski, T., Potts, S.G., Reemer, M., Settele, J., Straka, J., Schweiger, O., 2015. Climatic risk and distribution atlas of European bumblebees. Biorisk 10 (Special Issue). 246 pp. https://doi.org/10.3897/biorisk.10.4749

Redhead, J.W., Dreier, S., Bourke, A.F.G., Heard, M.S., Jordan, W.C., Sumner, S., Wang, J., Carvell, C., 2016. Effects of habitat composition and landscape structure on worker foraging distances of five bumble bee species. Ecol. Appl. 26, 726–739. https://doi.org/10.1890/15-0546/suppinfo

Requier, F., Jowanowitsch, K.K., Kallnik, K., Steffan-Dewenter, I., 2020. Limitation of complementary resources affects colony growth, foraging behavior, and reproduction in bumble bees. Ecology 101. https://doi.org/10.1002/ecy.2946

Roulston, T.H., Cane, J.H., 2000. Pollen nutritional content and digestibility for animals. Plant Syst. Evol. 222, 187–209. https://doi.org/10.1007/BF00984102

Rotheray, E.L., Osborne, J.L., Goulson, D., 2017. Quantifying the food requirements and effects of food stress on bumble bee colony development. J. Apic. Res. 56, 288–299. https://doi.org/10.1080/00218839.2017.1307712

Ruedenauer, F.A., Raubenheimer, D., Kessner-Beierlein, D., Grund-Mueller, N., Noack, L., Spaethe, J., Leonhardt, S.D., 2020. Best be(e) on low fat: linking nutrient perception, regulation and fitness. Ecol. Lett. 23, 545–554. https://doi.org/10.1111/ele.13454

Ruedenauer, F.A., Spaethe, J., Leonhardt, S.D., 2016. Hungry for quality—individual bumblebees forage flexibly to collect high-quality pollen. Behav. Ecol. Sociobiol. 70, 1209–1217. https://doi.org/10.1007/s00265-016-2129-8

Rundlöf, M., Persson, A.S., Smith, H.G., Bommarco, R., 2014. Late-season mass-flowering red clover increases bumble bee queen and male densities 172, 138–145. https://doi.org/10.1016/j.biocon.2014.02.027

Samuelson, A.E., Gill, R.J., Brown, M.J.F., Leadbeater, E., 2018. Lower bumblebee colony reproductive success in agricultural compared with urban environments. Proceedings of the Royal Society B: Biological Sciences. Royal Society Publishing. https://doi.org/10.1098/rspb.2018.0807

Schellhorn, N.A., Gagic, V., Bommarco, R., 2015. Time will tell: Resource continuity bolsters ecosystem services. Trends Ecol. Evol. 30, 524–530. https://doi.org/10.1016/j.tree.2015.06.007

Schmid-Hempel, R., Eckhardt, M., Goulson, D., Heinzmann, D., Lange, C., Plischuk, S., Escudero, L.R., Salathé, R., Scriven, J.J., Schmid-Hempel, P., 2014. The invasion of southern South America by imported bumblebees and associated parasites. J. Anim. Ecol. 83, 823–837. https://doi.org/10.1111/1365-2656.12185

Schweiger, O., Biesmeijer, J.C., Bommarco, R., Hickler, T., Hulme, P.E., Klotz, S., Kuhn, I., Moora, M., Nielsen, A., Ohlemuller, R., Petanidou, T., Potts, S.G., Pysek, P., Stout, J.C., Sykes, M.T., Tscheulin, T., Vila, M., Walther, G.R., Westphal, C., Winter, M., Zobel, M. & Settele, J. (2010). Multiple stressors on biotic interactions: how climate change and alien species interact to affect pollination. Biological Reviews, 85, 777-795. https://doi.org/10.1111/j.1469-185X.2010.00125.x.

Schweiger, S., Beyer, N; Hass, A. L.; Westphal, C., 2021: Code and data from "Pollen richness and parasitism but not landscape composition determine reproductive success of bumblebees in agricultural landscapes". Figshare. Dataset. https://doi.org/10.6084/m9.figshare.14256386.v1

Spear, D.M., Silverman, S., Forrest, J.R.K., 2016. Asteraceae Pollen Provisions Protect Osmia Mason Bees (Hymenoptera : Megachilidae) from Brood Parasitism 187. https://doi.org/10.1086/686241

Sperfeld, E., Martin-Creuzburg, D., Wacker, A., 2012. Multiple resource limitation theory applied to herbivorous consumers: Liebig's minimum rule vs. interactive co-limitation. Ecol. Lett. 15, 142–150. https://doi.org/10.1111/j.1461-0248.2011.01719.x

Tasei, J.N., Aupinel, P., 2008. Nutritive value of 15 single pollens and pollen mixes tested on larvae produced by bumblebee workers (Bombus terrestris, Hymenoptera: Apidae). Apidologie 39, 397–409. https://doi.org/10.1051/apido:2008017

Udy, K.L., Reininghaus, H., Scherber, C., Tscharntke, T., 2020. Plant–pollinator interactions along an urbanization gradient from cities and villages to farmland landscapes. Ecosphere 11. https://doi.org/10.1002/ecs2.3020

Vaidya, C., Fisher, K., Vandermeer, J., 2018. Colony development and reproductive success of bumblebees in an urban gradient. Sustain. 10, 1–14. https://doi.org/10.3390/su10061936

Vanbergen, A.J., Garratt, M. P., Vanbergen, A.J., Baude, M., Biesmeijer, J.C., Britton, N.F., Brown, M.J.F., Brown, M., Bryden, J., Budge, G.E., Bull, J.C., Carvell, C., Challinor, A.J., Connolly, C.N., Evans, D.J., Feil, E.J., Garratt, Mike P., Greco, M.K., Heard, M.S., Jansen, V.A.A., Keeling, M.J., Kunin, W.E., Marris, G.C., Memmott, J., Murray, J.T., Nicolson, S.W., Osborne, J.L., Paxton, R.J., Pirk, C.W.W., Polce, C., Potts, S.G., Priest, N.K., Raine, N.E., Roberts, S., Ryabov, E. V., Shafir, S., Shirley, M.D.F., Simpson, S.J., Stevenson, P.C., Stone, G.N., Termansen, M., Wright, G.A., 2013. Threats to an ecosystem service: Pressures on pollinators. Front. Ecol. Environ. 11, 251–259. https://doi.org/10.1890/120126

Veloso, M.M., MATEUS, C., JOSÉ SUSO M., 2016. An overview of Vicia faba role in ecosystems sustainability and perspectives for its improvement. Revista de Ciências Agrárias 39 (4): 490–505. https://doi.org/10.19084/RCA16098

Westphal, C., Steffan-Dewenter, I., Tscharntke, T., 2009. Mass flowering oilseed rape improves early colony growth but not sexual reproduction of bumblebees. J. Appl. Ecol. 46, 187–193. https://doi.org/10.1111/j.1365-2664.2008.01580.x

Westphal, C., Steffan-Dewenter, I., Tscharntke, T., 2006^a. Bumblebees experience landscapes at different spatial scales: Possible implications for coexistence. Oecologia 149, 289–300. https://doi.org/10.1007/s00442-006-0448-6

Westphal, C., Steffan-Dewenter, I., Tscharntke, T., 2006b. Foraging trip duration of bumblebees in relation to landscape-wide resource availability. Ecol. Entomol 31:389-394. https://doi.org/ 10.1111/j.1365-2311.2006.00801.x

Westphal, C., Steffan-Dewenter, I., Tscharntke, T., 2003. Mass flowering crops enhance pollinator densities at a landscape scale. Ecol. Lett. 6, 961–965. https://doi.org/10.1046/j.1461-0248.2003.00523.x

Westrich, P., 2018. Die Wildbienen Deutschlands. Eugen Ulmer KG, Stuttgart.Williams, N.M., Regetz, J., Kremen, C., 2012. Landscape-scale resources promote colony growth but not reproductive performance of bumble bees, Ecology 93, 1049–1058. https://doi.org/10.1890/11-1006.1

Williams, P.H., Osborne, J.L., 2009. Bumblebee vulnerability and conservation world-wide. Apidologie 40, 367–387. https://doi.org/10.1051/apido/2009025

Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problems. Methods Ecol. Evol. 1, 3–14. https://doi.org/10.1111/j.2041-210x.2009.00001.x

Supplementary Material

Calculation of landscape diversity

For each study landscape, landscape diversity was calculated as Shannon index (Krauss et al., 2003; Steffan-Dewenter et al., 2002) of twelve different land-use types using the *vegan* package (Oksanen et al., 2019). Following land-use types were utilized: arable land, urban area, water bodies, forest, groves, hedgerows, intensive grasslands, extensive/calcareous grasslands, orchard meadows, succession sites, fallows/ruderal sites, sown flower strips or fields.

References

Krauss J, Steffan-Dewenter I, Tscharntke T (2003) How does landscape context contribute to effects of habitat fragmentation on diversity and population density of butterflies? Journal of Biogeography 30: 889-900.

Steffan-Dewenter I, Münzenberg U, Bürger C, Thies C, Tscharntke T (2002) Scale-dependent effects of landscape context on three pollinator guilds. Ecology 83: 1421–1432. https://doi.org/10.1890/0012-9658(2002)083[1421:SDEOLC]2.0.CO;2

Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn M, Minchin R, O´Hara RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E, Wagner H (2019) vegan: Community Ecology Package. R package version 2.5-6. https://CRAN.R-project.org/package=vegan

Figures

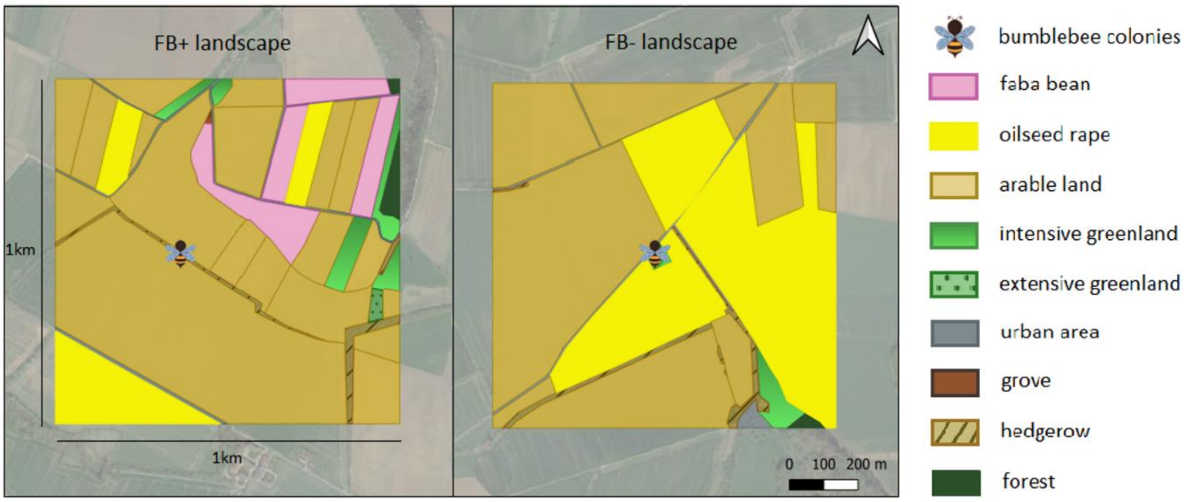

Figure A.1 Example of a landscape pair (FB+ and FB- landscape) with mapped landscape composition and the position of two neighbouring bumblebee colonies in the middle of the 1x1 km study landscape.

Figure A.2 Experimental setup of the *B. terrrestris* colonies in the study landscapes. In each landscape two bumblebee colonies were placed next to each other. They were placed on stones and covered by wooden roofs for protection.

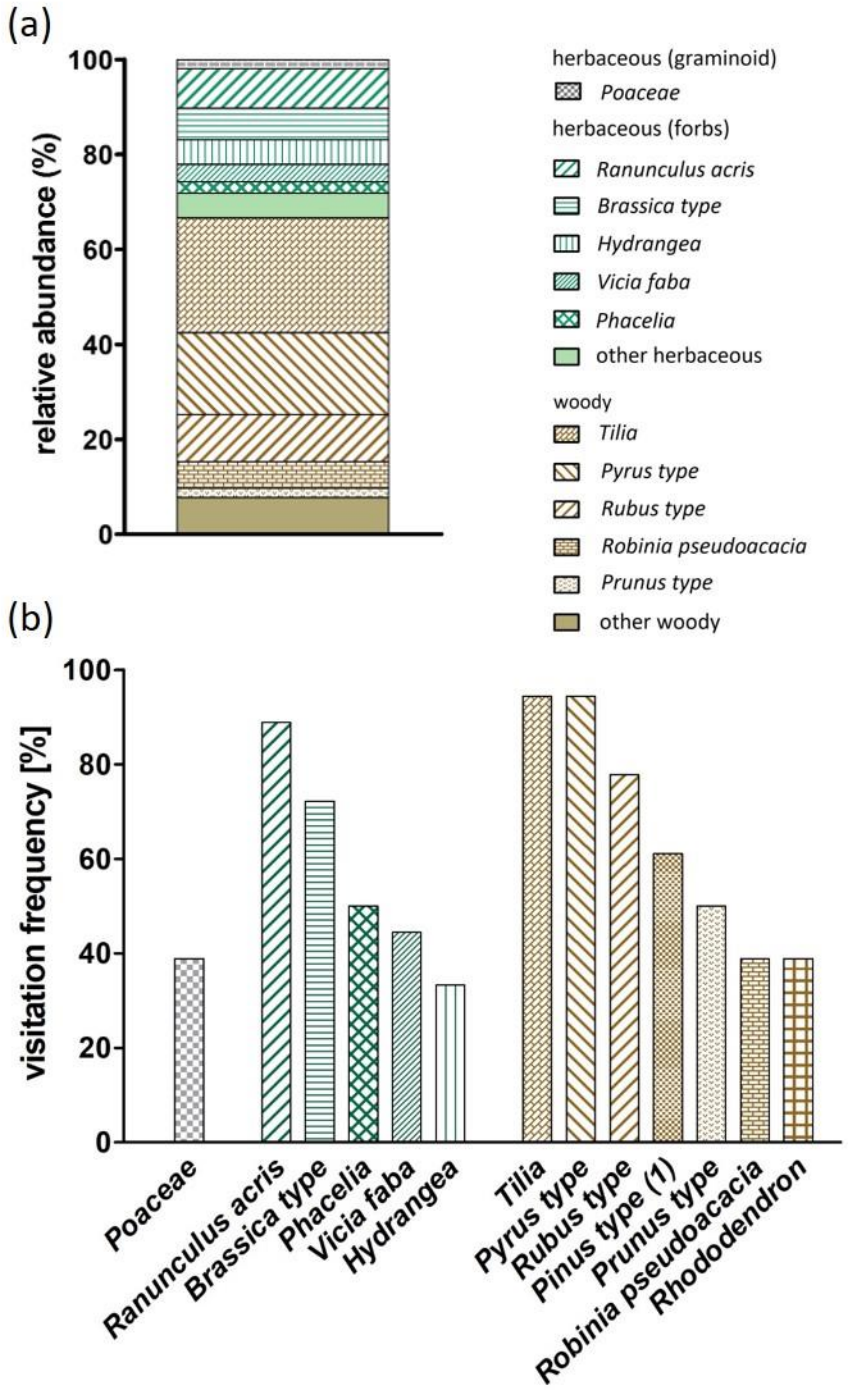

Figure A.3 Composition of the collected pollen samples. (**a**) Percentage of pollen types categorized according to plant functional groups giving the number of counted pollen grains added up over all landscapes and all sampling rounds. Pollen types with >500 pollen grains (see also Table A.3) were presented separately, pollen types with less than 500 grains were grouped. (**b**) The most frequently collected pollen types (collected in more than 30% of our landscapes) indicating dominant pollen sources for bumblebees.

Tables

Table A.1 Definitions of all habitat types (grassy and woody) considered as semi-natural habitats (SNH) in our study.

Habitat type	**Habitat category**	**Definition**
Extensive grassland	grassy	extensively managed (calcerous) grassland with diverse and flower-rich character; no shrubs present
Succession	woody or grassy	initial state of succession; emerging shrubs are present but grassy vegetation still dominating most of the area habitat area is mainly covered with grassy vegetation (>50%)
Grove	woody	woody structure; mainly trees; width > 10 m; not part of a larger forest patch but isolated in the arable matrix
Hedgerow	woody	Linear woody structure; mainly shrubs; longer than wide; width ≤ 10 m
Flower strip / area	grassy	Linear or areal habitat with flowering plants sown as an agri-environmental measurement
Orchard meadows	grassy	Grass-dominated areal habitat with a stand of old fruit trees; extensively managed or abandoned
Fallows	grassy	Areal fallow land; dominated by naturally occurring pioneer vegetation (e.g. *Cirium spp.; Arctium spp.; Urtica dioica; Atriplex spp.)*
Ruderal site	woody	open soil; dominated by pioneer vegetation

Table A.2 Time interval of the visitation rounds and MFC main blooming status at the time of visitation

Visitation round	**Time period**	**Mass flowering**
1	11/05 - 16/05/2018	*B. napus*
2	28/05 - 03/06/2018	*V. faba (in the most)*
3	05/06 - 11/06/2018	*V. faba (only in some)*
4	15/06 - 21/06/2018	no
5	22/06 - 25/06/2018	no

Table A.3 Pollen types with plant families, identified from the collected pollen samples (*Beug* 2015) of *Bombus terrestris* L. workers in our study landscapes within round 1-3, grouped by woody or herbaceous character. The total sum of counted pollen grains across all study landscapes was calculated as the sum of the mean numbers of grains per pollen type and landscape based on all three sampling rounds The number of landscapes where the pollen type was present is given. Pollen type *Smilax* could not be clearly attributed to woody or herbaceous because the genus contains species of both characteristics. Graminoid Poaceae were considered separately from the other herbaceous forbs. Pollen types were identified by Melissopal – Pollenanalytik (Hammoor, Germany). The first 500 pollen grains of three subsamples of each pollen mixture (overall 4500 pollen grains per landscape) were identified using a light microscope and following the guidelines of pollen identification in honey samples (Dustmann 2006).

Pollen type	**Plant family**	**Total sum of counted pollen grains**	**Number of landscapes**
Herbaceous (forbs)			
Ranunculus acris	Ranunculaceae	2266	16
Brassica type	Brassicaceae	1802	13
Hydrangea	Hydrangeaceae	1412	6
Vicia faba	Fabaceae	990	8
Phacelia	Boraginaceae	659	9
Trifolium pratense	Fabaceae	357	2
Lotus corniculatus	Fabaceae	267	1
Liliaceae spec.	Liliaceae	205	1
Trifolium repens	Fabaceae	178	2
Papaver	Papaveraceae	73	4
Symphytum/Pulmonaria	Boraginaceae	63	3
Centaurea cyanus	Asteraceae	60	2
Nymphaea	Nymphaeaceae	42	3
Fragaria	Rosaceae	37	2
Allium	Amaryllidaceae	20	2
Viola tricolor	Violaceae	20	4
Potentilla	Rosaceae	17	1
Achillea	Asteraceae	15	1
Taraxacum	Asteraceae	15	1
Plantago	Plantaginaceae	13	1
Foeniculum	Apiaceae	12	2
Xanthium	Asteraceae	12	1
Filipendula	Rosaceae	10	1
Urtica	Urticariaceae	7	1
Centaurea jacea	Asteraceae	5	1
Echium	Boraginaceae	5	1
Scrophulariaceae spec.	Scrophulariaceae	5	1
Herbaceous (graminoid)			
Poaceae spec.	Poaceae	521	7
Woody plants			
Tilia	Malvaceae	6550	17
Pyrus type	Rosaceae	4692	17
Rubus type	Rosaceae	2695	14
Robinia pseudoacacia	Fabaceae	1497	7
Prunus type	Rosaceae	542	9
Buddleja	Scrophulariaceae	465	2
Castanea sativa	Fagaceae	265	1
Rhododendron	Ericaceae	255	7
Sambucus	Adoxaceae	175	4
Magnolia	Magnoliaceae	165	2
Aesculus	Sapindaceae	137	3
Quercus	Fagaceae	108	2
Pinus type _(1)_	Pinaceae	93	11
Cornus	Cornaceae	88	5

Rhamnus frangula	Rhamnaceae	78	2
Lonicera	Caprifoliaceae	62	5
Acer	Sapindaceae	48	3
Pinus* type *(2)	Pinaceae	32	3
Salix	Salicaceae	23	2
Ilex	Aquifoliaceae	18	2
Liriodendron	Magnoliaceae	13	1
Corylus avellana	Betulaceae	10	1
Gleditsia	Fabaceae	10	1
Viburnum	Adoxaceae	10	2
Crataegus	Rosaceae	5	1
Vitis	Vitaceae	5	1
others			
Smilax	Smilacaceae	5	1

Table A.4 Global models with response and explanatory variables which were pre-analysed for final structural equation model using linear mixed effect models. Landscape pairs were included in the models as random effect.

Response variable	Explanatory variable
Number of young queens ~	number of broodcells (Nbroodcells)
	availability of faba bean (FB)
	cover of oilseed rape (OSR) cover of semi-natural habitats (SNH) cover of urban area
	pollen diversity
	landscape diversity
	weight of wax moth
	FB: cover of OSR FB: cover of SNH FB: cover of urban area FB: pollen diversity FB: landscape diversity
	pollen diversity: weight of wax moth pollen diversity: cover of OSR pollen diversity: cover of SNH pollen diversity: cover of urban area pollen diversity: landscape diversity
Number of broodcells~	availability of faba bean (FB)
	cover of oilseed rape (OSR) cover of semi-natural habitats (SNH) cover of urban area
	pollen diversity
	landscape diversity
	weight of wax moth
	FB: cover of OSR FB: cover of SNH FB: cover of urban area FB: pollen diversity FB: landscape diversity
	pollen diversity: weight of wax moth pollen diversity: cover of OSR pollen diversity: cover of SNH pollen diversity: cover of urban area pollen diversity: landscape diversity
Pollen diversity ~	availability of faba bean (FB)
	cover of oilseed rape (OSR) cover of semi-natural habitats (SNH) cover of urban area
	landscape diversity
	FB: cover of OSR FB: cover of SNH FB: cover of urban area FB: landscape diversity
Weight of wax moth larvae ~	availability of faba bean (FB)
	cover of oilseed rape (OSR) cover of semi-natural habitats (SNH) cover of urban area
	pollen diversity
	landscape diversity
	FB: cover of OSR FB: cover of SNH FB: cover of urban area FB: pollen diversity FB: landscape diversity

Contrasting effects of past and present mass-flowering crop cultivation on bee pollinators shaping yield components in oilseed rape

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Abstract

The cultivation of mass-flowering crops (MFC) can promote pollinators by providing floral resources. However, there is missing knowledge about the effect of MFC cultivation history on bees and their pollination services in agricultural landscapes. We investigated how bee densities in oilseed rape (*Brassica napus* L.) (OSR) fields were affected by past (cultivation area of the preceding three years) and current MFC area coverages in the surrounding landscape. Moreover, we analyzed how insect pollination, its possible interaction with the plants` pod numbers and MFC covers influence yield components of individual OSR plants and calculated yields (t/ha). To test this, we conducted pollinator surveys and a pollinator exclusion experiment in one oilseed rape field in 17 agricultural landscapes in Germany. We found that wild bee densities were positively affected by past MFC covers and negatively impacted by current OSR covers, indicating enhanced pollinator populations due to previous MFC cultivation and contemporary pollinator dilution. In contrast, honeybees showed opposite responses to past and present MFC cultivation. Furthermore, seed weight per plant of open pollinated plants was positively correlated with past MFC covers. Pollinator exclusion decreased the seed number per pod and increased thousand-seed weight, while yields were unaffected. Pod number interacted with insect pollination in shaping yields, such that pollinator exclusion led to a steeper increase of yield with higher pod numbers. Insect pollination compensated for low pod numbers by increasing the plants` seed number per pod and ultimately yields. Our findings demonstrate a beneficial effect of high MFC covers in the past on bee densities and potentially yield components in the current year. Our study highlights the need for further research on how past and present landscape composition in terms of MFC cultivation interactively affect pollinator communities and their pollination services in agricultural landscapes.

Keywords

ecosystem services, honeybees, landscape history, landscape composition, *Vicia faba*, carry-over effects

Introduction

Insect pollination leads to yield increases in many agricultural grown crops and is essential for the preservation of wild plant diversity (Klein et al., 2007; Kremen et al., 2007). 75 % of the most important food crops worldwide benefit from animal pollination (Klein et al., 2007) and most essential nutrients are obtained from those plants (Eilers et al., 2011). The economic value of crop pollination has been estimated 153 billion € per year worldwide (Gallai et al., 2009). Hence, to ensure high and stable yields of pollinator-dependent crops, it is necessary to preserve diverse pollinator communities (Garibaldi et al., 2014; Woodcock et al., 2019).

Wild pollinators are associated with heterogeneous landscapes comprising various resources and nesting sites that are threatened by landscape simplification (Potts et al., 2010). Thus, the landscape surrounding croplands is influencing yields of flowering crops via pollinators and their pollination services (Dainese et al., 2019; Martin et al., 2019). Diverse landscapes with high amounts of semi-natural habitats and a higher habitat connectivity have been shown to increase yields in different crops (Castle et al., 2019; Petersen and Nault, 2014). Besides, the cultivation of mass-flowering crops (MFC), like oilseed rape (*Brassica napus* L.) or faba beans (*Vicia faba* L.) can enhance pollinator densities and species richness (Beyer et al., 2020; Diekötter et al., 2014; Westphal et al., 2003), alter plant pollinator interactions (Diekötter et al., 2010; Shaw et al., 2020) and affect the distribution of pollinators in agricultural landscapes (Holzschuh et al., 2016, 2011). The high attractiveness of MFC might also lead to pollinator dilution effects with negative implications for the pollination of co-flowering wild plants or crops (Bänsch et al., 2020a; Grab et al., 2017; Holzschuh et al., 2016, 2011; Riedinger et al., 2015). But, positive carry-over effects on wild bee densities from high covers of MFC in the previous year are also likely (Kallioniemi et al., 2017; Riedinger et al., 2015).

Although short-term effects of MFC on pollinators and pollination services are well studied, less focus has been on the effect of land-use history on present biodiversity and associated ecosystem functions, which are highly relevant for ecosystem management and conservation (Foster et al., 2003). So far, only few studies tested the effects of land-use legacy on present-day diversity that might be the result of historic rather than of contemporary land-use or landscape structure (Harding et al., 1998; Lindborg and Eriksson, 2004). Historical land-use might also affect community responses to present-day landscape changes (Aguirre-Gutiérrez et al., 2015). More research is needed on whether land-use history, such as MFC cultivation history (i.e. the amount of MFC in the previous years) affects wild bee densities and their pollination services in agricultural systems.

The most productive oleaginous crop and most grown MFC in the EU is oilseed rape (*Brassica napus* L.) (OSR) (FAOSTAT, 2020). OSR is predominantly self-pollinated but benefits from wind and cross-pollination through insects (Becker et al., 1992; Perrot et al., 2018). Yields of OSR are known to be positively correlated with the abundance and diversity of pollinators (Jauker et al., 2012a; Perrot et al., 2018; Zou et al., 2017). Yield increases, measured as seed weight per plant, between 12 and 20 % due to insect pollination have been reported (Bartomeus et al., 2014; Bommarco et al., 2012; Zou et al., 2017) and even an 46 % higher seed weight per m^2 following honeybee hive addition (Sabbahi et al., 2005). Moreover, insect pollination has been shown to increase the OSR seed oil content (Bartomeus et al., 2014; Bommarco et al., 2012; Marini et al., 2015), resulting in a 20 % higher market value (Bommarco et al., 2012). OSR flowers are visited by a variety of different insects and honeybees are most common visitors (Garratt et al., 2014; Marini et al., 2015; Perrot et al., 2018). Nevertheless, wild bees have been shown to be most effective pollinators of OSR due to a higher probability of stigmal contact (Woodcock et al., 2013).

It has been shown that OSR plants compensate for lower seed numbers with a higher seed weight following pollinator exclusion (Geisler, 1988; Grosse et al., 1992; Hudewenz et al., 2014; Marini et al., 2015; Zou et al., 2017). For this reason, it is important to consider the whole plant when analyzing pollination services and yield components (Ouvrard and Jacquemart, 2019). Another important determinant of OSR yield is the number of pods which besides leaves and stems, plays an important role in providing assimilates. 40 – 50 % of the assimilates stored in the seeds are obtained from photosynthesis of the pods (Geisler, 1988) and a higher assimilation area of pod hulls is positively correlated with the seed number per pod (Grosse et al., 1992). However, most recent studies do not consider effects of pod numbers on yield components. Hence, to fully understand how pod numbers shape OSR yields in interaction with biotic factors, like insect pollination, more knowledge is needed.

We conducted a pollinator exclusion experiment and surveyed wild bees in one OSR field in 17 landscapes in Germany with differing landscape composition in terms of MFC cultivation, in the current and the past three years. Regarding past MFC cultivation, we considered the last three years as we expected that it takes several years for wild bee populations to build up and thus for effects on bee densities and pollination services to be detected (three years according to Blaauw & Isaacs, 2014). We analyzed the effects of current and past MFC covers on honeybee and wild bee densities in OSR fields and the associated effects of insect pollination services on pod number, bee densities, past and present MFC covers on OSR yield components and yields. We tested the following hypotheses: (1) bee densities in OSR fields are diluted by high coverages of co-flowering OSR, (2) wild bee densities are enhanced by high coverages of MFC in the preceding years, (3) Insect pollination enhances OSR yield and interacts with the plants` pod number in determining yield and (4) past and present MFC cultivation interact with wild bee densities in shaping OSR yields.

Material and Methods

Study fields and landscape metrics

The study was conducted in the summer of 2018. We selected seventeen conventionally managed OSR fields (*Brassica napus* L.) in Lower Saxony in Germany (Fig. A1). All OSR rape fields were sown with a hybrid winter OSR variety, but varieties differed between study landscapes and could not be controlled during recruitment of collaborating farmers. OSR fields were at least 3 km apart to prevent wild bees, with foraging ranges up to several kilometers, to visit more than one study OSR field (Westphal et al., 2006). We characterized the landscape composition of the current and the past years within a buffer of 1000 m around each OSR field.. As landscape history metrics we utilized the area coverage (ha) of the two main MFC, grown in Germany, i.e. OSR (*Brassica napus* L.) and faba bean (*V. faba* L.) within the preceding three years (2015 – 2017) (MFC cover history). Both MFC have been shown to impact pollinators in agricultural landscapes (e.g. Beyer et al., 2020; Westphal et al., 2003). We summed the area coverage of OSR and faba bean (ha) within the 1000 m buffer over the preceding three years. Landscape composition of the current year was determined by the area coverage of OSR (ha) in 2018 (OSR cover). To test potential pollinator dilution effects through co-flowering MFC, we only focused on OSR here. That is because the bee surveys in our study OSR fields took place during the period of oilseed rape full bloom, which had already ended before *V. faba* started to bloom. Therefore, we do not expect faba beans to impact pollinator densities and yields of our study OSR fields. Since we focused on present OSR and MFC history, we did not record other landscape metrics. The amount of semi-natural habitats in a landscape is relatively stable over time and an analysis based on unpublished data from similar landscapes in the same study region, revealed that the cover of semi-natural habitats was not correlated with the cover of past and present MFC.

Experimental design

We randomly chose forty-four individual oilseed rape plants in every of the 17 oilseed rape fields before the onset of flowering during mid/end of April 2018. Plants were located in four different plots per field, i.e. 11 plants per plot (Fig. A2). Of the four plots, two were at the field border (maximum 5 m from field border) and two in the field center (at least 15 m from any field border). Individual plots were at least 10 m apart from each other. We assigned the 11 plants per plot to two different treatments: pollinator exclusion (five plants) and open pollination (six plants to account for potentially higher variability). We ensured that plants had a similar developmental stage and were at least 1 m apart from each other. For the pollinator exclusion treatment, we installed a bag made of fine mesh (mesh size 0.8 x 0.8 mm) around individual oilseed rape plants (20 plants per field) to prevent insects from visiting the flowers (bagged plants). Wind- and self-pollination was still possible. Every bag was fixed with four bamboo poles, which were fixed in the ground. Bags were big enough to prevent growing plants to be affected or damaged by the bag. We removed bags from oilseed rape plants after they had finished blooming (end of May) to enable plants to mature under natural conditions. The plants of the open pollination treatment (24 per field) were marked and not covered to enable natural insect pollination (open plants). Additionally, we recorded plant density at three different locations close to the field edge and at three locations in the field center by counting the number of all oilseed rape plants per m^2. Mean plant density was calculated for the field edge and the field center.

Pollinator surveys

We surveyed bees within every study oilseed rape field with two standardized transect walks (50 x 2 m, 5 min) per field: one close to the field edge and one in the field center, next to the experimental plots. Surveys took place on days with air temperature above 15 °C, low wind speed and no rain from 10 a.m. until 6:15 p.m (Westphal et al. 2008). We repeated transect walks two times during the oilseed rape bloom from 04 to 16 May 2018. The number of all flower visiting wild bees and honeybees was recorded and wild bees were sampled, when possible, for species identification. Since we observed very few wild bees, we focused on densities and did not analyze species richness. We additionally estimated the local flower cover (%) of the study OSR field during every transect walk.

Yield components and yield

Fully ripened plants were harvested manually just before fields got harvested at the beginning of July (in total 748). We counted the total number of pods per plant in the field and stored them in individual paper bags. Thereafter, we counted the total number of seeds per pod for 10 randomly chosen pods per plant. All counted seeds per plant were pooled and dried at 60 °C for 12 hours and weighted afterwards. This weight was divided by the respective total number of counted seeds (per 10 pods) to determine the average single seed weight per plant. Finally, we calculated the following yield components per plant: (1) the average number of seeds per pod, (2) the thousand seed weight (TSW) in g (average single seed weight * 1000), (3) the total seed weight per plant in g. Ultimately, we calculated the yields per plot in t/ha, which is the total seed weight per plant averaged across each individual plot, multiplied by the plant density of the respective plot location (edge or center), divided by 100.

Statistical analyses

Statistical analyses were done in R version 3.6.1 (R Core Team, 2019). To test the effect of landscape metrics on pollinator densities (bees per 100 m^2 and 5 min) (Hypothesis 1 & 2), we used a generalized linear mixed effects models with the *glmmTMB* package (Brooks et al., 2017). Explanatory variables were percentage flower cover of the study OSR field (FC), area coverage of OSR of the current year (OSR cover), the area coverage of MFC in the previous years (MFC cover history) and bee group (honeybees/wild bees) as well as all possible two-way interactions including bee group and the interaction between OSR cover and MFC history. We included sampling run nested in field ID as random effect. The global model was fitted with negative binomial family due to overdispersion.

To test how landscape composition and insect pollination affect yield components and yield in OSR, we conducted two separate analyses, using linear mixed effects models of the *nlme* package (Pinheiro et al., 2019). First, we analyzed the effect of insect pollination and plants` pod number on the yield components of OSR, comparing open pollinated and bagged plants (Hypothesis 3). Our response variables were the average number of seeds per pod, TSW, seed weight per plant and yield per plot. Predictor variables included in all models were treatment (bagged/open), bee density (honeybee and wild bees summed) and the plants` pod number and all possible two-way interactions with treatment. We analyzed yield components on plant level and yields on plot level by using the average number of pods per plant for every plot as response. Field ID and plot were included as nested random effects in all models. As we expect MFC cultivation to only affect open pollinated plants via pollinators, we analyzed MFC cultivation effects and potential interactions with bee densities on yield parameters of open pollinated OSR plants in a second step (Hypothesis 4). We used the same response variables as described above. Explanatory variables were honeybee densities, wild bee densities, OSR cover, MFC cover history and the interactions between landscape metrics and wild bee densities, between landscape metrics and between honeybee and wild bee densities. Field ID and plot were added as random effects for yield components and for yields only field ID was included. To meet normality assumptions, seed weight per plant and yield were square root transformed and for the analyses with the open pollinated plants seed weight per plant was log transformed. Furthermore, we standardized all continuous explanatory variables (FC, OSR cover, MFC cover history, pod number) to a mean of zero and a standard deviation of one to improve model convergence. For the case of analyses for seed weight per plant and yield, the variable pod number was square root transformed to meet linearity assumptions. We used the variance inflation factor (VIF) to test for potential collinearity between explanatory variables and VIF was below 2 in all cases (Zuur et al., 2010). To address potential problems with spatial autocorrelation we fitted global models with and without exponential and Gaussian spatial autocorrelation structures and compared models via AICc. In all cases, the model without spatial autocorrelation had the lowest AICc.

We followed a multimodel inference approach by Burnham & Anderson (2002). Based on the global models for pollinator densities and yield components, we fitted candidate models, containing all possible combinations of predictor variables with the *dredge* function of the *MuMIn* package (Barton, 2019). Candidate models were ranked by second order Akaike Information Criterion (AICc). We used Akaike weights (w_i) to estimate relative support of a model across all models (Burnham and Anderson, 2002). Moreover, we calculated the sum of Akaike weights (Σw_i) of all predictor variables across all models that included the variable as its relative importance. We interpreted all models with a delta AICc < 2 compared to the best fitting model and we report all predictor variables with $\Sigma w_i > 0.2$. In addition, if more than one best-fitting model was identified, we report full and conditional model averaged coefficients with 95 % confidence intervals in the supplementary material (Fig. A3), calculated with the *MuMIn* package (Barton, 2019). We inspected residual plots to validate model assumptions and calculated the marginal (R_m^2) and conditional (R_c^2) R^2 values (Nakagawa et al., 2017) with the *performance* package (Lüdecke et al., 2020) to evaluate the goodness of fit of our models. To test for differences of yield components between pollinator exclusion treatments we applied post hoc tests with the *emmeans* package (Lenth, 2019) and alpha level of 0.05. Additionally, concerning seed weight per plant and yield we used post hoc tests to test for differences between treatments at a low and a high pod number per plant using the 10th and the 90th quantile respectively. We obtained predictions and confidence intervals in scatter plots from the *effects* package (Fox & Weisberg, 2019) and generated all figures using *ggplot2* (Wickham, 2016).

Results

Mass-flowering crop cover effects on pollinators

In total, we observed 353 honeybee and 81 wild bee individuals (11 different species) visiting oilseed rape flowers. Sampled wild bees belonged to the genus *Andrena* (63.5 %) and *Bombus*. There were two best models explaining landscape composition and landscape history effects on honeybee and wild bee densities. The best-fitting model included pollinator group, the cover of OSR and the cover of MFC in the previous years, as well as their interactions with pollinator group (Table A1). All those variables had a sum of Akaike weights between 0.82 and 1.00 (Table A2). The second-best model additionally included the local flower cover ($\Sigma w_i = 0.40$). Wild bee densities were negatively correlated with the cover of OSR in the surrounding landscape, while honeybees showed a slight increase (Fig. 1a). Increasing cover of MFC in the preceding years had a positive effect on the densities of wild bees and a negative effect on honeybee densities (Fig. 1b). Bee densities (honeybees and wild bees) increased with enhanced local flower cover of the study OSR field (Fig. A4).

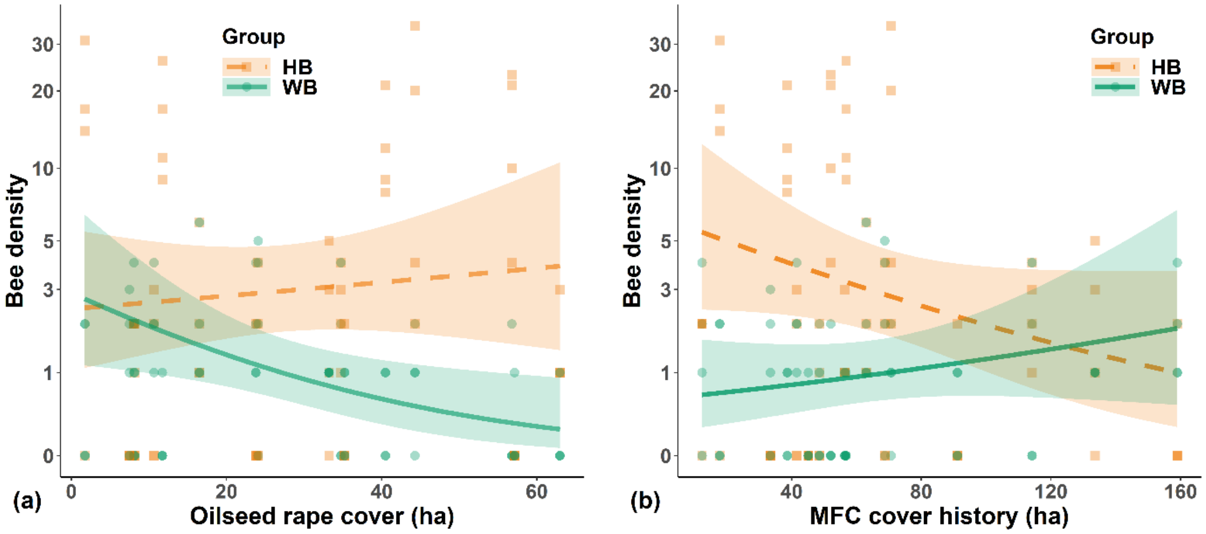

Figure 1 **(a)** Effect of oilseed rape cover (ha) in the current year on honey- (HB) and wild bee (WB) densities. **(b)** Effect of mass-flowering crop (MFC) cover history (ha; area coverage of the preceding three years) on honey- and wild bee densities. Lines depict model predictions with 95 % confidence intervals. Predictions were obtained from the best-fitting model *bee1* (Table A1).

Pollinator exclusion and pod number effects on yield components and yields

The seed number per pod was explained by three-best fitting models, including the pollinator exclusion treatment ($\Sigma w_i = 1.00$), number of pods ($\Sigma w_i = 1.00$), their interaction ($\Sigma w_i = 0.91$), bee density ($\Sigma w_i = 0.61$) and its interaction with treatment ($\Sigma w_i = 0.43$) (Table A3 & A4). The second and third best-fitting models were subsets of the best explaining model. The plants in the open pollinated treatment had on average 8.1 % more seeds per pod than bagged plants (Fig. 2a). The number of seeds per pod increased with increasing number of pods per plant, while this increase was stronger for bagged than open pollinated plants (Fig. 3a). For plants with a low pod number, open pollinated plants had more seeds per pod than bagged plants ($p<0.001$), while this difference disappeared for plants with a high pod number. Higher bee densities increased the number of seeds per pod, but only for open pollinated plants (Fig. 3b).

The best of the four candidate models within delta AICc < 2 for the thousand-seed weight included only treatment ($\Sigma w_i = 1.00$) (Table A3 & A4). The other best-fitting models contained, besides treatment, either bee density ($\Sigma w_i = 0.58$), the interaction between treatment and bee density ($\Sigma w_i = 0.25$) or pod number ($\Sigma w_i = 0.39$) (Table A3 & A4). Open pollinated plants had on average 5.5 % lower TSW than bagged plants (Fig. 2b). Bee density tended to negatively affect TSW of open pollinated plants (Fig. A5a). The plants` number of pods had no effect on TSW.

For seed weight per plant, there were seven best-fitting models (Table A3). The model with the lowest AICc contained treatment ($\Sigma w_i = 0.69$) and pod number ($\Sigma w_i = 1.00$). All best-fitting models were subsets of the last best-fitting model, which included treatment, pod number, bee density ($\Sigma w_i = 0.48$) and all interactions with treatment ($\Sigma w_i \leq 0.24$) (Table A3 & A4). Seed weight per plant did not differ between open and bagged plants (Fig. 2c) but was positively correlated with the number of pods per plant (Fig. 3c). Bee densities did not affect seed weight per plant.

The yields per plot were explained by four models within delta AICc < 2 (Table A3). The best fitting-model included pod number ($\Sigma w_i = 1.00$) and bee densities ($\Sigma w_i = 0.79$). The other models included in addition to the variables in the best-fitting model treatment ($\Sigma w_i = 0.64$), the interaction between pod number and treatment ($\Sigma w_i = 0.41$) and the interaction between bee density and treatment ($\Sigma w_i = 0.21$) (Table A3 & A4). Yield between open and bagged plants did not differ (Fig. 2d) but was positively correlated with the plants` pod number with stronger increase for bagged plants (Fig. 3c). For plants with a low pod number open pollinated plants tended to have higher yields than bagged plants ($p=0.07$), whereas for plants with a high pod number this difference disappeared (Fig. 3d). Bee densities had a negative influence on yield (Fig. A5b).

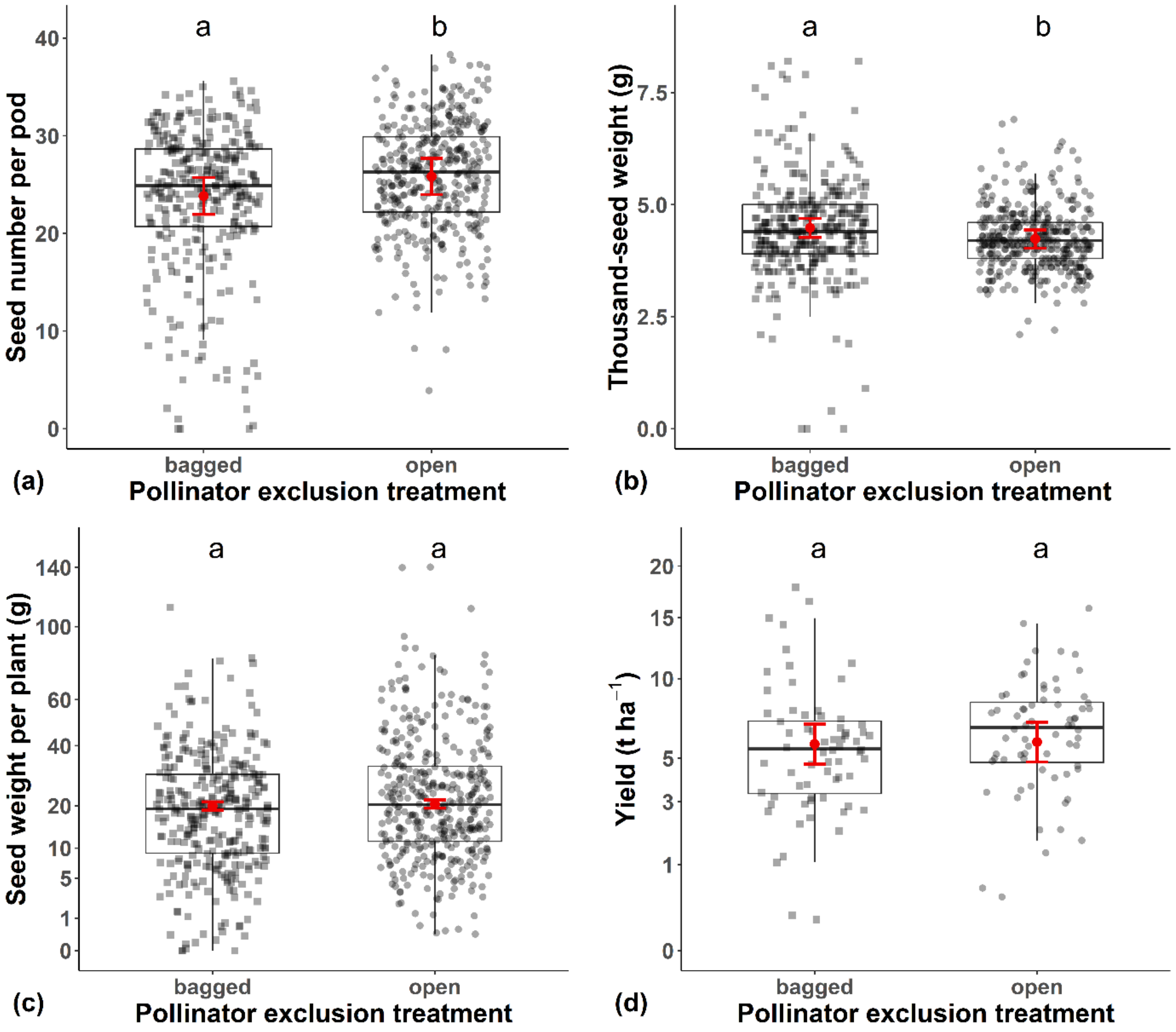

Figure 2 Effects of pollinator exclusion treatment on the **(a)** seed number per pod, **(b)** thousand-seed weight (g), **(c)** seed weight per plant (g) and **(d)** the yield (t/ha) in oilseed rape. Model predictions and 95 % confidence intervals are shown in red and were obtained from the respective best-fitting models *sn1, sw1, sp1* and the fourth best model *y4* for the case of yield (Table A3). Different letters above boxes indicate significant differences between bagged plants and open pollinated plants.

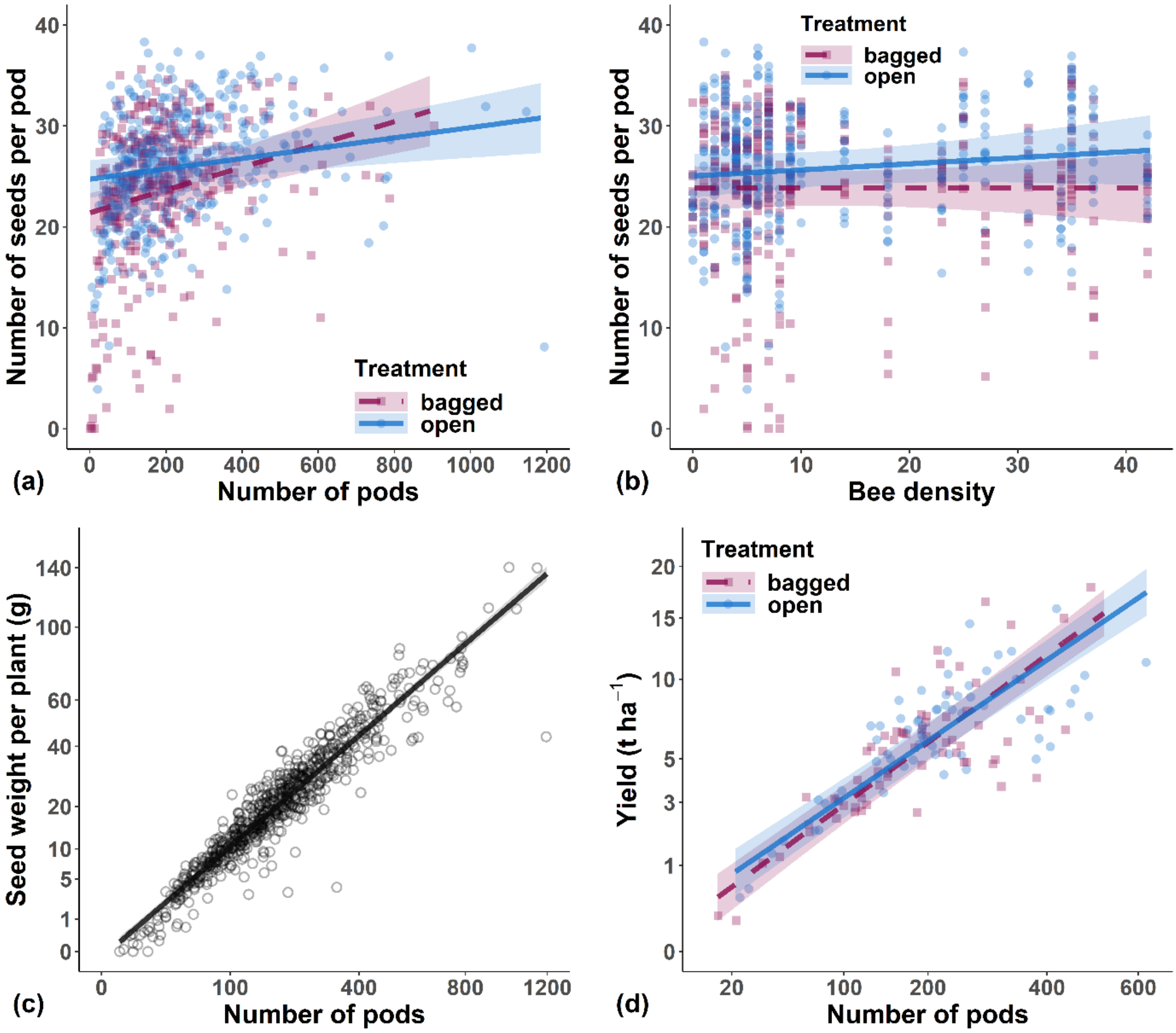

Figure 3 Effect of **(a)** pod number and of **(b)** bee density on the seed number per pod for open pollinated and bagged plants. Effect of pod number on **(c)** the seed weight per plant (g) and **(d)** yield in oilseed rape for bagged and open pollinated plants. Lines depict model predictions with 95 % confidence intervals. Model predictions were obtained from the respective best-fitting model *sn1*, *sp1* and the second-best fitting model *y2* for the case of yield (Table A3). Y- and x-axes in (c) and (d) are sqrt transformed.

Mass-flowering crop cover and pollinator effects on yield components and yields

Seed number per pod and yields of open pollinated plants were neither explained by past or present MFC cover, nor by honeybees or wild bee densities. In both cases, the null model was the model with the lowest AICc (Table A5). Thousand seed-weight was explained by the density of honeybees (Σw_i = 0.60) in terms of a decreasing seed weight of open pollinated plants with increasing bee densities. The null model was however the second-best fitting model with a dAICc of 0.18 and AIC weight almost as good as the best-fitting model (Table A5), which indicates a low support of the best model. For seed weight per plant, there were four best-fitting models within delta AICc < 2 (Table A5). The best-fitting model included MFC cover history (Σw_i = 0.83) and honeybee densities (Σw_i = 0.60), while additional to them, wild bee densities (Σw_i = 0.53) were included in the second-best model (Table A5&A6). The other models were subsets of the second-best one. MFC cover history (Fig. 4), honeybee densities and wild bee densities (Fig. A6) positively affected the seed weight per plant.

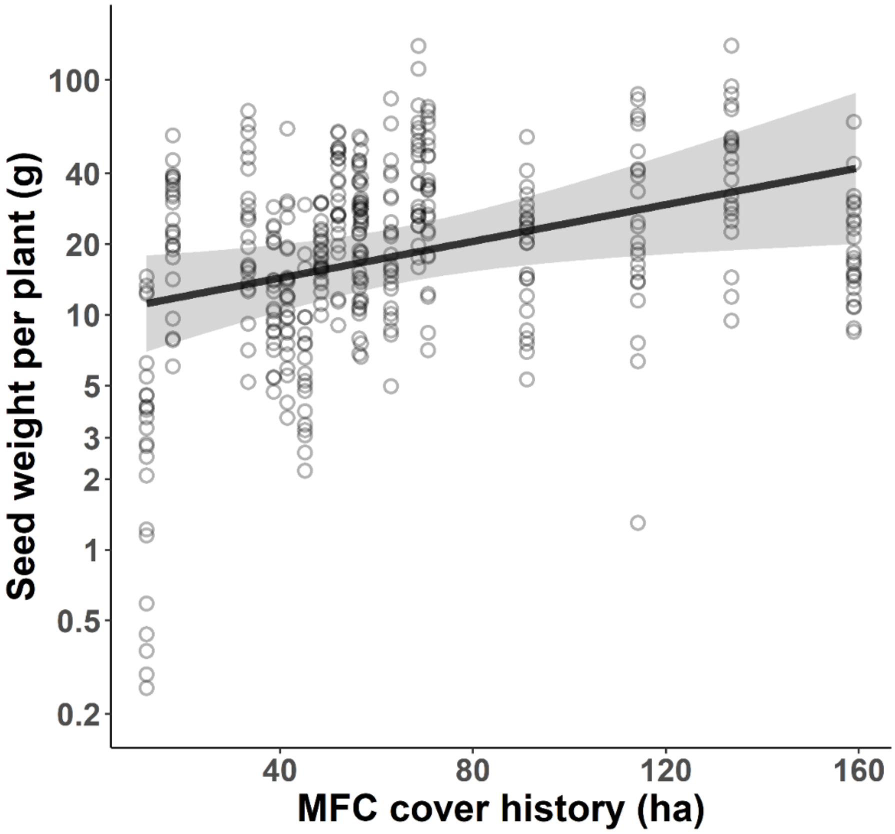

Figure 4 Effect of mass-flowering crop (MFC) cover history (ha; area coverage of the preceding three years on the seed weight per plant (g) for open pollinated oilseed rape plants. Lines depict model predictions with 95 % confidence intervals. Model predictions were obtained from the best-fitting model *spo1* (Table A5).

Discussion

In this study we investigated how past and present cover of availability of MFC affects pollinator densities and the provisioning of pollination services in OSR. We found that increasing OSR covers in the current year decreased wild bee densities in our study OSR fields, while a high cover of MFC in the past three years enhanced wild bee densities in OSR fields. Interestingly, compared to wild bees, honeybees showed contrasting effects to past and present MFC cultivation. Furthermore, seed weight per plant of open pollinated OSR plants was positively associated with high past MFC covers.

Mass-flowering crop cover effects on pollinators

High OSR covers dilute bee densities in OSR fields

Wild bee densities were affected in an opposite manner by MFC history and current OSR cover in the surrounding landscape. Moreover, wild bees and honeybees responded contrarily to MFC cultivation (see 4.1.3). Unlike honeybees, wild bee densities declined with increasing OSR covers in the present year. This suggests a dilution of wild bee pollinators due to high proportions of attractive OSR, which might negatively impact crop yields (Grab et al., 2017; Shaw et al., 2020). Considering that honeybee densities increased with higher OSR cover, bee densities would be similar in landscapes with a high and a low OSR cover. However, since wild bees are assumed to be the more effective OSR pollinators, (Woodcock et al., 2013), implications for crop yields are likely, independent of honeybees (Garibaldi et al., 2013). Besides pollination success of crops, also the pollination of wild plants might be adversely affected by a high amount of co-flowering crops in agricultural landscapes (Holzschuh et al., 2016, 2011), because wild bees move between crop and non-crop habitats according to their changing resource availability (Mandelik et al., 2012, Bänsch et al. 2020b). The contrasting positive effect of contemporary OSR cover on honeybee densities might mirror the number of hives in our study landscapes since beekeepers usually place honeybee hives in proximity to MFC. However, we did not record hive densities in the surroundings of the study fields.

High MFC covers in the past increase bee densities in the current year

In contrast, a high coverage of MFC in the past years enhanced wild bee densities in our study OSR fields. Similarly, a beneficial effect from high covers of MFC in the previous year has been shown to enhance wild bee densities (Kallioniemi et al., 2017; Riedinger et al., 2015). Moreover, landscape history can have an impact on current plant or insect species richness: Lindborg and Eriksson (2004) demonstrated that plant species richness is positively correlated with habitat connectivity 50 and 100 years ago and Aguirre-Gutiérrez et al. (2015) showed that pollinator species responses to landscape change were modified by historic landscape characteristics. However, we are not aware of any study showing MFC cultivation in the previous three years to promote wild bees in the current year. This finding emphasizes the importance of continuously available flowering resources in agricultural landscapes for pollinators. OSR and faba beans are both known to promote pollinators by providing short-term pulses of floral resources (Beyer et al., 2020; Diekötter et al., 2014; Westphal et al., 2003). Jauker et al. (2012b) found that the number of produced offspring in a solitary bee was positively affected by OSR cover. Though, other studies showed that the positive effect of MFC on bumblebee densities translated to neither a higher reproductive success (Westphal et al., 2009), nor in higher numbers of colonies (Herrmann et al. 2007). In our study, wild bee densities in OSR fields were increased in the long-term by MFC cultivation, which hints towards positive effects of MFC on wild bee reproductive success. Nevertheless, we cannot exclude the influence of confounding, random factors about which we have no information, such as other landscape features or management practices. There is an urgent need for studies addressing past and present landscape effects on wild bee survival as population-level effects have rarely been quantified (but see Carvell et al., 2017). Besides, further studies are needed to test how past and present MFC cultivation interactively shape bee densities and communities in agricultural landscapes. Possible negative impacts on MFC yields arising from a high percentage of co-flowering crops (Bänsch et al., 2020a; Shaw et al., 2020) might have been possibly outweighed by the positive long-term effect of MFC on pollinator densities. Nevertheless, we found no interaction effect of MFC history and OSR cover on bee densities.

Wild bees and honeybees show contrasting effects in response to MFC cultivation

Unlike wild bees, honeybee densities decreased with increasing historical cover of MFC. Though, the availability of floral resources at landscape scale determines the composition of honeybee diets (Bänsch et al., 2020c; Requier et al., 2015) and shortages in pollen availability can result in brood reductions and colony losses (Requier et al., 2017), honeybee densities are mainly correlated with the number of managed hives (e.g. Lindström et al., 2016). We did not record the number of honeybee colonies in and in proximity of our study landscapes. Therefore, we cannot preclude that study landscapes with a high MFC cover in the past simply contained fewer managed honeybee hives. The contrasting reactions of honey- and wild bee densities in response to landscape composition hint towards competition between the two pollinator groups. A displacement of wild bees in oilseed rape fields by increasing honeybee densities has already been observed (Lindström et al., 2016). Negative competition effects on wild bees from honeybees might be especially critical in homogenous landscapes with few floral resources (Herbertsson et al., 2016). Thus, a wildlife-friendly landscape management that aims at increasing heterogeneity and floral resource supply might reduce pressure on pollinators, which face multiple challenges and stressors (Potts et al., 2016; Vanbergen and Insect Pollinators Initiative, 2013).

Pollinator, pod number and mass-flowering crop cover effects on yield parameters and yields

Pollinator exclusion and bee densities affect yield components

Insect pollination was an important factor explaining yields and yield components of our OSR plants. As expected, pollinator exclusion decreased the number of seeds per pod and enhanced the thousand-seed weight . Accordingly, an increased bee density enhanced the seed number per pod and decreased the seed weight, but only in open pollinated plants. A difference between open pollinated and bagged plants was only visible at high bee densities, which indicates that high pollinator densities are necessary to obtain yield increases. An enhanced pollinator density and visitation has already been shown to increase OSR yields (Bartomeus et al., 2014; Jauker et al., 2012a). Yields in our study were however not significantly increased by insect pollination or high bee densities. This might be due to the extreme weather conditions in 2018 with very high temperatures and drought during summer (DWD, 2019) with implications for plants and insects. Resulting low bee densities might have been the reason for the lacking yield increase in open pollinated compared to bagged plants (see also Samnegård et al., 2016). Temperature is an important predictor of insect pollinator activity, which decreases with extreme high temperatures (Kühsel and Blüthgen, 2015; Kwon and Saeed, 2003). We only observed on average 1.2 wild bees and 5.2 honeybees per transect (100 m^2 and 5 min). In contrast, Sabbahi et al. (2005) reports a yield increase of about 46 % due to the addition of three honeybee hives per ha, which led to 5.8 times higher bee densities than in our fields. Additional to low bee densities, heat stress due to elevated temperatures could have negatively impacted OSR seed set and yields (Peltonen-Sainio et al., 2010; Young et al., 2004). Extreme weather might have damaged OSR plants, which is indicated by the very low and variable plant densities recorded (range from 11 to 55 plants per m^2, mean of 28.5). Since we calculated yields from the seed weight per plant (which did not respond to bee densities) multiplied by the plant density, diverging plant densities are likely to be responsible for patterns like declining yield with increasing bee densities. Other confounding factors, like pests or different varieties, which we did not account for, could be a further explanation (Grass et al., 2018; van Gils et al., 2016; Hudewenz et al., 2014). We cannot preclude possible variety effects on the plants` responses to insect pollination. Though, Perrot et al. (2018) used 28 different varieties of OSR for an pollination experiment and found no effect of OSR type (hybrid or conventional) on yield, as well as no evidence of an dependence of pollinator contribution to yield on plant variety or on fertilizer and pesticide input. Other studies however, show that pest control and fertilization can affect the contribution of pollinators to yield via changing resource availability of plants (Tamburini et al., 2019).

Pod number interacts with insect pollination in explaining yields

Pod number was an important driver of OSR yields (Diepenbrock, 2000). Seed number, seed weight per plant and overall yield was positively correlated with pod number. Pods play an important role in providing assimilates to the seeds through photosynthesis of the pod hulls and high levels of assimilates increase yield (Geisler, 1988; Grosse et al., 1992). Accordingly, we found a positive relationship between number of seeds per pod and pod number and hence higher yields due to increased allocation of resources to seed number rather than to seed weight. Furthermore, we found the effect of pod number on yield parameters to be modulated by the pollination treatment. To our knowledge, there are no studies showing an interaction between insect pollination and pod number in explaining OSR yields. For plants with few pods and therefore fewer assimilates to allocate to seed production, seed number per pod and yields were enhanced for open pollinated plants. This indicates that insect pollination can compensate for a low pod number and assimilate provisioning by enhancing seed number per pod and ultimately yields. Similar results have been shown by Marini et al. (2015), where insect pollination compensated for low nutrient inputs.

High MFC covers in the past increase seed weight per plant

We found a higher seed weight of open pollinated OSR plants in landscapes with a high cover of MFC, which might be driven by higher pollinator densities. We found enhanced wild bee densities in landscapes with high MFC covers and we found seed weight per plant to increase with honeybee- and wild bee densities. While honeybees have been shown to be most common OSR visitors (Marini et al., 2015; Perrot et al., 2018) wild bees might be the more effective OSR pollinators (Woodcock et al., 2013) and honeybees cannot replace wild bees` contribution to crop yields (Bänsch et al., 2020b; Garibaldi et al., 2013, 2014). Thus, wild pollinator conservation is of mayor importance for food production (Garibaldi et al., 2014; Klein et al., 2007). However, the contribution of other drivers to the observed seed weight increases, such as differing field management or climate conditions, cannot be ruled out. Management can interact with insect pollination in shaping yields (Marini et al., 2015; Tamburini et al., 2019). Since we do not have information about management practices of our fields, we cannot test those effects. Further research is needed to investigate if positive carry-over effects from past MFC cultivation on yields originate from the promotion of wild bees in the long term.

Conclusions

Our study shows that past and present MFC cultivation differentially affect wild bee densities in OSR fields and that insect pollination and high bee densities affect OSR yield components. Pollinator exclusion led to less, but heavier seeds, emphasizing the high compensation potential of OSR (Diepenbrock, 2000; Pinet et al., 2015). Moreover, the production of only few pods can be compensated by enhanced insect pollination. Further research is needed about how pod number interacts with environmental and biotic factors in shaping oilseed rape yields.

While high OSR covers in the current year led to decreased wild bee densities, a high coverage of MFC in the past enhanced wild bee densities in the present year and was positively correlated with the OSR seed weight per plant. MFC are known to have beneficial effects on pollinators (e.g. Westphal et al. 2003), but studies about long-term carry over effects are largely missing. There is a need for investigations about how landscape history interacts with present landscape metrics in shaping pollinator communities and how this in turn affects crop yields. Our results provide some evidence that past MFC cultivation has the potential to positively impact pollinators and MFC yields. Since co-flowering crops can also dilute pollinators (Holzschuh et al., 2011) and since pollinator diversity is enhanced by functional diversity of farmland plants (Sutter et al., 2017), it might be important, to consider the diversity, morphology and phenology of flowering crops grown in a landscape to achieve maximum benefits for pollinating insects and for crop pollination.

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References

Aguirre-Gutiérrez, J., Biesmeijer, J.C., van Loon, E.E., Reemer, M., Wallisdevries, M.F., Carvalheiro, L.G., 2015. Susceptibility of pollinators to ongoing landscape changes depends on landscape history. Divers. Distrib. 21, 1129–1140. https://doi.org/10.1111/ddi.12350

Bänsch, S., Tscharntke, T., Ratnieks, F.L.W., Härtel, S., Westphal, C., 2020a. Foraging of honey bees in agricultural landscapes with changing patterns of flower resources. Agric. Ecosyst. Environ. 291, 106792. https://doi.org/10.1016/j.agee.2019.106792

Bänsch, S., Tscharntke, T., Gabriel, D., Westphal, C., 2020b. Crop pollination services: complementary resource use by social vs solitary bees facing crops with contrasting flower supply. J. Appl. Ecol. https://doi.org/10.1111/1365-2664.13777

Bänsch, S., Tscharntke, T., Wünschiers, R., Netter, L., Brenig, B., Gabriel, D., Westphal, C., 2020c. Using ITS2 metabarcoding and microscopy to analyze shifts in pollen diets of honey bees and bumble bees along a mass-flowering crop gradient. Mol. Ecol. https://doi.org/10.1111/mec.15675

Bartomeus, I., Potts, S.G., Steffan-Dewenter, I., Vaissière, B.E., Woyciechowski, M., Krewenka, K.M., Tscheulin, T., Roberts, S.P.M., Szentgyörgyi, H., Westphal, C., Bommarco, R., 2014. Contribution of insect pollinators to crop yield and quality varies with agricultural intensification. PeerJ 2, e328. https://doi.org/10.7717/peerj.328

Barton, K., 2019. MuMIn: Multi-Model Inference. R package version 1.43.6.

Becker, H.C., Damgaard, C., Karlsson, B., 1992. Environmental variation for outcrossing rate in rapeseed (Brassica napus). Theor. Appl. Genet. 84, 303–306. https://doi.org/10.1007/BF00229487

Beyer, N., Gabriel, D., Kirsch, F., Schulz-Kesting, K., Dauber, J., Westphal, C., 2020. Functional groups of wild bees respond differently to faba bean (Vicia faba L.) cultivation at landscape scale. J. Appl. Ecol. 57, 2499-2508. https://doi.org/10.1111/1365-2664.13745

Blaauw, B.R., Isaacs, R., 2014. Flower plantings increase wild bee abundance and the pollination services provided to a pollination-dependent crop. J. Appl. Ecol. 51, 890-898. https://doi.org/ doi: 10.1111/1365-2664.12257

Bommarco, R., Marini, L., Vaissière, B.E., 2012. Insect pollination enhances seed yield, quality, and market value in oilseed rape. Oecologia 169, 1025–1032. https://doi.org/10.1007/s00442-012-2271-6

Brooks, M.E., Kristensen, K., Benthem, K.J. van, Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Maechler, M., Bolker, B.M., 2017. glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. R J. 9, 378–400.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference. A Pracitcal Information-Theoretic Approach, 2nd ed. ed. Springer-Verlag.

Carvell, C., Bourke, A.F.G., Dreier, S., Freeman, S.N., Hulmes, S., Jordan, W.C., Redhead, J.W., Summer, S., Wang, J., Heard, M.S. 2017. Bumblebee family lineage survival is enhanced in high-quality landscapes. Nature 543, 547–549.

Castle, D., Grass, I., Westphal, C., 2019. Fruit quantity and quality of strawberries benefit from enhanced pollinator abundance at hedgerows in agricultural landscapes. Agric. Ecosyst. Environ. 275, 14–22. https://doi.org/10.1016/j.agee.2019.01.003

Dainese, M., Martin, E.A., Aizen, M.A., Albrecht, M., Bartomeus, I., Bommarco, R., Carvalheiro, L.G., Chaplin-kramer, R., Gagic, V., Garibaldi, L.A., Ghazoul, J., Grab, H., Jonsson, M., Karp, D.S., Letourneau, D.K., Marini, L., Poveda, K., Rader, R., Smith, H.G., Takada, M.B., Taki, H., Tamburini, G., Tschumi, M., Steffan-Dewenter, I., 2019. A global synthesis reveals biodiversity-mediated benefits for crop production. Sci. Adv. 5, eaax0121.

Diekötter, T., Kadoya, T., Peter, F., Wolters, V., Jauker, F., 2010. Oilseed rape crops distort plant-pollinator interactions. J. Appl. Ecol. 47, 209–214. https://doi.org/10.1111/j.1365-2664.2009.01759.x

Diekötter, T., Peter, F., Jauker, B., Wolters, V., Jauker, F., 2014. Mass-flowering crops increase richness of cavity-nesting bees and wasps in modern agro-ecosystems. GCB Bioenergy 6, 219–226. https://doi.org/10.1111/gcbb.12080

Diepenbrock, W., 2000. Yield analysis of winter oilseed rape (Brassica napus L.): A review. F. Crop. Res. 67, 35–49. https://doi.org/10.1016/S0378-4290(00)00082-4

DWD (Deutscher Wetterdienst) 2019. Rückblick auf das Jahr 2018 - das bisher wärmste Jahr in Deutschland. https://www.dwd.de/DE/leistungen/besondereereignisse/temperatur/20190102_waermstes_jahr_in_deutschland_2018.html?nn=510076#download=1 (accessed 11 September 2020).

Eilers, E.J., Kremen, C., Greenleaf, S.S., Garber, A.K., Klein, A.M., 2011. Contribution of pollinator-mediated crops to nutrients in the human food supply. PLoS One 6. https://doi.org/10.1371/journal.pone.0021363

FAOSTAT, 2020. (Food and Agriculture Organisation of the United States) [WWW Document]. URL http://www.fao.org/faostat/en/#data/QC (accessed 9 October 2020).

Foster, D., Swanson, F., Aber, J., Burke, I., Brokaw, N., Tilman, D., Knapp, A., 2003. The importance of land-use legacies to ecology and conservation. BioScience 53:77–88.

Fox, J. and Weisberg, S. 2019. An R Companion to Applied Regression, 3rd Edition. Thousand Oaks, CA. URL: *http://tinyurl.com/carbook*

Gallai, N., Salles, J.M., Settele, J., Vaissière, B.E., 2009. Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. Ecol. Econ. 68, 810–821. https://doi.org/10.1016/j.ecolecon.2008.06.014

Garibaldi, L. A. et al. 2013. Wild pollinators enhance fruit set of crops regardless of honey bee abundance. Science 339, 1608–1611. https://doi.org/10.1126/science.1230200.

Garibaldi, L.A., Carvalheiro, L.G., Leonhardt, S.D., Aizen, M.A., Blaauw, B.R., Isaacs, R., Kuhlmann, M., Kleijn, D., Klein, A.M., Kremen, C., Morandin, L., Scheper, J., Winfree, R., 2014. From research to action: Enhancing crop yield through wild pollinators. Front. Ecol. Environ. 12, 439–447. https://doi.org/10.1890/130330

Garratt, M.P.D., Coston, D.J., Truslove, C.L., Lappage, M.G., Polce, C., Dean, R., Biesmeijer, J.C., Potts, S.G., 2014. The identity of crop pollinators helps target conservation for improved ecosystem services. Biol. Conserv. 169, 128–135. https://doi.org/10.1016/j.biocon.2013.11.001

Geisler, G., 1988. Pflanzenbau: Ein Lehrbuch - Biologische Grundlagen und Technik der Pflanzenproduktion, 2nd ed. Paul Parey, Berlin; Hamburg.

Grab, H., Blitzer, E.J., Danforth, B., Loeb, G., Poveda, K., 2017. Temporally dependent pollinator competition and facilitation with mass flowering crops affects yield in co-blooming crops. Sci. Rep. 7, 1–9. https://doi.org/10.1038/srep45296

Grass, I., Bohle, V., Tscharntke, T., Westphal, C., 2018. How plant reproductive success is determined by the interplay of antagonists and mutualists: Ecosphere 9. https://doi.org/10.1002/ecs2.2106

Grosse, F., Léon, J., Diepenbrock, W., 1992. Ertragsbildung und Ertragsstruktur bei Winterraps (Brassica napus L.) II. Vergleich zwischen Elternlinien und deren F1- und F2-Generationen. J. Agron. Crop Sci. 169, 94–103. https://doi.org/10.1111/j.1439-037X.1992.tb01187.x

Harding, J.S., Benfield, E.F., Bolstad, P.V., Helfman, G.S., Jones, E.B.D., 1998. Stream biodiversity: The goast of land use past. Proc. Natl. Acad. Sci. USA 95, 14843-14847.

Herbertsson, L., Lindström, S.A.M., Rundlöf, M., Bommarco, R., Smith, H.G., 2016. Competition between managed honeybees and wild bumblebees depends on landscape context. Basic Appl. Ecol. 17, 609–616. https://doi.org/10.1016/j.baae.2016.05.001

Holzschuh, A., Dainese, M., González-Varo, J.P., Mudri-Stojnić, S., Riedinger, V., Rundlöf, M., Scheper, J., Wickens, J.B., Wickens, V.J., Bommarco, R., Kleijn, D., Potts, S.G., Roberts, S.P.M., Smith, H.G., Vilà, M., Vujić, A., Steffan-Dewenter, I., 2016. Mass-flowering crops dilute pollinator abundance in agricultural landscapes across Europe. Ecol. Lett. 19, 1228–1236. https://doi.org/10.1111/ele.12657

Holzschuh, A., Dormann, C.F., Tscharntke, T., Steffan-Dewenter, I., 2011. Expansion of mass-flowering crops leads to transient pollinator dilution and reduced wild plant pollination. Proc. R. Soc. B Biol. Sci. 278, 3444–3451. https://doi.org/10.1098/rspb.2011.0268

Hudewenz, A., Pufal, G., Bögeholz, A.L., Klein, A.M., 2014. Cross-pollination benefits differ among oilseed rape varieties. J. Agric. Sci. 152, 770–778. https://doi.org/10.1017/S0021859613000440

Jauker, F., Bondarenko, B., Becker, H.C., Steffan-Dewenter, I., 2012a. Pollination efficiency of wild bees and hoverflies provided to oilseed rape. Agric. For. Entomol. 14, 81–87. https://doi.org/10.1111/j.1461-9563.2011.00541.x

Jauker, F., Peter, F., Wolters, V., Diekötter, T., 2012b. Early reproductive benefits of mass-flowering crops to the solitary bee Osmia rufa outbalance post-flowering disadvantages. Basic Appl. Ecol. 13, 268–276. https://doi.org/10.1016/j.baae.2012.03.010

Kallioniemi, E., Åström, J., Rusch, G.M., Dahle, S., Åström, S., Gjershaug, J.O., 2017. Local resources, linear elements and mass-flowering crops determine bumblebee occurrences in moderately intensified farmlands. Agric. Ecosyst. Environ. 239, 90–100. https://doi.org/10.1016/j.agee.2016.12.039

Klein, A.M., Vaissière, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Tscharntke, T., 2007. Importance of pollinators in changing landscapes for world crops. Proc. R. Soc. B Biol. Sci. 274, 303–313. https://doi.org/10.1098/rspb.2006.3721

Kremen, C., Williams, N.M., Aizen, M.A., Gemmill-Herren, B., LeBuhn, G., Minckley, R., Packer, L., Potts, S.G., Roulston, T., Steffan-Dewenter, I., Vázquez, D.P., Winfree, R., Adams, L., Crone, E.E., Greenleaf, S.S., Keitt, T.H., Klein, A.M., Regetz, J., Ricketts, T.H., 2007. Pollination and other ecosystem services produced by mobile organisms: A conceptual framework for the effects of land-use change. Ecol. Lett. 10, 299–314. https://doi.org/10.1111/j.1461-0248.2007.01018.x

Kühsel, S., Blüthgen, N., 2015. High diversity stabilizes the thermal resilience of pollinator communities in intensively managed grasslands. Nat. Commun. 6. https://doi.org/10.1038/ncomms8989

Kwon, Y.J., Saeed, S., 2003. Effect of temperature on the foraging activity of Bombus terrestris L. (Hymenoptera: Apidae) on greenhouse hot pepper (Capsicum annuum L.). Appl. Entomol. Zool.

38, 275–280. https://doi.org/10.1303/aez.2003.275

Lenth, R., 2019. emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.4.1. URL: https://CRAN.R-project.org/package=emmeans.

Lindborg, R., Eriksson, O., 2004. Historical Landscape Connectivity Affects Present Plant. Ecol. Soc. Am. 85, 1840–1845.

Lindström, S.A.M., Herbertsson, L., Rundlöf, M., Bommarco, R., Smith, H.G., 2016. Experimental evidence that honeybees depress wild insect densities in a flowering crop. Proc. R. Soc. B Biol. Sci. 283, 1–8. https://doi.org/10.1098/rspb.2016.1641

Lüdecke, D., Makowski, D., Waggoner, P., Patil, I., 2020. performance: Assessment of Regression Models Performance. R package version 0.4.5.

Mandelik, Y., Winfree, R., Neeson, T., Kremen, C., 2012. Complementary habitat use by wild bees in agro-natural landscapes. Ecol. Appl. 22, 1535–1546. https://doi.org/10.1890/11-1299.1

Marini, L., Tamburini, G., Petrucco-Toffolo, E., Lindström, S.A.M., Zanetti, F., Mosca, G., Bommarco, R., 2015. Crop management modifies the benefits of insect pollination in oilseed rape. Agric. Ecosyst. Environ. 207, 61–66. https://doi.org/10.1016/j.agee.2015.03.027

Martin, E.A., Dainese, M., Clough, Y., Báldi, A., Bommarco, R., Gagic, V., Garratt, M.P.D., Holzschuh, A., Kleijn, D., Kovács-Hostyánszki, A., Marini, L., Potts, S.G., Smith, H.G., Al Hassan, D., Albrecht, M., Andersson, G.K.S., Asís, J.D., Aviron, S., Balzan, M. V., Baños-Picón, L., Bartomeus, I., Batáry, P., Burel, F., Caballero-López, B., Concepción, E.D., Coudrain, V., Dänhardt, J., Diaz, M., Diekötter, T., Dormann, C.F., Duflot, R., Entling, M.H., Farwig, N., Fischer, C., Frank, T., Garibaldi, L.A., Hermann, J., Herzog, F., Inclán, D., Jacot, K., Jauker, F., Jeanneret, P., Kaiser, M., Krauss, J., Le Féon, V., Marshall, J., Moonen, A.C., Moreno, G., Riedinger, V., Rundlöf, M., Rusch, A., Scheper, J., Schneider, G., Schüepp, C., Stutz, S., Sutter, L., Tamburini, G., Thies, C., Tormos, J., Tscharntke, T., Tschumi, M., Uzman, D., Wagner, C., Zubair-Anjum, M., Steffan-Dewenter, I., 2019. The interplay of landscape composition and configuration: new pathways to manage functional biodiversity and agroecosystem services across Europe. Ecol. Lett. 22, 1083–1094. https://doi.org/10.1111/ele.13265

Nakagawa, S., Johnson, P.C.D., Schielzeth, H., 2017. The coefficient of determination R2 and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. J. R. Soc. Interface 14. https://doi.org/10.1098/rsif.2017.0213

Ouvrard, P., Jacquemart, A.L., 2019. Review of methods to investigate pollinator dependency in oilseed rape (Brassica napus). F. Crop. Res. 231, 18–29. https://doi.org/10.1016/j.fcr.2018.11.006

Peltonen-Sainio, P., Jauhiainen, L., Trnka, M., Olesen, J.E., Calanca, P., Eckersten, H., Eitzinger, J., Gobin, A., Kersebaum, K.C., Kozyra, J., Kumar, S., Dalla Marta, A., Micale, F., Schaap, B., Seguin, B., Skjelvåg, A.O., Orlandini, S., 2010. Coincidence of variation in yield and climate in Europe. Agric. Ecosyst. Environ. 139, 483–489. https://doi.org/10.1016/j.agee.2010.09.006

Perrot, T., Gaba, S., Roncoroni, M., Gautier, J.L., Bretagnolle, V., 2018. Bees increase oilseed rape yield under real field conditions. Agric. Ecosyst. Environ. 266, 39–48. https://doi.org/10.1016/j.agee.2018.07.020

Petersen, J.D., Nault, B.A., 2014. Landscape diversity moderates the effects of bee visitation frequency to flowers on crop production. J. Appl. Ecol. 51, 1347–1356. https://doi.org/10.1111/1365-2664.12287

Pinet, A., Mathieu, A., Jullien, A., 2015. Floral bud damage compensation by branching and biomass allocation in genotypes of Brassica napus with different architecture and branching potential. Front. Plant Sci. 6, 1–13. https://doi.org/10.3389/fpls.2015.00070

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., R Core Team, 2019. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-140. URL: https://CRAN.R-project.org/package=nlme.

Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O., Kunin, W.E., 2010. Global pollinator declines: Trends, impacts and drivers. Trends Ecol. Evol. 25, 345–353. https://doi.org/10.1016/j.tree.2010.01.007

Potts, S.G., Imperatriz-Fonseca, V., Ngo, H.T., Aizen, M.A., Biesmeijer, J.C., Breeze, T.D., Dicks, L. V., Garibaldi, L.A., Hill, R., Settele, J., Vanbergen, A.J., 2016. Safeguarding pollinators and their values to human well-being. Nature 540, 220–229. https://doi.org/10.1038/nature20588

R Core Team, 2019. R: A language and environment for statistical computing.

Requier, F., Odoux, J.F., Tamic, T., Moreau, N., Henry, M., Decourtye, A., Bretagnolle, V., 2015. Honey bee diet in intensive farmland habitats reveals an unexpectedly high flower richness and a major role of weeds. Ecol. Appl. 25, 881–890. https://doi.org/10.1890/14-1011.1

Requier, F., Odoux, J.F., Henry, M., Bretagnolle, V. 2017. The carry-over effects of pollen shortage decrease the survival of honeybee colonies in farmlands. J. Appl. Ecol., 54, 1161-1170.

Riedinger, V., Mitesser, O., Hovestadt, T., Steffan-Dewenter, I., Holzschuh, A., Rosenheim, J.A., 2015. Annual dynamics of wild bee densities: Attractiveness and productivity effects of oilseed rape. Ecology 96, 1351–1360. https://doi.org/10.1890/14-1124.1

Sabbahi, R., De Oliveira, D., Marceau, J., 2005. Influence of honey bee (Hymenoptera: Apidae) density on the production of canola (Crucifera: Brassicacae). J. Econ. Entomol. 98, 367–372. https://doi.org/10.1093/jee/98.2.367

Samnegård, U., Hambäck, P.A., Lemessa, D., Nemomissa, S., Hylander, K., 2016. A heterogeneous landscape does not guarantee high crop pollination. Proc. R. Soc. B Biol. Sci. 283. https://doi.org/10.1098/rspb.2016.1472

Shaw, R.F., Phillips, B.B., Doyle, T., Pell, J.K., Redhead, J.W., Savage, J., Woodcock, B.A., Bullock, J.M., Osborne, J.L., 2020. Mass-flowering crops have a greater impact than semi-natural habitat on crop pollinators and pollen deposition. Landsc. Ecol. 35, 513–527. https://doi.org/10.1007/s10980-019-00962-0

Sutter, L., Jeanneret, P., Bartual, A.M., Bocci, G., Albrecht, M., 2017. Enhancing plant diversity in agricultural landscapes promotes both rare bees and dominant crop-pollinating bees through complementary increase in key floral resources. J. Appl. Ecol. 54, 1856–1864. https://doi.org/10.1111/1365-2664.12907

Tamburini, G., Bommarco, R., Kleijn, D., van der Putten, W.H., Marini, L., 2019. Pollination contribution to crop yield is often context-dependent: A review of experimental evidence. Agric. Ecosyst. Environ. 280, 16–23. https://doi.org/10.1016/j.agee.2019.04.022

van Gils, S., van der Putten, W.H., Kleijn, D., 2016. Can above-ground ecosystem services compensate for reduced fertilizer input and soil organic matter in annual crops? J. Appl. Ecol. 53, 1186–1194. https://doi.org/10.1111/1365-2664.12652

Vanbergen, A.J., Insect Pollinators Initiative, 2013. Threats to an ecosystem service: Pressures on pollinators. Front. Ecol. Environ. 11, 251–259. https://doi.org/10.1890/120126

Westphal C., Steffan-Dewenter I., Tscharntke T., 2009. Mass flowering oilseed rape improves early colony growth but not sexual reproduction of bumblebees. J Appl Ecol 46: 187–193. https://doi.org/10.1111/j.1365-2664.2008.01580.x

Westphal C., Bommarco R., Carré G., Lamborn E., Morison N., Petanidou T., Potts S.G., Roberts S.P.M., Szentgyörgyi H., Tscheulin T., Vaissière B.E., Woyciechowski M., Biesmeijer J.C., Kunin W.E., Settele J., Steffan-Dewenter I., 2008. Measuring bee diversity in different European habitats and biogeographical regions. Ecological Monographs 78: 653–671. https://doi.org/10.1890/07-1292.1

Westphal, C., Steffan-Dewenter, I., Tscharntke, T., 2006. Bumblebees experience landscapes at different spatial scales: Possible implications for coexistence. Oecologia 149, 289–300. https://doi.org/10.1007/s00442-006-0448-6

Westphal, C., Steffan-Dewenter, I., Tscharntke, T., 2003. Mass flowering crops enhance pollinator densities at a landscape scale. Ecol. Lett. 6, 961–965. https://doi.org/10.1046/j.1461-0248.2003.00523.x

Wickham, H. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York, 2016.

Woodcock, B.A., Edwards, M., Redhead, J., Meek, W.R., Nuttall, P., Falk, S., Nowakowski, M., Pywell, R.F., 2013. Crop flower visitation by honeybees, bumblebees and solitary bees: Behavioural differences and diversity responses to landscape. Agric. Ecosyst. Environ. 171, 1–8. https://doi.org/10.1016/j.agee.2013.03.005

Woodcock, B.A., Garratt, M.P.D., Powney, G.D., Shaw, R.F., Osborne, J.L., Soroka, J., Lindström, S.A.M., Stanley, D., Ouvrard, P., Edwards, M.E., Jauker, F., McCracken, M.E., Zou, Y., Potts, S.G., Rundlöf, M., Noriega, J.A., Greenop, A., Smith, H.G., Bommarco, R., van der Werf, W., Stout, J.C., Steffan-Dewenter, I., Morandin, L., Bullock, J.M., Pywell, R.F., 2019. Meta-analysis reveals that pollinator functional diversity and abundance enhance crop pollination and yield. Nat. Commun. 10, 1–10. https://doi.org/10.1038/s41467-019-09393-6

Young, L.W., Wilen, R.W., Bonham-Smith, P.C., 2004. High temperature stress of Brassica napus during flowering reduces micro- and megagametophyte fertility, induces fruit abortion, and disrupts seed production. J. Exp. Bot. 55, 485–495. https://doi.org/10.1093/jxb/erh038

Zou, Y., Xiao, H., Bianchi, F.J.J.A., Jauker, F., Luo, S., van der Werf, W., 2017. Wild pollinators enhance oilseed rape yield in small-holder farming systems in China. BMC Ecol. 17, 1–7. https://doi.org/10.1186/s12898-017-0116-1

Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problems. Methods Ecol. Evol. 1, 3–14. https://doi.org/10.1111/j.2041-210x.2009.00001.x

Supplementary Material

Figures

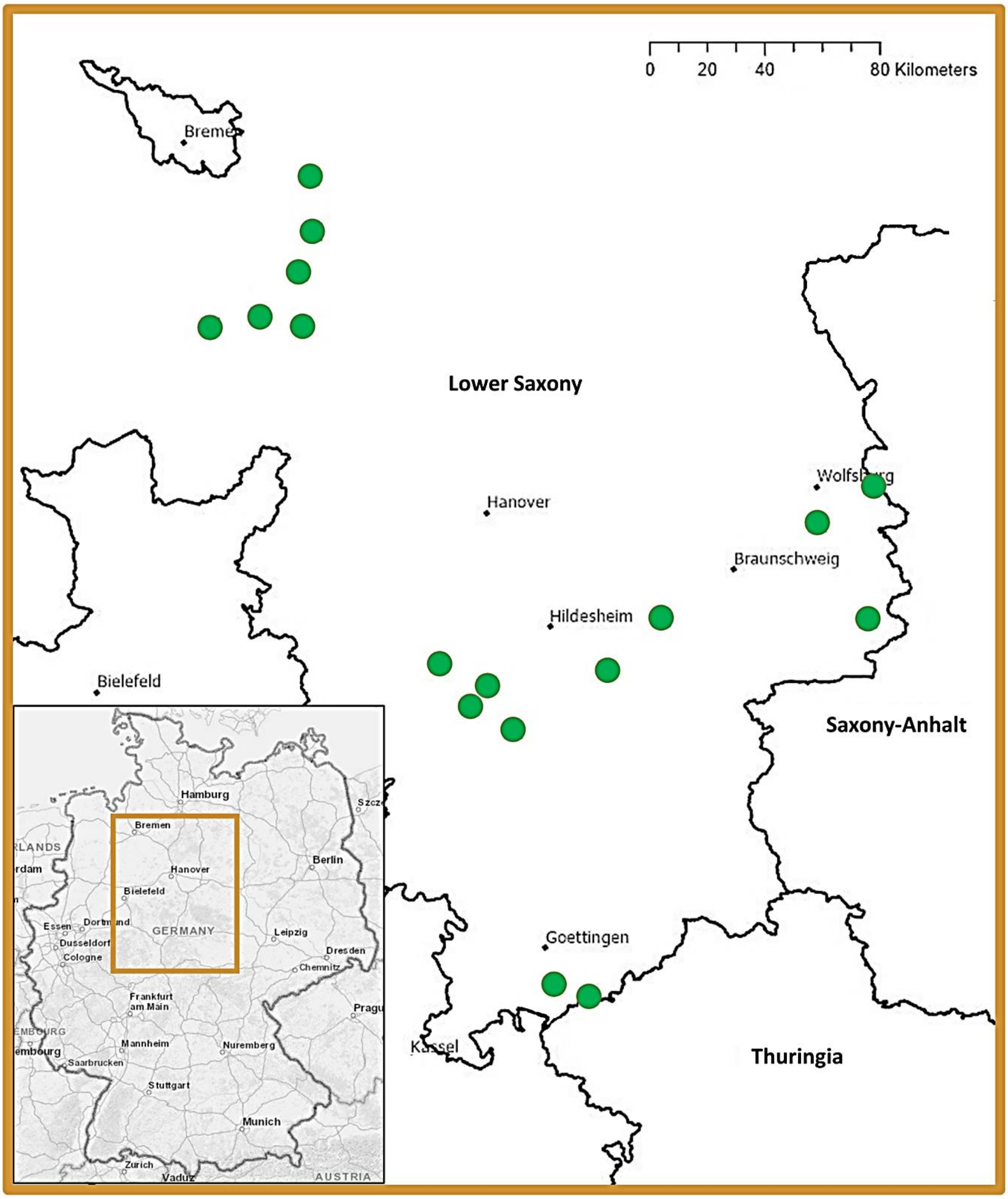

Figure A1 Schematic map showing the location of the study landscapes in Lower Saxony, Germany (depicted as green circles).

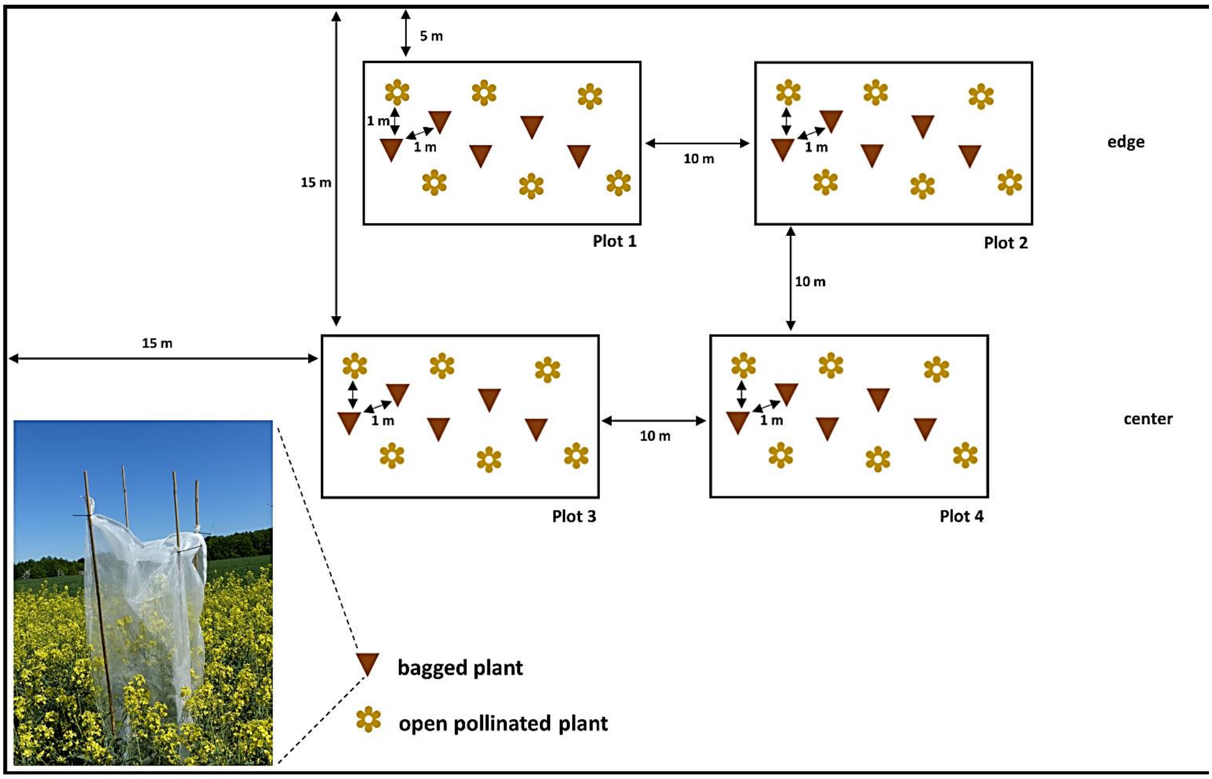

Figure A2 Schematic map of the study design. Arrangement of the four plots at the edge and in the center of the oilseed rape fields. Within every plot five randomly chosen plants were covered with a bag to exclude all insect pollinators (bagged plants) and six randomly chosen plants were marked and not covered with a bag to enable natural insect pollination (open pollinated plants).

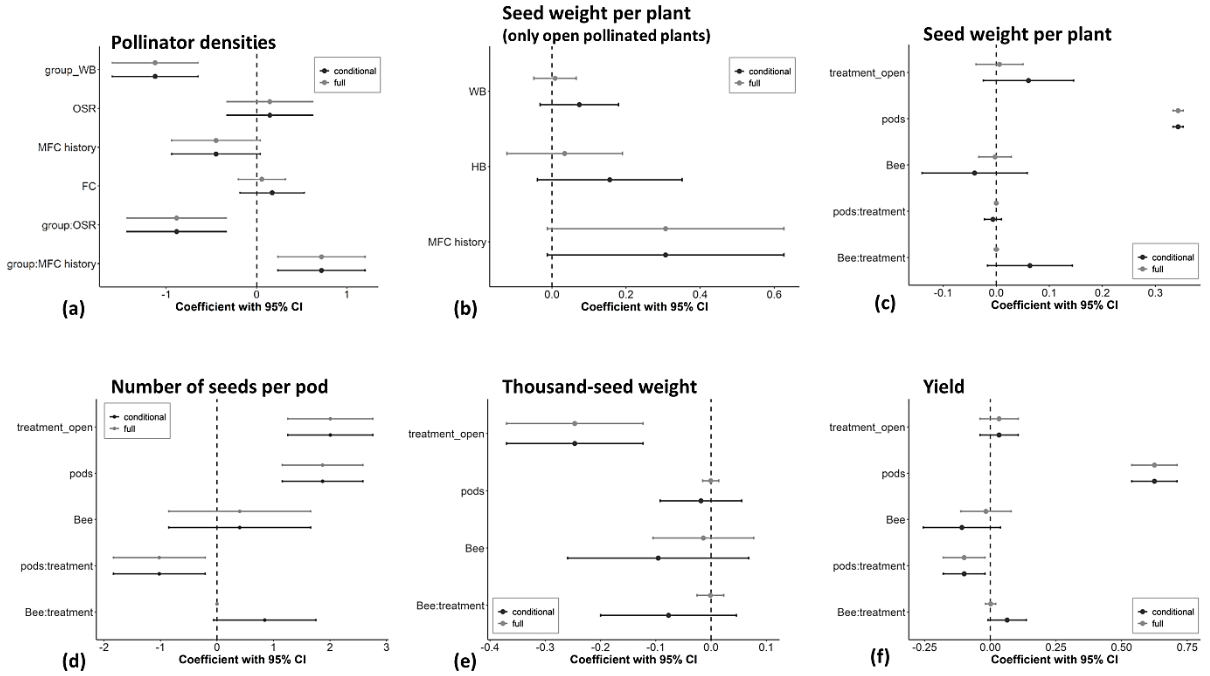

Figure A3 Model averaged coefficients with 95 % confidence intervals (CI) for the best-fitting models examining (a) bee density and landscape effects on seed weight per plant for only open pollinated plants (Table A5) and for best-fitting models explaining pollinator exclusion, bee density and pod number effects on (b) seed weight per plant, (c) thousand-seed weight, (d) number of seeds per pod and (e) yield (per plot) in open and bagged oilseed rape plants (Table A3). MFC history: MFC cover of the past three years, FC: local flower cover of study oilseed rape field, WB: wild bee densities, HB: honeybee densities, treatment: pollinator exclusion treatment (open/bagged), pods: number of pods per plant (average number of pods per plant per pod for yield), Bee: bee densities (HB and WB summed). The conditional average includes only the models in which the respective parameter appears. The full average uses the whole model set and for the models in which a parameter is absent a value of zero is substituted.

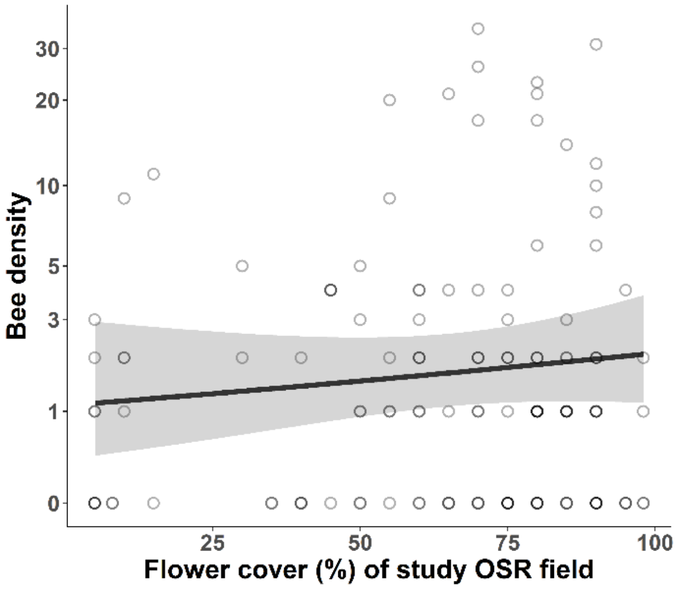

Figure A4 Effect of local flower cover (%) of study OSR fields on bee densities (honey- and wild bees). Line depicts model predictions with 95 % confidence intervals. Predictions were obtained from the second-best fitting model *bee2* (Table A1).

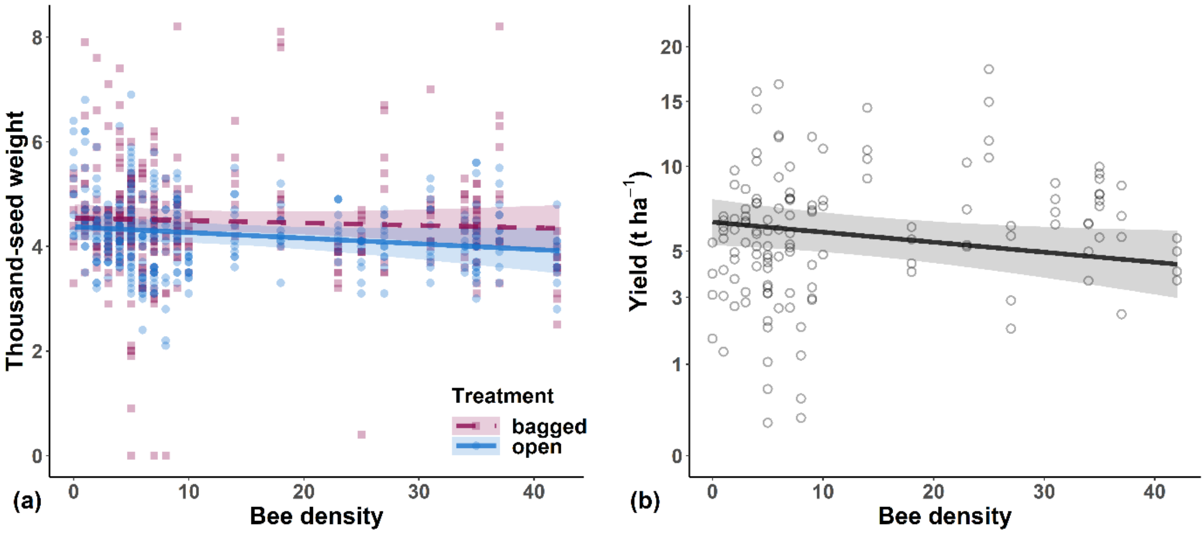

Figure A5 Effect of bee density on **(a)** the thousand-seed weight (TSW) and **(c)** yield in oilseed rape for bagged plants and open pollinated plants. Line depicts model predictions with 95 % confidence intervals. Predictions were obtained from the third-best fitting model *sw3* for TSW and the best fitting-model *y1* for the case of yield (Table A3).

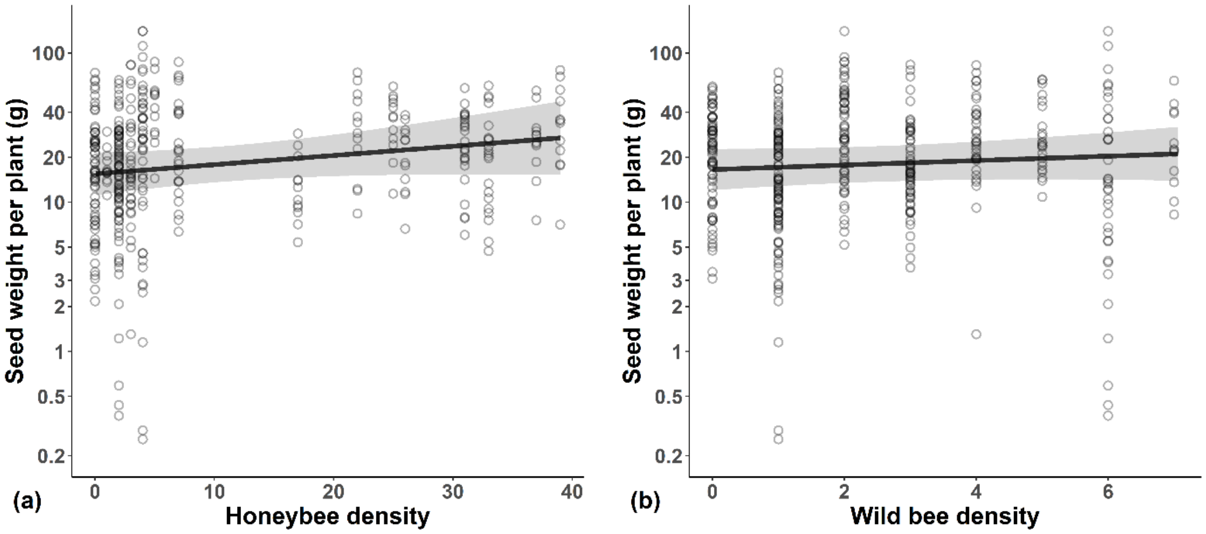

Figure A6 Effect of **(a)** honeybee density and **(b)** wild bee density on the seed weight per plant (g) for open pollinated oilseed rape plants. Line depicts model predictions with 95 % confidence intervals. Predictions were obtained from the second best-fitting model *spo2* (Table A5).

Tables

Mass-flowering crop cover effects on pollinators

Table A1 Summary of the best fitting candidate models (dAIC<2) and null models for **landscape metrics effects on bee densities**. Models were fitted with negative binomial family. Marginal (R_m^2) and conditional (R_c^2) R^2 values are given as a measure of the model´s goodness of fit. n: number of observations, FC: local flower cover of study oilseed rape field, OSR: area of oilseed rape in 2018, MFC_{hist}: area of mass-flowering crops from 2015-2017, group: bee group (honeybees/wild bees).

response variable	model	df	AICc	deltaAIC	AIC weight	explanatory variables	R_m^2	R_c^2
Bee density (n=136)	bee1	9	564.18	0.00	0.35	group + OSR + MFC_{hist} + group:OSR + group:MFC_{hist}	0.31	0.61
	bee2	10	565.56	1.38	0.18	Group + OSR + MFC_{hist} + group:OSR + group:MFC_{hist} + FC	0.32	0.62
	bee0	4	582.82	18.64	0.00	1	-	-

Table A2 The relative importance of explanatory variables expressed by Σw_i (sum of Akaike weights) for models to explain **landscape metrics effects on bee densities** (best fitting models are shown in table A1). Model parameters having $\Sigma w_i > 0.2$ for all response variables are shown. FC: local flower cover of study oilseed rape field, OSR: area of oilseed rape in 2018, MFC_{hist}: area of mass-flowering crops from 2015-2017, group: bee group (honeybees/wild bees).

model	response variable	group	OSR	MFC_{hist}	FC	group: OSR	group: MFC_{past}	OSR:MFC_{hist}
a.bee	Bee density	1.00	0.93	0.88	0.40	0.90	0.82	0.21

Pollinator exclusion and pod number effects on yield components and yields

Table A3 Summary of the best fitting candidate models (dAIC<2) and null models for the effects of **treatment, bee densities and plants` pod number on yield components and yield** in oilseed rape. Marginal (R_m^2) and conditional (R_c^2) R^2 values are given as a measure of the model´s goodness of fit. Treatment: pollinator exclusion treatment (bagged/open pollinated), pods: number of pods per OSR plant, Bee: bee density.

response variable	model	df	AICc	deltaAIC	AIC weight	explanatory variables	R_m^2	R_c^2
seed no. per pod (n=712)	**sn1**	9	4416.72	0.00	0.41	Treatment + pods + Bee + pods:treatment + Bee:treatment	0.12	0.15
	sn2	7	4417.04	0.32	0.35	Treatment + pods + pods:treatment	0.12	0.14
	sn3	8	4418.68	1.96	0.15	Treatment + pods + Bee + pods:treatment	0.12	0.14
	sn0	4	4475.68	58.96	0.00	1	-	-
TSW (n=708)	**sw1**	5	1817.41	0.00	0.26	Treatment	0.02	0.17
	sw2	6	1817.84	0.43	0.21	Treatment + Bee	0.03	0.18
	sw3	7	1818.36	0.95	0.16	Treatment + Bee + Bee:treatment	0.03	0.18
	sw4	6	1819.18	1.78	0.11	Treatmtent + pods	0.02	0.16
	sw0	4	1830.60	13.19	0.00	1	-	-
seed weight per plant (n=707)	**sp1**	6	1200.39	0.00	0.21	Treatment + pods	0.90	0.90
	sp2	5	1200.48	0.09	0.20	pods	0.90	0.90
	sp3	8	1201.36	0.97	0.13	Treatment + pods + Bee + Bee:treatment	0.90	0.90
	sp4	7	1201.73	1.35	0.11	Treatment + pods + Bee	0.90	0.90
	sp5	6	1201.78	1.39	0.11	Pods + Bee	0.90	0.90
	sp6	7	1201.84	1.45	0.10	Treatment + pods + pods:treatment	0.90	0.90
	sp7	9	1202.10	1.71	0.10	Treatment + pods + Bee + pods:treatment + Bee:treatment	0.90	0.90
	a.sp0	4	2657.15	1456.77	0.00	1	-	-
yield (n=136)	**y1**	6	25.3	0.00	0.23	Pods + Bee	0.63	0.93
	y2	8	26.0	0.72	0.19	Treatment + pods + Bee + pods:treatment	0.63	0.93
	y3	9	26.4	1.06	0.16	Treatment + pods + Bee + pods:treatment + Bee:treatment	0.63	0.93
	y4	7	26.9	1.58	0.12	Treatment + pods + Bee	0.63	0.93
	y0	4	215.4	190.09	0.00	1	-	-

Table A4 The relative importance of explanatory variables expressed by Σw_i (sum of Akaike weights) for models to explain the effects of **treatment, bee densities and plants` pod number on yield components and yield** in oilseed rape for all 22 study landscapes (best fitting models are shown in table A3). Model parameters having $\Sigma w_i > 0.2$ for all response variables are shown. Treatment: pollinator exclusion treatment (bagged/open pollinated), pods: number of pods per OSR plant, Bee: bee density.

Model	response variable	treatment	pods	Bee	pods: treatment	Bee: treatment
sn	**seed no. per pod**	1.00	1.00	0.61	0.91	0.43
sw	**TSW**	1.00	0.38	0.58	-	0.25
sp	**seed weight per plant**	0.69	1.00	0.48	0.24	0.22
y	**yield**	0.64	1.00	0.79	0.41	0.21

Mass-flowering crop cover and pollinator effects on yield components and yields

Table A5 Summary of the best fitting candidate models (dAIC<2) and null models for the effects of **landscape metrics and bee densities on yield components and yield** in open pollinated oilseed rape. Marginal (R_m^2) and conditional (R_c^2) R^2 values are given as a measure of the model´s goodness of fit. HB: honeybee densities, WB: wild bee densities, MFC_{hist}:area of mass-flowering crops from 2015-2017.

response variable	model	df	AICc	deltaAIC	AIC weight	explanatory variables	R_m^2	R_c^2

seed no. per pod (n=397)	**sno0**	4	2333.74	0.00	0.17	1	-	-
TSW (n=395)	**swo1**	5	777.08	0.00	0.13	HB	0.03	0.22
	swo0	4	777.30	0.18	0.12	1	-	-
seed weight per plant (n=395)	**spo1**	6	865.48	0.00	0.15	HB + MFC_{hist}	0.13	0.48
	spo2	5	866.23	0.76	0.10	HB + WB + MFC_{hist}	0.12	0.48
	spo3	7	866.48	1.01	0.09	MFC_{hist}	0.10	0.49
	spo4	6	867.33	1.86	0.06	WB + MFC_{hist}	0.10	0.50
	spo0	4	868.16	2.69	0.04	1	-	-
yield (n=68)	**yo0**	3	104.66	0.00	0.22	1	-	-

Table A6 The relative importance of explanatory variables expressed by Σw_i (sum of Akaike weights) for models to explain the effects of **landscape metrics and bee densities on yield components and yield** in open pollinated oilseed rape (best fitting models are shown in table A5). Model parameters having $\Sigma w_i > 0.2$ for all response variables are shown. HB: honeybee densities, WB: wild bee densities; MFC_{hist}:area of mass-flowering crops from 2015-2017, OSR: area of oilseed rape in 2018.

Model	**response variable**	**HB**	**WB**	**OSR**	**MFC_{hist}**
sno	**seed no. per pod**	0.37	0.40	0.34	0.45
swo	**TSW**	0.60	0.53	0.36	0.41
spo	**seed weight per plant**	0.60	0.53	0.37	0.83
yo	**yield**	0.32	0.40	0.31	0.37

Chapter 5

Landscape composition modifies pollinator densities, foraging behavior and yield formation in faba beans

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Article in preparation

Abstract

Wildlife-friendly management practices promote pollinators and pollination services in agricultural landscapes. Wild bee densities are driven by landscape composition, as they benefit from an increased availability of nesting and foraging resources at landscape scale. However, effects of landscape composition on bee foraging decisions and consequences for crop pollination have rarely been studied. We investigated, how landscape composition affects bee densities and foraging behavior in faba bean (*Vicia faba* L.) fields and how this impacts faba bean yield. We recorded densities and nectar robbing behavior of honeybees, long- tongued and short-tongued bumblebees in faba bean fields in eleven landscapes with varying landscape composition (e.g. land cover of oilseed rape, faba bean and semi-natural habitats). Moreover, we assessed yield components of faba beans via pollinator exclusion experiments. Increasing covers of faba bean and semi-natural habitats positively influenced bumblebee densities, while high oilseed rape covers negatively affected short-tongued bumblebee densities in bean fields. Increased faba bean covers enhanced the proportion of nectar robbing short-tongued bumblebees and honeybees. Yield components, i.e. number of beans per pod, seed weight per plant and dry matter yield (plot level) were increased by insect pollination, these effects however depended on variety. Yield components of open pollinated plants increased with increasing faba bean and semi-natural habitat cover, whereas we observed decreases in landscapes with high oilseed rape covers. Landscape composition interacted with bee densities in shaping yield formation in *V. faba*. Our study emphasizes the importance of considering landscape management to maximize crop yields, as shown for the case of faba beans. A high amount of semi-natural habitats in agricultural landscapes can promote both, wild bees and high crop yields.

Keywords

grain legumes, ecosystem services, mass-flowering crops, broad bean weevil, resource allocation

Introduction

Agriculture depends on ecosystem services, like crop pollination or pest control (Power, 2010) and the provisioning of such services is threatened by the loss of biodiversity, which has raised concerns (Cardinale et al., 2012). Thus, the topic has become an issue in EU agricultural policy and farmers get financial incentives for implementing biodiversity friendly farming practices. Most effective measures are those increasing the amount of semi-natural habitats in agricultural landscapes (European Commission, 2020). A high cover of semi-natural habitats benefits wild bees (Nayak et al., 2015; Steffan-Dewenter et al., 2002) and increases their densities in flowering crop fields (Carré et al., 2009;

Nayak et al., 2015) with implications for crop yields, which were shown to be enhanced in more diverse landscapes (Andersson et al., 2014; Petersen and Nault, 2014).

Furthermore, mass-flowering crops, like oilseed rape or faba bean can enhance pollinator densities by providing ample nectar and pollen resources (Beyer et al., 2020; Westphal et al., 2003) which can have positive effects on colony development and increase worker numbers (Westphal et al. 2009). Mass-flowering crops can also lead to pollinator shifts and dilution if individual plants or plant species compete for a limited number of pollinators (Holzschuh et al., 2011). Pollinators might be attracted to the flowering fields (Bänsch et al., 2021) and disperse within the crop when high covers are available. This can lead to a lower visitation of individual crop plants and of alternative co-flowering plants with negative implications for pollination services (Holzschuh et al., 2016; Shaw et al., 2020, but see Bänsch et al., 2021). Moreover, early mass-flowering crops can change the community composition of pollinators as it has been shown for a decreased density of long-tonged bumblebees on late-flowering red clover with increasing amounts of early-flowering oilseed rape in the landscape (Diekötter et al., 2010). The authors explain the patterns with competition through short-tongued bees, which strongly profited from oilseed rape and increased their nectar robbing activity on red clover (Diekötter et al., 2010). While the effect of landscape composition on pollinator densities and richness is well studied, landscape effects on foraging decisions of bee pollinators have been rarely examined (but see Bänsch et al., 2020; Grab et al., 2017; Raderschall et al., 2021). The availability of flowers within a certain habitat and the spatial distribution of foraging habitats at landscape scale affect the pollinators` foraging decisions and therefore drives the distribution of pollinators in the landscape (Holzschuh et al., 2011, Westphal et al., 2006). Also, the cover of semi-natural habitats in a landscape has been found to affect foraging decisions of bumblebees, as shown for a reduced proportion of pollen foragers when high amounts of semi-natural habitats are available (Requier et al., 2020).

The faba bean (*Vicia faba* L.) is an example for a crop, in which flower morphology constrains the visiting pollinator community and thereby impacts the bees` foraging behavior. A long tongue and some force are necessary to reach faba bean nectar, which is located deep in the long corollas (Bailes et al., 2018). Thus, most efficient pollinators are long-tongued bumblebee species, like *Bombus hortorum*, which mainly conduct legitimate flower visits, leading to highest rates of cross-fertilization (Marzinzig et al., 2018). In contrast, short-tongued bumblebees usually rob nectar by biting holes into the corolla tubes, which are then commonly used by honeybees (Bond and Poulsen, 1983; Marzinzig et al., 2018). While nectar robbing can negatively impact plant reproduction (Irwin et al., 2010), robbers might also indirectly act as pollinators by shaking the flowers (Kendall and Smith, 1975; Maloof and Inouye, 2000). However, knowledge is scarce about how bee pollinators with species-specific foraging behaviors affect yield formation in faba beans while the combined effects of landscape composition and conspecific crop pollinator species on yield parameters are not well understood.

Insect pollination increases the seed weight per plant of faba beans by 16 - 40 % (Bartomeus et al., 2014; Bishop et al., 2016; St-Martin and Bommarco, 2016) and yield is reduced by, on average, one third without pollination (Bishop & Nakagawa, 2020). The contribution of insect pollination to yield differs between varieties and interacts with other environmental factors or management practices (Bishop et al., 2020; Bishop & Nakagawa, 2020; St-Martin and Bommarco, 2016; Tamburini et al., 2019).

Here, we investigated landscape effects on bumblebees and honeybees and their foraging behavior in faba bean fields as well as the effect on faba bean yield. We tested following hypotheses: (1) High land covers of semi-natural habitats increase bumblebee densities in faba bean fields. (2) High covers of oilseed rape, blooming prior to faba beans, increase bumblebee densities in faba bean fields. (3) Increasing faba bean covers lead to a pollinator dilution and therefore lower bee densities in faba bean fields. (4) Landscape composition influences the bees` foraging behavior, i.e. nectar robbing of short tongued honeybees and bumblebees. (5) Insect pollination increases pod and bean number, seed weight, dry matter yield and protein yield of faba beans, dependent on the bean variety. (6) Landscape composition and bee densities interactively determine faba bean yield of open pollinated plants.

Material and Methods

Study fields and landscape metrics

In 2018, eleven study landscapes of 1 km^2 size were chosen in Germany (Appendix A: Fig. A1). Study landscapes were at least 8 km apart from each other. Each landscape contained at least one faba bean (*Vicia faba* L.) and oilseed rape (*Brassica napus* L.) field. Seven of the eleven bean fields were grown with the summer faba bean variety Fuego and four with Tiffany and all fields were conventionally managed. All crop and habitat types with a minimum area of 10 m^2 were mapped in each study landscape by site inspections (on the basis of maps derived from Google (2018), DigitalGlobe, GeoBasis-DE/BKG, GeoContent). Landscape composition metrics (percentage land cover of oilseed rape, faba bean and semi-natural habitats) within the 1 km^2 study landscapes were calculated using QGIS version 3.10 (QGIS Development Team, 2016). Semi-natural habitats were defined as hedgerows, groves, flower strips and flower fields, extensive grasslands, calcareous grasslands, fallows, orchards, ruderal and succession sites.

Experimental design

We established a pollinator exclusion experiment in one faba bean field per study landscape. The experiment was conducted in four different plots per field, two at the field edge (max. 5 m from field border) and two in the field center (at least 15 m from any border) (Appendix A: Fig. A2). In every plot 13 faba bean plants with similar developmental stage were randomly selected. Five plants were covered with a fine mesh bag (mesh size 0.8 x 0.8 mm) to exclude all insect pollinators (bagged treatment). Bags were big enough to cover whole plants and were fixed with four bamboo poles to not affect growth or to damage plants. Wind and self-pollination were still possible. Plants were bagged before the onset of flowering (mid/end of May) and bags were removed after flowering had ceased (mid/end of June) to allow plants and pods to mature under natural conditions. Eight study plants in each plot were left uncovered to allow natural pollination (open treatment). We counted the number of faba bean plants per 1 m^2 close to the edge and center study plots of every field (three times per location) and calculated the mean plant density per field location.

Pollinator surveys

Within every faba bean field, we surveyed bees with two standardized transect walks (50 x 2m, 5 min) (one at the field edge and one in the center). Surveys were repeated twice during faba bean flowering (28.05. – 03.06.2018 and 05.06. – 10.06.2018). During survey period, full bloom of oilseed rape had already ended with bloom completely finished by the end of May. Transect walks were conducted under weather conditions suitable for pollinators on days with air temperature above 15 °C, without rain and with low wind speed, from 10 a.m. until 6:15 p.m at the latest (Westphal et al., 2008). We recorded all flower visiting honeybees and bumblebees and their foraging behavior (legitimate visitors or nectar robbers). No other wild bee species were foraging on the bean flowers during our transect walks. Bumblebees were grouped into short-tongued (*Bombus terrestris, B. lucorum, B. lapidarius*) and long-tongued bumblebees (*B. hortorum, B. pascuorum, B. sylvarum*) following von Hagen and Aichhorn (2014). All bees visiting the front of the flowers were considered as legitimate visitors and potential pollinators, whereas all bees collecting nectar from the base of the corollas were considered nectar robbers. Additionally, we estimated the local flower cover (%) of the faba bean fields during every survey.

Yield components

We manually harvested all mature study bean plants at the end of July/beginning of August (in total 572 plants). Twenty-two of our study plants died or got damaged during the experiment and 57 plants were heavily infested by aphids and were therefore excluded from the analyses. We counted the number of pods per plant and the number of seeds per pod (for every pod and plant). Seeds were dried at 80 °C for 24 hours, the weight of all seeds per plant was quantified (seed weight per plant [g]) and the mean seed weight of an individual seed was calculated (individual seed weight [g]). We calculated dry matter yield per plot by multiplying plant density with the average seed weight per plant (of all plants per plot), divided by 100 [t/ha]. Furthermore, we assessed the protein yield [t/ha] per plot for eight study landscapes (for details see Appendix B). Moreover, the numbers of seeds infested by the broad been weevil (*Bruchus rufimanus* Boheman) were counted as number of seeds with circular weevil exit holes (results on weevil infestation are presented in Appendix B: Table B1&B2, Fig.B1).

Statistical analyses

Statistical analyses were conducted in R version 3.6.1 (R Core Team, 2019) using generalized linear mixed effects models with the *glmmTMB* package (Brooks et al., 2017). To test landscape composition effects on densities and foraging behavior of the three pollinator groups, we used following response variables: number of observed bees per 100 m^2 transect area (bee density) and proportion of bees robbing nectar from bean flowers (proportion of nectar robbers) of all observed bees. Explanatory variables included in these models were the percentage cover of oilseed rape, of faba bean, of semi-natural habitats, the local flower cover of the transect area, pollinator group (honeybees, short-, long-tongued bumblebees) and all possible two-way interactions with pollinator group. For bee densities, we used a negative binomial distribution due to overdispersion, and for the proportion of nectar robbers a binomial distribution was chosen. Landscape and field location were used as nested random effects (landscape/location).

Faba bean yield components were analyzed in two steps. First, we analyzed the effect of insect pollination and variety on plant yield for six different response variables, i.e. number of beans per pod (mean across all pods per plant), individual seed weight, number of pods, seed weight per plant, dry matter yield and protein yield. Pollinator exclusion treatment (bagged, open), bee density per field location (summed across all bee groups and runs), faba bean variety (Fuego, Tiffany) and all possible interactions were added as explanatory variables. Yield component analyses were conducted at plant level and dry matter yield and protein yield analysis at plot level.

In a second step, we tested whether yield components, dry matter yield and protein yield are affected by landscape composition in interaction with bee densities. We only used the open pollinated plants and the same yield response variables as described above. We included all landscape composition metrics, bee density per field location and the interactions between bee density and each landscape composition metrics as explanatory variables. Models for number of beans per pod and individual seed weight were fitted with Gaussian family and for number of pods negative binomial distribution was used. For seed weight per plant, dry matter yield and protein yield we used Gamma family and log link. Landscape and plot were used as nested random effects (landscape/plot) but for the dry matter yield and protein yield model only landscape was added.

After global models were fitted, we used the multimodel inference approach by Burnham & Anderson (2002) for model selection. Candidate models were ranked by second order Akaike Information Criterion (AICc) and we interpreted all models within delta AICc < 2. We used Akaike weights (w_i) to estimate the relative support of a model to have the best fit across all models and sum of Akaike weights (Σw_i) as measure of the relative importance of predictor variables. For more details see Appendix B.

Results

Landscape composition effects on bee pollinator density and foraging behavior

We observed in total 532 honeybees and 284 bumblebees, of which 70.8 % were short-tongued. Most observed honeybees (90.4%) and short-tongued bumblebees (85.0%), robbed nectar, while 84.1 % of all long-tongued bumblebee visits were legitimate visits (Appendix A: Table A1).

The multimodel inference for landscape composition effects on bee densities revealed three best-fitting models, including local flower cover ($\Sigma w_i = 1.00$), pollinator group ($\Sigma w_i = 1.00$) and all landscape composition metrics (Σw_i between 0.55 and 0.85) and the pollinator group x faba bean cover and group x oilseed rape cover interaction (Σw_i= 0.29 and 0.70 respectively) (Appendix A: Table A2 & A3). Increasing semi-natural habitat covers led to increasing bee densities (Fig. 1a). High faba bean covers positively affected bumblebee but not honeybee densities (Fig. 1b). High oilseed rape covers negatively influenced short-tongued bumblebee densities (Fig. 1c). Bee densities in faba bean fields increased with increasing local flower cover of the transect area (Appendix A: Fig. A3a).

There were three models within delta AICc < 2 for the proportion of nectar robbers, including pollinator group ($\Sigma w_i = 1.00$), local flower cover ($\Sigma w_i = 0.75$), faba bean cover ($\Sigma w_i = 0.56$), group x faba bean and group x flower cover interaction (Σw_i 0.42 and 0.61 respectively) (Appendix A: Table A2 & A3). The proportion of nectar robbing long-tongued bumblebees declined with increasing faba bean cover, while the opposite effect was observed for short-tongued bumblebees. (Fig. 1d). The proportion of nectar robbing long-tongued bumblebees increased with local flower cover contrary to honeybees (Appendix A: Fig. A3b). However, this effect was driven by an influential data point (at flower cover of 60%). The analysis without the influential point shows the proportion of nectar robbing long-tongued bumblebees to decrease with local flower cover, while the effect of faba bean cover on the proportion of nectar robbers does not change (results of the analysis without the influential data point are shown in Appendix A: Table A2 & A3; Fig. A3c & d).

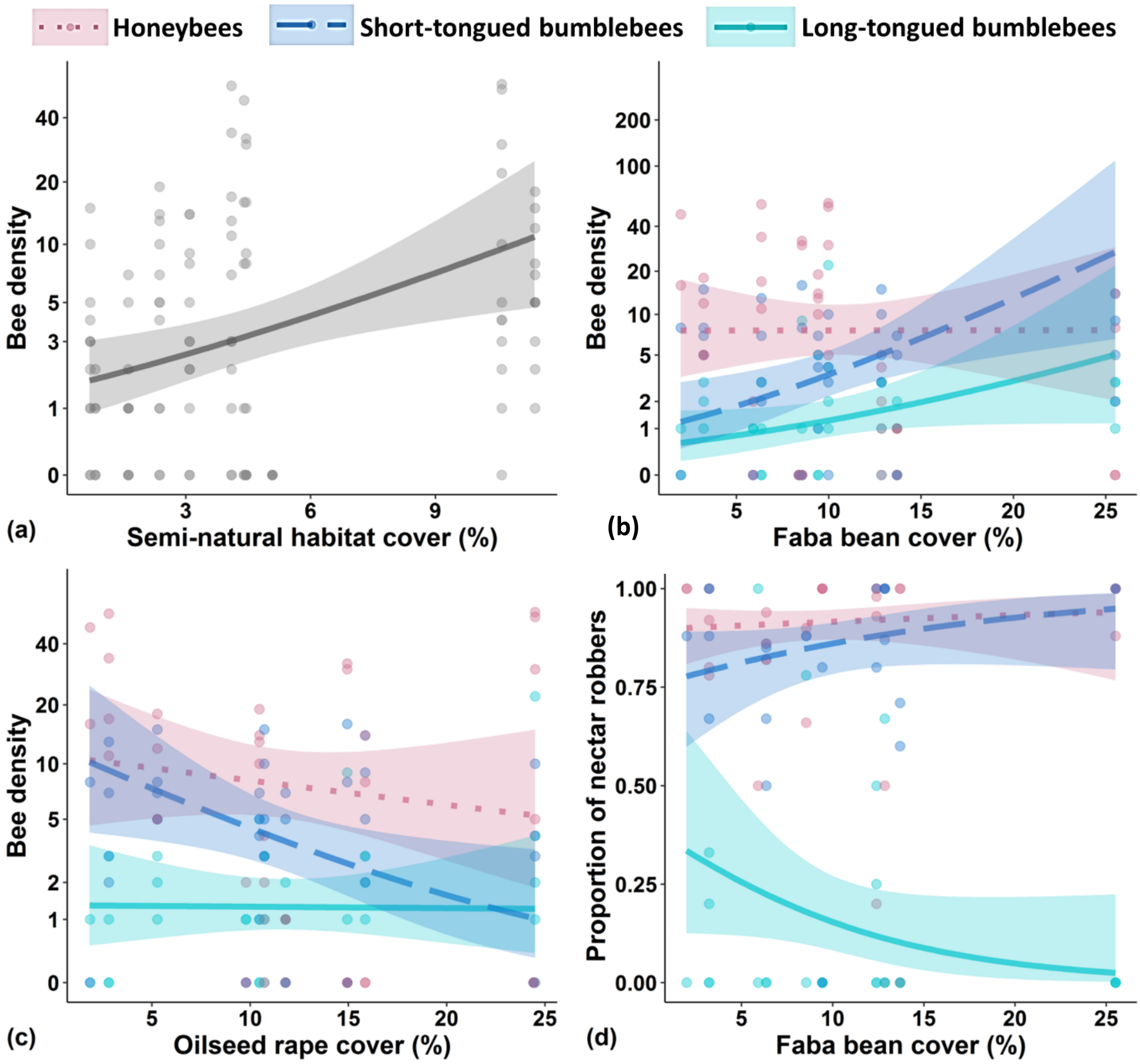

Figure 1 Effects of (**a**) semi-natural habitat cover, (**b**) faba bean cover and (**c**) oilseed rape cover on bee densities in faba bean fields. Effect of (**d**) faba bean cover on the proportion of nectar robbers. Different pollinator groups are depicted in different colors. Lines show predicted means with 95 % confidence intervals. Predictions are obtained from models *bee1* (a-c) and *rob3* (d) (Appendix A: Table A2).

Bee pollination effects on faba bean yield components

The number of beans per pod was explained by three best-fitting models, which included pollinator exclusion treatment ($\Sigma w_i = 1.00$), bee density ($\Sigma w_i = 0.95$), variety ($\Sigma w_i = 0.95$), the bee density x variety interaction ($\Sigma w_i = 0.65$) and the variety x treatment interaction ($\Sigma w_i = 0.41$) (Appendix A: Table A4 & A5). Mean bean number per pod was 57.9 % higher in open pollinated compared to bagged plants for variety Fuego and 37.0 % higher for Tiffany (Fig. 2a). Bee densities increased the number of beans per pod for Fuego but not for Tiffany (Appendix A: Fig. A4a).

For individual seed, the global model was the best-fitting model, including treatment, variety, bee density (Σw_i between 0.90 and 0.98), all possible two-way interactions (Σw_i between 0.42 and 0.70) and the three-way interaction ($\Sigma w_i = 0.25$) (Appendix A: Table A4 & A5). Individual seed weight was 10.9 % higher in bagged compared to open pollinated plants for Fuego and did not differ between treatments for Tiffany (Fig. 2b). Individual seed weight increased with bee density, but stronger for bagged than open plants for the case of Fuego, while for Tiffany a decrease was detected (Appendix A: Fig. A4b).

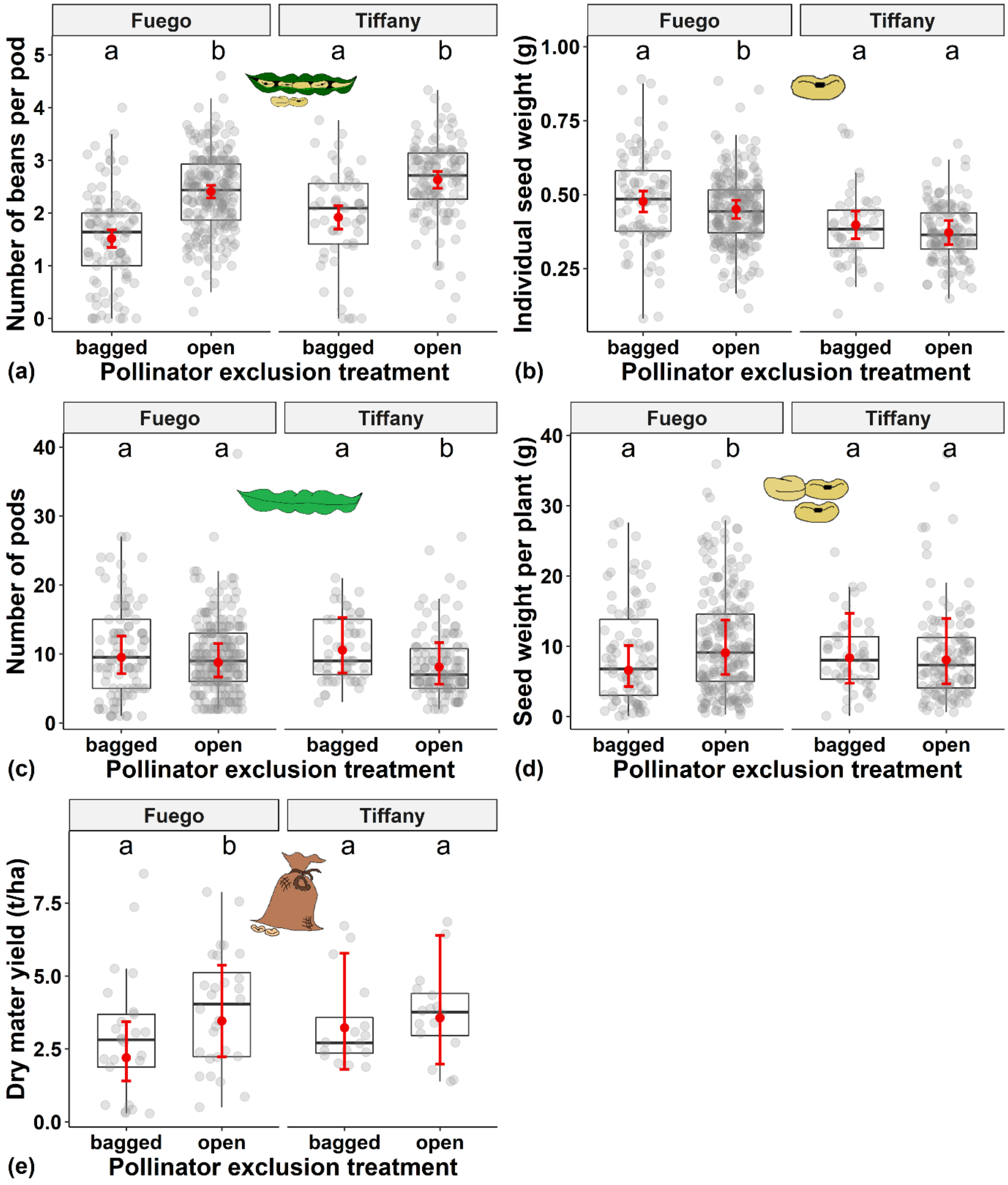

Figure 2 The effect of pollinator exclusion treatment on **(a)** the mean number of beans per pod, **(b)** the individual seed weight (g), **(c)** the number of pods, **(d)** the seed weight per plant (g) and **(e)** dry matter yield (t/ha) for the two faba bean varieties Fuego and Tiffany. Predicted means and 95 % confidence intervals are depicted in red. Different letters above boxplots

indicate significant differences between treatments. Predictions are obtained from the best-fitting models *sw1* (b) and *sp1* (d) and the second-best models *b2* (a), *p2* (c) *y2* (e) (Appendix A: Table A4).

The best-fitting model for pod number included only treatment ($\Sigma w_i = 0.99$) (Table S3 & S4). The three other models within dAICc < 2 contained additionally variety ($\Sigma w_i = 0.59$), bee density ($\Sigma w_i = 0.45$) and the interaction between variety and treatment ($\Sigma w_i = 0.42$). The number of pods per plant was 12.4 % higher in bagged compared to open pollinated plants for Tiffany and did not differ between treatments for Fuego (Fig. 2c). Bee densities had no effect on pod number.

Seed weight per plant was explained by one best-fitting model, including treatment ($\Sigma w_i = 0.99$), variety ($\Sigma w_i = 0.85$) and their interaction ($\Sigma w_i = 0.79$) (Appendix A: Table A4 & A5). The seed weight per plant was 17.6 % higher for open pollinated plants compared to bagged ones for Fuego, while no difference was detected for Tiffany (Fig. 2d).

The best-fitting model for dry matter yield included only treatment ($\Sigma w_i = 1.00$). The other two models within dAICc < 2 contained additionally variety ($\Sigma w_i = 0.59$) and the interaction between treatment and variety ($\Sigma w_i = 0.42$) (Appendix A: Table A4 & A5). Dry matter yield was 57.5 % higher in open pollinated than in bagged plants for Fuego, but not higher for Tiffany (Fig. 2e).

For protein yield the best-fitting model included treatment ($\Sigma w_i = 0.67$), but protein yield between open and bagged plants did not differ. The second-best fitting model was the null model with a dAICc of 0.97, indicating a low support of the best-fitting model.

Landscape composition effects on faba bean yield components

There were one to eight best-fitting models explaining the effect of landscape composition and bee density on the number of beans per pod, individual seed weight, number of pods per plant, seed weight per plant, dry matter yield and protein yield (Appendix A: Table A4). Bee density, all landscape composition metrics and various interactions were included in the models for all yield components. Oilseed rape cover (Σw_i between 0.62 and 0.99) generally had a negative effect on yield components (Fig. 3c&f; Appendix A: Fig. A5a-d). Faba bean cover (Σw_i between 0.34 and 0.93) and semi-natural habitat cover (Σw_i between 0.47 and 0.88) generally had a positive effect on yield components (Fig. 3 a&d; Appendix A: Fig. A5e-k). Bee density (Σw_i between 0.73 and 0.97) positively affected yield components but effects depended on landscape composition (Appendix A: Table A4 & A6).

Higher bee densities increased number of beans per pod (Fig. 3d), individual seed weight (Appendix A: Fig. A6d), number of pods (Appendix A: Fig. A6e) only in landscapes with a high cover of semi-natural habitats. Increasing bee densities had a positive effect on pod number in landscapes with a high cover of faba bean (Fig. 3e). Higher bee densities increased seed weight per plant (Fig. 3f), number of beans per pod (Appendix A: Fig. A6a), pod number (Appendix A: Fig. A6b) and dry matter yield (Appendix A: Fig. A6c) but only in landscapes with a high oilseed rape cover.

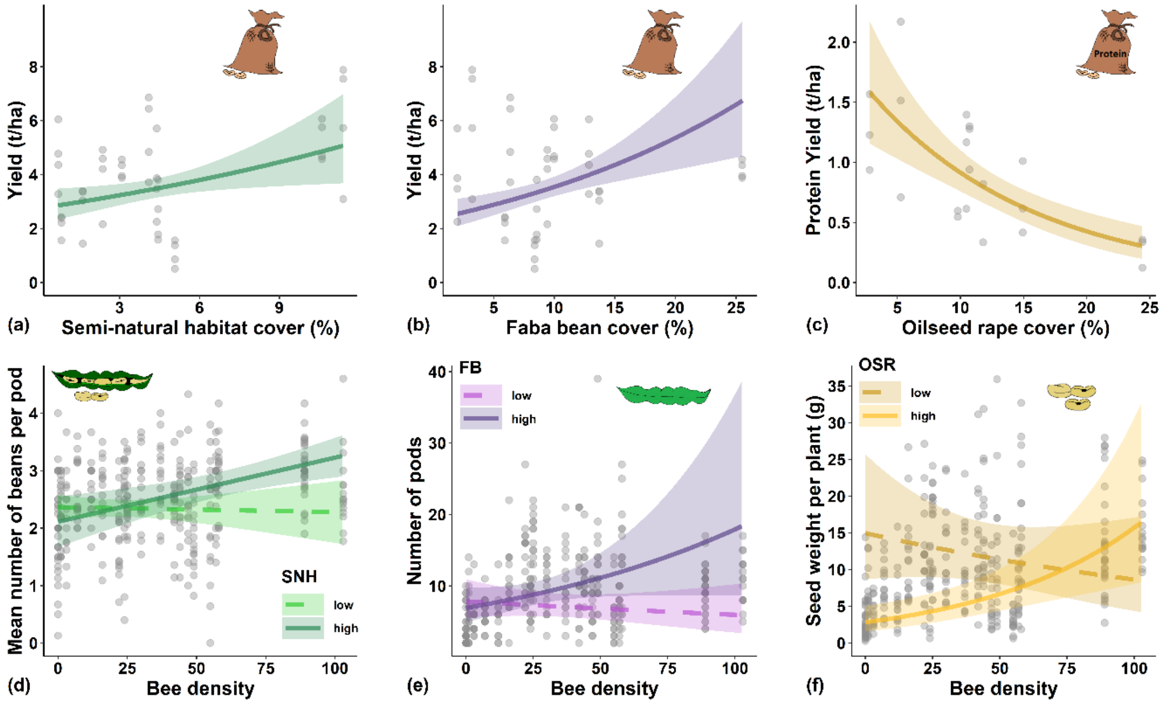

Figure 3 Effect of (**a**) semi-natural habitat cover (%) and of (**b**) faba bean cover (%) on yield per plot (t/ha). Effect of (**c**) oilseed rape cover (%) on protein yield (t/ha). Effect of bee density on (**d**) bean number/pod for high and low (equals 10.60 % (80th percentile) and 0.82 % (20th percentile) respectively; see Appendix B) covers of semi-natural habitats (SNH) (%). Effect of bee density on (**e**) pod number for high and low (equals 13.70 % (80th percentile) and 3.23 % (20th percentile) respectively) covers of faba bean (FB) (%). Effect of bee density on (**f**) seed weight per plant for landscapes high and low (equals 24.42 % (80th percentile) and 2.81 % (20th percentile) respectively) covers of oilseed rape (OSR) (%). Lines show predicted means with 95% confidence intervals. Predictions are obtained from the best-fitting models oy1 (a, b), opy1 (c), *ob1 (d), op1 (e), osp1 (f)* (Appendix A: Table A4).

Discussion

Landscape composition effects on bee pollinator density and foraging behavior

Our study revealed that landscape composition influences densities and foraging behavior of pollinators. The positive effect of semi-natural habitat cover on bee densities in bean fields is in line with other studies (Carré et al., 2009; Nayak et al., 2015; Raderschall et al., 2021). Generally, semi-natural habitats are known to promote wild bees (e.g. Steffan-Dewenter et al., 2002) and to improve their reproductive success (Requier et al., 2020). Landscapes with high semi-natural habitat covers presumably contained higher bumblebee densities, which foraged in bean fields during their flowering. Especially short-tongued bumblebees responded positively to high faba bean covers, which might be explained by their attraction to mass-resources (Walther-Hellwig and Frankl, 2000). Besides, high faba bean covers might have increased worker numbers of bumblebee colonies, similarly as known from mass-flowering oilseed rape (e.g. Herrmann et al., 2007; Westphal et al., 2003) and as indicated by higher bumblebee densities in landscapes with faba bean cultivation (Beyer et al., 2020). The cover of oilseed rape, which flowered prior to faba bean, had negative impacts on short-tongued bumblebee densities in bean fields, which contradicts our expectations. Several studies show positive effects of oilseed rape on pollinator densities (e.g. Herrmann et al., 2007; Westphal et al., 2003) but Kallioniemi et al. (2017) found a negative relationship between the area of early flowering crops and bumblebee densities and species richness. The authors mention competition from honeybees (see Lindström et al., 2016) or agrochemical applications in early flowering crops as possible reasons. Alternatively, bumblebees might have been attracted to particularly attractive semi-natural habitats in landscapes with high oilseed rape covers, leading to lower densities in bean fields. However, we did not record flowering plants in semi-natural habitats.

As expected, long-tongued bumblebees, which are most effective faba bean pollinators (Marzinzig et al., 2018), conducted lowest levels of nectar robbing. They conducted nectar robbing more frequently, when faba bean fields had higher local flower covers, analogously to Marzinzig et al. (2018). However, this effect was driven by one influential data point. If it is removed from the analyses, the effect reverses and thus needs to be interpreted with great care. Beyond, landscape composition affected bumblebees` foraging behavior in crop fields, which has rarely been observed (but see Raderschall et al. 2021). To our knowledge, no study to date has observed that landscape composition differentially affects the foraging behavior of different functional pollinator groups. With increasing *V. faba* land cover, short-tongued and long-tongued bumblebees increasingly conducted the foraging behavior related to their species-specific morphology. Short-tongued bumblebees increased their nectar robbing activity and thus made increased use of faba beans as nectar source. The lower nectar robbing activity of long-tongued bumblebees with increasing faba bean land covers might in contrast indicate an increased use of bean flowers as pollen source.

Bee pollination effects on faba bean yield components

Pollinator exclusion negatively affected yield components of *V. faba*. As expected, the number of beans per pod was enhanced in open pollinated plants compared to bagged plants (e.g. Bishop et al., 2016). This increase was stronger for variety Fuego and increasing bee densities led to more beans per pod in Fuego only. Individual seed weight did only differ between treatments for Fuego with heavier seeds in bagged plants. Surprisingly, seed weight in bagged plants increased with increasing bee densities, which might be the result of other interacting factors, such as differing management practices, which we could not control for. Bartomeus et al. (2014) observed enhanced yields with increasing bee densities for bagged flowers and suggest airborne pollen release by foraging bees as possible explanation (Pierre et al., 2010). While seed weight per plant and dry matter yield were not enhanced in open pollinated Tiffany plants, dry matter yield was enhanced by 57.5 % for Fuego. It is known that the effect of insect pollination is context and variety dependent (Bishop et al., 2020; Bishop & Nakagawa 2020). Fuego plants produced fewer but heavier seeds in response to insect exclusion (e.g. Geisler, 1988). Contrastingly, Li and Yang (2014) found no trade-offs between seed number and size in faba bean but instead a negative correlation between pod number and seed number per pod, alike the response of Tiffany to insect exclusion. The contrasting reactions of Fuego and Tiffany demonstrate two different plant strategies of resource allocation in response to the lack of insect pollination. Since plants only have limited resources, trade-offs between yield components are commonly observed (Li and Yang, 2014). It is moreover known that different cultivars of the same crop species can differ in their level of pollinator dependency influencing pollinator effectiveness and yields (Bishop & Nakagawa 2020; Kendall et al., 2020).

Landscape composition effects on faba bean yield components

High faba bean and semi-natural habitat covers enhanced faba bean yield components, which corresponds with higher bumblebee densities in such landscapes. It is known that the surrounding landscape can influence yield of flowering crops via pollinators (Dainese et al., 2019) and an enhanced availability of foraging and nesting habitats has been found to enhance faba bean seed set and yield (Andersson et al., 2014; Raderschall et al., 2021). Contrastingly, landscapes with increased oilseed rape covers had reduced yield components, which might result from lower bumblebee densities in those landscapes. Similarly, Diekötter et al. (2010) showed that high oilseed rape covers resulted in lower long-tongued bumblebee densities on red clover, but no effect on seed set was detected. Contrastingly, high oilseed rape covers positively affected the weight of strawberries flowering later in the season (Herbertsson et al., 2017). To our knowledge, our study is the first evidence of negative effects of early-flowering oilseed rape on pollinator densities in and yield of later flowering faba beans. Furthermore, we showed that the effect of increasing bee densities on faba bean yield formation was modulated by landscape composition. This might be the result of different pollinator communities in landscapes with high and low covers of the respective landscape composition metrics. Moreover, the foraging behavior of the different functional bee groups varied according to changing landscape composition (Bänsch et al., 2020). For instance, results indicate that in landscapes with low faba bean covers, honeybees outnumbered bumblebees, in contrast to landscapes with high bean covers where bumblebees were predominant. It is likely that the presence of bumblebees is decisive for successful pollination and yield formation in *V. faba*. Accordingly, long-tongued bumblebees are known to be most effective faba bean pollinators (Marzinzig et al., 2018) and pollination benefits tend to be higher for bumblebees than honeybees (Bishop & Nakagawa, 2020). Thus, visitor communities dominated by honeybees might be less effective, as indicated by our results.

Concluding, this study contributes to increasing evidence that crop pollinators respond to resource availability at landscape scale and adapt their foraging behavior respectively (Bänsch et al., 2020, Grab et al., 2017). Landscape composition modulated bee densities, bees` foraging behavior and pollination services. Our study adds further evidence on the high value of semi-natural habitats on ecosystem services, such as crop pollination. Further research is needed on how pollinators` foraging behavior in crops is affected by landscape composition and on how early flowering crops modulate pollinators` community composition and pollination services in later flowering crops.

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References

Andersson, G.K.S., Ekroos, J., Stjernman, M., Rundlöf, M., Smith, H.G., 2014. Effects of farming intensity, crop rotation and landscape heterogeneity on field bean pollination. Agric. Ecosyst. Environ. 184, 145–148. https://doi.org/10.1016/j.agee.2013.12.002

Bailes, E.J., Pattrick, J.G., Glover, B.J., 2018. An analysis of the energetic reward offered by field bean (Vicia faba) flowers: Nectar, pollen, and operative force. Ecol. Evol. 8, 3161–3171. https://doi.org/10.1002/ece3.3851

Bänsch, S., Tscharntke, T., Gabriel, D., Westphal, C., 2021. Crop pollination services: complementary resource use by social vs solitary bees facing crops with contrasting flower supply. J. Appl. Ecol. 58, 476-485. https://doi.org/10.1111/1365-2664.13777

Bartomeus, I., Potts, S.G., Steffan-Dewenter, I., Vaissière, B.E., Woyciechowski, M., Krewenka, K.M., Tscheulin, et al., 2014. Contribution of insect pollinators to crop yield and quality varies with agricultural intensification. PeerJ 2, e328. https://doi.org/10.7717/peerj.328

Beyer, N., Gabriel, D., Kirsch, F., Schulz-Kesting, K., Dauber, J., Westphal, C., 2020. Functional groups of wild bees respond differently to faba bean (Vicia faba L.) cultivation at landscape scale. J. Appl. Ecol. 57: 2499-2508. https://doi.org/10.1111/1365-2664.13745

Bishop, J., Garratt, M.P.D., Breeze, T.D., 2020. Yield benefits of additional pollination to faba bean vary with cultivar, scale, yield parameter and experimental method. Sci. Rep. 10, 1–11. https://doi.org/10.1038/s41598-020-58518-1

Bishop, J., Jones, H.E., Lukac, M., Potts, S.G., 2016. Insect pollination reduces yield loss following heat stress in faba bean (Vicia faba L.). Agric. Ecosyst. Environ. 220, 89–96. https://doi.org/10.1016/j.agee.2015.12.007

Bond, D.A., Poulsen, M.H., 1983. Pollination. In: Hebblethwaite, P. D., Ed., The Faba Bean (Vicia faba L.). Butterworths, London, 77-101.

Brooks, M.E., Kristensen, K., Benthem, K.J. van, Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., et al., 2017. glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. R J. 9, 378–400.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference. A Practical Information-Theoretic Approach, 2nd ed. ed. Springer-Verlag.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., et al., 2012. Biodiversity loss and its impact on humanity. Nature 486, 59–67. https://doi.org/10.1038/nature11148

Carré, G., Roche, P., Chifflet, R., Morison, N., Bommarco, R., Harrison-Cripps, J., Krewenka, K., Potts, S.G., et al., 2009. Landscape context and habitat type as drivers of bee diversity in European annual crops. Agric. Ecosyst. Environ. 133, 40–47. https://doi.org/10.1016/j.agee.2009.05.001

Dainese, M., Martin, E.A., Aizen, M.A., Albrecht, M., Bartomeus, I., Bommarco, R., Carvalheiro, L.G., et al., 2019. A global synthesis reveals biodiversity-mediated benefits for crop production. Sci. Adv. 5, eaax0121.

Diekötter, T., Kadoya, T., Peter, F., Wolters, V., Jauker, F., 2010. Oilseed rape crops distort plant-pollinator interactions. J. Appl. Ecol. 47, 209–214. https://doi.org/10.1111/j.1365-2664.2009.01759.x

European Commission, 2020. Evaluation of the impacts of the CAP on habitats, landscape, biodiversity. Final Report. Publications Office of the European Union. Luxembourg.

Geisler, G., 1988. Pflanzenbau: Ein Lehrbuch - Biologische Grundlagen und Technik der Pflanzenproduktion, 2nd ed. Paul Parey, Berlin; Hamburg.

Grab, H., Blitzer, E.J., Danforth, B., Loeb, G., Poveda, K., 2017. Temporally dependent pollinator competition and facilitation with mass flowering crops affects yield in co-blooming crops. Sci. Rep. 7, 1–9. https://doi.org/10.1038/srep45296

Herbertsson, L., Rundlöf, M., Smith, H.G., 2017. The relation between oilseed rape and pollination of later flowering plants varies across plant species and landscape contexts. Basic Appl. Ecol. 24, 77–85. https://doi.org/10.1016/j.baae.2017.08.001

Herrmann, F., Westphal, C., Moritz, R.F.A., Steffan-Dewenter, I., 2007. Genetic diversity and mass resources promote colony size and forager densities of a social bee (Bombus pascuorum) in agricultural landscapes. Mol. Ecol. 16, 1167–1178. https://doi.org/10.1111/j.1365-294X.2007.03226.x

Holzschuh, A., Dainese, M., González-Varo, J.P., Mudri-Stojnić, S., Riedinger, V., Rundlöf, M., Scheper, J., et al., 2016. Mass-flowering crops dilute pollinator abundance in agricultural landscapes across Europe. Ecol. Lett. 19, 1228–1236. https://doi.org/10.1111/ele.12657

Irwin, R.E., Bronstein, J.L., Manson, J.S., Richardson, L., 2010. Nectar Robbing: Ecological and Evolutionary Perspectives. Annu. Rev. Ecol. Evol. Syst. 41, 271–292. https://doi.org/10.1146/annurev.ecolsys.110308.120330

Kallioniemi, E., Åström, J., Rusch, G.M., Dahle, S., Åström, S., Gjershaug, J.O., 2017. Local resources, linear elements and mass-flowering crops determine bumblebee occurrences in moderately intensified farmlands. Agric. Ecosyst. Environ. 239, 90–100. https://doi.org/10.1016/j.agee.2016.12.039

Kendall, A.D.A., Smith, B.D., 1975. The Pollinating Efficiency of Honeybee and Bumblebee Visits to Field Bean Flowers (Vicia faba L.) 12, 709–717.

Kendall, L.K., Gagic, V., Evans, L.J., Cutting, B.T., Scalzo, J., Hanusch, Y., Jones J., Rocchetti, M., Sonter, C., Keir, M., Rader, R. 2020. Self-compativle blueberry cultivars require fewer floral visits to maximize fruit production than a partially self-incompatible cultivar. J. Appl Ecol. 57: 2454-2462. https:// doi.org/10.1111/1365-2664.13751

Li, X., Yang, Y., 2014. A novel perspective on seed yield of broad bean (Vicia faba L.): Differences resulting from pod characteristics. Sci. Rep. 4, 1–6. https://doi.org/10.1038/srep06859

Lindström, S.A.M., Herbertsson, L., Rundlöf, M., Bommarco, R., Smith, H.G., 2016. Experimental evidence that honeybees depress wild insect densities in a flowering crop. Proc. R. Soc. B Biol. Sci. 283, 1–8. https://doi.org/10.1098/rspb.2016.1641

Maloof, J.E., Inouye, D.W., 2000. ARE NECTAR ROBBERS CHEATERS OR MUTUALISTS? Ecology 81.

Marzinzig, B., Brünjes, L., Biagioni, S., Behling, H., Link, W., Westphal, C., 2018. Bee pollinators of faba bean (Vicia faba L.) differ in their foraging behaviour and pollination efficiency. Agric. Ecosyst. Environ. 264, 24–33. https://doi.org/10.1016/j.agee.2018.05.003

Nayak, G.K., Roberts, S.P.M., Garratt, M., Breeze, T.D., Tscheulin, T., Harrison-Cripps, J., Vogiatzakis, I.N., et al., 2015. Interactive effect of floral abundance and semi-natural habitats on pollinators in field beans (Vicia faba). Agric. Ecosyst. Environ. 199, 58–66. https://doi.org/10.1016/j.agee.2014.08.016

Pierre, J., Vaissière, B., Vallée, P., Renard, M., 2010. Efficiency of airborne pollen released by honeybee foraging on pollination in oilseed rape: A wind insect-assisted pollination. Apidologie 41, 109–115. https://doi.org/10.1051/apido/2009056

Power, A.G., 2010. Ecosystem services and agriculture: Tradeoffs and synergies. Philos. Trans. R. Soc. B Biol. Sci. 365, 2959–2971. https://doi.org/10.1098/rstb.2010.0143

QGIS Development Team, 2016. QGIS Geographic Information System. Open Source Geospatial Foundation Project. Retrieved from http:// qgis.osgeo.org.

R Core Team, 2019. R: A language and environment for statistical computing.

Raderschall, C.A., Bommarco, R., Lindström, S.A.M., Lundin, O., 2021. Landscape crop diversity and semi-natural habitat affect crop pollinators, pollination benefit and yield. Agric. Ecosyst. Environ. 306, 107189. https://doi.org/10.1016/j.agee.2020.107189

Requier, F., Jowanowitsch, K.K., Kallnik, K., Steffan-Dewenter, I., 2020. Limitation of complementary resources affects colony growth, foraging behavior, and reproduction in bumble bees. Ecology 101, 0–3. https://doi.org/10.1002/ecy.2946

Shaw, R.F., Phillips, B.B., Doyle, T., Pell, J.K., Redhead, J.W., Savage, J., Woodcock, B.A., et al., 2020. Mass-flowering crops have a greater impact than semi-natural habitat on crop pollinators and pollen deposition. Landsc. Ecol. 35, 513–527. https://doi.org/10.1007/s10980-019-00962-0

Soper, M.M.H., 1952. A study of the principal factors affecting the establishment and development of the field bean (vicia faba). J. Agric. Sci. 42, 335–346. https://doi.org/10.1017/S0021859600057233

St-Martin, A., Bommarco, R., 2016. Soil compaction and insect pollination modify impacts of crop rotation on nitrogen fixation and yield. Basic Appl. Ecol. 17, 617–626. https://doi.org/10.1016/j.baae.2016.07.001

Steffan-Dewenter, I., Münzenberg, U., Bürger, C., Thies, C., Tscharntke, T., 2002. Scale-dependent effects of landscape context on three pollinator guilds. Ecology 83, 1421–1432. https://doi.org/10.1890/0012-9658(2002)083[1421:SDEOLC]2.0.CO;2

Tamburini, G., Bommarco, R., Kleijn, D., van der Putten, W.H., Marini, L., 2019. Pollination contribution to crop yield is often context-dependent: A review of experimental evidence. Agric. Ecosyst. Environ. 280, 16–23. https://doi.org/10.1016/j.agee.2019.04.022

von Hagen, E., Aichhorn, A., 2014. Hummeln. bestimmen, ansiedeln, vermehren, schützen, 6th ed.

Fauna Verlag, Nottuln.

Walther-Hellwig, K., Frankl, R., 2000. Foraging habitats and foraging distances of bumblebees, Bombus spp. (Hym., Apidae), in an agricultural landscape. J. Appl. Entomol. 124, 299–306. https://doi.org/10.1046/j.1439-0418.2000.00484.x

Westphal C., Steffan-Dewenter I. & Tscharntke T., 2009. Mass flowering oilseed rape improves early colony growth but not sexual reproduction of bumblebees. Journal of Applied Ecology, 46, 187-193.

Westphal, C., Bommarco, R., Carré, G., Lamborn, E., Morison, N., Petanidou, T., Potts, S.G., et al., 2008. Measuring bee diversity in different European habitats and biogeographical regions. Ecol. Monogr. 78, 653–671. https://doi.org/10.1890/07-1292.1

Westphal C., Steffan-Dewenter I. & Tscharntke T., 2006. Foraging trip duration of bumblebees in relation to landscape-wide resource availability. Ecological Entomology, 31, 389-394.

Westphal, C., Steffan-Dewenter, I., Tscharntke, T., 2003. Mass flowering crops enhance pollinator densities at a landscape scale. Ecol. Lett. 6, 961–965. https://doi.org/10.1046/j.1461-0248.2003.00523.x

Supplementary material

Appendix A

Figures

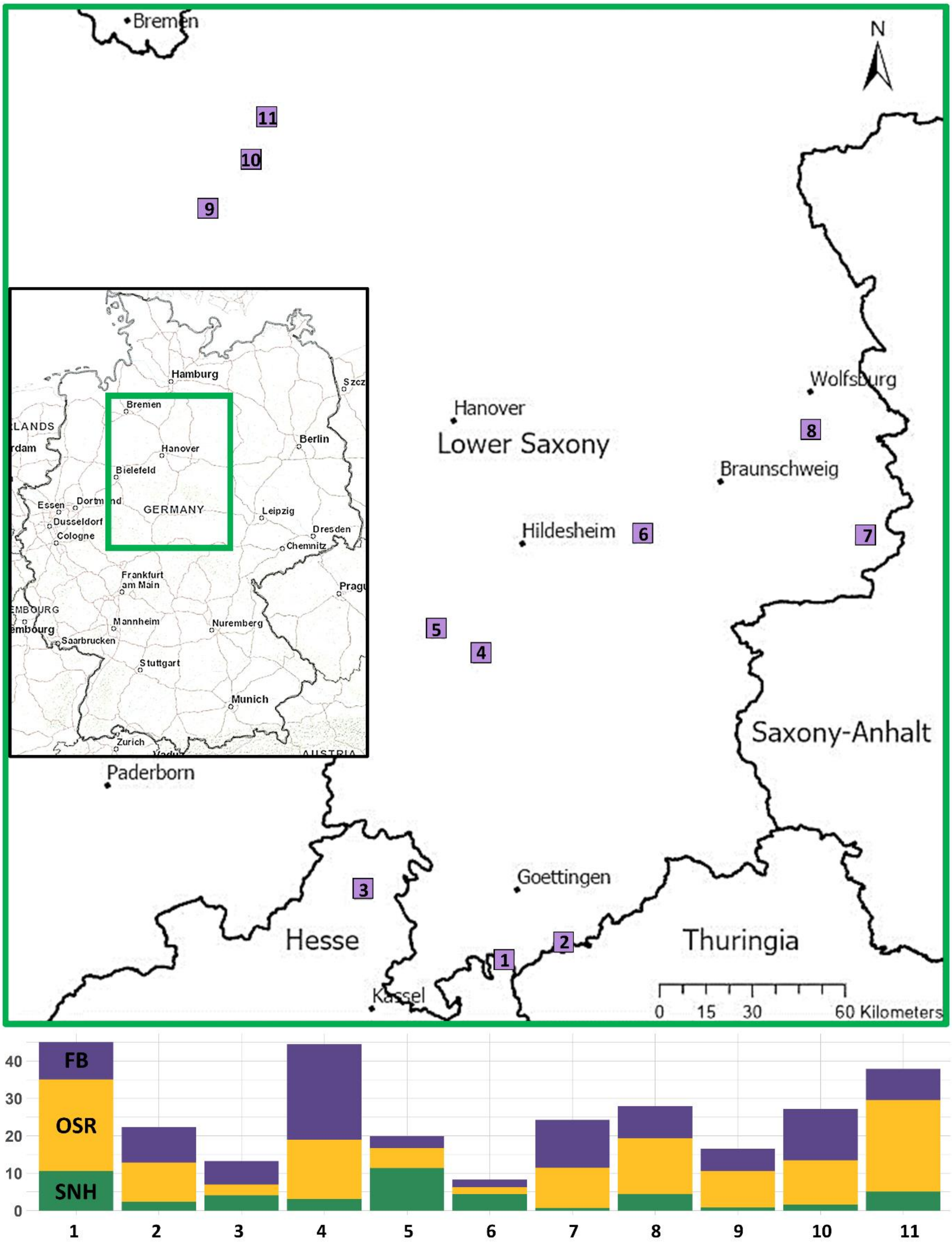

Figure A1 Schematic map showing the location of the study landscapes in Germany (depicted as purple squares) Below, the composition of the individual study landscapes is shown: the area proportion (%) of faba bean (FB, in puple), of oilseed rape (OSR, in yellow) and of semi-natural habitats (SNH, in green) of each study landscape.

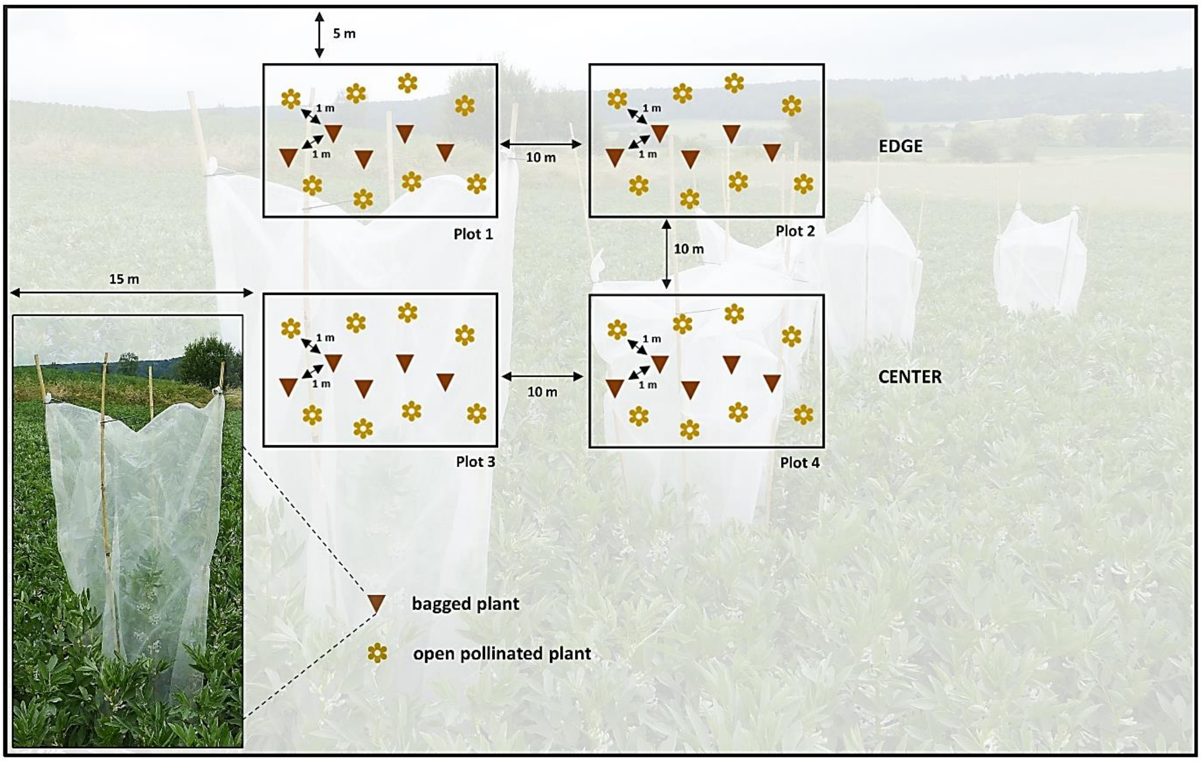

Figure A2 Study design of pollinator exclusion experiment. In each faba bean fields four individual plants per plot (two at field center and two at field edge) were bagged (see photograph) and eight open pollinated plants were marked and left unbagged to allow natural pollination.

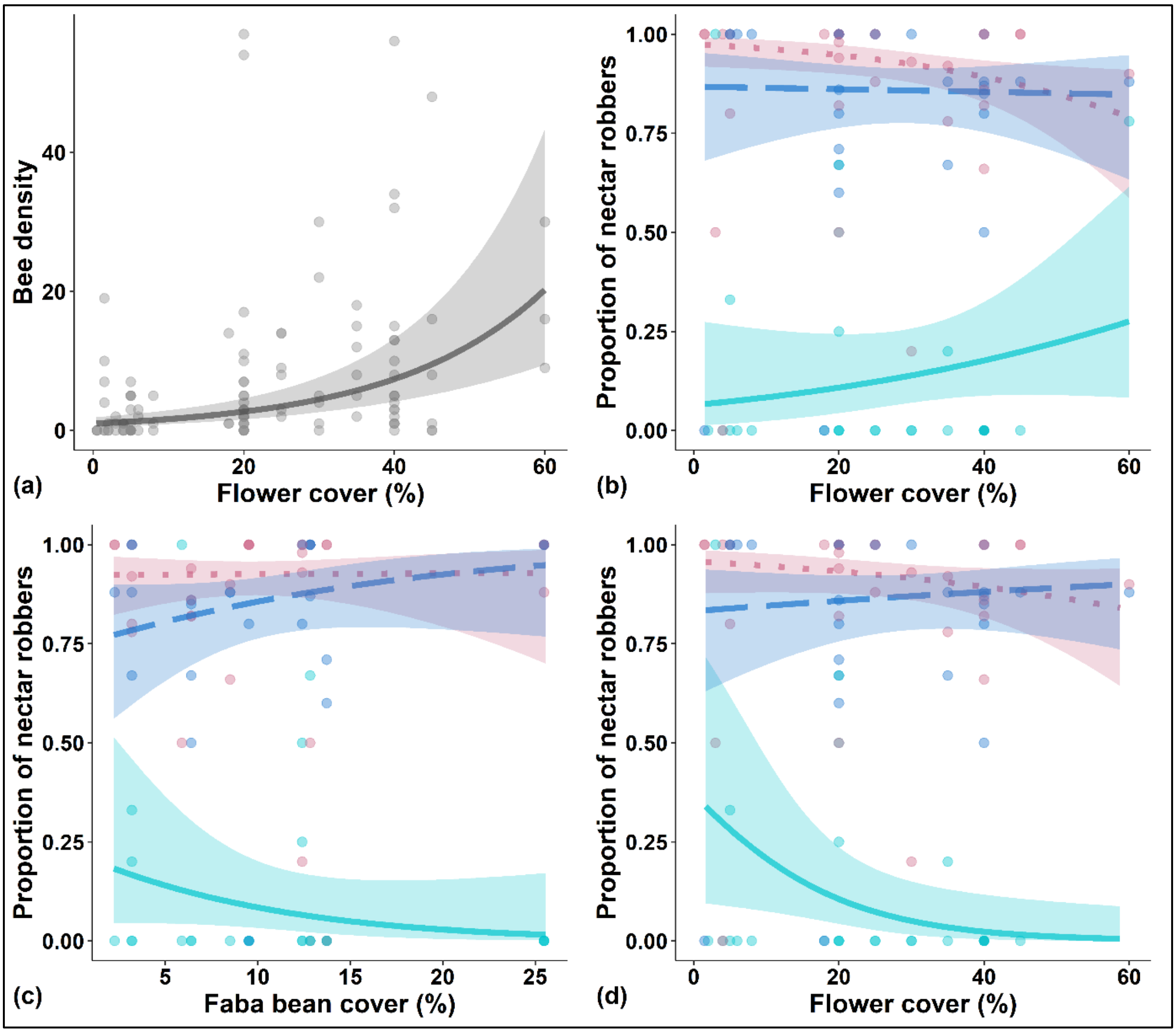

Figure A3 The effect of local flower cover (%) of transect area on (a) bee density and on (b) the proportion of nectar robbers for the three pollinator groups (depicted in different colors) - for the whole data set. Effect of (c) faba bean cover (%) and of (d) local flower cover (%) on the proportion of nectar robbers for the three pollinator groups - for the data set without the influential data point at flower cover = 60 %. Lines show predicted means with 95 % confidence intervals. Predictions are obtained from the respective best-fitting models *bee1* (a) and *rob1* (b) and from the third-best fitting model *robB3* (c, d) (Table A2).

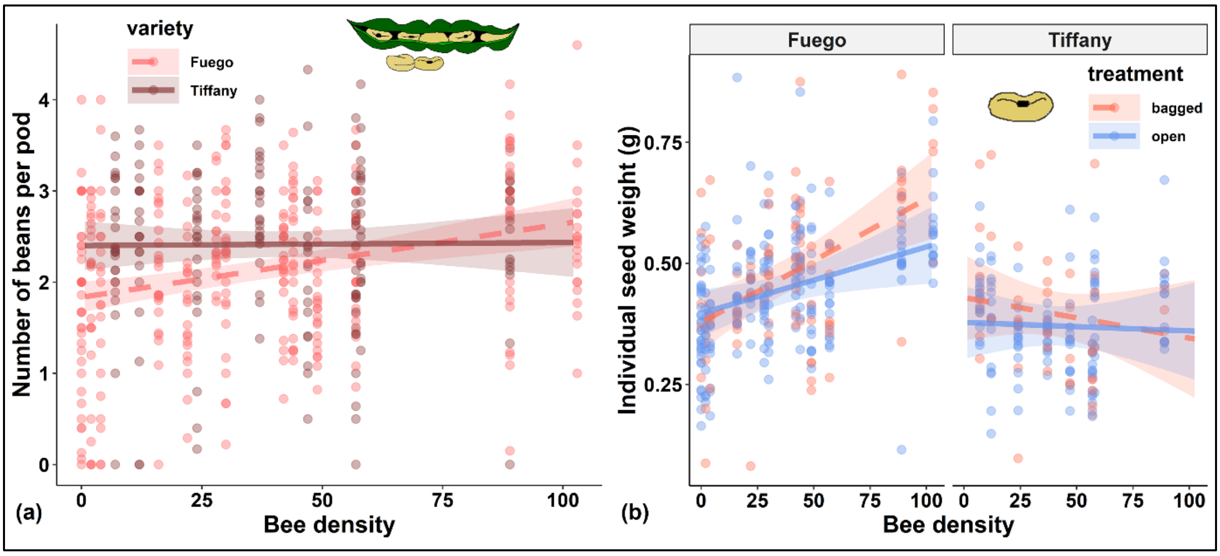

Figure A4 The effect of bee density on (a) the number of beans per pod for the two different bean varieties and the effect of bee density on (b) the individual seed weight (g) for open and bagged plants and for both varieties. Predicted means and 95 % confidence intervals are shown. Predictions are obtained from the second-best model *b2* (a) and the best-fitting model *sw1* (b) (Table A4).

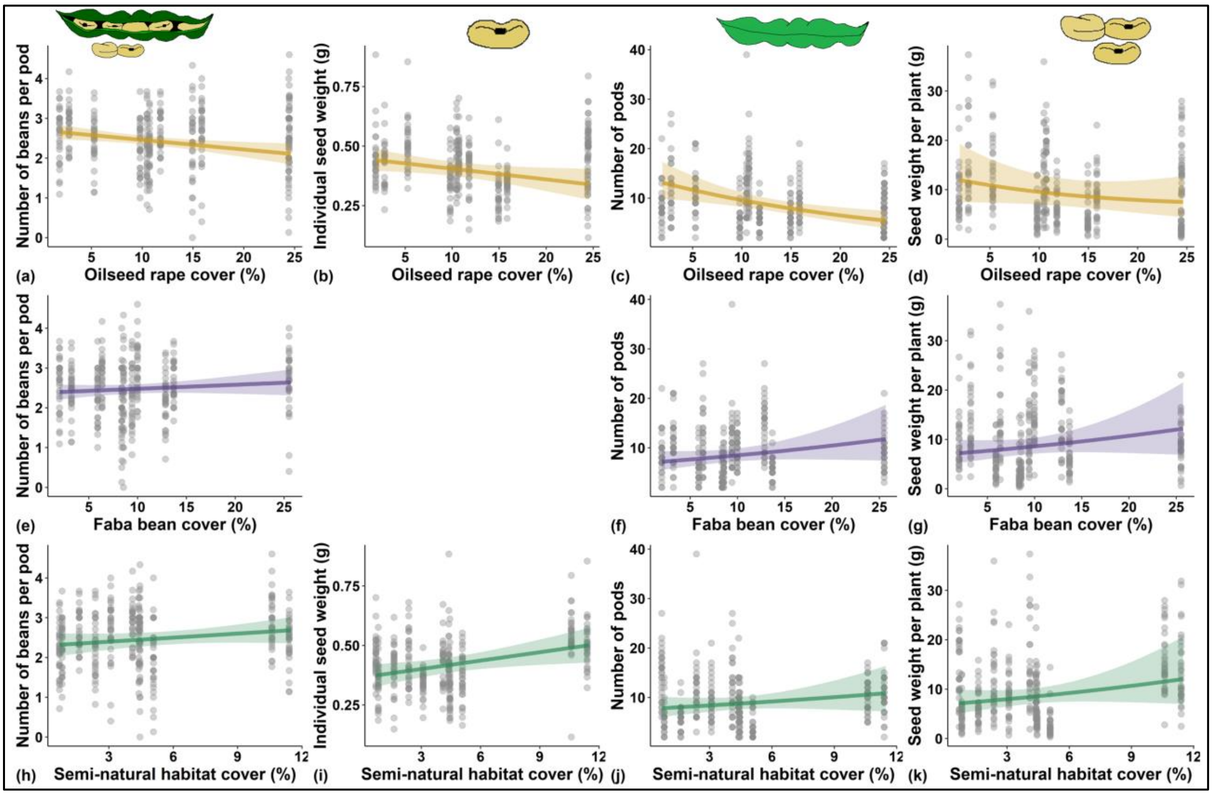

Figure A5 Effects of (a-d) oilseed rape cover (%), (e-g) faba bean cover (%) and of (h-k) semi-natural habitat cover on yield components. Predicted means and 95 % confidence intervals are shown. Predictions are obtained from models *ob1* (a&h), *ob3* (e), *osw1* (b), *osw2* (i), *osw7* (f), *op3* (c), *op4* (f), *op6* (j), *osp1* (d), *osp2* (g), *osp3* (k) (Table A4).

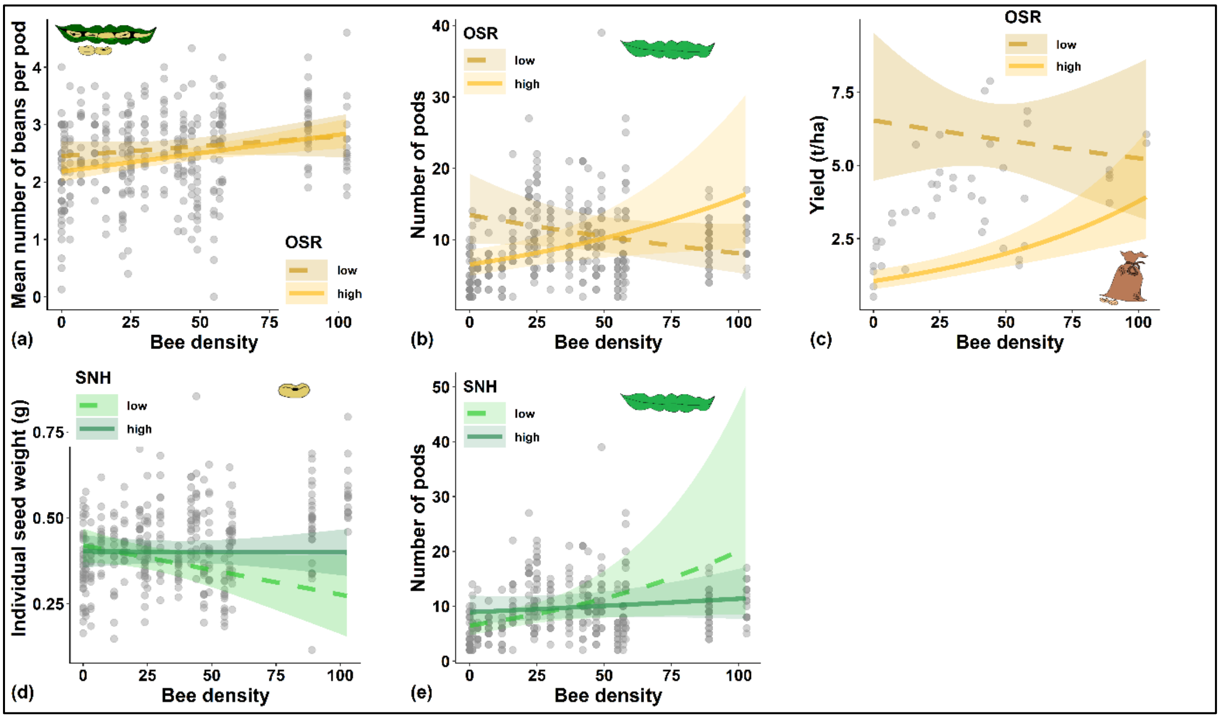

Figure A6 The effect of bee density (a) on the mean number of beans per pod, (b) on the number of pods per plant and (c) on yield (t/ha) for a high and a low (equals 24.42 % and 2.81 % respectively) level of oilseed rape cover. The effect of bee density on (d) the individual seed weight (g) and on (e) the number of pods per plant for high and low (equals 10.60 % and 0.82 % respectively) covers of semi-natural habitats. Lines show predicted means with 95% confidence intervals. Predictions are obtained from models *ob5* (a), *op5* (b, e), oy1 (d) and *osw1* (d) (Table A4).

Tables

Table A1 Total number of observed honeybees, short-tongued bumblebees and long-tongued bumblebees as well as their observed pollination behavior on faba beans (during transect walks).

	Honeybees	Short-tongued Bumblebees	Long-tongued Bumblebees
observed in total	520	201	83
legitimate visit	49	29	69
nectar robbing	471	163	14

Table A2 Summary of the best fitting candidate models (dAIC<2), null and full models for the effects of landscape composition on bee densities and foraging behavior in faba bean fields. Analyses of the proportion of nectar robbers were conducted with the full data set (rob) and without an influential data point (robB). Marginal (R_m^2) and conditional (R_c^2) R^2 values are given as a measure of the model´s goodness of fit. group: pollinator group (honeybees, long-tongued bumblebees, short-tongued bumblebees), FB: faba bean cover (%), FC: local flower cover of faba bean fields, OSR: oilseed rape cover (%), SNH: semi-natural habitat cover (%).

response variable	model	df	AICc	deltaAIC	AIC weight	explanatory variables	R_m^2	R_c^2
Bee densities (n=120)	**bee1**	14	600.67	0.00	0.19	group + FB + FC + OSR + SNH + group:FB + group:OSR	0.66	0.74
	bee2	11	600.69	0.02	0.18	group + FB + FC + SNH + group:FB	0.63	0.71
	bee3	12	601.37	0.70	0.13	group + FB + FC + OSR + SNH + group:FB	0.64	0.73
	bee0	4	656.96	56.29	0.00	1	0.00	0.51
	bee.full	18	611.15	10.48	0.00	group + FB + FC + OSR + SNH + group:FB + group:sOSR + group:sSNH + group:sFC	0.66	0.74

Proportion of nectar robbers (n=83)	**rob1**	8	260.75	0.00	0.19	group + FC + group:FC	0.53	0.60
	rob2	11	261.68	0.93	0.12	group + FB + FC + group:FB + group:FC	0.55	0.62
	rob3	8	262.63	1.88	0.07	group + FB + group:FB	0.55	NA
	rob0	3	451.61	190.86	0.00	1	0.00	0.11
	rob.full	17	269.26	8.50	0.00	group + FB + FC + OSR + SNH + group:FB + group:OSR + group:SNH + group:FC	0.66	0.71
Proportion of nectar robbers (n=82; without influential data point)	**robB1**	8	242.57	0.00	0.14	group + FC + group:FC	0.58	0.63
	robB2	6	243.61	1.03	0.09	group + FC	0.55	0.61
	robB3	11	243.61	1.04	0.09	group + FB + FC + group:FB + group:FC	0.59	0.64
	robB4	5	243.82	1.25	0.08	group	0.55	0.61
	robB0	3	448.61	206.04	0.00	1	0.00	0.11
	robB.full	17	255.37	12.79	0.00	group + FB + FC + OSR + SNH + group:FB + group:OSR + group:SNH + group:FC	0.61	0.66

Table A3 The relative importance of explanatory variables expressed by Σw_i (sum of Akaike weights) for models to explain the effects of landscape composition on bee densities and foraging behavior of bees in faba bean fields (best fitting models are shown in Table A2). Analyses of the proportion of nectar robbers were conducted with the full data set (rob) and without an influential data point (robB). Model parameters having $\Sigma w_i > 0.2$ for all response variables are shown. group: pollinator group (honeybees, long-tongued bumblebees, short-tongued bumblebees), FB: faba bean cover (%), FC: local flower cover of faba bean fields, OSR: oilseed rape cover (%), SNH: semi-natural habitat cover (%).

Model	response variable	group	FB	FC	SNH	OSR	group: FB	group: FC	group: SNH	group: OSR
bee	**Bee densities**	1.00	0.85	1.00	0.85	0.55	0.70	-	-	0.29
rob	**Prop. robbers**	1.00	0.56	0.75	0.26	0.25	0.42	0.61	-	-
robB	**Prop. robbers**	1.00	0.45	0.73	0.25	0.25	0.27	0.47	-	-

Table A4 Summary of the best fitting candidate models (dAIC<2) and null models for the effects of bee pollination on faba bean yield components and for bee density and landscape composition effects on yield components of open pollinated faba bean plants. Marginal (R_m^2) and conditional (R_c^2) R^2 values are given as a measure of the model´s goodness of fit. Treatment: pollinator exclusion treatment (bagged/open pollinated), Bee: bee densities, variety: faba bean variety (Tiffany/Fuego), FB: faba bean cover (%), OSR: oilseed rape cover (%), SNH: Semi-natural habitat cover (%), Bee: bee densities.

response variable	model	df	AICc	deltaAIC	AIC weight	explanatory variables	R_m^2	R_c^2
Bee pollination effects on yield components								
Beans per pod (n=493)	b1	8	1145.89	0.00	0.28	Bee + treatment + variety + Bee:variety	0.25	0.28
	b2	9	1146.65	0.76	0.19	Bee + treatment + variety + Bee:variety + treatment:variety	0.25	0.28
	b3	7	1147.87	1.98	0.10	Bee + treatment + variety	0.24	0.28
	b0	4	1261.61	115.71	0.00	1	0.00	0.08
	b.full	11	1150.51	4.62	0.03	Bee + treatment + variety + Bee:treatment + Bee:variety + treatment:variety + Bee:treatment:variety	0.25	0.28
Individual seed weight (n=493)	sw1 & sw.full	11	-765.24	0.00	0.25	Bee + treatment + variety + Bee:treatment + Bee:variety + treatment:variety + Bee:treatment:variety	0.22	0.36
	sw2	9	-764.86	0.38	0.21	Bee + treatment + variety + Bee:treatment + Bee:variety	0.21	0.36
	sw3	8	-763.76	1.48	0.12	Bee + treatment + variety + Bee:variety	0.20	0.35
	sw0	4	-756.22	9.02	0.00	1	0.00	0.36
Seed weight per plant (n=480)	sp1	7	2879.79	0.00	0.43	treatment + variety + treatment:variety	0.02	0.46
	sp0	4	2888.39	8.60	0.01	1	0.00	0.43
	sp.full	11	2886.47	6.68	0.02	Bee + treatment + variety + Bee:treatment + Bee:variety + treatment:variety + Bee:treatment:variety	0.03	0.46
Pod number (n=493)	p1	5	2803.62	0.00	0.25	treatment	0.01	0.44
	p2	7	2803.90	0.28	0.21	treatment + variety + treatment:variety	0.02	0.45
	p3	6	2805.27	1.64	0.11	Bee + treatment	0.02	0.42
	p4	8	2805.61	1.98	0.09	Bee + treatment + variety + treatment:variety	0.03	0.42
	p0	4	2812.40	8.77	0.00	1	0.00	0.43

	p.full	11	2809.72	6.10	0.01	Bee + treatment + variety + Bee:treatment + Bee:variety + treatment:variety + Bee:treatment:variety	0.03	0.43
Dry matter yield (n=85)	y1	5	301.76	0.00	0.25	treatment	0.05	0.69
	y2	7	301.96	0.19	0.23	treatment + variety + treatment:variety	0.09	0.71
	y3	6	303.75	1.98	0.09	treatment + variety	0.07	0.69
	y0	4	311.73	9.97	0.00	1	0.00	0.61
	y.full	11	308.93	7.17	0.01	Bee + treatment + variety + Bee:treatment + Bee:variety + treatment:variety + Bee:treatment:variety	0.13	0.70
Protein Yield (n=43)	py1	5	440.74	0.00	0.23	treatment	0.03	0.68
	py0	4	441.72	0.97	0.14	1	0.00	0.64
	py.full	-	-	-	-	-	0.57	0.73
Landscape composition effects on yield components (open pollinated plants)								
Beans per pod (n=344)	ob1	9	746.39	0.00	0.11	Bee + FB + OSR + SNH + Bee:SNH	0.10	0.11
	ob2	5	746.67	0.29	0.10	Bee	0.05	0.16
	ob3	6	747.70	1.31	0.06	Bee + FB	0.06	0.16
	ob4	7	747.82	1.44	0.05	Bee + FB + OSR	0.07	0.16
	ob5	8	747.94	1.55	0.05	Bee + FB + OSR + Bee:OSR	0.09	0.17
	ob6	10	748.09	1.70	0.05	Bee + FB + OSR + SNH + Bee:OSR + Bee:SNH	0.10	0.11
	ob7	6	748.22	1.83	0.04	Bee + OSR	0.05	0.16
	ob0	4	748.84	2.45	0.03	1	0.00	0.17
	ob.full	11	750.18	3.79	0.02	Bee + OSR + SNH + FB + Bee:OSR + Bee:SNH + Bee:FB	0.10	0.11
Individual seed weight (n=342)	osw1	8	-606.73	0.00	0.20	Bee + OSR + SNH + Bee:SNH	0.23	0.39
	osw2	5	-605.38	1.35	0.10	SNH	0.12	0.38
	osw0	4	-602.56	4.17	0.02	1	0.00	0.38
	osw.full	11	-600.42	6.31	0.01	Bee + OSR + SNH + FB + Bee:OSR + Bee:SNH + Bee:FB	0.23	0.39
Seed weight per plant (n=342)	osp1	7	2036.95	0.00	0.20	Bee + OSR + Bee:OSR	0.27	0.51
	osp2	8	2037.54	0.59	0.15	Bee + FB + OSR + Bee:OSR	0.30	0.51
	osp3	9	2037.90	0.95	0.12	Bee + FB + OSR + SNH + Bee:OSR	0.32	0.52
	osp4	8	2038.71	1.76	0.08	Bee + OSR + SNH + Bee:OSR	0.27	0.52
	osp0	4	2042.07	5.12	0.02	1	0.00	0.51
	osp.full	11	2041.42	4.47	0.02	Bee + OSR + SNH + FB + Bee:OSR + Bee:SNH + Bee:FB	0.32	0.51
Pod number (n=344)	op1	9	1887.55	0.00	0.14	Bee + FB + OSR + Bee:FB + Bee:OSR	0.28	0.50
	op2	7	1887.96	0.41	0.12	Bee + OSR + Bee:OSR	0.25	0.52
	op3	8	1888.02	0.47	0.11	Bee + FB + OSR + Bee:FB	0.22	0.46
	op4	8	1888.08	0.53	0.11	Bee + FB + OSR + Bee:OSR	0.28	0.52
	op5	9	1888.40	0.85	0.09	Bee + OSR + SNH + Bee:OSR + Bee:SNH	0.27	0.52
	op6	9	1888.94	1.39	0.07	Bee + FB + OSR + SNH + Bee:FB	0.24	0.47
	op7	10	1889.14	1.59	0.06	Bee + FB + OSR + SNH + Bee:FB + Bee:OSR	0.28	0.50
	op8	10	1889.28	1.72	0.06	Bee + FB + OSR + SNH + Bee:OSR + Bee:SNH	0.30	0.52
	op0	4	1892.97	5.42	0.01	1	0.00	0.48
	op.full	11	1890.39	2.83	0.03	Bee + OSR + SNH + FB + Bee:OSR + Bee:SNH + Bee:FB	0.29	0.50
Dry matter yield (n=40)	oy1	8	152.72	0.00	0.44	Bee + FB + OSR + SNH + Bee:OSR	0.67	0.68
	oy0	3	163.60	10.88	0.00	1	0.66	0.00
	oy.full	10	159.17	6.45	0.02	Bee + OSR + SNH + FB + Bee:OSR + Bee:SNH + Bee:FB	0.67	0.68
Protein Yield (n=22)	opy1	4	22.65	0.00	0.53	OSR	0.60	-
	opy0	3	31.99	9.34	0.00	1	0.00	0.54
	opy.full	-	-	-	-	Bee + OSR + SNH + FB + Bee:OSR + Bee:SNH + Bee:FB	0.70	-

Table A5 The relative importance of explanatory variables expressed by Σw_i (sum of Akaike weights) for models to explain the effects of bee pollination on faba bean yield components (best fitting models are shown in Table A4). Model parameters having $\Sigma w_i > 0.2$ for all response variables are shown. Treatment: pollinator exclusion treatment (bagged/open pollinated), sBee: bee densities, variety: faba bean variety (Tiffany/Fuego).

Insect pollination effects on yield parameters and yield								
Model	**response variable**	**treatment**	**variety**	**Bee**	**treatment: variety**	**Bee: treatment**	**Bee:variety**	**Bee:treatment :variety**
b	**Beans per pod**	1.00	0.95	0.95	0.41	0.28	0.65	-
sw	**Individual Seed weight**	0.98	0.93	0.90	0.41	0.65	0.68	0.23
sp	**Seed weight per plant**	0.99	0.85	0.43	0.79	-	-	-
p	**Pod number**	0.99	0.59	0.44	0.42	-	-	-
y	**Dry matter yield**	1.00	0.59	0.42	0.41	-	-	-

py	**Protein yield**	0.67	0.39	0.51	-	-	-	-

Table A6 The relative importance of explanatory variables expressed by Σw_i (sum of Akaike weights) for models to explain the effects of landscape composition and bee density on faba bean yield components of open pollinated plants (best fitting models are shown in Table A4). Model parameters having $\Sigma w_i > 0.2$ for all response variables are shown. FB: faba bean cover (%), OSR: oilseed rape cover (%), SNH: semi-natural habitat cover (%), Bee: bumblebee densities.

Landscape composition effects of yield parameters and yield (open pollinated plants)								
Model	**response variable**	**Bee**	**FB**	**OSR**	**SNH**	**Bee:FB**	**Bee:OSR**	**Bee:SNH**
ob	**Beans per pod**	0.87	0.63	0.64	0.53	-	0.23	0.28
osw	**Individual Seed weight**	0.73	0.34	0.62	0.88	-	-	0.51
osp	**Seed weight per plant**	0.92	0.61	0.95	0.52	0.24	0.77	-
op	**Pod number**	0.96	0.71	0.96	0.47	0.47	0.71	0.22
oy	**Dry matter yield**	0.97	0.93	0.99	0.84	-	0.80	0.25
opy	**Protein Yield**	-	0.20	0.99	-	-	-	-

Appendix B

Details on the statistical approach

We used the multimodel inference approach by Burnham & Anderson (2002) for model selection. Based on the global models, candidate models, containing all possible combinations of predictor variables were fitted with the *dredge* function of the *MuMIn* package (Barton, 2019). They were ranked by second order Akaike Information Criterion (AICc) and Akaike weights (w_i) were used to estimate relative support of a model to have the best fit across all models (Burnham and Anderson, 2002). The number of variables in the candidate models for all protein yield models was restricted to a maximum of five. The sum of Akaike weights (Σw_i) of all predictor variables across all models that include the respective variable were used as measure of the relative importance. We interpreted all models with a delta AICc < 2 compared to the best fitting model and we interpret the effects of all predictor variables with $\Sigma w_i > 0.2$. We calculated the marginal (R_m^2) and conditional (R_c^2) R^2 values (Nakagawa et al., 2017) with the *performance* package (Lüdecke et al., 2020) to evaluate the models' goodness of fit. We inspected residual plots to validate model assumptions. We used the variance inflation factor (VIF) to test for collinearity and VIFs were below 3 for all cases (Zuur et al., 2010). We tested for spatial autocorrelation in residuals using the Moran`s I test, which was non-significant ($p > 0.05$) for all models. To test for differences between pollinator groups and between pollinator exclusion treatments, we applied post hoc tests with the *emmeans* package (Lenth, 2019) and alpha level of 0.05. To visualize interaction effects between bee density and landscape composition metrics (two continuous explanatory variables) on yield components, we plotted predictions of the effect of bee density on yield components for a low and a high level of the respective landscape composition metrics. Those levels represent the 20th and 80th percentile of the landscape composition metrics, respectively.

References

Barton, K., 2019. MuMIn: Multi-Model Inference. R package version 1.43.6.

Lenth, R., 2019. emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.4.1. URL: https://CRAN.R-project.org/package=emmeans.

Lüdecke, D., Makowski, D., Waggoner, P., Patil, I., 2020. performance: Assessment of Regression Models Performance. R package version 0.4.5.

Nakagawa, S., Johnson, P.C.D., Schielzeth, H., 2017. The coefficient of determination R2 and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. J. R. Soc. Interface 14. https://doi.org/10.1098/rsif.2017.0213

Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problems. Methods Ecol. Evol. 1, 3–14. https://doi.org/10.1111/j.2041-210x.2009.00001.x

Measurement of the beans` nitrogen content and calculation of protein yield

The seeds` nitrogen (N) content was assessed using 79 samples from eight study fields. For 3-6 bagged and open pollinated plants per landscape, beans of different pods were milled. N content of flour was determined by high temperature combustion (analysis with Vario el cube, Elementar). Two samples per plant were analyzed and averaged (in total 158 individual samples). We calculated protein yield [t/ha] per plot by multiplying dry matter yield with the mean bean protein content (N*6.25 (Jones, 1941)), averaged across all plants per plot.

References

Jones, D., 1941. Factors for converting percentages of nitrogen in foods and feeds into percentages of protein. Washington, DC.

Landscape composition effects on seed infestation with the broad been weevil (*Bruchus rufimanus* Boheman)

Results

The multi-model inference revealed eight models within delta AICc < 2 explaining landscape composition effects on seed infestation with the broad bean weevil (Appendix B: Table B1). The proportion of seeds infested with *B. rufimanus* decreased with the cover of semi-natural habitats in the landscape (Σwi = 0.94), slightly stronger so at the field edge compared to the field center (location x SNH: Σwi = 0.41; Appendix B: Table B2, Fig. B1a). Weevil infestation decreased with increasing faba bean cover (Σwi = 0.73) and this decrease was stronger at the field edge (Appendix B: Fig. B1b). Weevil infestation did not differ between the field edge and the field center (Σwi = 0.89; p=0.10). The proportion of weevil infested seeds decreased with increasing number of pods per plant (Σwi = 0.81; Appendix B: Fig. B1c) and increased with increasing oilseed rape land cover (Σwi = 0.47; Appendix B: Fig. B1d).

Table B1 Summary of the best fitting candidate models (dAIC<2) and null models for the landscape composition effects on seed infestation with the broad bean weevil. Marginal (R_m^2) and conditional (R_c^2) R^2 values are given as a measure of the model´s goodness of fit. FB: faba bean cover (%), SNH: Semi-natural habitat cover (%), location: field location (edge/center), pods: number of pods per faba bean plant.

Landscape composition effects on seed infestation with the bread been weevil (open pollinated plants)								
response variable	**model**	**df**	**AICc**	**deltaAIC**	**AIC weight**	**explanatory variables**	**R_m^2**	**R_c^2**
Proportion of weevil infested seeds (n=343)	we1	8	1811.35	0.00	0.08	location + FB + pods + SNH + location:FB	0.15	0.29
	we2	9	1811.98	0.63	0.06	location + FB + OSR + pods + SNH + location:FB	0.17	0.29
	we3	8	1811.99	0.64	0.06	location + FB + pods + SNH + location:SNH	0.15	0.29
	we4	9	1812.40	1.05	0.05	location + FB + pods + SNH + location:FB + location:SNH	0.15	0.29
	we5	7	1812.66	1.31	0.04	location + FB + pods + SNH	0.15	0.29
	we6	9	1812.89	1.54	0.04	location + FB + OSR + pods + SNH + location:SNH	0.17	0.29
	we7	10	1813.08	1.73	0.04	location + FB + OSR + pods + SNH + location:FB + location:SNH	0.17	0.29
	we8	6	1813.19	1.84	0.03	FB + pods + SNH	0.15	0.29
	we0	3	1819.13	7.78	0.00	1	0.00	0.28
	we.full	12	1817.31	5.96	0.00	location + FB + OSR + pods + SNH + location:FB + location:OSR + location:pods + location:SNH	0.17	0.29

Table B2 The relative importance of explanatory variables expressed by Σw_i (sum of Akaike weights) for models to explain the effects of landscape composition and plants` pod number on the seed infestation with the broad bean weevil (best fitting models are shown in Table B1). Model parameters having $\Sigma w_i > 0.2$ for all response variables are shown. FB: faba bean cover (%), OSR: oilseed rape cover (%), SNH: semi-natural habitat cover (%), location: field location (edge/center), pods: number of pods per faba bean plant.

Landscape composition effects on seed infestation with the bread been weevil (open pollinated plants)								
Model	**response variable**	location	pods	FB	OSR	SNH	location:FB	location:SNH
we	**Prop. weevil infest.**	0.89	0.81	0.90	0.47	0.94	0.45	0.41

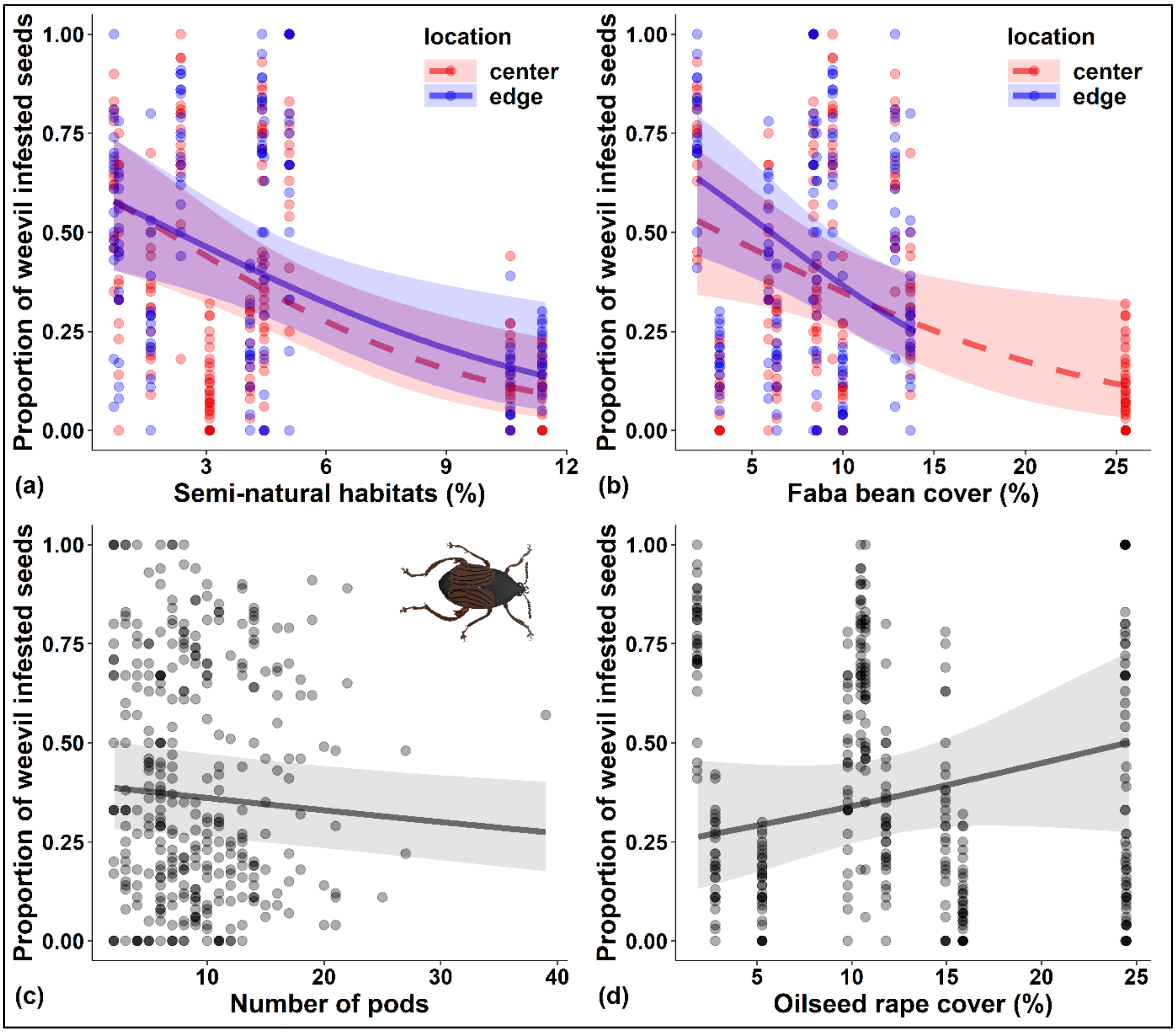

Fig. B1 The effect of (**a**) cover of semi-natural habitats (%), (**b**) faba bean cover (%), (**c**) number of pods per plant and (**d**) oilseed rape cover (%) on the proportion of seeds infested with the broad bean weevil. In (a, b) for plants at the field edge and in the field center. Lines show predicted means with 95% confidence intervals. Predictions are obtained from model *we1* (Appendix B: Table B1).

Discussion

The broad bean weevil is a major pest in faba beans and infestation lowers the seed quality as food or feed product with resulting price declines (Bachmann et al., 2020). We found the proportion of seeds with *B. rufimanus* damage to decrease with increasing number of pods per plant and with increasing faba bean cover. This might be the result of a dilution of weevils if more faba bean pods or plants are available in a landscape. The decrease of weevil infestation with increasing faba bean cover was stronger at the field edge, from which beetles migrate into the field from the surroundings. Bean weevils overwinter under tree bark, in leaf litter, in seeds or in the soil and move into bean fields usually in May (Pölitz and Reike, 2019; Seidenglanz and Huňady, 2016). Pölitz and Reike (2019) observed that weevils particularly used plants at the field edges for oviposition. Contrary, our results do not show a higher infestation of plants at the field edge compared to the field center. Field center in our study was defined as 15 m from the field edge, which might have been a too short distance from the edge to observe significant differences between field edge and field center. Furthermore, the proportion of infested seeds decreased with increasing covers of semi-natural habitats. The promotion of natural enemies of weevil pests in heterogeneous landscapes might have been the reason for that. For aphids for instance, a positive effect of landscape heterogeneity on pest control has been found (Plećaš et al., 2014). However, we did not record the occurrence of the weevil`s natural enemies and the parasitism rates. A parasitism by the wasp *Triaspis thoracicus* might lower weevil densities (Seidenglanz and Huňady, 2016). Since weevil larvae bore into seeds directly after hatching and develop within the seeds, a control of the larval stage through insecticides is difficult (Pölitz and Reike, 2019; Seidenglanz and Huňady, 2016). Therefore, it might be promising to gain more knowledge on how *B. rufimanus* infestations can be lowered through biological pest control. Further research is needed on whether the availability of semi-natural habitats in agricultural landscapes can indeed enhance pest control and lower pest pressure of weevils on faba beans. Finally, we found an increased weevil infestation with increasing oilseed rape land covers. A possible explanation is that weevils fed on the pollen of oilseed rape during its bloom until the end of May. Pölitz and Reike (2019) observed broad been weevils to feed on faba bean nectar and pollen but also on the pollen of flowers in the surroundings with no preference for specific flower species. Weevils might have been benefited from the resources of a nearby oilseed rape field flowering directly before faba beans start to bloom.

References

Bachmann, M., Kuhnitzsch, C., Martens, S.D., Steinhöfel, O., Zeyner, A., 2020. Control of bean seed beetle reproduction through cultivar selection and harvesting time. Agric. Ecosyst. Environ. 300, 1–2. https://doi.org/10.1016/j.agee.2020.107005

Plećaš, M., Gagić, V., Janković, M., Petrović-Obradović, O., Kavallieratos, N.G., Tomanović, Ž., Thies, C., et al., 2014. Landscape composition and configuration influence cereal aphid-parasitoid-hyperparasitoid interactions and biological control differentially across years. Agric. Ecosyst. Environ. 183, 1–10. https://doi.org/10.1016/j.agee.2013.10.016

Pölitz, B., Reike, H.P., 2019. Studies on Biology and Infestation Dynamics of the Bean Seed Beetle (Coleoptera, Bruchidae: Bruchus Rufimanus) in Saxony. Gesunde Pflanz. 79–85. https://doi.org/10.1007/s10343-019-00459-5

Seidenglanz, M., Huňady, I., 2016. Effects of faba bean (Vicia faba) varieties on the development of Bruchus rufimanus. Czech J. Genet. Plant Breed. 52, 22–29. https://doi.org/10.17221/122/2015-CJGPB

Synthesis

In this thesis, I studied the effect of faba bean cultivation on bee pollinators, i.e. their densities, species richness, reproduction, resource utilization and their functional community composition. Furthermore, I focused on the effect of landscape composition on bee pollinators and analyzed how insect pollinators shape yield components of mass-flowering crops in interaction with landscape composition. I found evidence for a beneficial effect of the cultivation of *V. faba* on bees and thereby I provide an example for an effective on-field greening measure. Nevertheless, the cultivation of a single mass-flowering crop alone cannot sustain insect diversity in agroecosystems. As demonstrated, mass-flowering crops promote certain functional groups of pollinators, which are associated with the morphology of the crops` flowers. While faba beans promoted predominantly bumblebees and bees with foraging preferences for Fabaceae, oilseed rape enhanced the proportion of social bees in the pollinator communities. These findings indicate that crop diversity is an important factor for sustaining a high pollinator diversity, as it has been already indicated in regard of a high functional diversity of farmland plants (Sutter et al., 2017).

Another major aspect for bee conservation is the presence of large amounts of high quality semi-natural habitats in agricultural landscapes. I found semi-natural habitats to enhance bee densities. Moreover, I observed indications for enhanced pest control in landscapes with a high semi-natural habitat cover, in terms of lower proportions of weevil infested bean seeds. Beyond the quantity of semi-natural habitats, their quality might be decisive for bee conservation. I found the flower cover of semi-natural habitats to be the main driver of non-*Bombus* wild bee densities in these habitats and landscape diversity to enhance wild bee species richness. Furthermore, the cover of semi-natural habitats did not affect the reproduction of bumblebee colonies, but landscape diversity positively affected the number of young queens. These findings indicate that in addition to the quantity of semi-natural habitats, their quality as well as the diversity of agricultural landscapes are essential prerequisites for the promotion of bees. Concluding, I recommend the implementation of both, on-field and off-field biodiversity measures to conserve beneficial insects in agricultural landscapes. High amounts and diversity of semi-natural habitats provide a continuous supply of resources for the whole pollinator community, while mass-flowering crops merely promote certain pollinator groups and predominantly the common crop pollinators (Kleijn et al., 2015).

Beyond that, I found evidence for legacy effects, i.e. that landscape composition in the current year and even in the past years affects actual bee pollinators in crop fields and the crop yield. Mass-flowering crop cultivation in the past enhanced bee densities in oilseed rape fields, whereas mass-flowering crops in the actual year led to a pollinator dilution. Insect pollination and past mass flowering crop cover positively affected crop yield. This emphasizes the importance of taking landscape composition history into account when analyzing crop pollination services in agricultural landscapes.

Moreover, I found landscape composition to affect bee densities and bees` foraging behavior in faba bean fields as well as faba bean yield components. The landscape cover of semi-natural habitats and of faba bean positively affected bee densities and crop yield, while oilseed rape had negative impacts. Additionally, landscape composition interacted with bee densities in shaping faba bean yield, indicating that landscape composition needs to be considered for achieving maximum crop yields.

My results add further evidence to the role of landscape complexity on beneficial insects in agricultural landscapes (Benton et al., 2003; Bukovinszky et al., 2017; Tscharntke et al., 2005). My thesis provides new insights into the complex relationships between landscape composition, bee densities, bees` foraging behavior and mass-flowering crop yields. Moreover, it indicates that on- and off-field management practices can improve landscape composition and promote pollinators and their vital pollination services. I encourage the implementation of biodiversity measures aiming at a high semi-natural habitat quantity and quality and at increasing temporal and spatial crop diversity as well as high landscape diversity in order to sustain beneficial insects in agricultural landscapes and to conserve ecosystem services, such as pollination for future generations.

References

Benton, T.G., Vickery, J.A., Wilson, J.D., 2003. Farmland biodiversity: Is habitat heterogeneity the key? Trends Ecol. Evol. 18, 182–188. https://doi.org/10.1016/S0169-5347(03)00011-9

Bukovinszky, T., Verheijen, J., Zwerver, S., Klop, E., Biesmeijer, J.C., Wäckers, F.L., Prins, H.H.T., Kleijn, D., 2017. Exploring the relationships between landscape complexity, wild bee species richness and reproduction, and pollination services along a complexity gradient in the Netherlands. Biol. Conserv. 214, 312–319. https://doi.org/10.1016/j.biocon.2017.08.027

Kleijn, D., Winfree, R., Bartomeus, I., Carvalheiro, L.G., Henry, M., Isaacs, R., Klein, A.M., Kremen, C., et al., 2015. Delivery of crop pollination services is an insufficient argument for wild pollinator conservation. Nat. Commun. 6. https://doi.org/10.1038/ncomms8414

Sutter, L., Jeanneret, P., Bartual, A.M., Bocci, G., Albrecht, M., 2017. Enhancing plant diversity in agricultural landscapes promotes both rare bees and dominant crop-pollinating bees through complementary increase in key floral resources. J. Appl. Ecol. 54, 1856–1864. https://doi.org/10.1111/1365-2664.12907

Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I., Thies, C., 2005. Landscape perspectives on agricultural intensification and biodiversity - Ecosystem service management. Ecol. Lett. 8, 857–874. https://doi.org/10.1111/j.1461-0248.2005.00782.x

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List of publications

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Declaration

I hereby confirm that I have written this doctoral thesis independently, that I have not used other sources or facilities other than the ones mentioned, that I have not used unauthorized assistance and that I have not submitted this thesis previously in any form for another degree at any university or institution.

Göttingen, November 2020

Nicole Beyer