Prolonged blooming season of flower plantings increases wild bee abundance and richness in agricultural landscapes

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Abstract

Flower plantings can increase the abundance of bees and improve pollination services in the surrounding landscape. However, uncertainty remains as to whether flower plantings play a role in wild bee conservation. The aim of this study has been to examine the contribution of the composition and management of flower plantings to the attraction of bees, particularly of endangered species. In a large-scale monitoring project, wild bee data were collected on 60 flower plantings and 120 semi-natural reference plots in 20 study sites over 2 years. In total, we recorded 60,335 bees belonging to 351 species. In flower plantings, bee species richness and abundance were intricately linked to high plant richness and constant blooming throughout the season. In the first year of this study, a complementary blooming phenology of annual and perennial plants resulted in a more constant bloom on flower plantings. In the second year, partial mowing of flower plantings mid-season enhanced floral resources during the late season. As a result, bee richness and abundance in flower plantings increased from the first to the second year. Nevertheless, the compositional heterogeneity of bees over all 20 sites in Germany did not increase from the first to the second year. We conclude that diverse and constant blooming throughout the season is the most important factor for promoting bees in flower plantings. To ensure sufficient beta diversity over a large spatial scale, we recommend the adjustment of seed mixtures according to the geographical region.

Keywords Flower strips · Wildflower plantings · Floral resources · Red List · Threatened bees · Agri-environment scheme

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Introduction

Wild bees provide key pollination services within natural ecosystems and croplands (Kearns et al. 1998; Bommarco et al. 2012; Holzschuh et al. 2012). Therefore, they play a major role for global food security and in the maintenance of ecosystem stability and biodiversity (Klatt et al. 2013; Potts et al. 2016). Evidence is however growing for a world-wide decline of wild bees (Brittain et al. 2010; Bartomeus et al. 2013a; Powney et al. 2019; Zattara and Aizen 2021). This has prompted concerns about not only the safety of the pollination service provided by wild bees, but also the intrinsic value of wild bee biodiversity (Kleijn et al. 2015). As a result, the aim of several ongoing projects is to safeguard and promote wild bees in agricultural landscapes (Knop et al. 2006; Melathopoulos et al. 2015; Jönsson et al. 2015; Chopra et al. 2015; Ouvrard et al. 2018; Neumüller et al. 2020).

Semi-natural habitats such as extensively managed grassland or ruderal areas offer a diverse set of feeding and nesting sources for wild bees (Steffan-Dewenter et al. 2002; Kennedy et al. 2013; Krimmer et al. 2019; Neumüller et al. 2020). Driven by the agricultural intensification in Europe, many of these valuable habitats have been lost during the last few decades (Stoate et al. 2001) and many flowering plants are in decline (Eichenberg et al. 2021). These observations suggest that the shortage of available floral resources is one of the main drivers of the current wild bee decline (Tilman et al. 2001; Biesmeijer et al. 2006; Scheper et al. 2014). Accordingly, the provision of adequate floral resources is considered to be essential for sustainable habitat management targeting wild bees (Scheper et al. 2014; Sutter et al. 2017). Nevertheless, the restoration or establishment of new semi-natural habitats is often expensive or impossible (von Haaren and Reich 2006). Alternatively, the establishment of flower plantings on tilled arable land has become an important approach for providing additional floral resources for bees (Haaland et al. 2011). Flower plantings can efficiently increase wild bee abundance and related pollination services in the surrounding landscape (Carvalho et al. 2012; Blaauw and Isaacs 2014), although only a few plantings have been adapted to the specific needs of the local bee community and have been shown to enhance wild bee richness (Scheper et al. 2015).

Studies investigating the value of flower plantings have mostly focused on their beneficial effects for a few common generalist bee species (Sutter et al. 2017; Grab et al. 2019; Ahrenfeldt et al. 2019; Albrecht et al. 2020) that are abundant in agroecosystems (Kleijn et al. 2015; Sutter et al. 2017). Among these species are honeybees or common bumblebee species that choose host plants in respect of quantity or nutritional requirements (Leonhardt and Blüthgen 2012). The abundance of bees is strongly driven by the availability of feeding sources in the same location (Holzschuh et al. 2013). In contrast, bee species richness is predominately moderated by the composition and richness of available plant species (Potts et al. 2003; Scheper et al. 2015; Neumüller et al. 2020). In particular, rare bee species mostly rely on key plant species different from those used by most of the important crop pollinators (Sutter et al. 2017; Westrich 2018; Danforth et al. 2019). In this context, many bee species have been shown to prefer specific taxonomic groups of plants and are only active for a limited time period of the year (Westrich 2018; Danforth et al. 2019).

In central Europe, government-funded seed mixtures that fulfil the criteria of agri-environmental schemes are often limited in the number of plant species that they contain and are designed to implement flower plantings that are re-established every year (Carvell et al. 2007; Batáry et al. 2015; Agrarmarkt Austria 2021; Landwirtschaftskammer Nordrhein-Westfalen 2021; Mastel et al. 2021). Although annual flower plantings have been shown to promote common crop pollinators and the associated pollination

service in a landscape (Jönsson et al. 2015; Campbell et al. 2017; Rundlöf et al. 2018; Klatt et al. 2020), evidence has been presented that species-rich and adequately managed flower plantings support a greater spectrum of bee species (Carvell et al. 2007; Pfiffner et al. 2019). On this basis, the mixing of annual and perennial plants and mowing during the season in flower plantings might therefore promote more constant blooming throughout the season and might attract complementary groups of wild bee species (Williams et al. 2015; Kirmer et al. 2018; Martins et al. 2018). The temporal continuity of floral resources is important for high bee species richness as it strongly affects the stability of a bee community (Blüthgen and Klein 2011; Scheper et al. 2015; Williams et al. 2015; Crowther and Gilbert 2020). If the goals of the establishment of a flower planting is not only to promote pollination service, but also to conserve wild bee diversity, then we need to provide flower plantings that serve both target groups: common crop pollinators and rare species (Sutter et al. 2017). Enhancement of wild bee diversity has been shown to increase pollination success in crop cultures (Klein et al. 2003; Hoehn et al. 2008) by stabilizing pollination over space and time (Hector et al. 2010; Blüthgen and Klein 2011; Bartomeus et al. 2013b). Hence, multiple goals can be achieved by promoting general bee diversity.

Bee communities greatly differ between regions because of the high grade of habitat specialization of wild bees. They require a range of floral and nesting resources and are adapted to specific climatic conditions (Westrich 2018). As a result, the composition of wild bee communities shows a high geographical turnover, resulting in a high compositional heterogeneity of bees on a large spatial scale (Rubene et al. 2015; Winfree et al. 2018; Orr et al. 2021). A previous study involving a comparison of bee communities in semi-natural habitats and locally adapted flower plantings has revealed that the grade of compositional heterogeneity (compositional turnover between sample plots) of bees is reduced on flower plantings in the first year after establishment, when compared with surrounding semi-natural habitats (Neumüller et al. 2020). However, uncertainty remains as to whether flower plantings with a longer succession can attain a similar compositional heterogeneity to that of semi-natural habitats.

In this large-scale study over 20 study sites in Germany, we investigated wild bee communities in flower plantings (flower strips) containing annual and perennial plant species over 2 years. We explored changes in plant and bee communities in the flower plantings from the first year of establishment to the second year (Fig. 1). To control for yearly changes in bee occurrence in the flower plantings, we also monitored, at each site, the bee communities on two different semi-natural habitats. Bee communities in flower plantings were explored while paying special attention to bee species classified as threatened or vulnerable (Red list of Germany, Westrich et al. 2011).

As wild bee communities strongly depend on floral resources, we expected that, in flower plantings, the abundance and richness of bees would be determined by the local availability and diversity of the flowering plants. In this context, we furthermore hypothesized that, in the second year of the study, perennial plants would produce a more diverse and continuous flowering aspect throughout the year. Rare bee species are predicted to depend on specific plant species and are therefore hypothesized to benefit particularly from enhanced flowering in the second year. Previous observations on field margins suggest that mowing during the season can promote constant blooming throughout the season (Kirmer et al. 2018). Hence, we hypothesized that, in the second year, partial mowing of the flower plantings mid-season would enhance flower cover during the late summer. Finally, by providing enhanced floral resources in the second year of this study, flower plantings might attract a broader spectrum of bees from the local community. Hence, we hypothesized that

Fig. 1 Flower planting for wild bee conservation established at the 20 study sites [photos H. R. Schwenninger (A) and H. Burger (B–D)]. The images show various developmental stages of the same flower planting (A) in the first year (dominating flowers: *Anthemis tinctoria*, followed by *Centaurea cyanus*), B in the second year after establishment (flowers such as *Echium vulgare*, *Reseda luteola* and *Carduus nutans*) and C late flowers after partial mowing (left: unmown, right: mown part with dominating *Daucus carota* flowers, followed by *Centaurea jacea*). D Examples of wild bees visiting flowers of the plantings (from top left to bottom right): *Andrena flavipes* on *Tripleurospermum perforatum*, *Bombus sylvarum* on *Trifolium pratense*, *Bombus pascuorum* on *Carduus nutans*, *Halictus tumulorum* on *Anthemis tinctoria*)

compositional heterogeneity between flower plantings over whole Germany would increase from the first to the second year.

Methods

This study is part of the BienABest project that aims to safeguard the ecosystem service of pollination and to enhance wild bee diversity in agricultural landscapes (www.bienabest.de). The project incorporates extensive wild bee monitoring, which has provided wild bee data for this study. The methodology of the data acquisition in this study is congruent with that of Neumüller et al. (2020).

Study sites

The study was conducted in 2018 and 2019 in 180 sampling plots in 20 different study sites distributed over seven federal states of Germany (Neumüller et al. 2020). The total study area extended over 708 km longitudinally and 507 km latitudinally, with an altitude between 20 and 580 m above sea level (Fig. 2). The mean distance between all study sites was 323.35 kms with a minimum distance of 6.5 kms and a maximum distance of 779.79

Fig. 2 Map of Germany showing the 20 study sites in which the study was performed. Each dot represents a site. Green areas indicate a low topographical elevation; red areas indicate a high topographical elevation (BKG 2013)

kms (also see Fig. 2). The selection of the sites was based mainly on the presence of semi-natural grassland embedded in an agricultural landscape matrix. To evaluate whether the established flower plantings were successful in promoting the local bee communities, we used two semi-natural habitats for comparison. In each study site, the sampling plots were located within a radius of 500 m around a centroid that was, in turn, calculated from the centroids of the nine sampling plots, except for 23 plots that lay close (less than 350 m) to the outer boundary of the 500 m radius.

Flower plantings

Within each of the study sites, we established three 0.3-ha flower plantings (flower strips) on tilled arable land, either during the autumn or the spring prior to the first field surveys in 2018. The shape of the flower plantings was quadratic to rectangular. Each flower planting acted as a 0.3-ha sampling plot for variable transect walks (Westphal et al. 2008), resulting in a total of 60 sampling plots of wildflower planting. The planting areas were sown with seed mixtures consisting of between 41 and 53 species encompassing regionally native, naturalized and cultured (non-invasive) plant species with a complementary flower phenology to provide floral resources throughout the season (see Supplementary Material Table S1 for detailed information about our seed mixtures). For the compilation of seed mixtures, previously existing bee-plant interaction data recorded in the ‘Wildbienen

Kataster Baden-Württemberg' (<http://www.wildbienen-kataster.de>) were evaluated and the most attractive plant species for bees in a respective region were included in the seed mixtures. Although the seed mixtures were similar for all sites, plant composition was adapted to match the distribution of each plant species in a geographic region. In addition to the plants included in the seed mixtures, the spontaneous growth of non-sown wild flowering plants was registered on all flower plantings. In 2019, half of the area of each sampling plot of the flower plantings was mown between the middle of June and the middle of July. Mowing was performed at a height of about 15 cm to encourage further blooming. In the horticultural literature, this practice is referred to as “deadheading” and is known to prolong the bloom period (DeGomez 2002; García-Sogo et al. 2010). In 2018, flower plantings were not mown until the last field survey was performed, because partial mowing was assumed to have no beneficial effect on the annual plant community present in the first year.

Semi-natural habitats

To evaluate the success of the established flower plantings, we used two semi-natural habitats as a reference: grassland and residual habitats. Grassland plots were characterized by extensive management and a high diversity of native flowering plants. The grasslands were managed either by mowing once or twice a year or by grazing by sheep, goats or donkeys. Residual habitats were sampled to monitor bee communities commonly present in agricultural areas. Hence, they were composed of rarely used field paths, field margins and small ruderal areas. Within each of the 20 study sites, we established three 0.3-ha sampling plots for each of the semi-natural habitat types, resulting in a total of 120 reference sampling plots. Additionally, nesting hills were established close to the study plots in all research areas in order to provide nesting resources for bees.

Wild bee surveys

Bee data were collected on the three described habitat types: flower plantings, grassland and residual habitat elements. Bee data from 2018 were taken from Neumüller et al. (2020). Following the methodology of Neumüller et al. (2020), the sampling of each plot in 2019 was performed during five sampling events. Individual events were evenly distributed between April to September, starting with the flowering of dandelion and continuing every 3 to 4 weeks depending on the weather conditions. Sampling was only conducted during sunny weather (cloud cover less than 30%), at temperatures higher than 10 °C and under low wind conditions.

While sampling, collectors could freely move within the plots, following the distribution of relevant nesting and feeding resources for the bees (Westphal et al. 2008; Schindler et al. 2013). To account for intra-day bee phenology, each plot was sampled during two subunits of 25 min, one before and one after 12:30, with a minimum of 120 min between the two sampling events. On structure-rich plots, which were covered by a range of different habitat components, small habitat patches (e.g. flower patches dominated by one plant species or nesting sites) were sampled for a maximum of 5 min. All encountered bee individuals were caught with an entomological net, except for those that could be determined at first sight and identified to species level on the spot. After sampling, all caught bee individuals were inspected with a field microscope or a magnifying glass and released once they had been clearly determined. Individuals that could still not be identified in the field

were killed for further determination by wild bee taxonomists. To minimize collector bias and to guarantee reliable species determination, sampling was performed only by wild bee experts (see acknowledgements).

Flower resource availability

Before and during each bee survey, the vegetation of the visited area for the bee survey was visually inspected and the mean flower cover and all encountered flowering plant species that might act as feeding resources for bees were recorded. The flower cover was categorized in one of four categories: less than 1%, 1 to 10%, 11 to 40% and more than 40%. Voucher specimens of flowering plants that could not be identified to species level in the field were later determined in the laboratory.

Statistical analysis

Comparison of bee species richness and abundance between the 2 years and the three habitat types

Bee data before noon and after noon were pooled for each of the five sampling events within each year. Since all 180 sampling plots were sampled ten times in 2 years, aggregation of the data resulted in 1800 individual data points. In the next step, we separated bee data into two categories: vulnerable, extremely rare or threatened species (from here on called rare species), as classified by the Red List of Germany (Westrich et al. 2011), and non-Red List species (from here on called common species). Hence, we separately compared bee species richness and abundance for both datasets between the three habitat types and the 2 years. During the analysis of the data, we detected a strong non-linear temporal pattern in the dataset. By using the function *gam* of the R package *mgcv* (Wood 2019), we applied spatiotemporal generalized additive models (GAMs) with a negative binomial distribution following Wood (2017). This allowed us to model non-linear effects of time. The first two GAMs included either species richness or abundance as a dependent variable and an interaction between the three habitat categories (flower plantings, grassland and residual habitat elements) and year as an independent variable. To account for differing sampling dates, the day of the year (Julian date) for each sampling event was added as a thin plate spline to the model structure. To test for a spatial dependence in our data derived from the distribution of our sampling sites, we followed (Zuur et al. 2017) and fitted experimental variograms as implemented in the package *geoR* (Ribeiro et al. 2003). The variograms indicated spatial dependencies that were later confirmed when models with a spatial correlation structure explained a higher proportion of the total variation in our data than generalized additive mixed models with a random structure (plot nested in site). To account for this spatial dependence, we included a spatial correlation structure by adding longitudinal and latitudinal coordinates as a thin plate smooth interaction spline to the model. This allowed the model to account for spatial closeness of study sites (Wood 2017). After the running of the models, we used the package *emmeans* (Lenth et al. 2019) for post-hoc analyses to compare pairwise either bee species richness or abundance between the 2 years and the three habitat types. For the smooth variables, we let the package select the number of basis functions (*k*). Model diagnostics were performed using the function *gam.check* implemented in the package *mgcv* (Wood 2019) to ensure an adequate fit of all models.

No adaptations to improve the model fit were necessary. During inspection of all GAM curves, non-overlapping confidence intervals of two curves were interpreted as significant difference (MacGregor-Fors and Payton 2013).

Correlation of species richness of bees and flowering plants

In the next step, we explored any correlations in changes in species richness in bees and flowering plants in the three habitat types. In this regard, we calculated a generalized additive mixed model with bee species richness as the dependent variable, setting flower richness in an interaction with habitat type as the independent variable. Additionally, we applied the same spatiotemporal correlation structure as described previously but added sampling year as a random factor and not as an independent variable. Subsequently, we performed post-hoc analyses for a pairwise slope comparison between habitat types by using the package *emmeans* (Lenth et al. 2019). As for the other models, we let the package select the number of basis functions for our smooth parameters and performed model evaluation.

Temporal patterns of bees and plants

To test for temporal patterns, data before noon and after noon were pooled for each of the five sampling events within each year. Subsequently, spatiotemporal generalized additive models were applied using the function *gam* (Wood 2019). In four models, flower richness, flower cover, bee richness or bee abundance were set as dependent variables. All models were implemented with a negative binomial distribution, except for the model containing cover as the depended variable, which was implemented with a beta distribution. The Julian date in combination with a factor-smooth interaction of a combination of year and habitat type was added as a thin plate spline to each model. Furthermore, the longitudinal and latitudinal centroid-coordinates of each pot were added as an interaction term to account for the spatial distribution of the data.

To explore whether annual and perennial plant species showed differences in flowering phenology, we calculated similar temporal models to those for plant richness and flower cover. However, this time, the data were divided between annual and perennial (including biennial) plants and the Julian date was set in a factor-smooth interaction with growth type (annual/perennial). As for the other models, we let the package select the number of basis functions for our smooth parameters and performed model evaluation.

Compositional heterogeneity of bees and plants

Compositional heterogeneity of bee communities in flower plantings was compared between the 2 years by using the *vegan* package (Oksanen et al. 2019). We used the *vegdist* function to calculate the Bray–Curtis dissimilarity between individual sampling plots and the *betadisper* function to calculate the dispersion of each group. Subsequently, the *TukeyHSD* function was used to compare the compositional heterogeneity between the first and the second years. The same analysis was performed to compare the compositional heterogeneity of plant communities between the three habitat types.

Results

During the 2 years of sampling, we recorded a total of 60,335 bee individuals belonging to 351 bee species, representing 59% of all known German bee species (Westrich 2018). In flower plantings, a total of 25,507 bee individuals were recorded from 279 species. Regarding rare species, we recorded a total of 11,471 individuals from 134 species (Table S2).

Comparisons between habitat types and years

In flower plantings, both the species richness and abundance of rare and common bees significantly increased from the first to the second year (Fig. 3a, b). In grasslands, only bee species richness of common bees increased from 2018 to 2019, whereas species richness of rare bees did not change between the 2 years. Over all three habitat types, the highest species richness of rare bees was found in grassland in the first year and in flower plantings in the second year (Table S4). In the first year, the bee abundance of common and rare species was similar in all habitat types but, in the following year (2019), the abundance in flower

Fig. 3 Comparison of bee richness and abundance between the 2 years and three habitat types for common (a) and rare (b) species. Predicted values with 95% confidence intervals derived from the calculated GAM models. Bars with asterisks indicate significant differences: * $p < 0.05$, *** $p < 0.001$. Coefficients of the underlying GAMs with post-hoc comparisons, including comparisons between habitat types, are given in the Supplementary Material (Table S3, S4)

plantings exceeded those in grassland and residual habitats, making flower plantings generally the habitat type with the highest bee abundance.

Temporal patterns of plants

From early to mid-season of the second year, the flower richness in flower plantings was similar to that of the first year but, after the partial mowing event, kept increasing until the end of the season (Fig. 4a). This resulted in a significantly higher plant species richness in the late season of the second year than in the first year.

In both years, the flower cover in flower plantings reached similar maxima around the middle of June during a particularly abundant bloom of *Anthemis tinctoria* (Fig. 4b). Whereas maximum cover occurred as a short peak in the first year, a high cover of blooming plants was retained over a longer period after the partial mowing event in the second year. The temporal distribution of flower cover and flower richness in grassland and residual habitats showed no strong divergences between the 2 years (see Supplementary Material Fig. S1).

In flower plantings, perennial plants strongly increased total flower richness during the late season in both years (Fig. 5a, b). Remarkably, in the first year, the richness of perennial and annual plants showed a strong complimentary temporal pattern with more annual plants from the early to the mid-season and more perennial plants from the mid to the late season. This resulted in overall more stable floral resources throughout the season (compare to Fig. 4a, b). In the second year, annual plants appeared to

Fig. 4 Temporal patterns of flower richness (a), flower cover (b), bee richness (c) and bee abundance (d) in flower plantings for the first and the second years. Shaded areas represent 95% confidence intervals. The grey line indicates the partial mowing event in 2019. Complete estimate values of the underlying GAMs are given in the Supplementary Material (Table S5)

Fig. 5 Comparison of temporal patterns of flower richness and flower cover in flower plantings for the years 2018 (a) and 2019 (b) for annual and perennial plants. Shaded areas around the lines represent 95% confidence intervals. The grey line indicates the partial mowing event in 2019. Complete estimate values of the underlying GAMs are given in the Supplementary Material (Table S6)

decrease, whereas perennial plants increased in dominance and retained a high flower cover from the mid to the late season. The plants *Medicago sativa*, *Trifolium pratense* and *Achillea millefolium* showed particularly high flower cover in the late season (Supplementary Material Table S8 presents those plants producing the highest flower cover in each sampling event).

Temporal patterns of bees

Although a strong linear relationship was observed between plant richness and bee richness in all three habitat types, it was particularly pronounced in flower plantings (Fig. 6). In accordance with this interdependence, the temporal patterns in bee abundance and richness in flower plantings appeared to follow the availability of floral resources. During late summer, the species richness and abundance of bees strongly increased from the first to the second year (Fig. 4c, d). Conversely, bee data showed similar temporal patterns from early to mid-season when compared between the 2 years. Species richness and abundance in grassland and residual habitats followed similar temporal patterns in both years (Supplementary Material Fig. S1).

Heterogeneity of bee communities

Compositional heterogeneity of the bee community in flower plantings was almost identical in both years (Fig. 7). The compositional heterogeneity of plant communities in flower plantings was lower than those in the two semi-natural habitat categories (Supplementary

Fig. 6 Correlation of bee richness and flower richness in the three habitat types. Brackets with asterisks indicate significantly different slopes: * $p < 0.05$, *** $p < 0.001$. Coefficients of the slope comparison are given in the Supplementary Material (Table S7)

Fig. 7 Compositional heterogeneity of bee communities between flower plantings did not increase from the first (2018) to the second year (2019). Boxes represent the median and 25th/75th percentile of the distances to group centroid calculated with betadisper. Whiskers extend to 1.5 times the interquartile range. Coefficients of the underlying analysis are given in the Supplementary Material (Table S9)

Material Fig. S2). In a comparison of the composition of flowering plants between habitats, flower plantings differed substantially from the two semi-natural habitat categories, which were comparably similar in this regard (Supplementary Material Fig. S3).

Discussion

In our study, flower plantings attracted more bee species and individuals in the second year after establishment, when floral resources were enhanced compared with the first year. This positive trend was mainly observed in flower plantings and not in the two other habitat types and was particularly pronounced for rare species. As hypothesized, increases in bee species richness and abundance from the first to the second year mainly happened during late summer, when a more constant bloom attributable to multi annual flower plantings and partial mowing resulted in a higher plant species richness and flower cover. Despite the locally increased diversity of bee species and enhanced floral resources in the flower plantings of the second year, the compositional heterogeneity of bee communities over all 20 sites in Germany did not increase as compared with the first year.

Bee richness and abundance depend on floral resources

The species richness of wild bees in our study was intricately linked to the flower richness in our sampling sites. Hence, the increases in species richness and abundance of bees in the second year of this study must have been caused by the observed improvements in floral resources, which attracted additional bees from the surrounding landscape (Neumüller et al. 2020). Specialized bee species are easily limited by a lack of suitable host plants (Biesmeijer et al. 2006; Weiner et al. 2014; Sutter et al. 2017). This might explain the particular enhancement of the species richness and abundance of rare bee species in the second year, concomitant with the higher richness of plants. Therefore, our results clearly show that plant species composition in seed mixtures is a critical aspect when designing flower plantings (Carvell et al. 2007).

In our study, both plant and bee communities were enhanced in the second year of the study. This suggests that multi annual flower plantings are superior to annual flower plantings, particularly as the frequent tillage of flower plantings might hinder the emergence of ground-nesting bees that build their nests on flower plantings (Ullmann et al. 2016). Furthermore, it remains unclear how the discontinuance of flower plantings will affect wild bee communities that are adapted to abundant feeding resources.

Prolonged floral resource availability through partial mowing and a mixture of annual and perennial plants

Many bee species have only one generation per year and the adult females of such species often have short life spans of only a few weeks (Westrich 2018). As a result, seasonal species turnover often accounts for a large part of total diversity in wild bee communities (Rollin et al. 2015). By covering a wider spectrum of temporal niches in the second year, the flower plantings were able to attract and feed more bee species than in the first year. This was certainly a main reason for the increased bee abundance and richness in flower plantings of the second year. Bee species that occupy a narrow temporal niche are predicted to be more vulnerable to temporal declines of floral resources (Blüthgen and Klein 2011). Hence, the species richness of the rare bees in our flower plantings probably increased strongly not only because of a higher flower resource diversity, but potentially also because the flower plantings covered temporal niches that were critical for some rare species.

In the first year of the study, the flower cover of the plantings showed a pronounced peak in the middle of the season but was much lower before this time point and showed

a severe drop after it. In order to prolong the blooming in our flower plantings, half of the area of each flower planting plot was mown in the mid-season of the second year. The partial mowing appeared to be successful; in the second year, flower cover was significantly higher towards the end of the season. During the mowing event and shortly afterwards, the unmown part of the plot was still in full bloom and thus compensated for the loss of floral resources on the other half of the plot. The cut part of the flower plantings bloomed again a few weeks after the mowing event, resulting in high flower cover and richness (Fig. 1C). A second bloom after cutting was predominantly observed in perennial plants and not in annual ones. In addition, we observed that in flower plantings an increase in richness occurred at the end of the season and that this increase was partly attributable to late-flowering plant species. Partial mowing in the second year of this study resulted in more constant floral resources being available towards the end of the season. This time of the year was previously described as a resource bottleneck for bees (Timberlake et al. 2021). Concordantly with floral resources, increases in bee species richness and abundance from the first to the second year were also noted after the partial mowing event. As mowing was only performed in the second year, the positive effects on flower plantings might also be explained by succession dynamics from the first to the second year. Nevertheless, the finding that increases in bees and plants almost exclusively occurred a few weeks after the partial mowing event, together with our personal observation (Fig. 1C), provides strong indications that mowing plays an important role.

In addition to the positive effects of mowing, perennial plants provided stable floral resources even in the first year of our study. Against our expectations, many perennial plants bloomed in the first year, probably because the seed mixtures were sown early (autumn or early spring). When the richness of annual plants declined during the mid-season of the first year, perennial plant richness persisted until the end of the season. Our results are in agreement with the recommendations by Williams et al. (2015) that perennial plants will enhance flower plantings that are designed to exist for 1 year only. Hence, the inclusion of a balanced mixture of annual and perennial plants is a good option for increasing the ecological value of seed mixtures used in agri-environmental schemes that are often dominated by annual plants.

Compositional heterogeneity in bees depends on variation in flowering plants

Even though plant species richness in flower plantings increased in the second year of our study, the mean compositional heterogeneity of the plant and bee communities over all study sites stayed almost the same, as compared with the first year (Neumüller et al. 2020). Hence, the previously observed reduced grade of heterogeneity on flower plantings (Neumüller et al. 2020) did not increase from the first to the second year. Although the composition of the seed mixtures was adapted for the various geographical sites, most annual and perennial plant species were the same for all sites. Nevertheless, the species composition of the flower plantings differed substantially from those in the two semi-natural habitats and, in both years, the compositional heterogeneity of plants was lower on flower plantings than on the two other habitat types. The strong habitat specialization of many wild bee species has been argued to drive the species turnover of wild bee communities (Rubene et al. 2015; Scheuchl and Willner 2016; Westrich 2018; Neumüller et al. 2020). Therefore, the reduced compositional heterogeneity of plants was probably the main cause for the reduced compositional heterogeneity of bees in the flower plantings.

Conclusion

Based on the results of our study, we conclude that the diversity of food plants in flower plantings is an important factor for promoting diverse bee communities. Selecting local plant species that are not common in an agricultural landscape can increase the potential for supporting rare and specialized bee species. By the constant offering of flowers throughout the season, flower plantings can compensate for shortages of feeding resources in a landscape and thus support bees with a differing phenology. In annual flower plantings, this can be achieved by mixing annual and perennial plant species. Partial mowing of areas of flower plantings during mid-season is a method for extending the blooming period in flower plantings further into the late season. As our seed mixture attracted large numbers of rare species, it seems to have been successful in conserving wild bee diversity. Moreover, common pollinators profited and together with rare species probably increased pollination success in the surroundings. The compositional heterogeneity over all study plots did not increase from the first to the second year. Hence, we recommend altering seed mixtures according to the climatic conditions or geographic region in which they are applied, especially when the aim is to promote locally endangered and rare bee species.

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Author contributions HS, KW and MA conceived the study concept; UN and HB performed analyses and interpreted the results under the supervision of MA; UN wrote the original draft of the manuscript with contributions from HB; all authors commented on previous versions and approved the final manuscript.

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Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Code availability Codes of our statistical analyses will be provided upon request.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All persons who collected bees for this study received the necessary authorization to do so from the competent authority.

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