

RESEARCH ARTICLE

Wild bee communities benefit from temporal complementarity of hedges and flower strips in apple orchards

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Abstract

1. Wild bees importantly pollinate both crop and wild plants. Yet, in intensive agricultural landscapes, wild bees are rare due to resource limitations of nectar and pollen. Flower strips and hedges are often used as resource enhancements for wild bees to overcome this shortage, but provide floral resources only during specific time periods. To sustain diverse and stable bee communities, bee-attractive flowers need to be available during the entire growing season. This may be achieved by combining flower strips and hedges to complement each other and provide continuous floral resources.
2. Over three subsequent years, we compared the phenology of flower and wild bee communities in perennial flower strips, hedges and improved hedges (complemented with a sown herb layer) in conventional apple orchards in Southern Germany, a pollination-dependent crop system.
3. Hedges provided floral resources in the early season while the flower strips took over later in the season.
4. Bees visited the hedges mostly from March to June, whereas they visited the flower strips from June to August in the first year, and in the second year already from April onwards. Flower strips were visited with an overall higher abundance and species richness than both the hedges and the improved hedges.
5. *Synthesis and application.* For enhancing wild bees in intensive apple orchards, hedges and perennial flower strips are complementary in providing flower resources. Yet, flower strips bloom more constantly and during periods of flower scarcity, and thus attract a higher diversity of bees than hedges. Perennial flower strips of different age classes should be preferred over annual strips, at best in a network with some well-maintained hedges, as perennial flower strips of different age attract different bee communities and thus potentially a higher bee diversity on the landscape level.

KEYWORDS

annual variation, apple orchard, hedgerow, intensive agriculture, perennial flower strip, phenology, wild bee conservation, wildflower planting

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1 | INTRODUCTION

Wild bee decline has become a major concern in the field of agro-ecology and in the wider public. Wild bees (from now on referred to as 'bees') provide pollination to wild and crop plant species, and diverse pollinator communities provide more robust pollination services (Garibaldi et al., 2013; IPBES, 2016; Klein et al., 2007). However, bee persistence depends on adequate floral resources across their flight period (Westrich, 2018). In intensively managed agricultural landscapes these resources are often scarce due to a reduction of flower-rich semi-natural habitats and flowering crops (Le Féon et al., 2010). This is exacerbated by the fact that floral resources are often not available over the full vegetation period, for example, because meadows are frequently mown and mass-flowering crop monocultures like fruit trees typically provide flowers only for a short time (Eeraerts et al., 2021; Le Féon et al., 2010). This limited resource period poses problems to both social and solitary bees. Social bees like bumblebees require floral resources from spring to late summer to build up healthy colonies and to produce enough queens for the next generation (Bommarco et al., 2021; Carvell et al., 2017). Irregular flower availability was shown to reduce bumblebee colony growth in comparison to continuous flower supply (Hemberger et al., 2020). Solitary bees typically have specific flight periods of some weeks, in which they rely on the availability of suitable flowers (Balfour et al., 2018). Thus, continuous floral resources are crucial to promote and sustain diverse bee communities (Glaum et al., 2021; Neumüller et al., 2021).

The most common measure used to enhance floral resources for bees are flower strips, which are financially funded in the form of agri-environmental schemes in the EU and the United States (Albrecht et al., 2020). Flower strips indeed were found to increase the diversity of bees in agricultural landscapes (Ganser et al., 2021; Jönsson et al., 2015; Lowe et al., 2021; Scheper et al., 2015). For example, bumblebee queens were more abundant in landscapes with flower strips (Bommarco et al., 2021; Klatt et al., 2020). Even rare species benefit under certain conditions (Buhk et al., 2018; Neumüller et al., 2021). Hedges are also attractive for bees (Garratt et al., 2017; Morandin & Kremen, 2013; Ponisio et al., 2016). They consist mainly of different early flowering shrub and tree species and ideally a later flowering herb layer along the edge (Maudsley, 2000), and thus have the potential to provide floral resources over the entire season.

Flower strips and hedges typically peak in flower availability at different periods of the year. Hedges typically provide most flowers in spring and early summer (Balfour et al., 2018), benefiting early flying solitary bee species and foundresses of social bee species such as bumblebees (Carvell et al., 2017; Scheper et al., 2015; Westrich, 2018). However, the value of hedges as foraging habitat for bees depends on the flowering plant species richness and composition of hedges (Garratt et al., 2017; Von KönigsLöw et al., 2021). The overall value of hedges for bees furthermore depends on the presence of an herb layer, which ideally provides flowers also in summer, similar to flower strips (Hannon & Sisk, 2009; Miñarro & Prida, 2013). When herb layers are absent, sowing herb plant seeds may help to extend the flowering period. Flower strips in contrast reportedly

provide the highest abundance of flowers in summer (Campbell et al., 2017; Neumüller et al., 2021; Ouvrard et al., 2018). In the summer months, floral resources frequently became scarce in intensively managed agricultural landscapes in the last decades due to fewer flower-rich habitats. For this reason the suite of bee species that fly during summer months appears to be more vulnerable than early-flying species (Balfour et al., 2018; Hofmann et al., 2019). Flower strips may thus be valuable management measures that bridge the low flower availability for bee species flying in summer months.

For future enhancements of bees, it is important to create landscapes with complimentary flower habitats to provide floral resources across the growing season. However, redundancy, provided by hedge herb layers and flower stripes flowering in the same period could also be valuable to stabilise bee populations (Burkle et al., 2020). Furthermore, the floral resource dynamics may differ from year to year, especially in newly established vegetation types like flower strips and sown hedge herb layers. Flower strips start blooming only in early summer in the first year (Campbell et al., 2017; Ouvrard et al., 2018). In perennial flower strips the beginning of flowering might shift forward in subsequent years due to differences in plant developmental stages and species composition, which might in turn have an effect on bee communities. The same should be true for sown hedge herb layers.

In this study, we investigate temporal trends (between and within years) of different bee enhancement measures, namely perennial flower strips, hedges and improved hedges (complemented with a sown herb layer). We compare flower cover and wild bee diversity between these enhancement measures monthly over three consecutive years. The study was conducted in a landscape dominated by apple orchards, a pollination-dependent production system (Garratt et al., 2014). Orchard edge ground vegetation was therefore used as control. We tested the following hypotheses: (1) The availability of flowers in the enhancement measures changes across the season and between years. (2) The enhancement measures differ in bee abundance and species composition across the season and from year to year. Overall, we expect that hedges and flower strips complement each other in providing continuous floral resources to attract bees.

2 | MATERIALS AND METHODS

2.1 | Study sites

We selected 18 study sites at the edge of apple orchards in the Lake Constance region (Baden-Württemberg), one of the major apple growing regions in Germany. The sites were at least 1 km distant from each other (except one case). All sites were managed according to Integrated Pest Management (IPM), involving preventive and corrective use of chemical pesticides besides nonchemical pest and weed control measures. As bees were shown to respond on landscape composition in a radius of 500m, the sites were selected to be surrounded by a large proportion of apple orchards ($53 \pm 13\%$) and a low proportion of forest ($6 \pm 9\%$) in this radius (Kleijn & van

Langevelde, 2006). There were no larger semi-natural habitats in the surrounding area (for further details on study sites see Von Königslöw et al., 2021).

At each orchard, different pollinator enhancement measures were established: flower strips ($n = 4$), existent hedges ($n = 4$), existent hedges complemented with an herb layer (improved hedge, $n = 5$) or no enhancement (control, $n = 5$). The flower strips and the hedge herb layers were established in April 2018 with two different flower-rich perennial seed mixtures of regional provenance, both containing annual and perennial species (flower strips: mixture of native wild and non-native cultivated plants; hedge herb layers: only wild plants; Species lists see Appendix S1). The seed beds were prepared with a stone burrier or a motorised rotary tiller. The seeds were sown manually and pressed onto the soil with a roller. The flower strips, but not the hedge herb layers, were mown in autumn 2018 and 2019 (for details on establishment and maintenance see Appendix S2). All flower strips were 2.5 m, all hedge herb layers 0.5 m wide and both 25 m long. The hedges were at least 10 years old and were composed of variable shrub species in varying density. The length of the hedges was between c. 40 and 170 m (mean 124 ± 49 m). Unimproved hedges had no or only narrow herb layers composed nearly exclusively by grasses.

2.2 | Bee sampling

Bee samplings were generally conducted at least once per month between April to September 2018, March to August 2019 and March to September 2020. The number of samplings per site varied between 9 and 14 per year, yielding in total 33–37 observations per site. Sampling took place on warm and calm days without rain ($25.4 \pm 4.7^\circ\text{C}$, min 13°C ; wind speed 2.1 ± 2.1 m/s, max 11 m/s). To avoid time-of-the-day effects, sampling took place at varying times of the day at all study sites.

The sampling scheme consisted of bee observations and flower identification. On each observation day, we selected three 1 m^3 plots (including vertical vegetation) on predefined 25 m transects within the measures or the orchard edge (in and between apple tree rows). We selected plots in areas with maximum flower diversity.

We observed each plot for 5 min and caught all bees we could not reliably identify in the field for later identification to species level. We categorised bees to social (including primitive eusocial) or solitary based on Westrich (2018) (see Appendix S3). In each plot, we counted the number of flowers for all individual flowering plant species. Tiny or composite flowers were counted as floral units.

An official permission for sampling bees was given by the Regional Administrative Council in charge (Regierungspräsidium Tübingen). An ethical approval was not required.

2.3 | Statistical analysis

For testing differences between months across years, we calculated abundance and species richness of bees per site, month and year,

receiving in total 303 data points (3 years \times 6 months \times 18 sites minus few missing observations e.g. due to bad weather or pesticide application on sampling date). To account for unequal numbers of observations per month and year, we divided abundance and species richness by the number of observations so that we received mean values per month. To account for potential differences in sampling efficiency in the measures, we conducted the analysis also with estimate species (R function 'estimateR' from VEGAN package, see Oksanen, 2020), but received equivalent results and therefore used untransformed species richness.

We used generalised linear models ('GLMs') with a gamma distribution and log-link to test the relation of plant and social and solitary bee abundance or species richness with the interaction of enhancement measure and year. Furthermore, we built subsets for each measure and used GLMs with a gamma distribution and log-link on the relation of flower and social and solitary bee abundance or species richness with the interaction of year and month. The interaction was used to allow different responses within month across years. As the gamma distribution does not cover zeros, we added 0.1 to all values. For comparing the effects of the months and years, we calculated pairwise comparisons with the R-function emmeans with Bonferroni-Holm adjustment of p -values (EMMEANS package, Lenth, 2016).

To test whether bee abundance and species richness changed from year to year in the measures, we calculated the mean values per site and year. We used GLMs with a gamma distribution and log-link to test the relation of bee abundance and species richness and included an interaction for measure and year. We constructed one model for the following bee groups: social and solitary bees, red-listed solitary bees and red-listed bumblebees. We used emmeans with Bonferroni-Holm adjustment to compare annual effects.

To test for community differences over the course of the year, we generated monthly species' abundances per enhancement measure and year. We calculated Morisita-Horn dissimilarities of communities and applied mutational multivariate analyses of variance ('adonis'; Anderson, 2001) with $n = 10,000$ permutations to test community change across years with month as explaining variable. For illustrating the species variation, we used nonmetric multidimensional scaling (three-dimensional) based on bray dissimilarities ('metaMDS', R package VEGAN; Oksanen et al., 2019). To analyse community differences within the enhancement measures across the 3 years, we aggregated the data by site and year and extracted subsets for the measures. We applied 'adonis' on each subset (based on Morisita-Horn dissimilarities) and if year had a significant effect we plotted the metaMDS for illustration.

3 | RESULTS

Over the 3-year study period, we observed 2040 wild bees (65% social, 35% solitary bees), which belonged to 93 species (Table S3).

Across the season the enhancement measures varied strongly in flower abundance and species richness: The hedges (improved and unimproved) and the orchards dominated the flower provision

in March and April (Figure 1A; Table 1). Although hedges provided more than 1.5 times more flowers than the control, the difference was not significant. From June on, the flower strips, which established largely successfully, dominated with partly the double amount of flowers than the improved hedges, at which the establishment success of the sown hedge herb layers varied between sites from poor to high flower covers. Flower species richness followed a similar pattern as flower abundance, but the differences between the measures were smaller (Table 1). Across the season, all three measures complemented each other in providing flowers.

The bee abundance and species richness per month differed between the measures following flower availability in general. The flower strips attracted the highest abundance and species richness of bees over most of the season (Figure 1B,C; Table 1). Only during March did control and hedges attract significantly more bees. In the summer months from June to September the number of bees was up to more than three times higher in the flower strips than in the other enhancement measures. Bee species richness followed a similar pattern as abundance, but in lower magnitude. Social and solitary bees showed nearly identical patterns of abundance and species richness, although solitary bees showed an overall higher preference for (improved and unimproved) hedges and the difference in abundance was not as high as for social bees.

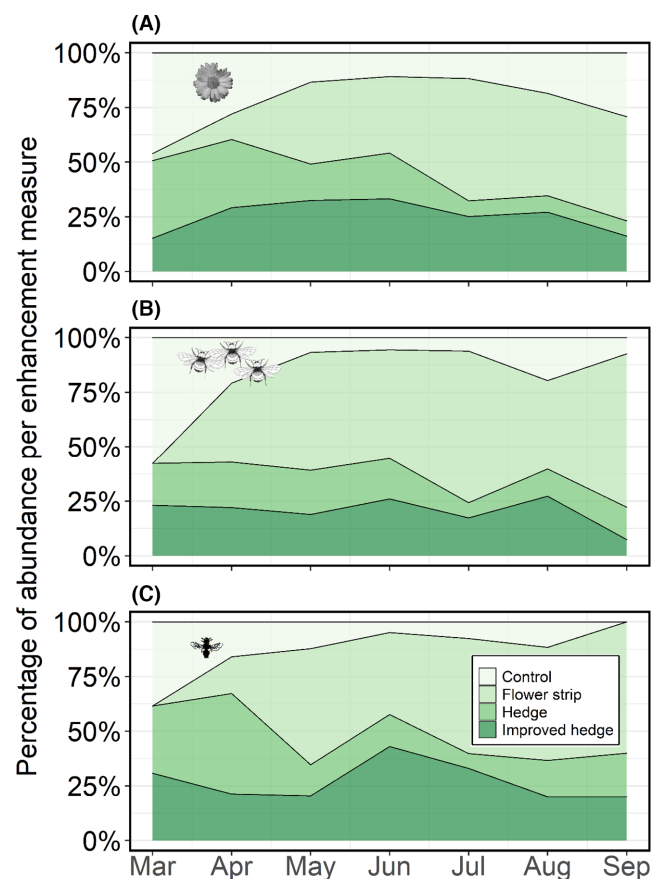


FIGURE 1 Abundance of (A) flowers, (B) social and (C) solitary wild bees across the season per enhancement measure. Shown is the relative mean contribution per month of all 3 years combined.

Flower and bee patterns varied not only between months but also between years (except for the control): The flower strips provided no floral resources until end-May in 2018, whereas in 2019 and 2020 they provided flowers from April onwards (Figure 2; Appendices S4 and S5). In congruence, flower strips supported higher abundance and species richness of bees in April and May 2019 and 2020; for example, social bee abundance was up to four times higher than the other enhancement measures in May 2019 (Figure 3; Appendix S6). From June onwards bee abundance and species richness in the flower strips were similar in all 3 years, although flower abundance was generally lower in the summer months 2018. In the hedges, bee abundance and species richness varied in the months from March to June, but with none of years being a clear frontrunner. At the improved hedges, flower abundance and species richness increased in 2019 and 2020 in comparison to 2018 in the months from May to August. In addition, solitary bee abundance and species richness increased from 2018 to 2019 and 2020 in the months from May to July, whereas social bees showed no significant differences.

When comparing the yearly overall abundance and species richness in the enhancement measures, we observed differences for flowers but not for bees. Flower abundance was up to three times higher in (improved and unimproved) hedges and four times higher in the flower strips in 2019 and 2020 than in 2018 (Appendices S7 and S8). Bee abundance and species richness of the tested bee groups, however, differed in none of the four measures. The only exception was the group of red-listed bumblebees, which were more than three times more abundant in 2018 in the flower strips. In absolute numbers, species richness was highest in 2019 in all measures (see Appendix S9).

The overall bee community differed between measures, months and year, but interactions were not significant (Figure 4a; adonis: measure $R^2 = 0.078$, $p < 0.001$; month $R^2 = 0.206$, $p < 0.001$; year $R^2 = 0.021$, $p = 0.012$). Among the four measures, only the bee communities of the flower strips differed between years (Flower strip $R^2 = 0.144$, $p = 0.029$; Hedge $R^2 = 0.110$, $p = 0.221$; Improved hedge $R^2 = 0.101$, $p = 0.137$; Control $R^2 = 0.032$, $p = 0.972$). Here, the bee community in 2018 was distinct from the communities in 2019 and 2020, which partly overlapped (Figure 4b).

4 | DISCUSSION

We found that the temporal complementarity of floral resources in the different enhancement measures in apple orchards affected how bees used these measures within and between years. All enhancement measures taken together enhanced a large bee species community, which gradually changed from spring to late summer.

4.1 | Phenology across the season

Orchards provided peak floral resources at the beginning of the season (similar to Rosa García & Miñarro, 2014). In March and April, *Taraxacum officinalis* flowered the interrow alleys and *Lamium*

TABLE 1 Monthly abundance and species richness of (A) flowers, (B) social bees and (C) solitary bees. Shown are model estimates (least square means). Letters indicate results of multiple comparisons of enhancement measures per month; measures with distinct letters were significantly different from each other.

Enhancement measure		Least square mean ± SE													
		Mar	Apr	May	Jun	Jul	Aug	Sep							
(A) Flowers															
Control															
Abundance		113.6 ± 36.6	b	192.1 ± 50.5	ab	70.5 ± 19.2	a	82.4 ± 21.7	a	64.1 ± 16.9	a	66.6 ± 17.5	ab	87.3 ± 28.1	ab
Species richness		3.1 ± 0.6	a	2.4 ± 0.4	a	2.9 ± 0.5	a	2.6 ± 0.4	a	2.6 ± 0.4	ab	1.9 ± 0.3	a	3.4 ± 0.7	b
Flower strip															
Abundance		16.5 ± 5.9	a	112.5 ± 33.1	a	193.9 ± 57	a	302.1 ± 88.8	b	445.5 ± 131	b	295.5 ± 86.9	c	177.6 ± 64	b
Species richness		1.5 ± 0.3	a	1.7 ± 0.3	a	3.8 ± 0.7	a	6.2 ± 1.1	b	5.7 ± 1.0	c	5.0 ± 0.9	b	6.0 ± 1.3	b
Hedge															
Abundance		154.4 ± 55.6	b	345.4 ± 101.5	b	107.3 ± 31.5	a	177.5 ± 52.2	ab	57.1 ± 16.8	a	46.5 ± 13.7	a	29.7 ± 11.4	a
Species richness		1.7 ± 0.4	a	2.1 ± 0.4	a	3.1 ± 0.5	a	2.4 ± 0.4	a	1.8 ± 0.3	a	1.7 ± 0.3	a	1.5 ± 0.4	a
Improved hedge															
Abundance		44.8 ± 15.2	ab	244.2 ± 66.5	ab	146.3 ± 39.8	a	249.7 ± 68	b	184.3 ± 50.2	b	149.2 ± 40.6	bc	60.6 ± 21.8	ab
Species richness		2.5 ± 0.5	a	2.4 ± 0.4	a	3.8 ± 0.6	a	4.2 ± 0.7	ab	4.4 ± 0.7	bc	3.7 ± 0.6	b	3.5 ± 0.7	ab
(B) Social bees															
Control															
Abundance		1.0 ± 0.4	b	0.5 ± 0.2	a	0.3 ± 0.1	a	0.6 ± 0.2	a	0.8 ± 0.3	a	2 ± 0.7	ab	0.3 ± 0.1	a
Species richness		0.6 ± 0.2	b	0.4 ± 0.1	a	0.2 ± 0.0	a	0.5 ± 0.1	a	0.7 ± 0.2	a	0.6 ± 0.2	a	0.3 ± 0.1	a
Flower strip															
Abundance		0.1 ± 0.0	a	0.6 ± 0.2	a	2.0 ± 0.7	b	6.7 ± 2.4	b	8.4 ± 3.1	b	4.5 ± 1.7	b	2.5 ± 1.1	b
Species richness		0.1 ± 0.0	a	0.4 ± 0.1	a	0.9 ± 0.3	b	3.1 ± 1.0	b	2.4 ± 0.8	b	2.0 ± 0.6	b	1.2 ± 0.5	b
Hedge															
Abundance		0.7 ± 0.3	b	0.4 ± 0.2	a	1.3 ± 0.5	b	2.1 ± 0.8	ab	1.2 ± 0.4	a	1.1 ± 0.4	a	0.7 ± 0.3	ab
Species richness		0.6 ± 0.2	b	0.3 ± 0.1	a	0.9 ± 0.3	b	1.3 ± 0.4	ab	0.9 ± 0.3	ab	0.6 ± 0.2	a	0.5 ± 0.2	ab
Improved hedge															
Abundance		0.7 ± 0.3	b	0.4 ± 0.1	a	0.9 ± 0.3	ab	3.1 ± 1	b	2.4 ± 0.8	ab	2.1 ± 0.7	ab	0.4 ± 0.2	a
Species richness		0.4 ± 0.2	b	0.3 ± 0.1	a	0.6 ± 0.2	b	1.6 ± 0.5	b	1.5 ± 0.4	ab	1.4 ± 0.4	ab	0.4 ± 0.1	ab
(C) Solitary bees															
Control															
Abundance		abu	abu	abu	abu	abu	abu	abu	abu	abu	abu	abu	abu	abu	abu
Species richness		0.9 ± 0.3	b	0.4 ± 0.1	a	0.2 ± 0.1	a	0.4 ± 0.1	a	0.3 ± 0.1	a	0.4 ± 0.1	a	0.1 ± 0.0	a

TABLE 1 (Continued)

		Least square mean \pm SE													
Enhancement measure		Mar	Apr	May	Jun	Jul	Aug	Sep							
Flower strip															
Abundance		0.1 \pm 0.0	a	0.5 \pm 0.2	a	1.4 \pm 0.5	b	2.6 \pm 0.9	b	2.4 \pm 0.9	c	1.5 \pm 0.6	b	0.5 \pm 0.2	a
Species richness		0.1 \pm 0.0	a	0.3 \pm 0.1	a	1.1 \pm 0.4	b	1.4 \pm 0.5	b	1.8 \pm 0.6	c	1.1 \pm 0.3	a	0.5 \pm 0.2	b
Hedge															
Abundance		1.6 \pm 0.7	b	1.1 \pm 0.4	a	0.5 \pm 0.2	ab	1 \pm 0.4	ab	0.5 \pm 0.2	ab	0.5 \pm 0.2	ab	0.2 \pm 0.1	a
Species richness		0.6 \pm 0.2	b	0.6 \pm 0.2	a	0.5 \pm 0.2	ab	0.7 \pm 0.2	ab	0.4 \pm 0.1	ab	0.5 \pm 0.2	a	0.2 \pm 0.1	ab
Improved hedge															
Abundance		1.3 \pm 0.6	b	0.5 \pm 0.2	a	0.6 \pm 0.2	ab	2.4 \pm 0.8	ab	1.5 \pm 0.5	bc	0.5 \pm 0.2	ab	0.2 \pm 0.1	a
Species richness		0.9 \pm 0.3	b	0.4 \pm 0.1	a	0.5 \pm 0.1	ab	0.7 \pm 0.2	ab	1.0 \pm 0.3	bc	0.4 \pm 0.1	a	0.2 \pm 0.1	ab

purpureum in the tree rows with *L. purpureum* attracting especially bumblebee queens. In late April, apple trees supplied bees with large quantities of flowers, although the number of apple flower-visiting wild bees was low compared to honeybees (von Königsłow et al., 2021). After apple trees finished blooming, alternative resources (mainly *Trifolium repens* and *Bellis perennis*) were mostly available only over short timespans or in spatially limited patches within the orchards due to herbicide application and frequent mowing. Generally, flower and bee diversity in the ground vegetation was higher in the more extensively managed orchards, but the diversity was overall limited (von Königsłow et al., 2021) presumably resulting in a uniform species composition in intensive orchard landscapes. Furthermore, ground vegetation within orchards typically had fewer flowers than at orchard edges, where sampling took place (von Königsłow et al., 2021). Enhancement measures complementing floral resources in apple orchards are therefore ecologically important across all seasons, but perhaps least so in spring.

Similar to the orchards, the hedges (improved and unimproved) produced large quantities of flowers in March and April, for example, *Salix* sp. or *Prunus spinosa*. After the flower of *Rubus fruticosus* agg. in June, the quantity of floral resources in hedges declined continuously into late summer. Despite the partially high flower availability, hedges were not necessarily visited by a high diversity of bees. An explanation for this is that some of the most prevalent shrub species in the studied hedges produced unattractive flowers for bees, for example, *Euonymus europaeus* (Westrich, 2018). Another reason for the fewer bee visits were the short flowering periods of shrubs and trees. Most hedges did not provide continuous floral resources, but rather a fluctuating mass supply, which was shown to reduce bumblebee diversity (Hemberger et al., 2020). The fluctuations are visible through the significant differences in bee abundance and species richness between the study years. As sampling did not take place at the exact same time in each year, we measured the flowering of different shrub species or missed mass blooms between study years. A further explanation for the comparatively low bee diversity in hedges lies in the life cycles of social and solitary bee species. Social bees are active over the entire season but typically have low population sizes in spring because at this time individual females found colonies that produce much higher individual numbers in summer (Westrich, 2018, Appendix S10). Solitary bees in contrast have species-specific flight periods and although many species fly in spring, the majority occur in summer (Balfour et al., 2018). In terms of bee life cycles, it is unsurprising that bee diversity in hedges was lower than in the later blooming flower strips. Yet, this lower diversity does not imply that hedges are unimportant to bee communities as they provide flowers at a crucial time for the foundation of healthy social bee colonies in summer and for many early flying solitary species, of which many have a preference for woody vegetation (Balfour et al., 2018; Carvell et al., 2017; Scheper et al., 2015). Increasing the diversity of bee-attractive shrubs and regular maintenance could help to increase the habitat quality of hedges.

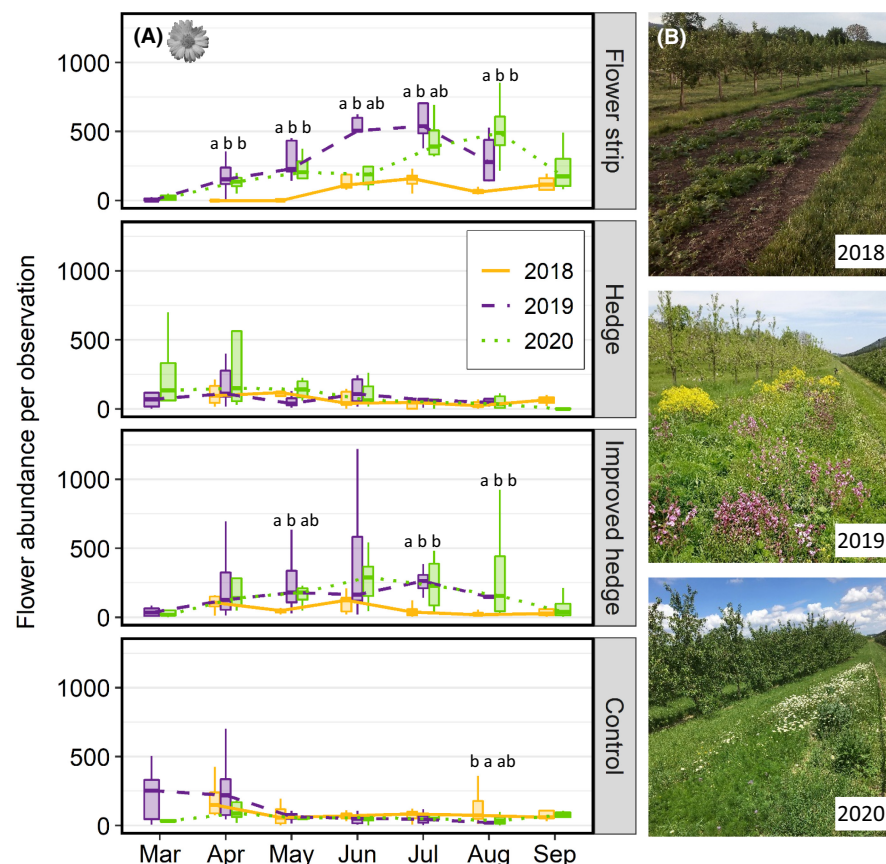


FIGURE 2 Monthly change of floral resources. (A) Abundance of flowers per enhancement measure across the season, separated per year. Shown are boxplots per month and year (outliers not shown). The y-axis shows the mean abundance per observation (number of flowers per month divided by number of observations). Letters indicate results of multiple comparisons (emmeans); years with distinct letters were significantly different from each other. If no letters are indicated, the years did not differ significantly. (B) Photos of the same flower strip in mid-May in the three subsequent years show the change of floral community.

The hedges coincided in large parts with the maximum flower supply in the orchards in spring, although they provided flowers longer into summer. During the mass flowering of apple trees, however, few shrub species flowered in hedges and were infrequently visited by bees. A reason for this may be that pollinators were diluted across the landscape due to the extremely high flower supply (Tschartnke et al., 2012). A further explanation may be that the dominant blooming tree in the hedges during apple boom was *Prunus padus*, which belongs to the same plant family as apples and as such attracts a similar bee species spectrum. This is supported by the fact that the bee species composition between apple flowers and hedge shrubs flowering at the same time did not differ (adonis $R^2 = 0.045$, $p = 0.458$).

Establishing herb layers elongated flower provision of improved hedges into July and August. The sown herb layers especially attracted solitary bees (nearly as many as the flower strips), whereas social bees preferred the flower strips, possibly due to the smaller size of the herb layers (Blaauw & Isaacs, 2014; Riggi et al., 2021). The establishment of herb layers along hedges can thus be a meaningful measure for creating a continuous flower supply, but their attractiveness depends on the establishment success and total flower production, which was highly variable in our experiment due to differing light availability (Scheper et al., 2021; Schmidt et al., 2021; von Königsłow et al., 2021). The establishment of an herb layer is thus only promising along the sun exposed side of hedges and if enough space is available.

In contrast to the hedges and the orchards, the flower strips provided maximum resources during the summer (June to mid-August),

which is similar to other studies (Neumüller et al., 2021; Ouvrard et al., 2018). Over this time span, they attracted a high diversity of social and solitary wild bees, which confirms their positive effects on bee diversity (Buhk et al., 2018; Ganser et al., 2021; Jönsson et al., 2015; Lowe et al., 2021; Scheper et al., 2015; Schubert et al., 2021). Flower strips provide complimentary resources near orchards and hedges as they provide flowers when these both are scarce in flowers.

4.2 | Phenology from year to year

In flower strips and herb layers of improved hedges, phenology differed not only across the season, but also across years. This variation especially differed between the year of establishment and subsequent years. The flower strips started flowering not before June in the year of sowing, whereas in the second and third year flowering started much earlier. This earlier bloom in the subsequent years was attributable to spontaneous early flowering vegetation like *Glechoma hederaceae*, which provided flowers already from early April (Ouvrard et al., 2018; Schmidt et al., 2021). Furthermore, early flowering plants from the seed mixtures started flowering in late-April (e.g. *Silene dioica*, *Isatis tinctoria*, *Leucanthemum vulgare*). Also the hedge herb layers started flowering earlier in the second year of establishment, but the floral supply was overall smaller and the flowering period was shorter than in the flower strips. This was due to differences in seed mixture, which lacked fast-growing annual plant

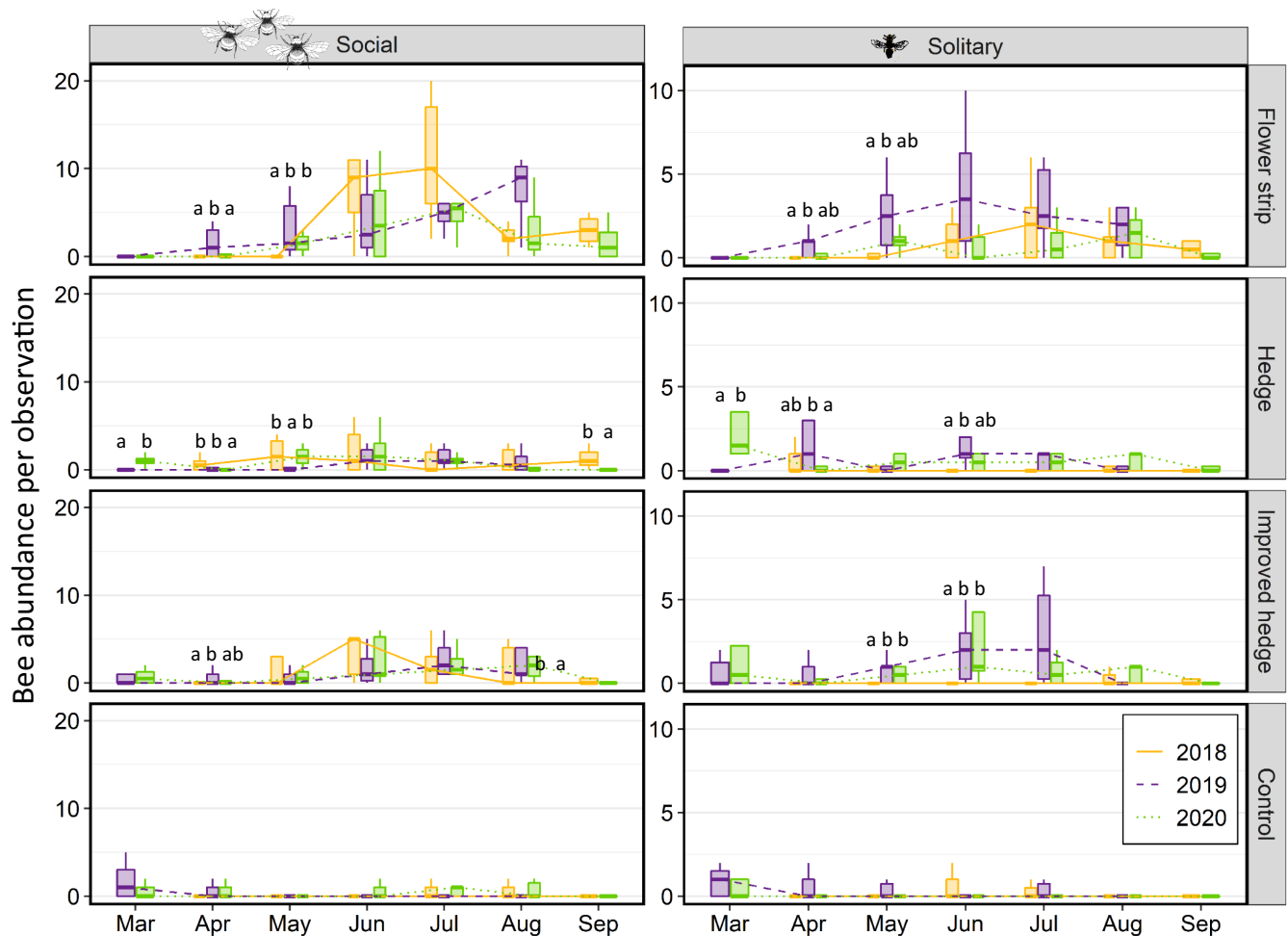
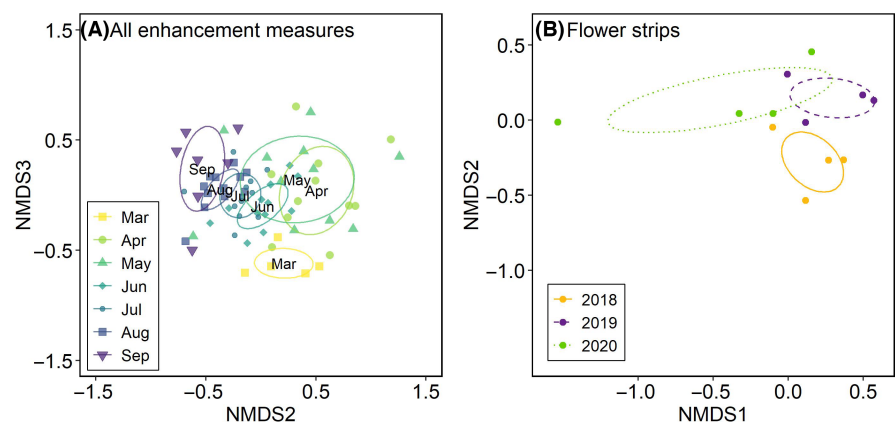


FIGURE 3 Abundance of social and solitary wild bees per enhancement measure across the season, separated per year. Shown are boxplots per month and year (outliers not shown). The y-axis shows the mean abundance per observation (number of bees per month divided by number of observations). Lines connect medians. Letters indicate results of multiple comparisons (emmeans); years with distinct letters were significantly different from each other. If no letters are indicated, the years did not differ significantly.

FIGURE 4 Bee species composition. (A) NMDS ordinations using Bray–Curtis dissimilarity of wild bee species composition across all enhancement measures per month (stress = 0.133). Dots represent bee communities per enhancement measure separated per month and year. (B) NMDS of bee species composition in the flower strips per year (stress = 0.148). Dots represent experimental sites. Ellipses represent covariance ellipses per month.



species, but also due to the less appropriate growth conditions along the hedges.

The flower strips hosted different bee communities from year to year. Early floral resources in second and third year benefited foundresses of long-lived social species and early-flying solitary species

by providing them with foraging possibilities before the end of their flight period in June (see Appendix S11; Balfour et al., 2018). This resource availability for early flying species may explain the differences in the bee communities between the study years. Furthermore, the plant species composition changed from year to year (see NMDS

in Appendix S12). In the first year annual plant species dominated, whereas biennial and perennial species took over in the second year, which attracted different bee species. *Osmia adunca* for example, which is oligolectic on *Echium* species, occurred only in the second and third year, but not in the first year when *Echium vulgare* did not flower.

Despite the additional attraction of early flying species, the effect of the longer flowering period on overall bee species richness remained ambiguous when considering the entire season. We found an overall higher bee diversity in the flower strips and hedge herb layers during the second year, but this may be attributable simply to inter-annual variation as bee diversity was higher in all enhancement measures in this particular year. Several studies found increases in bee species richness, especially of rare and specialised species, in flower strips over time (Buhk et al., 2018; Lowe et al., 2021; Schubert et al., 2021). Contrary to these findings, bee diversity, also of rare species, did not increase with time in our experiment in both the flower strip and the hedge herb layer. The mean bee species richness per site and the overall species richness of all flower strips combined even dropped largely from the second to the third year (Table S6). This can be explained by a decrease in the diversity of nectar- and pollen-rich plant species as grasses and specific flowering plant species started to dominate the plant community. Our results therefore indicate that bee species richness in flower strips does not under all conditions increase with time. Red-listed bumblebees, namely the two long-tongued species *Bombus sylvarum* and *Bombus humilis*, were even more abundant in the first year of establishment possibly due to a preference for plant species flowering mostly in the first year. For example, *B. sylvarum* was mostly observed on *Phacelia tanacetifolia*, which produced much less flowers in the second year. Both bumblebee species visited plant species that are rather nectar rich instead of pollen rich. This nectar source probably complements the pollen of *Trifolium repens*, which was frequently flowering in the orchard ground vegetation and is an important pollen source for long-tongued bumblebees (Carvell et al., 2006; Goulson et al., 2005). However, the availability of nectar-rich flowers in the second year was presumably similarly high as in the first year (e.g. *Echium vulgare*, *Malva* sp., *Melilotus* sp.). So these red listed bumble bee species either show more specific preferences for certain plant species, or may have been affected by the hot and dry conditions during the three study years.

5 | CONCLUSIONS

For enhancing wild bees in apple orchards, both hedges and flower strips are useful, especially when combined. However, flower strips complemented periods of flower scarcity in the orchards better than hedges and thus better promoted bee diversity. In contrast, hedges have more variable floral resources that predominantly overlap with orchard flowering in spring.

Perennial flower strips of different age classes should be preferred over the currently still more common annual strips as these

have the potential to enhance an overall higher diversity of bees due to temporal and floral complementarity. Maintenance measures like adapted mowing and renewing those parts of the flower strips that are no longer flower rich and diverse may contribute to maintain flower production and thus bee-attractive habitats across years. A network of perennial flower strips and some well-maintained hedges spanning landscapes with high proportions of intensive apple orchards could be a powerful tool for enhancing bee diversity. To increase the ability of hedges to complement periods of flower scarcity in the orchards, emphasis should be placed on increasing diversity of bee-attractive shrubs with complementary phenology.

AUTHOR CONTRIBUTIONS

Vivien von Königslöw and Alexandra-Maria Klein conceived the ideas and designed methodology; Vivien von Königslöw collected the data; Vivien von Königslöw and Felix Fornoff analysed the data; and Vivien von Königslöw led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST

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DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository under <https://doi.org/10.5061/dryad.z612jm6fj> and <https://doi.org/10.5281/zenodo.6976170> (Von Königslöw et al., 2022).

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Supporting Information

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