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Time since establishment drives bee and hoverfly diversity, abundance of crop-pollinating bees and aphidophagous hoverflies in perennial wildflower strips

Matthias Albrecht[a,*], Arthur Knecht[a,b], Matthias Riesen[b], Theres Rutz[a], Dominik Ganser[a]

[a]Agroecology and Environment, Agroscope, Reckenholzstrasse 191, CH-8046 Zurich, Switzerland
[b]Institute of Natural Resource Sciences, Zurich University of Applied Sciences, Grüentalstrasse 14, Postfach CH-8820 Wädenswil, Switzerland

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Abstract

Wildflower strips (WFS) are amongst the most commonly applied measures to promote pollinators and natural enemies of crop pests in agroecosystems. Their potential to enhance these functionally important insect groups may vary substantially with time since establishment of WFS. However, knowledge on their temporal dynamics remains scarce, hampering recommendations for optimized design and management. We therefore examined temporal dynamics of taxonomic and functional groups of bees and hoverflies in perennial WFS ranging from one to ≥6 years since sowing with a standardized species-rich seed mixture of flowering plants in 18 agricultural landscapes in Switzerland. The abundance of wild bees, honeybees and hoverflies declined after the second year by 89%, 62% and 72%, respectively. Declines in bee abundance and hoverfly species richness were linear and those of aphidophagous hoverflies exponential, while wild bee species richness peaked in the third year. Declines over time generally paralleled decreases in flower abundance (-83%) and flowering species richness (-61%) and an increase in grass cover (+70%) in WFS. Flowering plant species richness showed strong positive relationships with dominant crop-visiting wild bees and aphidophagous hoverflies. Furthermore, dominant crop-visiting wild bees, but not aphidophagous hoverflies, were positively related to the proportion of (semi-)open semi-natural habitat in the surrounding landscape (500 m radius), but negatively with forest. We conclude that the effectiveness of perennial WFS to promote pollinator diversity, crop-pollinating bees and aphidophagous hoverflies through foraging resources decreases after the first two to three years, probably due to a decline of diverse and abundant floral resources. Although older perennial WFS may still provide valuable nesting and overwintering opportunities for pollinators and natural enemies, our findings indicate that regular re-sowing of perennial WFS may be necessary to maintain adequate floral resource provisioning for effective pollinator conservation and promotion of crop pollination and natural pest control services in agricultural landscapes.

Keywords: Agroecology; Agri-environment schemes; Biodiversity restoration; Conservation biological control; Flower strips; Natural enemies; Pollinators; Secondary succession; Syrphidae; Temporal community dynamics

*Corresponding author.
E-mail addresses: matthias.albrecht@agroscope.admin.ch (M. Albrecht), matthias.riesen@zhaw.ch (M. Riesen), d_ganser@me.com (D. Ganser).

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Introduction

Intensive agriculture and the simplification of agroecosystems jeopardize farmland biodiversity and associated provisioning of ecosystem services, such as crop pollination and natural pest control services (Dainese et al., 2019; IPBES, 2016). In the last decades, however, considerable effort has been undertaken to mitigate the loss of biodiversity and to promote ecological intensification by harnessing biodiversity-based ecosystem services (e.g. Kovács-Hostyánszki et al., 2017). Wildflower plantings such as wildflower strips (WFS) are amongst the most commonly applied measures to foster rare species, biodiversity and ecosystem services in intensively managed agricultural landscapes (Albrecht et al., 2020; Haaland, Naisbit & Bersier, 2011; Scheper, Bommarco, Holzschuh, Potts & Riedinger, 2015; Tschumi, Albrecht, Entling & Jacot, 2015; Williams et al., 2015; Wratten, Gillespie, Decourtye, Mader & Desneux, 2012). In fact, their establishment in agricultural landscapes has been promoted by member states of the European Union as a type of Ecological Focus Areas (EFAs) part of the greening measures implemented in the framework of the Common Agricultural Policy (CAP) or Farm Bill programs in the USA (IPBES, 2016; Kovács-Hostyánszki et al., 2017; Venturini, Drummond, Hoshide, Dibble & Stack, 2017). For pollinators and natural enemies, WFS can offer vital resources such as floral and other food resources, shelter or overwintering habitat (Holland et al., 2016; M'Gonigle, Ponisio, Cutler & Kremen, 2015; Scheper et al., 2013). By promoting pollinator and natural enemies, WFS may also contribute to crop pollination and natural pest control services in nearby crops (e.g. Albrecht et al., 2020; Blaauw & Isaacs, 2014; Ganser, Mayr, Albrecht & Knop, 2018; Sutter, Albrecht & Jeanneret, 2018; Tschumi et al., 2015, 2016a,b).

However, the effectiveness of WFS in promoting rare species, diversity and functionally particularly important groups of bees and hoverflies, such as dominant crop-pollinating bees and natural enemies of crop pests, may strongly depend on the time since their establishment. Yet, knowledge on the temporal dynamics of pollinator and natural enemy communities during perennial WFS succession, and underlying drivers, remains scarce (Albrecht et al., 2020; Blaauw & Isaacs, 2014; Ganser, Knop & Albrecht, 2019). An increase in the number of pollinators and natural enemies with flower strip age is predicted by the expectation that the build-up and restoration of local crop pollinator populations requires time (Blaauw & Isaacs, 2014; Buhk et al., 2018; Venturini et al., 2017). However, dynamics of pollinator and natural enemy communities are also likely driven by temporal changes in other resources they rely on, such as floral food resources as a potential key driver of pollinators and natural enemies that consume such resources during certain life-history stages (Ganser, Albrecht, & Knop, 2020; Scheper et al., 2013, 2015; Sutter, Jeanneret, Bartual, Bocci & Albrecht, 2017; Tschumi et al., 2016a; Wäckers & van Rijn, 2012). In sown perennial WFS, flowering plant diversity might be highest in the second or third year, in the transition period from early succession stages dominated by annuals to later stages dominated by perennial flowering plants, while flower abundance and diversity in older WFS may be reduced through competitive exclusion by increasingly dominant grasses, as often observed in naturally regenerated field margins in Central European agroecosystems (De Cauwer, Reheul, D'hooghe, Nijs & Milbau, 2004; Steffan-Dewenter & Tscharnkte, 2001). Hence, successional changes in vegetation properties, in particular temporal shifts in the abundance and diversity of floral food resources (Kremen, M'Gonigle & Ponisio, 2018), should also strongly affect the effectiveness of WFS in promoting different groups of bees and hoverflies: rare species and the diversity of bees and hoverflies may particularly strongly respond to flowering plant diversity, and show a mid-successional peak, while the mostly generalist dominant crop-visiting wild bees, managed honey bees and aphidophagous hoverflies may mainly reflect temporal dynamics in flower abundance. Moreover, temporal changes in vegetation characteristics may also affect the potential of WFS as suitable nesting habitat for ground-nesting bee pollinators and as overwintering habitat of pollinators and natural enemies (Frank & Reichhart, 2004; Ganser et al., 2019), in contrast to managed honey bees, which should be mainly driven by temporal changes in the abundance of adequate foraging resources.

In addition to local WFS drivers, the effectiveness of WFS might also depend on the agricultural landscape context (Geppert et al., 2020; Grass et al., 2016) and the proportion of semi-natural habitats (SNHs) around them (Bátary, Baldi, Kleijn & Tscharntke, 2010; Jonsson et al., 2015). Simplified landscapes with low amounts of SNH likely have depleted source populations of pollinators and natural enemies, which should limit the potential of WFS to support pollinators and natural enemies. However, bee pollinators may require different types of SNH than hoverfly pollinators and natural enemies (Bartual et al., 2019; Jauker, Diekötter, Schwarzbach & Wolters, 2009; Shackelford et al., 2013). While for example woody SNH, such as forests, may be particularly important to sustain aphidophagous hoverflies and other dipteran natural enemies in agricultural landscapes, as they can provide for example suitable overwintering habitat and abundant alternative food resources (e.g. Bartual et al., 2019; Pfister et al., 2017; Schirmel et al., 2018), herbaceous open and semi-open SNHs rich in flowering plant species may be particularly important for bee pollinators (Bartual et al., 2019; Ganser, Albrecht, & Knop, 2020; Rollin et al., 2013; Sutter et al., 2017). However, our understanding of the temporal and spatial dynamic as potential drivers of the effectiveness of WFS to support pollinators and natural enemies remains surprisingly scarce (but see e.g. Steffan-Dewenter & Tscharntke, 2001). Yet, a better understanding of these factors is important to improve recommendations with respect to the design and management of WFS in agricultural landscapes.

Here, we examined the temporal dynamics of taxonomic and functional groups of bees and hoverflies in 18 perennial WFS ranging from 1 to 6 years since establishment sown with a standardized species-rich seed mixture of flowering plants across uncorrelated proportions of (semi-)open and forested SNH in the surrounding agricultural landscapes in Switzerland. Adult bees and hoverflies are important pollinators (IPBES, 2016; Jauker, Bondarenko, Becker & Steffan-Dewenter, 2012). Larvae of aphidophagous hoverflies are also key predators of crop aphids (Wäckers & van Rijn, 2012). We address the following questions:

(1) How do rare species, and the diversity and abundance of bees and hoverflies in WFS change with time since their establishment?
(2) How do the key functional groups dominant crop-visiting wild bees and aphidophagous hoverflies change with WFS age?
(3) What is the role of floral abundance and diversity, and grass cover, driving temporal dynamics of the different taxonomic and functional groups of bees and hoverflies?
(4) How does the proportion of (semi-)open and forested SNHs at the landscape scale affect the studied pollinators and natural enemies in WFS?

We hypothesized that the abundances of honey bees and dominant crop-visiting wild bees decline with WFS age parallel to an increase in grass cover, associated with a decrease in floral abundance, while rare species, bee diversity and hoverfly diversity will peak in medium-aged WFS parallel to a mid-successional peak in flowering plant species diversity, and potentially nesting habitat suitability. We expected wild bees in WFS to be positively related to the proportion of (semi-)open but not forested SNH in the surrounding landscape, while we predicted a contrasting response for hoverflies.

Materials and methods

Study design and study region

The study was conducted in agricultural landscapes of the Swiss Plateau in the cantons of Aargau, Bern and Zurich. The study region covering an area of approximately 130 × 70 km is characterized by a mixed farming system dominated by arable crop production. The dominant SNHs in the region are forest remnants, hedgerows and extensively managed grasslands (Ganser et al., 2018). In the study region, a total of 18 perennial WFS of different age were selected along independent gradients ($P = 0.464$) in the proportion of (semi-)open and forested SNH in the surrounding landscape. The age of the selected WFS (i.e. the time span from sowing date in spring until sampling in spring/summer) ranged from 1 to 8 years after sowing (2nd to 9th year WFS were on place). Not enough freshly sown WFS (first months directly after sowing, 1st succession year) fulfilling all criteria of the study design could be identified in the study region and they were therefore not sampled. The same number of WFS was sampled for each age (i.e. three WFS of each year after establishment, except for the oldest age class, which consisted of two WFS 6 years old and one 8-year-old WFS (hereafter ≥6 years old WFS). Sampled WFS were at least 1.0 km apart from each other. WFS of the same age were evenly distributed (no spatial clumping; visually assessed) within the study region and no significant correlation of WFS age and the proportion of SNH in the surrounding landscape was present (ANOVA; $F_{6,18}$, $P = 0.464$). The area of WFS ranged from 0.10 to 0.55 ha (mean ± 1 SE: 0.26 ± 0.03 ha); it was ensured that it was not confounded with proportion of SNH ($P = 0.582$) or the age of WFS (ANOVA, $F_{6,18}$, $P = 0.628$).

All selected WFS were sown with a standardized seed mixture according to the prescriptions of the most common type of sown flower strips (“Buntbrache Vollversion”) as part of the Swiss agri-environment scheme (Direktzahlungsverordnung DZV, 2013). The seed mixture contains some annual but mostly perennial flowering herbaceous plants and legumes (see species list provided in Appendix A: Table S1). The use of pesticides or fertilizer applications in WFS is not allowed, except for local herbicide use against problematic weeds, such as *Cirsium* sp. After 8 years, WFS normally have to be removed by farmers, as grasses usually become very dominant and outcompete sown flowering herbs and legumes after this time period (Direktzahlungsverordnung DZV, 2013; Ganser et al., 2019).

Sampling of bees and hoverflies

Bees and hoverflies were sampled with standardized sweep-netting (e.g. Albrecht et al., 2010; Ganser et al., 2018; diameter of sweep nets: 40 cm). A total of 50 sweeps (two transects of 25 sweeps each, separated by approximately 10 m) were performed during each of 5 sampling rounds from beginning of May to end of August 2016 in each WFS. Bees that could not be identified in the field were captured for later identification in the laboratory. Sweep netting and transect walks were carried out between 10.00 and 17.00 h only when weather conditions were suitable (according to Pollard and Yates (1994)). Time of day of the sampling of insects at a site was randomized across sites and sampling rounds. Collected insects were stored in a freezer at minus 20 °C before they were pinned and identified by taxonomic experts.

We were interested in the responses of species richness and abundance of the different groups of bees and hoverflies. We separately analysed repsonses of wild bee species richness and abundance, and that of the abundance of the managed Western honey bee, *Apis mellifera* L.. Moreover, we were particularly interested in the response of the wild bee and hoverfly species considered to be important as providers of pollination and natural pest control services in crops (functional groups of dominant crop-visiting wild bees and hoverflies potentially providing aphid control services); therefore, dominant crop-visiting wild bees were classified according to Kleijn et al. (2015); e.g. *Andrena haemorrhoa, Bombus pascuorum, Lasioglossum calceatum*, L. *politum*; Appendix A: Table S2) and hoverfly species predating on aphids in their larval stage were classified as aphidophagous hoverflies according to Speight (2011). Additionally, wild bees and hoverflies that are listed as vulnerable, endangered or critically endangered according to the Red Lists for the region (Red List of bees of Switzerland (Amiet, 1994) and Germany (Westrich et al., 2011); Red List of hoverflies of Baden-Württemberg (Doczkal, Rennwald & Schmid, 2001) were classified as threatened species of particular conservation concern (Appendix A: Table S3).

Vegetation surveys and assessments of flower abundance

During each sampling round, flower abundance of each flowering legume and herbaceous plant species was estimated in five plots of each 2 × 2 m, randomly located within the insect sampling area of each WFS as the percentage of the plot area covered with flowers of a species. Additionally, percentage of grass cover was estimated in each plot.

Assessments of the landscape context

Around each focal WFS the percentage of forests and (semi-) open SNH (i.e. extensively managed grasslands, other wildflower strips, ruderal areas, hedgerows) was quantified in a landscape sector of 500 m radius using existing maps available as GIS layers (TLM3D, swisstopo, Wabern). This radius was chosen based on the expected average foraging ranges of the mostly small-bodied wild bees and hoverflies with considered average foraging ranges of a few hundred meters (Greenleaf, Williams, Winfree & Kremen, 2007), especially in the small-scaled mosaic-type agricultural landscape of the study region, as indicated by previous studies of bees and hoverflies in the study region (e.g., Albrecht, Duelli, Müller, Kleijn & Schmid, 2007; Ganser, Albrecht, & Knop, 2020; Tschumi et al., 2016a). Calculations were performed using ArcMap 10.1 GIS software.

Statistical analysis

To analyse the effect of time since establishment of WFS on the major taxonomic groups of bees and hoverflies (number of counted number of insect specimens (abundance) and species (species richness)) generalized linear mixed-effects (GLMM) models with a Poisson distribution and the fixed explanatory variable year since establishment of the WFS (continuous variable: 1−6 years), WFS area as co-variate and site as random effect were run. Response variables were the abundance and species richness of the taxonomic groups wild bees and hoverflies, and the abundance of managed honey bees (*A. mellifera*), as well as the abundance of important functional groups of ecosystem service providers: the abundance of dominant crop-visiting wild bees and aphidophagous hoverflies sampled in each WFS and sampling round. In addition to linear relationships of insects with time since establishment of WFS we tested for exponential (log (linear)) and hump-shaped relationships with a peak at intermediate ages (2nd and 3rd polynomial). As the 2nd polynomial relationship showed a poor fit in all analyses, only results of linear, log(linear) and 3rd polynomial models are presented. For each response variable, the best-performing model was chosen based on AICc (Burnham & Anderson, 2002); this model with the best goodness of fit was then used for predictions and statistical inference (as e.g. suggested by Zuur, Ieno, N.J., Savelief and Smith (2009). To further test for significant differences in the effect of time since WFS establishment between the major taxonomic groups honey bees, wild bees and hoverflies, we also ran a GLMM model with binomial error distribution and the proportion of insect groups as response variable, and taxonomic group (factor with three levels: honey bees wild bees and hoverflies), time since establishment and their interaction as fixed explanatory variables, and site as a random factor. A significant time × pollinator group interaction indicates significant changes in the proportion of taxonomic pollinator groups with time since WFS establishment.

To analyse the role of potential local WFS drivers (flower abundance, flowering plant species richness, percentage grass cover) and landscape context (proportion of forest and proportion of (semi-)open (non-forest) SNH in the surrounding landscape) of the studied taxonomic and functional groups of bees and hoverflies GLMMs assuming a Poisson error distribution were run with site as random effect. Interaction terms were not included to avoid overfitting of the models. Potential co-linearity amongst explanatory variables was quantitatively assessed in all models, but none of the explanatory variables included together in a model were strongly correlated ($r < 0.6$; Zuur et al., 2009). For all models, we checked for overdispersion by including an observation-level random factor in the model and comparing it to a model without the random observation parameter, as recommended e.g. by Harris (2014) as a simple and robust approach to account for overdispersion of count data not associated with zero-inflation. In case of overdispersion the observation-level random factor significantly improved the models and was retained in the models (Bolker et al., 2009; Harris, 2014). All analyses were done in R version 3.2.1 (R Core Team, 2017), using the lme4 packages (Bates et al., 2015).

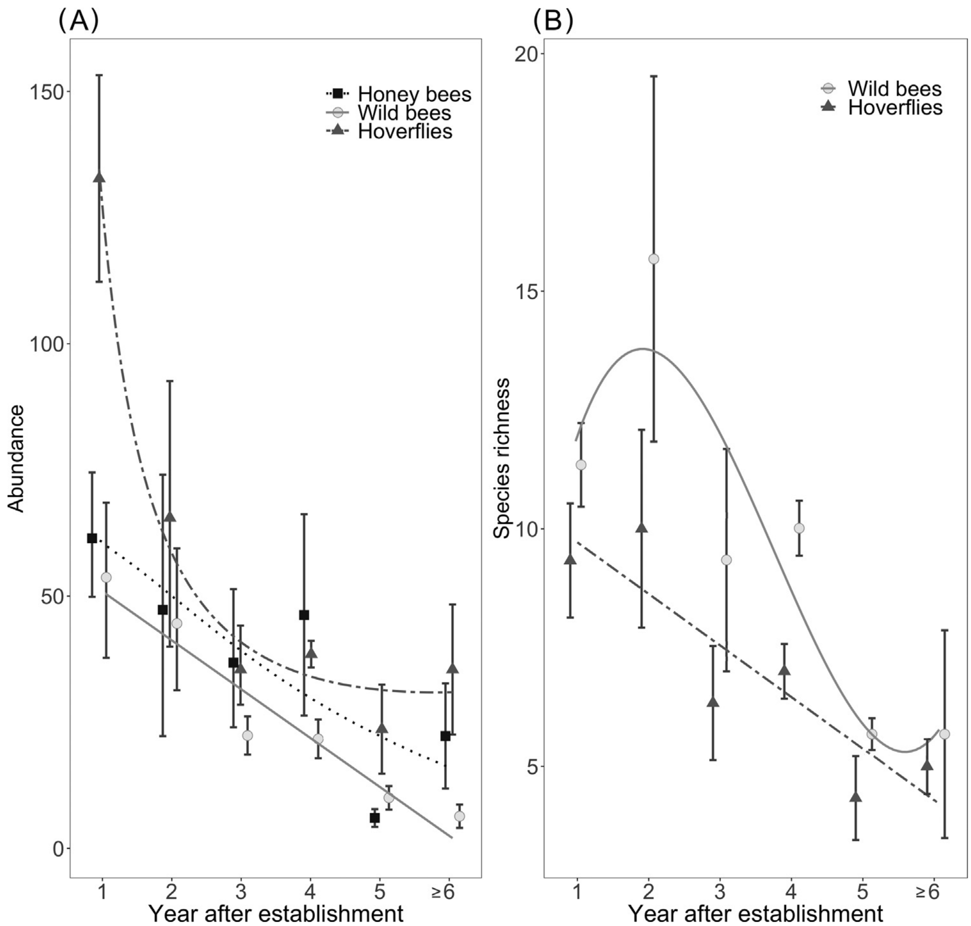

Fig. 1. Relationships of (A) the abundance of honey bees, wild bees and hoverflies and (B) the species richness of wild bees and hoverflies with time since establishment of wildflower strips (1 to ≥6 years). Predicted means and confidence intervals are shown for best-fitting relationship according to AICc. See methods section for detailed description of models.

Results

Effects of time since establishment of WFS on taxonomic and functional insect groups

A total of 1756 bees (474 wild bees of 50 species; 745 honey bees) and 1011 hoverflies of 36 species were sampled. Of the sampled wild bees, 218 individuals (46%), belonging to 13 species, are considered as dominant crop-visiting wild bees in Europe (according to Kleijn et al., 2015; Appendix A: Table S2). Only 28 individuals (2%) of 11 species (9 bee species; 2 hoverfly species) of the sampled wild bees and hoverflies are Red List species listed as threatened (Appendix A: Table S3).

Abundance and species richness of wild bees and hoverflies, as well as honey bee abundance declined with time since establishment (1 to ≥6 years after sowing; Fig. 1; Table 1). The decrease of hoverfly abundance with time since establishment was best predicted by a negative exponential relationship, while for the other response variables the linear models performed best according to AICc (Fig. 1; Table 1; Appendix A: Table S4). Similarly, abundance and species richness of dominant crop-visiting wild bees and abundance of honey bees declined linearly, whereas abundance, but not species richness, of aphidophagous hoverflies declined exponentially with time since establishment (Fig. 2; Appendix A: Table S5). The predicted decline in abundance 1 to ≥6 years after establishment was strongest for wild bees (89%), while honey bees and hoverflies declined by 62% and 72%, respectively. Accordingly, there was a shift towards a smaller proportion of wild bees with time since establishment compared to honey bees and hoverflies from 22 ± 4% in 1-year-old WFS to 9 ± 1% in ≥−6-year old WFS (Appendix A: Fig. S1; Appendix A: Table S6).

Effects of plant community temporal dynamics on bee and hoverfly communities

Both flower abundance and flowering species richness (not significantly correlated) decreased with year since

Table 1. Summary of results of generalized linear mixed effects model analyses of effects of year since establishment of the wildflower strips (Age WFS) and the co-variate area of WFS on the abundance of (a) managed honey bees, wild bees and hoverflies, and (b) species richness of wild bees and hoverflies. Estimated means (estimate) and standard errors (SE), and *P*-values (*P*; significant *P*-values (<0.05) in bold), are shown.

	Honey bees			Wild bees			Hoverflies		
	Estimate	*SE*	*P*	*Estimate*	*SE*	*P*	*Estimate*	*SE*	*P*
a) Abundance									
(Intercept)	5.67	0.86	<**0.001**	4.44	0.50	<**0.001**	1.70	0.63	**0.023**
Area WFS	−0.03	0.02	0.076	−0.02	0.01	0.981	0.01	0.01	0.300
Age WFS (linear)	−0.45	0.13	<**0.001**	−0.42	0.08	<**0.001**			
Age WFS (exponential)							−0.04	0.01	<**0.001**
b) Species richness									
(Intercept)				−0.37	0.79	<**0.001**	2.47	0.41	<**0.001**
Area WFS				0.01	0.01	0.973	−0.01	0.01	0.990
Age WFS (linear)							−0.16	0.07	**0.019**
Age WFS (3rd degree)				−0.01	0.01	<**0.001**			

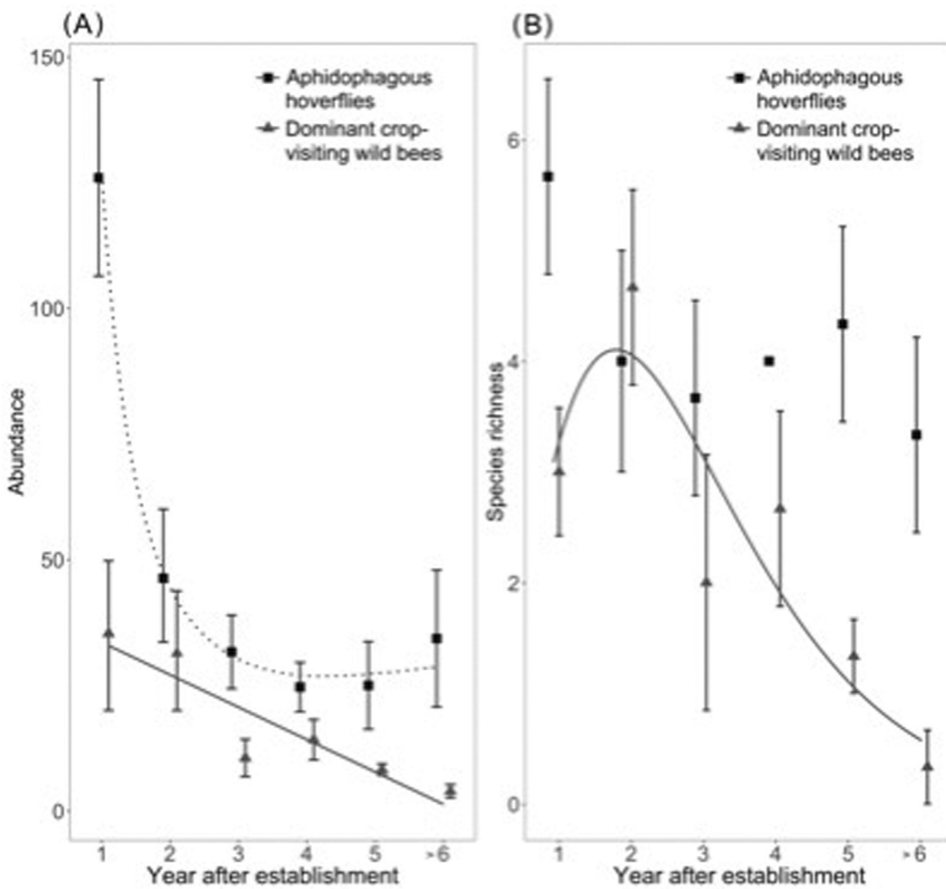

Fig. 2. Relationships of (A) the abundance and (B) the species richness of dominant crop-visiting wild bees (according to Kleijn et al., 2015) and aphidophagous hoverflies with time since establishment of wildflower strips (1 to ≥6 years after establishment). Predicted means and confidence intervals are shown for best-fitting relationship (according to AICc). See methods section for detailed description of models.

establishment of WFS (Fig. 3). Furthermore, flower abundance was positively related to honey bee and hoverfly abundance, and tended to be positively related to hoverfly species richness, whereas flowering species richness was positively related to wild bee and hoverfly abundance (Fig. 3; Table 2). Flowering species richness of WFS was also positively related to the abundance of dominant crop-visiting wild bees and aphidophagous hoverflies (Appendix

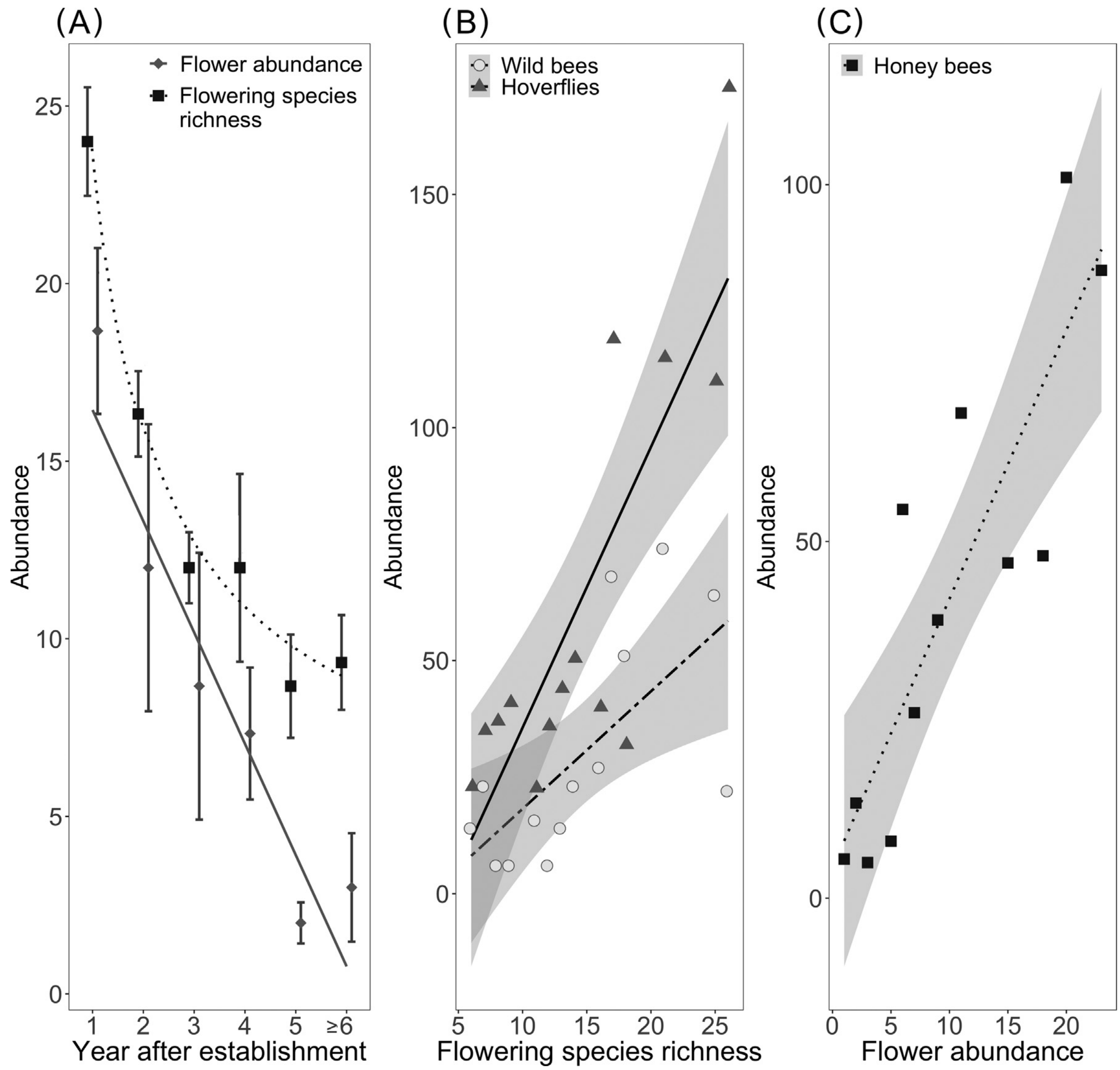

Fig. 3. Relationships of (A) flower abundance and flowering species richness and time since establishment of wildflower strips (1 to ≥6 years), (B) abundance of wild bees and hoverflies and flowering species richness, and (C) honey bee abundance and flower abundance. Predicted means and confidence intervals are shown. See methods section for detailed description of models.

A: Table S7). Moreover, grass cover (not significantly correlated with flower abundance or flowering species richness) was negatively related to hoverfly abundance (Table 2). Grass cover increased with year since establishment (Table 2).

Landscape context as potential driver of bees and hoverflies in WFS

Wild bee abundance was positively related to the proportion of (semi-)open (non-forest) SNH in the landscape surrounding WFS, and there was a trend for a positive relationship of wild bee species richness with (semi-)open SNH (Fig. 4; Table 2). The proportion of forest was, however, negatively related to wild bee abundance and tended to be negatively related to wild bee species richness (Table 2). Similarly, both the abundance and species richness of dominant crop-visiting wild bees were positively related to (semi-)open SNH in the surrounding landscape, while the proportion of forest was negatively related to their abundance (Fig. 4; Appendix A: Table S7). No significant relationships were found for effects of the proportion of forest or other SNH on honey bees or hoverflies (Table 2).

Discussion

Our study highlights that age of sown perennial WFS is a key driver of their effectiveness in promoting bees and hoverflies, revealing marked declines of bee and hoverfly abundances, including important crop pollinators and aphidophagous hoverflies 1 to ≥6 years after the sowing year (from the 2nd to the ≥7th year WFS were in place). In

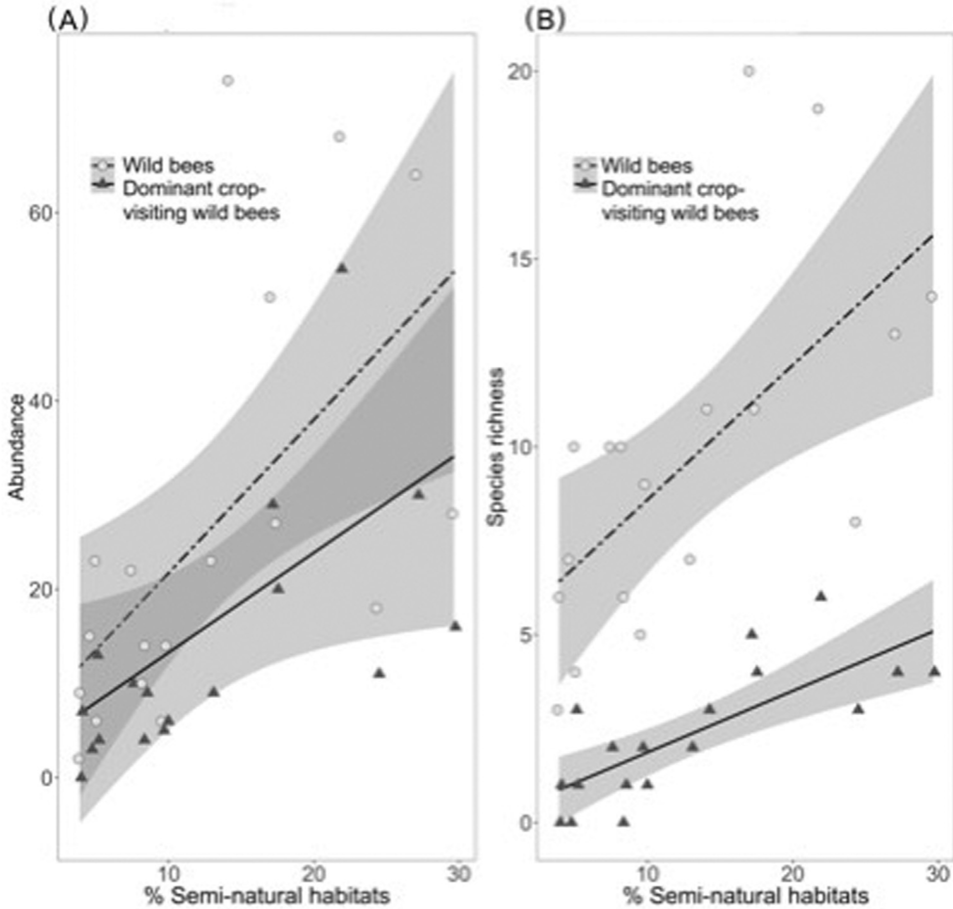

Fig. 4. Relationships of the (A) abundance and (B) species richness of wild bees (total number) and dominant crop-visiting wild bees (according to Kleijn et al., 2015) and the proportion of (semi-)open) (non-forest) SNH in a radius of 500 m around wildflower strips. Predicted means and confidence intervals are shown. See methods section for detailed description of models.

Table 2. Summary of results of generalized linear mixed effects model analysis of effects of local wildflower strip characteristics (flower abundance, flower species richness, grass cover) and the landscape context (percentage forest, percentage (semi-)open SNH) on (a) the abundance of honey bees, wild bees and hoverflies, and (b) the species richness of wild bees and hoverflies. Estimated means (estimate) and standard errors (SE), and *P*-values (*P*; significant *P*-values (<0.05) in bold) are shown.

	Honey bees			Wild bees			Hoverflies		
	Estimate	*SE*	*P*	*Estimate*	*SE*	*P*	*Estimate*	*SE*	*P*
a) Abundance									
(Intercept)	2.69	0.61	**<0.001**	1.54	0.42	**<0.001**	2.07	0.36	**<0.001**
Flower abundance	0.15	0.03	**<0.001**	0.01	0.02	0.349	0.06	0.02	**0.002**
Floral species richness	−0.07	0.04	0.103	0.08	0.03	**0.002**	0.06	0.02	**0.012**
Grass cover	<0.01	0.01	0.690	<0.01	0.01	0.628	0.01	<0.01	**0.005**
% forest landscape	0.40	0.38	0.284	−1.43	0.35	**<0.001**	0.21	0.22	0.341
% (semi-)open SNH	0.03	0.55	0.950	1.64	0.37	**<0.001**	0.50	0.31	0.112
b) Species richness									
(Intercept)				1.54	0.39	**<0.001**	1.78	0.46	**<0.001**
Flower abundance				0.03	0.02	0.179	0.04	0.02	0.072
Floral species richness				0.02	0.03	0.340	−0.01	0.03	0.745
Grass cover				0.00	0.01	0.570	0.00	0.01	0.630
% forest landscape				−0.63	0.34	0.060	0.19	0.39	0.616
% (semi-)open SNH				0.65	0.35	0.067	0.04	0.34	0.912

fact, in the 5 or ≥6 years old WFS roughly five times fewer flower-visiting wild bees, 2.5 times fewer honey bees and four times fewer hoverflies were recorded compared to 2-year-old WFS. This decline over time was relatively constant and linear for bees. Hoverfly numbers, in particular those of aphidophagous hoverflies, dropped markedly from the 2nd to 3rd year after establishment and remained low in older WFS, showing a negative exponential relationship with WFS age. Species richness of bees and hoverflies was also higher in young compared to older WFS; interestingly, however, wild bee species richness increased from the 2nd to the 3rd year after establishment before declining again strongly with increasing age of WFS. To our best knowledge, empirical data of other studies on temporal dynamics of bees or hoverflies with age of sown WFS are largely lacking (but see e.g. Dicks et al. (2014) for a review of evidence for effects of different types of WFS on different groups of flower-visiting insects). General theory for natural secondary succession would instead predict a steady increase in species richness of insects with age during succession driven by increasing niche diversity offered by the maturing vegetation (Parish & Bazzaz, 1979; Siemann, Haarstad & Tilman, 1999). However, these predictions for systems with natural regeneration of the vegetation cannot be directly applied to the establishment of wildflower plantings through sowing or planting of plant species. Our findings are in line with a study of 1 to 5-year-old set aside fields with natural regeneration (no seed mixture sown) in Germany, finding a decline of bee abundance and species richness after a peak in the second year (Steffan-Dewenter & Tscharnkte, 2001).

Irrespective of WFS age, only few red list species of bees and hoverflies were recorded. However, more than half of the sampled wild bees are considered dominant crop-pollinating wild bees in Europe according to Kleijn et al. (2015)). Although proportions of bumblebees (*Bombus* sp.) and andrenid bees (*Andrena* sp.) known to play important roles as crop pollinators in Europe were generally relatively low, species of these taxa such as *Bombus pascuorum* or *Andrena haemorrhoa* were regularly found in the WFS. However, the wild bee communities of WFS were dominated by halictid bees including several species in high numbers, such as *Lasioglossum calceatum* or L. *politum*, which are also considered dominant crop-visiting wild bees of a series of European crops (e.g., Hutchinson et al., 2021; Kleijn et al., 2015). Most of the not classified wild bee species were relatively widespread generalist bees, potentially also locally visiting crops, but not listed as dominant crop-visiting bees in Kleijn et al. (2015)). Moreover, most of the sampled hoverflies were considered potentially important predators of crop aphids (Speight, 2011). Thus, the studied WFS may not strongly contribute to the conservation of threatened bees and hoverflies, but should play an important role for promoting pollinators and natural enemies that provide crop pollination and pest control services. It needs to be noted that the studied WFS were not specifically designed to promote rare bees and hoverflies, more generally for biodiversity conservation of a broad range of taxonomic and functional groups plants and animals and associated multifunctionality in agroecosystems (e.g. Tschumi et al., 2016b).

Succession of WFS vegetation driving temporal dynamics of bee and hoverfly communities

As predicted for the succession of plant-flower visitor communities in natural regeneration systems, our results suggest that temporal dynamics of bee and hoverfly communities are driven by temporal changes in the WFS vegetation. The observed declines of bees and hoverflies paralleled strong decreases in flower abundance and flowering species richness during the studied time period of secondary succession. Similar declines of floral abundance and diversity have been observed in the first years of succession of sown field margins (De Cauwer et al., 2004) and for naturally regenerated wildflower areas after the 2nd year of succession (Steffan-Dewenter &Tscharntke, 2001). A high species richness of flowering plants in the second year can be expected in this transition period from early succession stages dominated by annuals to later stages dominated by perennial flowering plants (Steffan-Dewenter & Tscharnkte, 2001). While flower abundance was positively related to honey bee abundance (e.g. Ganser et al., 2018; Grass et al., 2016), we found that flowering species richness showed stronger positive relationships with wild bee and hoverfly richness than flower abundance. Positive relationships of flowering plant diversity and bee species richness in flower strips and other floral enhancement measures have been observed in previous studies (e.g. Albrecht et al., 2007; Kremen et al., 2018; Scheper et al., 2013; Steffan-Dewenter & Tscharnkte, 2001; Sutter et al., 2017; Wood, Holland & Goulson, 2017; but see Grass et al., 2016). However, our study shows that floral richness was a better predictor than flower abundance of both the abundance of dominant crop-visiting wild bees and aphidophagous hoverflies, highlighting the importance of a high diversity of flowering WFS plants to promote these providers of crop pollination and natural pest control services (Albrecht et al., 2020). Increased species richness of flowering plants is likely associated with increased functional trait complementarity in terms of floral resources for diverse flower visitor communities exhibiting a range of foraging preferences and feeding traits (Campbell, Biesmeijer, Varma & Wäckers, 2012; Kremen et al., 2018; Sutter et al., 2017; van Rijn & Wäckers, 2016; Wäckers & van Rijn, 2012; Warzecha, Diekötter, Wolters & Jauker, 2018). Moreover, a high flowering plant diversity ensures continuous resource availability over time (Balzan, Bocci & Moonen, 2014; Lundin, Ward & Williams, 2019; Schellhorn, Gagic & Bommarco, 2015) for a diversity of flower-visiting insects with different activity periods. Furthermore, it should provide positive selection effects, i.e. an increased likelihood of a diverse plant mixture to contain particularly important floral resource plants for different flower visitors. In fact, the presence of key floral resource plant species can be an important driver of bees and hoverflies (Bartual et al., 2019; Sutter et al., 2017; Tschumi et al., 2015;Tschumi et al., 2016a,b). For example, Warzecha et al. (2018) found that four top floral resource plants supported approximately 80% of flower visiting insects in WFS of different seed mixtures. The presence of these key plants was a better predictor of flower visitors than plant species diversity *per se*. Van Rijn and Wäckers (2016) showed that the number of zoophagous hoverflies in flowering field margins was highly correlated with the abundance of a limited range of flowering plant species that had flowers with nectar accessible for them. In the WFS studied here, Asteraceae, including annual, biannual and perennial species, dominated in young perennial WFS, whereas with increasing age, the flower abundance shifted towards higher proportions of perennial species, including in particular species of Lamiaceae, Onagraceae or Malvaceae (Appendix A: Fig. S2). The high proportion of Asteraceae, as well as other flowering plants with open flowers with nectar most likely accessible to hoverflies in the 2nd year after WFS, such as Apiaceae or Violaceae, likely contribute to the markedly higher numbers of hoverflies in these young WFS compared to older WFS (Hatt et al., 2019; van Rijn & Wäckers, 2016).

Interestingly, a recent quantitative synthesis of the effectiveness of flower strips and hedgerows on the provisioning of crop pollination and natural pest control services in adjacent crop fields found a positive saturating relationship of WFS age and pollination services in adjacent crops from the year of WFS establishment going on to the following few years (Albrecht et al., 2020). However, most studies that could be analysed in Albrecht et al. (2020) investigated less than 4-year-old WFS, and further research is needed to examine impacts on crop pollination services also of older WFS, and to further explore the temporal dynamics of the abundance and species richness of flowering herbaceous plants and their relationships with bees and hoverflies also in other regions than the Central European agricultural region studied here. This region is characterized by highly fertilized soils facilitating the observed increase in competition of flowering herbs and legumes with increasingly dominant grasses (see also De Cauwer et al., 2004; Ganser et al., 2019; Steffan-Dewenter & Tscharntke, 2001). An increase of wild pollinator abundance and pollination services in WFS-adjacent crops with flower strip age may also be explained by a greater provision of nesting and overwintering opportunities in older WFS. Such opportunities are likely scarce in short-lived annual flower strips that could even be ecological traps for overwintering arthropods (Ganser et al., 2019). For example, Frank and Reichhart (2004) observed an increase of overwintering of carabid and staphylinid beetles up to the third year after WFS establishment, while Ganser et al. (2019) found distinct successional changes in overwintering of different arthropod groups with time since establishment of perennial WFS. Populations of ground-nesting wild bees may increase over time of species showing nesting site fidelity (Potts & Willmer, 1997). On the other hand, most ground-nesting bees prefer well insolated bare or only sparsely vegetated ground as nesting habitat (Harmon-Threatt, 2020). The increased dominance and cover of grasses during WFS succession across years found in the present study suggests that the suitability of WFS as nesting habitat for ground-nesting bees may decrease after the first 3 to 4 years since establishment. However, the temporal dynamics of the nesting habitat potential of WFS for bees remains largely unexplored.

Effects of landscape context on bees and hoverflies in WFS

The abundance of wild bees and dominant crop-visiting wild bees was higher in WFS in agricultural landscapes with increased proportions of (semi-)open SNH. This finding is in line with the expectation that colonisation of sown WFS by arthropods should be higher in landscapes offering enough suitable habitat sustaining source populations (e.g. Ganser et al., 2019; Sutter et al., 2018). They are also in line with existing evidence that wild bees seem to show more consistent responses to the amount of SNH in agricultural landscapes than hoverflies, which often show less consistent responses (e.g. Haenke, Scheid, Schaefer, Tscharntke & Thies, 2009; Jauker et al., 2009; Meyer, Jauker & Steffan-Dewenter, 2009; Shackelford et al., 2013; Sutter et al., 2018). Interestingly, only the proportion of (semi-)open SNH resulted in increased numbers of wild bees in WFS, while the amount of forest was negatively related to wild bees. Increased numbers of wild bees can be associated with higher floral resource availability in more open compared to forested SNH in Central European agricultural landscapes (Bartual et al., 2019; Rollin et al., 2013); but also better nesting opportunities for the mainly ground-nesting bees observed in the WFS could explain this contrasting response of wild bees. Further research is required to improve our understanding of functional mechanisms underpinning insect pollinator and natural enemy responses to different SNH types in agricultural landscapes (Bartual et al., 2019; Blasi et al., 2021). Nevertheless, this finding highlights the importance of prioritizing diverse SNH for effective landscape management and conservation efforts. The establishment of WFS may, however, be even more effective and needed in simple agricultural landscapes, in which they can create a stronger ecological contrast in terms of enhanced resource availability for pollinators and natural enemies (Bátary et al., 2010; Scheper et al., 2013; Marja et al., 2019). Our study was not designed to test this hypothesis, or whether bees and hoverflies could be promoted also at the population level (Ganser, Albrecht, & Knop, 2020) or at least partly may also reflect concentration effects. Future research could address these questions with respect to WFS of different times since establishment.

Conclusions and implications

We conclude that the effectiveness perennial WFS to promote bee and hoverfly diversity, as well as dominant crop-pollinating bees and aphidophagous hoverflies, is strongly dependant on the time since their establishment, as highlighted by the pronounced decline of species richness and abundance of bees and hoverflies, including dominant crop-visiting wild bees and aphidophagous hoverflies, already after the first two to three years since the establishment of the studied WFS. Thus, although older WFS may still represent valuable overwintering and nesting sites for ground-nesting wild bees, as well as habitats for other components of farmland biodiversity, our findings indicate that it remains an important practical challenge to design and manage perennial flower strips in a way that ensures continued adequate floral food resource availability for bees, hoverflies and likely other flower-visiting insects in the longer term over several years. *Re*-sowing of perennial WFS may be necessary already after a few years to maintain diverse floral resource provisioning and to improve their effectiveness for pollinator conservation and the promotion of crop pollination and natural pest control services in the agricultural study area. Moreover, to improve colonisation of WFS by wild pollinators, sufficient amounts of (semi-)open SNH should be maintained in the surrounding agricultural landscape. Hence, our study highlights the importance of considering the landscape context and in particular WFS age and temporal dynamics driving their effectiveness when optimising the design and management of flower strips to more effectively promote conservation of insect communities providing pollination and natural pest control services in agricultural landscapes.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests.

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Supplementary materials

Supplementary material associated with this article can be found in the online version at doi:10.1016/j.baae.2021.10.003.

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