Agriculture, Ecosystems and Environment 319 (2021) 107570

Contents lists available at ScienceDirect

Agriculture, Ecosystems and Environment

journal homepage: www.elsevier.com/locate/agee

Flower availability drives effects of wildflower strips on ground-dwelling natural enemies and crop yield

Zulin Mei [a,*], Gerard Arjen de Groot [b], David Kleijn [a,b], Wim Dimmers [b], Stijn van Gils [c], Dennis Lammertsma [b], Ruud van Kats [b], Jeroen Scheper [a,b]

[a] Plant Ecology & Nature Conservation, Wageningen University, Droevendaalsesteeg 3a, 6708 PB Wageningen, The Netherlands
[b] Animal Ecology, Wageningen Environment Research, P.O. Box 47, 6700 AA Wageningen, The Netherlands
[c] Department of Terrestrial Ecology, Netherlands Institute of Ecology (NIOO-KNAW), P.O. Box 50, 6700 AB Wageningen, The Netherlands

ARTICLE INFO

Key words:
Agricultural production
Conservation biological control
Ecological intensification
Field margin
Flower diversity
Habitat management
Semi-natural habitat

ABSTRACT

Wildflower strips have been heralded as a promising way to enhance ecosystem services by providing organisms which may help make farming less dependent on external inputs. However, recent studies show inconsistent effects on delivery of ecosystem services and crop yield, warranting a more detailed analysis of the factors determining the effects of wildflower strips. We examined how the natural enemy groups of spider, carabid beetle and staphylinid beetle, as well as aphid pest and crop yield respond to wildflower strips. We furthermore determined whether the response of natural enemies, aphids and crop yield depends on flower cover and species richness, and how this is influenced by fertilizer and insecticide applications to the crop in 16 winter wheat fields in the Netherlands. We used an experimental approach with a nested design that included all combinations of wildflower strips (present/absent), fertilizer application (yes/no) and insecticide application (yes/no). Presence of wildflower strips did not affect ground-dwelling natural enemies, aphids or crop yield. However, flower availability across wildflower strips and control margins was positively related to the abundance of the pooled number of examined natural enemies, spiders and carabid beetles. Positive effects in the crop were observed over limited distances; up to 5 m from the edge for spiders and wheat yield. The effects of flower availability and on-field management practices on natural enemies, aphids and wheat yield did not interact suggesting that, in our study, effects of flowers were not influenced by insecticide or fertilizer applications but were mainly additive. Our study indicates that cover and richness of wildflowers in field margin habitat, rather than establishment of wildflower strips per se, drove increases in natural enemies and crop yield. This suggests that more attention should be given to the optimization of establishment success of seed mixtures and management practices enhancing wildflower cover and diversity. Furthermore, biodiversity enhancing management of the herbaceous vegetation in linear landscape elements may represent a cost-effective alternative to boost ecosystem services regulating crop production in agricultural landscapes.

1. Introduction

Expansion and intensification of agriculture since the Green Revolution in the 1960s have boosted agricultural production, but have had significant negative impacts on the environment (Matson et al., 1997). Conversion of natural ecosystems into farmland and excessive use of agrochemicals have resulted in loss and degradation of habitat and strong declines in farmland biodiversity (Tscharntke et al., 2005; Gámez-Virués et al., 2015). As biodiversity underpins the ecosystem services that are critical for agricultural production, such as pollination, natural pest control and nutrient cycling, long-term agricultural productivity may be jeopardized if current biodiversity declines continue (Tscharntke et al., 2005; Rusch et al., 2013; Dainese et al., 2019). With the global human population continuously increasing, meeting the growing demands for food in a sustainable way is a serious challenge for mankind in the next decades (Godfray et al., 2010).

Ecological intensification has been proposed as an approach to reduce anthropogenic pressure on the environment while maintaining agricultural productivity (Bommarco et al., 2013). Ecological intensification proposes to replace external inputs with ecosystem services to

* Corresponding author.
E-mail address: zulin.mei@wur.nl (Z. Mei).

https://doi.org/10.1016/j.agee.2021.107570
Received 12 November 2020; Received in revised form 29 June 2021; Accepted 2 July 2021
Available online 22 July 2021

increase the sustainability of farming. One of the key ecosystem services supporting crop production is natural pest control, with an estimated economic value of $4.5 billion per year in the USA alone (Losey and Vaughan, 2006). Delivery of pest control services in agricultural fields has been shown to depend on the composition of the surrounding landscape, with landscapes containing less semi-natural habitats providing less pest control services and lower crop yield (Dainese et al., 2019). This suggests that in simplified agricultural landscapes where few semi-natural habitats remain, creating new semi-natural habitats may be an effective way of enhancing natural pest control (Veres et al., 2013).

In intensively farmed landscapes, field margin habitats such as ditch banks, hedges and roadside verges make up a significant proportion of the semi-natural habitats. Field margins can provide less-disturbed overwintering sites to natural enemies, as well as essential resources when these are unavailable in the crop. The suitability of field margins as habitat for natural enemies can be further enhanced by expanding them and sowing wildflower mixtures, thereby providing pollen and nectar for flower-visiting species groups such as hoverflies and parasitoid wasps (Bianchi and Wäckers, 2008; Haaland et al., 2011). Such wildflower strips may benefit natural enemies that do not or rarely use floral resources, such as spiders, carabid beetles and staphylinid beetles as well because they can provide long-term stable shelters and complex vertical vegetation structures that are important for these organisms (Frank and Reichhart, 2004; Schmidt-Entling and Döbeli, 2009). However, while wildflower strips have generally been shown to benefit natural enemies (Blaauw and Isaacs, 2015; Tschumi et al., 2015), the effects of wildflower strips on ecosystem service delivery are less consistent, with studies showing positive, neutral and even negative effects on natural pest control in nearby crops (Pfiffner et al., 2009; Tscharntke et al., 2016; Tschumi et al., 2016a; Grab et al., 2018; Toivonen et al., 2018; Cahenzli et al., 2019; Albrecht et al., 2020). This makes it difficult to formulate clear recommendations that help entice farmers to integrate wildflower strips into farm management.

One reason for the varying effectiveness of wildflower strips in enhancing pest control could be variation in the quantity and quality of the floral resources they provide (Pollier et al., 2019; Albrecht et al., 2020). Flower abundance and diversity varies markedly between wildflower strips because different seed mixtures are being used (Haaland et al., 2011) or because of variation in establishment success at the species or even whole mixture level (Scheper et al., 2015). Furthermore, the quality of wildflower strips often decreases with time since establishment if management practices are inadequate (De Cauwer et al., 2005), potentially weakening their effectiveness in attracting and preserving natural enemies (Frank et al., 2012). Wildflower strip effectiveness is furthermore determined by the floral diversity of the pre-existing field margins. Sowing wildflowers next to an abundantly flowering margin creates a smaller ecological contrast may therefore result in lower impact than sowing wildflowers next to a field margin devoid of flowers (Kleijn et al., 2011; Scheper et al., 2013). While the diversity of wildflower strips is often considered as a variable explaining the effectiveness of wildflower strips (Scheper et al., 2013; Albrecht et al., 2020), the role of the diversity of the pre-existing field boundary is rarely examined (but see Bischoff et al., 2016; Pollier et al., 2018).

Another reason for the varying effectiveness of wildflower strips could be that the effects of wildflower strips depend on farm management (Sutter et al., 2018). For example, spraying insecticides may not only impact the target pest species but also negatively affect non-target species, such as natural enemies (Bommarco et al., 2011). Harming key predators may reduce effective longer-term suppression of the target pest species which could ultimately increase pest abundance or even result in outbreak of secondary pests (Hill et al., 2017). The use of insecticides may therefore counteract positive effects of establishing semi-natural habitats through unintentional side-effects on natural enemies (Gagic et al., 2019). Fertilizer application may also indirectly influence the effectiveness of wildflower strips through effects on both natural enemies and pests (Garratt et al., 2011). For instance, Garratt et al. (2018) found that the aphid species *Metopolophium dirhodum*, but not *Sitobion avenae*, was more abundant in fertilized than in unfertilized wheat crop plots. Gagic et al. (2017) also found that fertilizer application to wheat crops reduced activity density of wolf spiders but increased activity density of staphylinid beetles. Therefore, the net effects of fertilizer application on natural pest control probably depend on the local context, which is determined by, amongst others, crop, pest species and composition of natural enemy community (Birkhofer et al., 2008). How the effects of on-field management on natural pest control interact with effects of wildflower fields is virtually an unexplored territory.

Here, we examined the effects of wildflower strips on natural pest control and crop yield in winter wheat (*Triticum aestivum*) fields with contrasting management in the Netherlands. We selected eight fields bordering a 3–5 m wide wildflower strip on one side and eight fields without wildflower strips as control. Each field was subdivided into four plots that were subject to all combinations of fertilizer application (with, without) and insecticide application (with, without). We subsequently quantified the abundance of the total and most dominant groups of natural enemies and aphids, as well as crop yield and examined how this was influenced by presence and quality of wildflower strips and on-field management. We specifically asked (1) whether effects of wildflower strips on natural enemies, aphids and crop yield are affected by wildflower cover and diversity and (2) whether and how effects of wildflower strips on natural enemies, aphids and crop yield are influenced by insecticide and fertilizer applications.

2. Material and methods

2.1. Study system and site selection

The study area, the Flevopolder, is land that was reclaimed in the 1950s and 1960s from a former inner sea in the center of the Netherlands. Most of the land was shaped into a mosaic of square agricultural fields separated by roads and drainage ditches, although small forest areas were planted scattered throughout the area (Fig. 1). Soils mostly consist of sea clay and thus typically are mineral-rich, fine-textured and mostly low in percentage of organic material. Most farmers use a crop rotation scheme that includes potato, onion and wheat. In the study year 2014, about 20% of the total agricultural area in this region consisted of winter wheat (Statistics Netherlands (CBS), 2015).

We selected sixteen winter wheat fields (Fig. 1), all of which were located on clayey soils. At eight sites, a mixture of perennial flowering plant species had been sown in 2–4 m wide strips to replace the pre-existing field boundaries of the wheat fields. These wildflower strips had been sown at least one year prior to the experiment. The exact composition of the flower mixture varied between strips, but typically included *Trifolium repens*, *Lotus corniculatus*, *Cichorium intybus*, *Medicago sativa*, *Achillea millefolium* and *Leucanthemum vulgare*. The other eight wheat fields served as control sites and were bordered by a standard field boundary, which had similar characteristics as the pre-existing field boundaries where the wildflower strips had been sown: a width of about 2 m and usually a ditch bank, and vegetation dominated by coarse grass species. The average closest distance between experimental wheat field sites was 12.2 km (range from 0.35 to 36.4 km).

2.2. Experimental setup per site

In each wheat field we established an experimental site of 80×25 m, with the longer side adjacent to the wildflower strip or control field margin. Farmers were asked to avoid the application of organic or mineral fertilizer and the spraying of insecticides in this area, while otherwise maintaining all regular management practices. To assess the impact of fertilizer and insecticide application, each site was subdivided into four plots (20×25 m each), and all combinations of

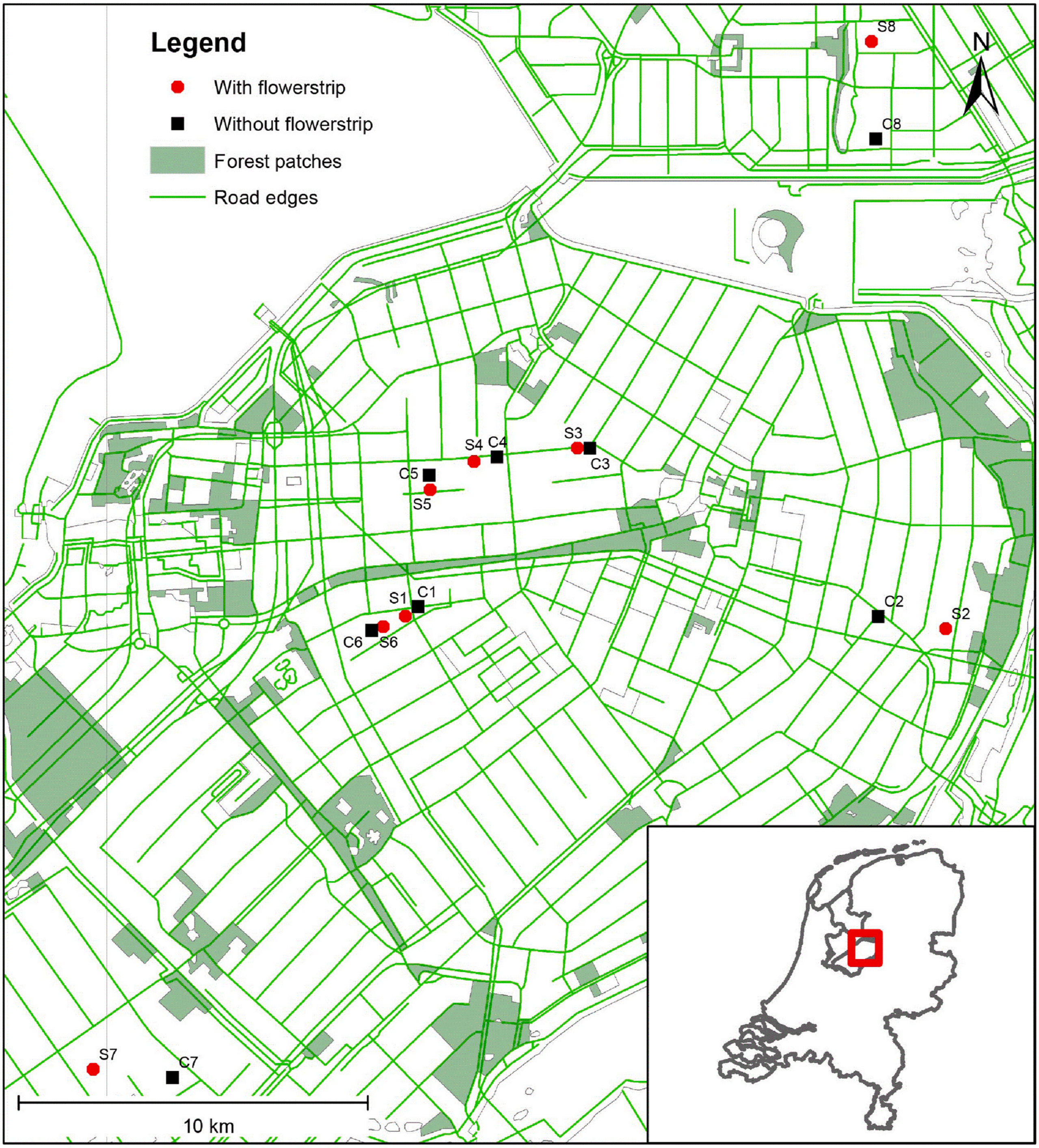

Fig. 1. Geographical map of the study area, showing the locations of the 16 study sites. C represents control sites without wildflower strips; S represents sites sown with wildflower strips.

fertilizer application (with, without) and insecticide application (with, without) were randomly assigned to four plots (Fig. S1a). The nitrogen fertilizer (two gifts of calcium ammonium nitrate) was applied in mid-March and early April, containing 80 and 90 kg N per hectare respectively. The insecticide (Karate Zeon® Syngenta, Bergen op Zoom, the Netherlands, main active ingredient lambda-cyhalothrin w/w = 2.5–10%) was sprayed in May at the heading stage of the wheat (BBCH 50; Zadoks et al., 1974) with a dosage of 50 mL/ha.

2.3. Flower characterization and pest and natural enemy surveys

Flower cover and species richness were assessed on 7 and 8 July 2014 in the pre-existing boundaries of the control sites and in the wildflower strips, just after the last survey round of pest and natural enemies had finished (see below) during the peak of floral resource availability. Flowering species were recorded in a 25 m transect by laying down a line and recording all species that had open flowers directly next to both sides of this line. Flower cover was assessed in three 1 m^2 plots per transect (on both ends and in the middle of the line) by visually estimating (from directly above the plot) the percent of ground area covered by open flower heads (Fig. S1a). Flower cover values were averaged per plot. All flower observations were done by the same person.

Per plot, abundance of pests (*Sitobion avenae*) and ground-dwelling predator were assessed during three inventory rounds, in April (stem elongation stage; BBCH 35), May (heading stage; BBCH 50) and June (flowering stage; BBCH 60). Inventories were conducted within field margins (wildflower strips and control; 0 m from field margin) and in the crop at distances of 5, 10 and 20 m from the field margin. The number of live aphids were counted on 17 wheat tillers in each of two transects per distance, with parallel alignment to the field margin ($17 \times 2 \times 3 = 102$ tillers inspected per plot). Ground-dwelling natural enemies were captured by pitfall traps (plastic beer cups, height 154.5 mm and diameter 95 mm), with four pitfall traps per plot: one within the field margin and three in the crop at distances of 5, 10 and 20 m (Fig. S1b). Each pitfall trap was filled with 200 mL of a mixture of 2/3 water and 1/3 glycol. After 5 days, pitfall traps were emptied and arthropods were collected and stored in 70% ethanol solution to be furthered classified. Specimens were subsequently sorted and counted and, for the purpose of this study, the number of individuals of the three most abundant groups of natural enemies was determined: Aranae (spider), Carabidae (carabid beetle) and Staphylinidae (staphylinid beetle).

2.4. Wheat yield measurements

Ripe wheat ears were manually harvested in all plots, within days before the whole field was harvested (late July 2014). Per plot, we harvested in total 1 m^2 at 5, 10 and 20 m distance from the field margin respectively, by placing four subplots of 0.25 m^2 along a line parallel to the margin at each distance (Fig. S1b). Harvested ears were transported in cotton bags and dried by hanging the open bags in a climate room with constant temperature of 25 °C and air humidity of 10%. After threshing, we measured the total fresh weight per replicate batch and the fresh and dry weight of a ~50 g subsample, in order to calculate total grain yield in g/m^2 (standardized to a moisture content of 14%).

2.5. Analysis

We excluded the unfertilized treatment plots from three fields (two wildflower strip sites, one control site) from the analyses as it turned out that the respective owners of the fields had accidentally fertilized these plots. As a result, we ended up with a total of 48 experimental plots, with 232 sampling points for the natural enemies (including those in the wildflower strip and control field margin) and 174 sampling points for the aphids and wheat yield.

Abundance data of ground-dwelling natural enemy (spider, carabid beetle and staphylinid beetle) and aphid were pooled over rounds per sampling point, and were ln (x + 1) transformed to improve normality and homoscedasticity of residuals.

The focus of our analyses was to experimentally test the effects of wildflower strips and on-field management on natural enemies, pests and crop yield. However, because the abundance of natural enemies and pests may be affected by landscape context, we first explored whether these were related to the proportion semi-natural habitat (forests, heathlands, orchards, roadside verges, dikes and hedgerows) in a 500 m radius around our experimental plots using linear mixed effects models with semi-natural habitat cover as fixed effect and field ID, with fertilizer and insecticide treatments nested in field ID, as random effects to correct for the multiple samples from the same site. Semi-natural habitat cover ranged from 1.1% to 26.5% (mean ± SD: 11.1 ± 8.2%) and was not significantly related to spiders ($\chi^2_{(1)} = 1.17$, $P = 0.28$), carabid beetles ($\chi^2_{(1)} = 0.09$, $P = 0.77$), staphylinid beetles ($\chi^2_{(1)} = 1.64$, $P = 0.20$) or aphids ($\chi^2_{(1)} = 0.50$, $P = 0.48$). We subsequently did not consider landscape context in the main analyses of our study.

Welch's *t*-test was used to compare flower cover and species richness between wildflower strips and control margins. We used linear mixed effects models and an information theoretic approach to analyze effects of wildflower strips and on-field management on abundance of natural enemies. Analyses were performed for each of the main natural enemy species groups separately: spider, carabid beetle and staphylinid beetle and total natural enemy. We constructed a global model that included wildflower strip treatment (yes/no), fertilizer application (yes/no), insecticide application (yes/no), distance from the field boundary (0, 5, 10, 20 m) and all their two-way interactions as fixed effects, and field ID, with fertilizer and insecticide treatments nested in field ID, as random effects. Next, we used the global model to construct an all-subsets model set consisting of all possible combinations of the fixed factors and their two-way interactions. We restricted our analyses to two-way interactions to limit model complexity and the total number of models considered, given the sample size (Burnham et al., 2011). To examine effects of floral quality of wildflower strips and control field margins, we furthermore added models in which we replaced the binary wildflower strip treatment variable with the continuous variables flower species richness and flower cover. Comparisons of the performance of model sets therefore included models with either presence of wildflower strips (yes/no) or, regardless of field margin type, flower cover or flower species richness of field margins. Flower cover was ln (x + 1) transformed to reduce positive skew. A similar approach was used to examine effects on aphid abundance and crop yield, with the exception that these analyses only concerned within-field data and distance from field boundary therefore only included data collected at 5, 10 and 20 m from field margins.

Models were ranked based on their Akaike Information Criterion values corrected for small sample size (AICc) and we restricted our candidate set to models with ΔAICc < 2 (Burnham et al., 2011). Akaike model weights (ω), which reflects the probability that a model is the best approximating model in the candidate set, were calculated for each model in the candidate set. In the interest of parsimony, in case models in a candidate set included more complex versions of a model with a lower AIC value, we based our inference on this simpler model (Richards, 2008; Richards et al., 2011). To aid interpretation of effects, we present significance tests for parameter estimates in Table S1. All analyses were performed using R version 3.5.0 (R Core Team, 2018).

3. Results

Trifolium sp., *Lotus corniculatus*, *Taraxacum officinale* and *Plantago lanceolata* were dominant species and presented in majority of wildflower strips. Floral quality varied a lot between different strips, with flower cover and species richness ranging from 1% to 55% and 3 to 11 respectively in the sown strips and ranging from 0% to 1% and 0 to 4 respectively in the control strips. Nevertheless, both flower cover ($t_{8.09} = -3.305$, $P = 0.011$) and species richness ($t_{9.60} = -4.2994$, $P = 0.002$) of wildflower strips were significantly higher than those of control sites. Flower cover and flower richness were significantly correlated across all sites ($r = 0.598$, $P = 0.014$).

3.1. Natural enemies

In total, 10,150 individuals of ground-dwelling natural enemies were captured during the experiment with 1349 spiders, 4423 carabid beetles, 4246 staphylinid beetles and 132 arthropods of other taxa. All natural enemies were captured in May and June and in April no natural enemies were captured at all. Presence of wildflower strips did not feature in majority of the best models explaining abundance of any of the natural enemy groups (Table 1). Flower cover and species richness on the other hand featured prominently, albeit in interaction with other factors, in the models that best explained abundance of total natural enemies, spiders and carabid beetles. Abundance of total natural enemies was best explained by a model including distance to field margins, flower cover and the interaction between the two factors (Table 1a and

Table 1
Candidate models (ΔAICc < 2) explaining the change in abundance of natural enemies (a, b, c, d) and aphids (e) and yield of winter wheat (f). AICc values of null models (intercept-only) are added for reference.

(a)Total natural enemies

Explanatory variable	Model set								Null model
	1	2	3	4	5	6	7	8	
D_5	0.11	0.11	0.11	0.11	0.11	0.11	0.11	0.11	
D_{10}	0.19	0.19	0.19	0.19	0.19	0.19	0.19	0.19	
D_{20}	0.25	0.25	0.25	0.25	0.25	0.25	0.25	0.25	
F		0.10	0.10	0.10			0.10	0.10	
I			0.11	0.11	0.11	0.11		0.11	
WFS									
FC	0.64	0.63	0.63	0.63	0.64	0.65	0.64	0.64	
FR									
FC×D_5	-0.70	-0.70	-0.70	-0.70	-0.70	-0.70	-0.70	-0.70	
FC×D_{10}	-0.54	-0.54	-0.54	-0.54	-0.54	-0.54	-0.54	-0.54	
FC×D_{20}	-0.92	-0.92	-0.92	-0.92	-0.92	-0.92	-0.92	-0.92	
FC×F		-0.35	-0.34	-0.34					
FC×I				-0.27		-0.27			
FR×D_5									
FR×D_{10}									
FR×D_{20}									
FR×F									
FR×I									
F×D_5									
F×D_{10}									
F×D_{20}									
I×D_5									
I×D_{10}									
I×D_{20}									
F×I									
d.f.	11	13	14	15	12	13	12	13	4
AICc	451.0	451.1	451.9	451.9	451.9	452.1	452.2	453.0	464.9
ΔAICc	0	0.07	0.86	0.87	0.89	1.10	1.12	1.99	13.9
ω	0.184	0.178	0.120	0.119	0.118	0.106	0.106	0.068	<0.001

(b) Spiders

Explanatory variable	Model set						Null model
	1	2	3	4	5	6	
D_5	-0.24	-0.24	-0.24	-0.24	-0.24	-0.24	
D_{10}	-0.53	-0.53	-0.53	-0.53	-0.53	-0.53	
D_{20}	-0.42	-0.42	-0.42	-0.42	-0.42	-0.42	
F	-0.31	-0.31	-0.31	-0.31	-0.31	-0.31	
I	0.03	-0.36	0.03	0.03	0.03	-0.36	
WFS							
FC	0.85	0.85	0.85	0.85	0.85	0.85	
FR							
FC×D_5	-0.39	-0.39	-0.39	-0.39	-0.39	-0.39	
FC×D_{10}	-0.81	-0.81	-0.81	-0.81	-0.81	-0.81	
FC×D_{20}	-0.92	-0.92	-0.92	-0.92	-0.92	-0.92	
FC×F			-0.24			-0.24	
FC×I				-0.22			
FR×D_5							
FR×D_{10}							
FR×D_{20}							
FR×F							
FR×I							
F×D_5							
F×D_{10}							
F×D_{20}							
I×D_5	-0.49		-0.49	-0.49	-0.49		
I×D_{10}	-0.49		-0.49	-0.49	-0.49		
I×D_{20}	-0.56		-0.56	-0.56	-0.56		
F×I					-0.15		
d.f.	16	13	17	17	17	14	4
AICc	495.4	496.3	496.4	496.6	497.2	497.3	538.4
ΔAICc	0	0.95	1.06	1.23	1.84	1.94	43
ω	0.283	0.176	0.167	0.153	0.113	0.107	<0.001

(c) Carabid beetles

Explanatory variable	Model set							Null model
	1	2	3	4	5	6	7	
D_5	0.05	0.05	0.05	0.05	0.05	0.05	0.05	
D_{10}	0.36	0.36	0.36	0.36	0.36	0.36	0.36	
D_{20}	0.41	0.41	0.41	0.41	0.41	0.41	0.41	
F	-0.46	-0.44	-0.19	-0.46	-0.19	-0.44	-0.46	
I		0.20			0.20		0.20	
WFS								
FC				0.49			0.49	

(continued on next page)

Table 1 (*continued*)

(a)Total natural enemies Explanatory variable	Model set								Null model
	1	2	3	4	5	6	7	8	
FR	0.44	0.44	0.44		0.44	0.44			
FC×D_5				-0.82			-0.82		
FC×D_{10}				-0.48			-0.48		
FC×D_{20}				-0.70			-0.70		
FC×F				-0.68			-0.68		
FC×I									
FR×D_5	-0.98	-0.98	-0.98		-0.98	-0.98			
FR×D_{10}	-0.73	-0.73	-0.73		-0.73	-0.73			
FR×D_{20}	-0.68	-0.68	-0.68		-0.68	-0.68			
FR×F						-0.23			
FR×I									
F×D_5			-0.05		-0.05				
F×D_{10}			-0.40		-0.40				
F×D_{20}			-0.56		-0.56				
I×D_5									
I×D_{10}									
I×D_{20}									
F×I									
d.f.	12	13	15	13	16	13	14	4	
AICc	618.1	618.8	618.9	619.5	619.6	619.9	620	635.2	
ΔAICc	0	0.62	0.73	1.4	1.42	1.75	1.9	17.1	
ω	0.236	0.173	0.164	0.118	0.116	0.098	0.095	<0.001	
(d) Staphylinid beetles									
Explanatory variable	Model set							Null model	
	1	2	3	4	5	6	7		
D_5									
D_{10}									
D_{20}									
F	0.75	0.75	0.75	0.75	0.75	0.75	0.75		
I			0.09	0.09	0.09				
WFS							-0.08		
FC									
FR		-0.21		-0.21	-0.21	-0.22			
FC×D_5									
FC×D_{10}									
FC×D_{20}									
FC×F									
FC×I									
FR×D_5									
FR×D_{10}									
FR×D_{20}									
FR×F						-0.17			
FR×I				-0.30					
F×D_5									
F×D_{10}									
F×D_{20}									
I×D_5									
I×D_{10}									
I×D_{20}									
F×I									
d.f.	5	6	6	8	7	7	6	4	
AICc	558.8	559.3	560.1	560.5	560.6	560.7	560.7	593.3	
ΔAICc	0	0.45	1.3	1.73	1.77	1.89	1.9	34.5	
ω	0.254	0.203	0.133	0.107	0.105	0.099	0.098	<0.001	
(e) Aphids									
Explanatory variable	Model set				Null model				
	1	2	3	4					
D_{10}		0.03	0.03						
D_{20}		0.02	0.02						
F									
I	-0.47	-0.47	-0.47	-0.47					
WFS				0.18					
FC		-0.53	-0.53						
FR									
FC×D_{10}		0.73	0.73						
FC×D_{20}		0.75	0.75						
FC×F									
FC×I			0.18						
FR×D_{10}									
FR×D_{20}									
FR×F									
FR×I									
F×D_{10}									

(*continued on next page*)

Table 1 (*continued*)

(a)Total natural enemies Explanatory variable	Model set								Null model
	1	2	3	4	5	6	7	8	
F×D_{20}									
I×D_{10}									
I×D_{20}									
F×I									
d.f.	5	10	11	6	4				
AICc	422.1	422.1	423.8	423.8	434.7				
ΔAICc	0	0.08	1.72	1.77	12.6				
ω	0.357	0.344	0.151	0.148	<0.001				
(f) Yield									
Explanatory variable	Model set		Null model						
	1	2							
D_{10}	86.25	86.25							
D_{20}	103.18	103.18							
F	567.87	573.16							
I									
WFS									
FC									
FR	103.38	103.33							
FC×D_{10}									
FC×D_{20}									
FC×F									
FC×I									
FR×D_{10}	-137.23	-137.51							
FR×D_{20}	-115.80	-115.37							
FR×F									
FR×I									
F×D_{10}		29.42							
F×D_{20}		-45.28							
I×D_{10}									
I×D_{20}									
F×I									
d.f.	10	12	4						
AICc	2239.4	2241	2378.3						
ΔAICc	0	1.61	138.9						
ω	0.691	0.309	<0.001						

Models are ranked in order of increasing differences in corrected Akaike Information Criterion (ΔAICc), Akaike model weights (ω) indicate the probability that a model is the best approximating model in the candidate set. Dx, distance from field margins (5 m, 10 m and 20 m); F, fertilizer application (yes/no); I, insecticide application (yes/no); WFS, treatment (wildflower strips/control sites); FC, flower cover; FR, flower species richness. Variables WFS, FC and FR were never included together in the same model.

S1). Although there were seven other candidate models within ΔAICc < 2, these were all more complex versions of the highest ranking model (Table 1a). In the field margins, total natural enemy abundance was higher in margins with many flowers than in margins with some or no flower, but this pattern did not extend into the adjacent fields (Fig. 2a). This effect was mostly caused by the response of the spiders. The highest ranking model explaining spider abundance included distance to field margins, flower cover, fertilizer and insecticide applications and interactions between distance and insecticide and between distance and flower cover. However, this model performed only marginally better than the more parsimonious second-highest ranking model without the interaction between distance and insecticide (ΔAICc = 0.95, Table 1b and S1). Fig. 2b therefore illustrates the relationships based on this more conservative parsimonious model and shows spider abundance being higher in margins with many flowers than in margins with some or no flowers. This pattern extended 5 m into the field as well, but is no longer apparent at 10 and 20 m from the field edge. Spider abundance was furthermore higher in unfertilized and unsprayed fields (Fig. 3a, b). Carabid beetle abundance was best explained by the effects of distance, fertilizer, flower richness and distance × flower richness (Tables 1c and S1). Six other high ranking models performed almost equally well but were less parsimonious than the highest ranking model (Table 1c), Consistent factors in all models were positive effects of distance, negative effects of fertilize, and a positive relationship with one of the flower variables. Fig. 2c illustrates the interacting relationship between flower richness and distance based on the highest ranking model, with fields with flower-rich field margins having more carabids at the field edge but less in the crop field itself. The best model explaining staphylinid beetle abundance only included fertilization which significantly promoted its abundance (Tables 1d and S1, Fig. 3d), however, this positive effect of fertilization on staphylinid beetles was in contrast to that on spiders and carabid beetles.

3.2. *Aphids*

A total of 725 aphids were observed on wheat tillers, all during the heading (386) or flowering stage (339) of the wheat. The best model explaining the abundance of aphids only included insecticide which significantly reduced aphid numbers (Tables 1e and S1, Fig. S2). The second-best model, whose ΔAICc was only 0.08, included a negative relationship of overall aphid numbers with flower cover, suggesting a potential contribution of wildflower strips to aphid control (Table 1e). However, this second-best model was far more complex than the insecticide-only model.

3.3. *Wheat yield*

Wheat yield was best explained by a model including fertilizer, distance, flower richness and the interaction between the last two factors (Table 1f and S1). Fertilizer application had the expected positive effect with a 48% yield reduction in unfertilized plots (Fig. 4a), Next to margins without flowers, wheat yield was 15% and 16% lower at 5 m than at 10 and 20 m from the margin respectively while next to flower-poor field margins, wheat yield was 10% lower at 5 m than at 10 and 20 m

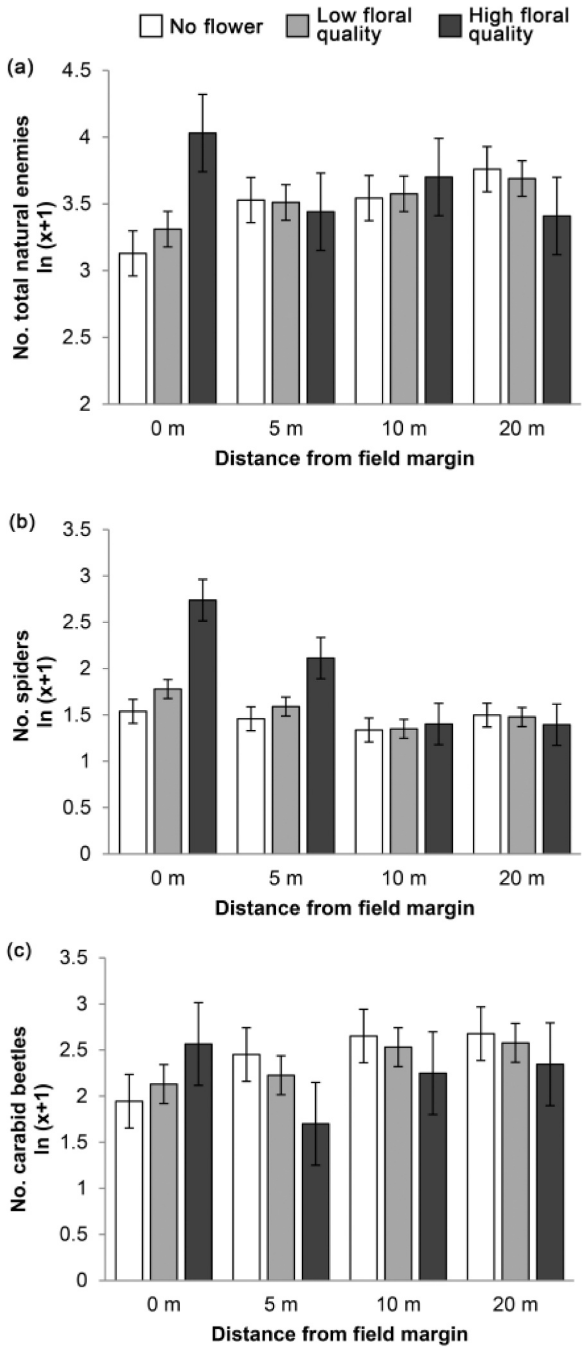

Fig. 2. Effects of floral quality and distance to field margins on mean abundance of (a) total natural enemies, (b) spiders and (c) carabid beetles in fields adjacent to margins with no flower (white, 10th quantile), low floral quality (light gray, 50th quantile) and high floral quality (dark gray, 90th quantile). For total natural enemies (a) and spiders (b), floral quality was defined as flower cover and for carabid beetles (c), floral quality was defined as flower species richness. Model-estimated means are shown, with error bars indicating SE.

from the margin (Fig. 4b). In contrast, next to flower-rich margins wheat yield at 5 m was slightly higher than yield at both 10 and 20 m from the margin. As a result, wheat yield at 5 m from flower-rich field margins was 15% and 10% higher than yields at 5 m from margins with no or some flowers respectively. These differences were no longer apparent at 10 and 20 m from the margins (Fig. 4b).

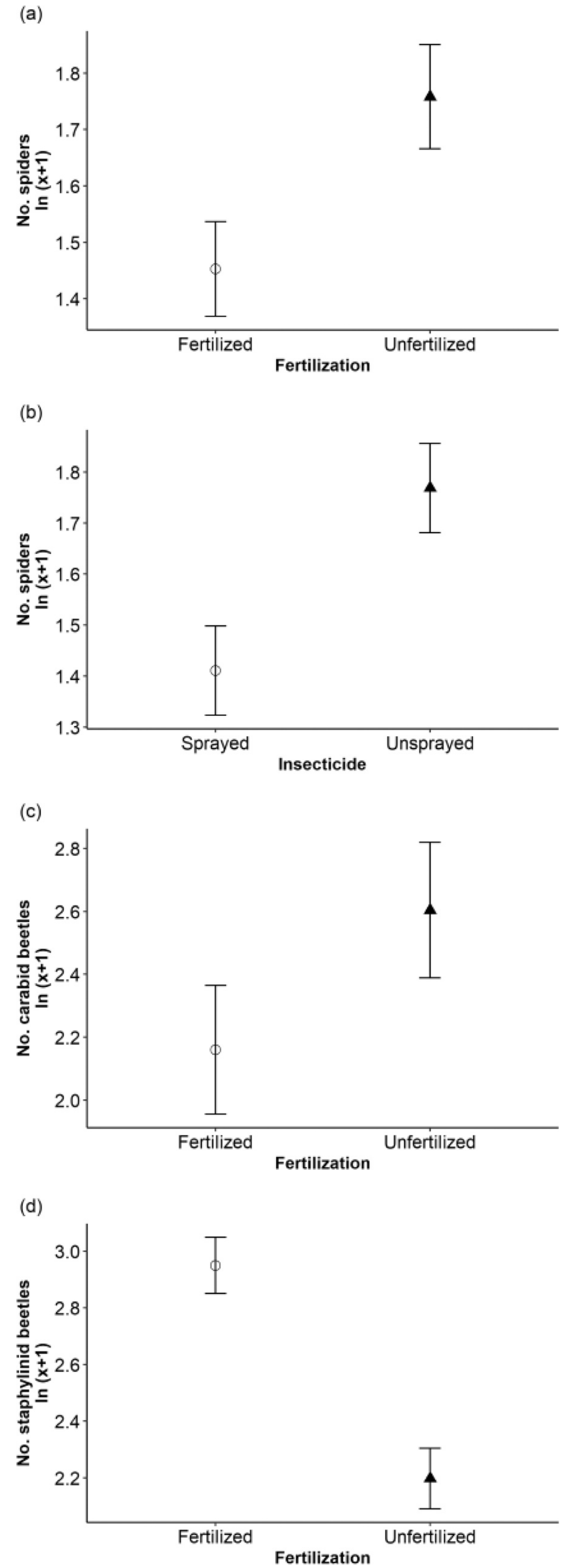

Fig. 3. Effects of on-field management on mean abundance of (a, b) spiders, (c) carabid beetles and (d) staphylinid beetles. Open circles represent intensive on-field management (fertilized or insecticide sprayed), filled triangles represent extensive on-field management (unfertilized or insecticide unsprayed). Model-estimated means are shown, with error bars indicating SE.

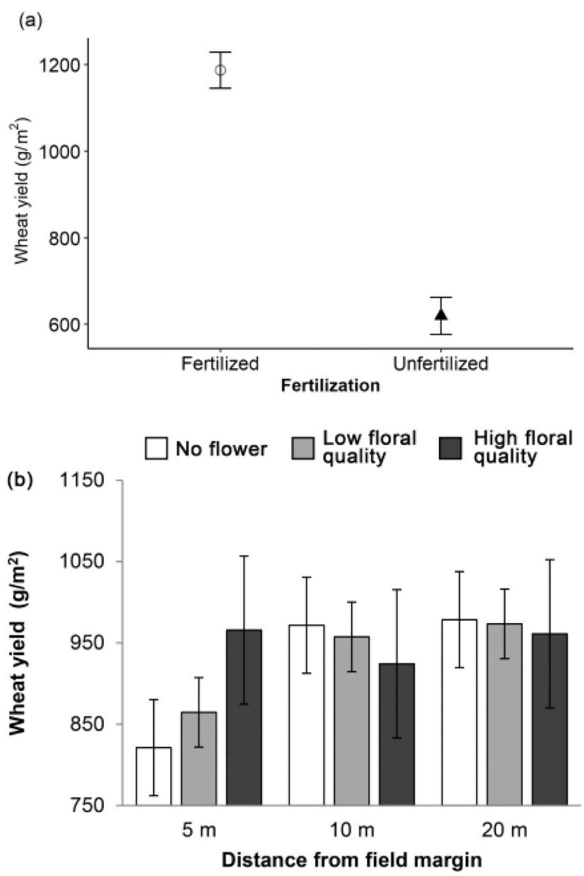

Fig. 4. (a) Effects of fertilization on mean wheat yield. Open circle represents fertilized fields and filled triangle represents unfertilized fields. (b) Effects of floral quality and distance to field margins on mean wheat yield in fields adjacent to margins with no flower (white, 10th quantile), low floral quality (light gray, 50th quantile) and high floral quality (dark gray, 90th quantile). Floral quality was defined as flower species richness. Model-estimated means are shown, with error bars indicating SE.

4. Discussion

The major result of our study is that it is not the establishment of wildflower strips that drives effects on ground-dwelling natural enemies and wheat yield, but it is the actual cover and diversity of wildflowers in field margins that determines effect size. These flowers can be introduced by establishment of wildflower strips but can also occur naturally in pre-existing field boundaries as well. Furthermore, we did not find any interactions between the effects of floral characteristics of field margins and those of on-field management on natural enemies, aphids and wheat yields indicating that in our study effects of wildflower strips were not masked by fertilizer or insecticide applications but were mainly additive.

The fact that presence of wildflower strips did not feature in any of the sets of candidate models was probably caused by the large variation in floral quality of the studied wildflower strips. Although on average flower cover and diversity were significantly higher in wildflower strips than in control field boundaries, there was considerable overlap, with the most flower-rich control boundary scoring better than three wildflower strips. Our results highlight that sowing wildflowers on farmland does not automatically result in high flower cover and diversity. The examined wildflower strips were supposed to be cut twice per year and cuttings had to be removed, such management is generally considered to promote wildflower cover (Piqueray et al., 2019). However, the high nutrient availability in the clayey arable soil could have made it difficult for wildflower species of non-local provenance to compete with the naturally occurring perennial grass species (Schmidt et al., 2020). Currently, schemes subsidizing farmers to establish biodiversity enhancing semi-natural landscape elements rarely include criteria regarding the quality that should be aimed for or management practices that should be implemented to provide successful outcomes (Cole et al., 2020). The results of our study suggest that including such criteria could not only increase biodiversity outcomes but also the delivery of ecosystem services regulating agricultural production.

Spiders and carabid beetles were positively related to cover and diversity of wildflowers respectively, this is unexpected since neither species group feeds on pollen or nectar. In a recent meta-analysis on the effects of wildflower strips, Albrecht et al. (2020) did not find a relationship between wildflower diversity and pest control services while the expected relationship between flower diversity and pollination services was indeed found. Natural enemies benefit from undisturbed overwintering sites, especially when there are no crops on the fields. Perennial wildflower strips can function as such and are known to support, for example, higher densities of carabid beetles than regularly disturbed crop edges (Ganser et al., 2019). More importantly, vegetation dominated by flowering forbs generally has a more open and complex vertical vegetation structure (Schmidt-Entling and Döbeli, 2009). The openness of the vegetation may allow beetles to move more easily through the vegetation while the more complex vertical structure provides more niches for invertebrates and allows, for instance, coexistence of higher densities of web-building and ground-dwelling spiders (Schmidt-Entling and Döbeli, 2009). Spiders could furthermore benefit from an increase in prey resources such as flower visiting insects that are attracted by the high flower cover (Dukas and Morse, 2003; Heiling et al., 2003). In sum, the promotion of abundance of spiders and carabid beetless was probably not driven by the floral food resources but by the more complex structure that flowers in field margins provided.

Interestingly, we did not find much support for interactions between the effects of floral resources in field margins and the effects of on-field management for any of the response variables suggesting that the two management strategies operated independently in our study. Staphylinid beetles were not affected by wildflower strips but their abundance in the field was positively affected by fertilizer application supporting earlier observations of Gagic et al. (2017). Abundance of spiders and carabid beetles was negatively related to fertilizer application and abundance of spiders was negatively related to insecticide applications. In the crop, the three groups of natural enemies thus all responded differently to wildflowers and on-field management. This may explain why recent meta-analyses find contrasting relationships between cover of semi-natural habitat and natural enemies in crops (Karp et al., 2018). Different species groups respond differently not only to the resources in semi-natural habitat, they also demonstrate different, sometimes opposite responses to on-field management. In this study, spiders and carabid beetles were negatively affected by fertilizer application while staphylinid beetles were positively affected, effectively neutralizing any overall response by total natural enemies. In the crop, activity density of spiders declined but that of carabid beetles increased with increasing distance from the margin (Fig. 2b, c). As a result, activity density of the pooled number of natural enemies in the crop showed very little difference between treatments but increased from margin to field center at low flower cover while it declined at high flower cover (Fig. 2a). Pitfall traps measuring activity density are known to be more effective in open habitats where ground-active species can move more rapidly (Phillips and Cobb, 2005). The numbers of observed specimens in the field margin with dense vegetation are therefore probably an underestimation of their relative abundance of the three species groups at this location.

Any observed positive effects of flowers in the margins on invertebrates in the crop were restricted to a narrow 5–10 m wide zone along the field margin. This was also the zone where positive effects of wildflowers on crop yield were detected (Fig. 4b) which is in line with recent findings of Albrecht et al. (2020) that delivery of pest control services generally does not extend very far into the field. The best model explaining crop yield was very similar to the best model explaining total natural enemy abundance. The only differences were the obvious positive effects of fertilizer application on crop yield, and flower richness rather than flower cover being related to crop yield (Table 1). As flower cover and flower species richness were significantly correlated, this may suggest a relationship between natural enemy abundance and crop yield. The reason why we did not find any effects of insecticide on wheat yield may result from the fact that the insecticide treatment was applied regardless of the actual pest pressure in the plots. We did not test for direct relationships between natural enemies and yield because natural enemies generally concentrate on locations with the highest densities of pests (Ramsden et al., 2015) which may lead to spurious correlations. The best model explaining aphid abundance did not include any wildflower variable and only insecticide application featured consistently in the candidate set of best models with aphid abundance being about 1.5 times higher in unsprayed fields than sprayed ones (Fig. S2). Insecticide spraying also negatively affected the abundance of spiders (Fig. 4b), one of the three most dominant natural enemy groups in this system. This confirms that insecticide application simultaneously reduces pests and some natural enemies (Bommarco et al., 2011; Regan et al., 2017) which may result in net effects on wheat yield that are not always positive. It is noteworthy that, compared to the field center, we did not observe higher yields in crop edges next to flower rich vegetation. The crops showed a typical reduction in yield towards the edge of the field when a margin contained no or few flowers. This yield depression was absent next to flower rich-field margins (Fig. 4b). A possible explanation could be that margins without any flowering forbs are a source of more pests than natural enemies while the reverse is true for flower-rich margins. Furthermore, pest species and groups of natural enemies that were not included in this study such as cereal leaf beetles and lacewings may also have affected the yield patterns observed in our study (Tschumi et al., 2015). Our results indeed suggest that the observed relationship between crop yield and field margin wildflowers originated from the impact of a wider set of natural enemies on a wider set of pest species than we sampled (Wäckers and van Rijn, 2012; Hatt et al., 2017).

5. Conclusion

Previous studies examining the effectiveness of wildflower strips in enhancing pest control services have focused on evaluating the effects of presence of wildflower strips and often excluded strips from analyses when mixtures failed to establish or wildflowers were overgrown by spontaneous weedy vegetation (e.g., Tschumi et al., 2015; Tschumi et al., 2016b). While such an approach gives valuable information on the potential of this management practice and provides a proof-of-concept, it fails to include variables that influence effectiveness under real-world conditions and does not consider the way in which they are typically being established and managed by farmers (Kleijn et al., 2006). The wildflower strips examined in this study were part of a government funded agri-environment scheme and were established and managed following the guidelines of that scheme. The fact that many of these strips comprised few wildflowers, sometimes even less than the pre-existing field boundary, is therefore a meaningful and important result. It suggests that more attention should be given to environmental factors impacting the quality of wildflower strips, which management practices can be used to enhance floral resources and how this can be incorporated into agri-environmental scheme design and prescriptions (Cole et al., 2020). A better understanding of how to enhance the desirable species, and to suppress the unwanted species in wildflower strips may furthermore reduce the reluctance of farmers to implement this measure (Kleijn et al., 2019) and possibly increase its uptake in agricultural landscapes. It furthermore suggests that management increasing flower cover and diversity in pre-existing field boundaries may be just as effective for ecosystem service delivery as establishing new wild flower strips. Since there are little or no opportunity costs associated with biodiversity enhancing management of the herbaceous vegetation in the linear landscape elements and such elements make up the green infrastructure in agricultural landscapes, this may be a much more cost-effective approach to improve ecosystem services regulating agricultural production than taking productive land out of production to sow wildflowers.

Funding

This paper has been written in the framework of the European Union funded FP7 project LIBERATION (grant 311781). The contribution of JS was made possible by the 2012 BiodivERsa/FACCE-JPI joint call for research proposals (project 832.14.007; ECODEAL), with the national funder NWO (Dutch Research Counsil, The Netherlands). These projects have no influence on the scientific output or on the conclusions and recommendations.

CRediT authorship contribution statement

GAG and DK designed the experiment. GAG, WD, SvG, DL and RvK collected data. JS and ZM performed analyses. ZM, DK and JS wrote the initial manuscript. All co-authors contributed significantly to improving the manuscript. All authors gave final approval for publication.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank all farmers that participated in this project and especially Coby Dekker of the Agri-environment Cooperative ‘Rondom het Greppelveld’ for her valuable assistance in the selection of field sites and input in the study setup. We also thank the editor and anonymous reviewers for their constructive suggestions and comments, which were of great help in improving the paper.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2021.107570.

References

Albrecht, M., Kleijn, D., Williams, N.M., Tschumi, M., Blaauw, B.R., Bommarco, R., Sutter, L., 2020. The effectiveness of flower strips and hedgerows on pest control, pollination services and crop yield: a quantitative synthesis. Ecol. Lett. 23 (10), 1488–1498.

Bianchi, F.J., Wäckers, F.L., 2008. Effects of flower attractiveness and nectar availability in field margins on biological control by parasitoids. Biol. Control 46 (3), 400–408.

Birkhofer, K., Bezemer, T.M., Bloem, J., Bonkowski, M., Christensen, S., Dubois, D., Mäder, P., 2008. Long-term organic farming fosters below and aboveground biota: implications for soil quality, biological control and productivity. Soil Biol. Biochem. 40 (9), 2297–2308.

Bischoff, A., Pollier, A., Lamarre, E., Salvadori, O., Cortesero, A.M., Le Ralec, A., Jaloux, B., 2016. Effects of spontaneous field margin vegetation and surrounding landscape on Brassica oleracea crop herbivory. Agric. Ecosyst. Environ. 223, 135–143.

Blaauw, B.R., Isaacs, R., 2015. Wildflower plantings enhance the abundance of natural enemies and their services in adjacent blueberry fields. Biol. Control 91, 94–103.

Bommarco, R., Miranda, F., Bylund, H., Björkman, C., 2011. Insecticides suppress natural enemies and increase pest damage in cabbage. J. Econ. Entomol. 104 (3), 782–791.

Bommarco, R., Kleijn, D., Potts, S.G., 2013. Ecological intensification: harnessing ecosystem services for food security. Trends Ecol. Evol. 28 (4), 230–238.

Burnham, K.P., Anderson, D.R., Huyvaert, K.P., 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. Behav. Ecol. Sociobiol. 65 (1), 23–35.

Cahenzli, F., Sigsgaard, L., Daniel, C., Herz, A., Jamar, L., Kelderer, M., Sekrecka, M., 2019. Perennial flower strips for pest control in organic apple orchards—A pan-European study. Agric. Ecosyst. Environ. 278, 43–53.

Cole, L.J., Kleijn, D., Dicks, L.V., Stout, J.C., Potts, S.G., Albrecht, M., Biesmeijer, J.C., 2020. A critical analysis of the potential for EU Common Agricultural Policy measures to support wild pollinators on farmland. J. Appl. Ecol. 57 (4), 681–694.
Dainese, M., Martin, E.A., Aizen, M.A., Albrecht, M., Bartomeus, I., Bommarco, R., Ghazoul, J., 2019. A global synthesis reveals biodiversity-mediated benefits for crop production. Sci. Adv. 5 (10), 0121.
De Cauwer, B., Reheul, D., D'hooghe, K., Nijs, I., Milbau, A., 2005. Evolution of the vegetation of mown field margins over their first 3 years. Agric. Ecosyst. Environ. 109 (1–2), 87–96.
Dukas, R., Morse, D.H., 2003. Crab spiders affect flower visitation by bees. Oikos 101 (1), 157–163.
Frank, T., Reichhart, B., 2004. Staphylinidae and Carabidae overwintering in wheat and sown wildflower areas of different age. Bull. Ѐntomol. Res. 94 (3), 209–217.
Frank, T., Aeschbacher, S., Zaller, J.G., 2012. Habitat age affects beetle diversity in wildflower areas. Agric. Ecosyst. Environ. 152, 21–26.
Gagic, V., Kleijn, D., Báldi, A., Boros, G., Jørgensen, H.B., Elek, Z., Marini, L., 2017. Combined effects of agrochemicals and ecosystem services on crop yield across Europe. Ecol. Lett. 20 (11), 1427–1436.
Gagic, V., Hulthen, A.D., Marcora, A., Wang, X., Jones, L., Schellhorn, N.A., 2019. Biocontrol in insecticide sprayed crops does not benefit from semi-natural habitats and recovers slowly after spraying. J. Appl. Ecol. 56 (9), 2176–2185.
Gámez-Virués, S., Perović, D.J., Gossner, M.M., Börschig, C., Blüthgen, N., De Jong, H., Scherber, C., 2015. Landscape simplification filters species traits and drives biotic homogenization. Nat. Commun. 6 (1), 1–8.
Ganser, D., Knop, E., Albrecht, M., 2019. Sown wildflower strips as overwintering habitat for arthropods: effective measure or ecological trap? Agric. Ecosyst. Environ. 275, 123–131.
Garratt, M.P.D., Wright, D.J., Leather, S.R., 2011. The effects of farming system and fertilizers on pests and natural enemies: a synthesis of current research. Agric. Ecosyst. Environ. 141 (3–4), 261–270.
Garratt, M.P.D., Bommarco, R., Kleijn, D., Martin, E., Mortimer, S.R., Redlich, S., van Gils, S., 2018. Enhancing soil organic matter as a route to the ecological intensification of European arable systems. Ecosystems 21 (7), 1404–1415.
Godfray, H.C.J., Beddington, J.R., Crute, I.R., Haddad, L., Lawrence, D., Muir, J.F., Toulmin, C., 2010. Food security: the challenge of feeding 9 billion people. Science 327 (5967), 812–818.
Grab, H., Poveda, K., Danforth, B., Loeb, G., 2018. Landscape context shifts the balance of costs and benefits from wildflower borders on multiple ecosystem services. Proc. Biol. Sci. 285 (1884), 20181102.
Haaland, C., Naisbit, R.E., Bersier, L.F., 2011. Sown wildflower strips for insect conservation: a review. Insect Conserv. Divers. 4 (1), 60–80.
Hatt, S., Lopes, T., Boeraeve, F., Chen, J., Francis, F., 2017. Pest regulation and support of natural enemies in agriculture: experimental evidence of within field wildflower strips. Ecol. Eng. 98, 240–245.
Heiling, A.M., Herberstein, M.E., Chittka, L., 2003. Crab-spiders manipulate flower signals. Nature 421 (6921), 334.
Hill, M.P., Macfadyen, S., Nash, M.A., 2017. Broad spectrum pesticide application alters natural enemy communities and may facilitate secondary pest outbreaks. PeerJ 5, 4179.
Karp, D.S., Chaplin-Kramer, R., Meehan, T.D., Martin, E.A., DeClerck, F., Grab, H., O'rourke, M.E., 2018. Crop pests and predators exhibit inconsistent responses to surrounding landscape composition. Proc. Natl. Acad. Sci. USA 115 (33), E7863–E7870.
Kleijn, D., Baquero, R.A., Clough, Y., Diaz, M., De Esteban, J., Fernández, F., Knop, E., 2006. Mixed biodiversity benefits of agri-environment schemes in five European countries. Ecol. Lett. 9 (3), 243–254.
Kleijn, D., Rundlöf, M., Scheper, J., Smith, H.G., Tscharntke, T., 2011. Does conservation on farmland contribute to halting the biodiversity decline? Trends Ecol. Evol. 26 (9), 474–481.
Kleijn, D., Bommarco, R., Fijen, T.P., Garibaldi, L.A., Potts, S.G., van der Putten, W.H., 2019. Ecological intensification: bridging the gap between science and practice. Trends Ecol. Evol. 34 (2), 154–166.
Losey, J.E., Vaughan, M., 2006. The economic value of ecological services provided by insects. Bioscience 56 (4), 311–323.
Matson, P.A., Parton, W.J., Power, A.G., Swift, M.J., 1997. Agricultural intensification and ecosystem properties. Science 277 (5325), 504–509.
Pfiffner, L., Luka, H., Schlatter, C., Juen, A., Traugott, M., 2009. Impact of wildflower strips on biological control of cabbage lepidopterans. Agric. Ecosyst. Environ. 129 (1–3), 310–314.
Phillips, I.D., Cobb, T.P., 2005. Effects of habitat structure and lid transparency on pitfall catches. Environ. Entomol. 34 (4), 875–882.
Piqueray, J., Gilliaux, V., Decruyenaere, V., Cornelis, J.T., Uyttenbroeck, R., Mahy, G., 2019. Management of grassland-like wildflower strips sown on nutrient-rich arable soils: the role of grass density and mowing regime. Environ. Manag. 63 (5), 647–657.
Pollier, A., Guillomo, L., Tricault, Y., Plantegenest, M., Bischoff, A., 2018. Effects of spontaneous field margin vegetation on the regulation of herbivores in two winter crops. Basic Appl. Ecol. 27, 71–82.
Pollier, A., Tricault, Y., Plantegenest, M., Bischoff, A., 2019. Sowing of margin strips rich in floral resources improves herbivore control in adjacent crop fields. Agric. For. Entomol. 21 (1), 119–129.
R Core Team 2018. R version 3.5.0. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
Ramsden, M.W., Menéndez, R., Leather, S.R., Wäckers, F., 2015. Optimizing field margins for biocontrol services: the relative role of aphid abundance, annual floral resources, and overwinter habitat in enhancing aphid natural enemies. Agric. Ecosyst. Environ. 199, 94–104.
Regan, K., Ordosch, D., Glover, K.D., Tilmon, K.J., Szczepaniec, A., 2017. Effects of a pyrethroid and two neonicotinoid insecticides on population dynamics of key pests of soybean and abundance of their natural enemies. Crop Prot. 98, 24–32.
Richards, S.A., 2008. Dealing with overdispersed count data in applied ecology. J. Appl. Ecol. 45 (1), 218–227.
Richards, S.A., Whittingham, M.J., Stephens, P.A., 2011. Model selection and model averaging in behavioural ecology: the utility of the IT-AIC framework. Behav. Ecol. Sociobiol. 65 (1), 77–89.
Rusch, A., Bommarco, R., Jonsson, M., Smith, H.G., Ekbom, B., 2013. Flow and stability of natural pest control services depend on complexity and crop rotation at the landscape scale. J. Appl. Ecol. 50 (2), 345–354.
Scheper, J., Holzschuh, A., Kuussaari, M., Potts, S.G., Rundlöf, M., Smith, H.G., Kleijn, D., 2013. Environmental factors driving the effectiveness of European agri-environmental measures in mitigating pollinator loss—a meta-analysis. Ecol. Lett. 16 (7), 912–920.
Scheper, J., Bommarco, R., Holzschuh, A., Potts, S.G., Riedinger, V., Roberts, S.P., Wickens, V.J., 2015. Local and landscape-level floral resources explain effects of wildflower strips on wild bees across four European countries. J. Appl. Ecol. 52 (5), 1165–1175.
Schmidt, A., Kirmer, A., Kiehl, K., Tischew, S., 2020. Seed mixture strongly affects species-richness and quality of perennial flower strips on fertile soil. Basic Appl. Ecol. 42, 62–72.
Schmidt-Entling, M.H., Döbeli, J., 2009. Sown wildflower areas to enhance spiders in arable fields. Agric. Ecosyst. Environ. 133 (1–2), 19–22.
Statistics Netherlands (Centraal Bureau voor de Statistiek, CBS) 2015. StatLine: Landbouw; gewassen, dieren en grondgebruik naar regio. Website: http://statline.cbs.nl/StatWeb (Accessed January 2015).
Sutter, L., Albrecht, M., Jeanneret, P., 2018. Landscape greening and local creation of wildflower strips and hedgerows promote multiple ecosystem services. J. Appl. Ecol. 55 (2), 612–620.
Toivonen, M., Huusela-Veistola, E., Herzon, I., 2018. Perennial fallow strips support biological pest control in spring cereal in Northern Europe. Biol. Control 121, 109–118.
Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I., Thies, C., 2005. Landscape perspectives on agricultural intensification and biodiversity–ecosystem service management. Ecol. Lett. 8 (8), 857–874.
Tscharntke, T., Karp, D.S., Chaplin-Kramer, R., Batáry, P., DeClerck, F., Gratton, C., Martin, E.A., 2016. When natural habitat fails to enhance biological pest control–five hypotheses. Biol. Conserv. 204, 449–458.
Tschumi, M., Albrecht, M., Entling, M.H., Jacot, K., 2015. High effectiveness of tailored flower strips in reducing pests and crop plant damage. Proc. Biol. Sci. 282 (1814), 20151369.
Tschumi, M., Albrecht, M., Bärtschi, C., Collatz, J., Entling, M.H., Jacot, K., 2016a. Perennial, species-rich wildflower strips enhance pest control and crop yield. Agric. Ecosyst. Environ. 220, 97–103.
Tschumi, M., Albrecht, M., Collatz, J., Dubsky, V., Entling, M.H., Najar-Rodriguez, A.J., Jacot, K., 2016b. Tailored flower strips promote natural enemy biodiversity and pest control in potato crops. J. Appl. Ecol. 53 (4), 1169–1176.
Veres, A., Petit, S., Conord, C., Lavigne, C., 2013. Does landscape composition affect pest abundance and their control by natural enemies? A review. Agric. Ecosyst. Environ. 166, 110–117.
Wäckers, F.L., Van Rijn, P.C., 2012. Pick and mix: selecting flowering plants to meet the requirements of target biological control insects. Biodiversity and Insect Pests: Key Issues for Sustainable Management, pp. 139–165.
Zadoks, J.C., Chang, T.T., Konzak, C.F., 1974. A decimal code for the growth stages of cereals. Weed Res. 14 (6), 415–421.