



The interplay of intercropping, wildflower strips and weeds in conservation biological control and productivity

Séverin Hatt^{1,2} · Thomas F. Döring¹

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Abstract

Different diversification practices have the potential to reduce pests and therefore pesticide use. Yet, their integration at the agroecosystem level and the evaluation of their multifunctional effects remain limited. Through a two-year field experiment conducted in Germany, we tested whether associating intercropping (faba bean-wheat, followed by breadseed poppy-barley) with pluriannual wildflower strips strengthens the biological regulation of aphid pests and weeds, and enhances cropping system productivity. The contribution of flowering weeds to conservation biological control was also analysed. Aphid but also predator colonization and predation rates on bean and poppy were consistently lower in intercropping compared to sole cropping. Wildflower strips enhanced aphid predation in bean-wheat intercropping, and further reduced aphid colonization at 10 m distance but not at 20 m in poppy-barley intercropping. Weed biomass was consistently reduced in intercropping compared to sole cropping bean and poppy, and did not significantly affect bean and poppy yields in intercropping. The cover of one flowering weed species, *Matricaria recutita*, was negatively correlated to aphid colonization and positively correlated to predation rate. *Matricaria recutita* flowers were also visited more often by predatory hoverflies in plots adjacent to wildflower strips. Finally, land equivalent ratio was consistently higher than 1, and the highest in bean-wheat intercropping associated to wildflower strips. The study demonstrates the benefits of associating wildflower strips to intercropping to strengthen biological control and cropping system productivity. Flowering weeds, maintained at an acceptable level through intercropping, turn out to be relevant functional biodiversity in interacting with wildflower strips for conservation biological control.

Keywords Agro-ecological crop protection · Agro-ecosystem diversification · Field margin management · Functional agrobiodiversity · Mixed cropping · Pesticide-free agriculture

Introduction

The detrimental effects of pesticides on the environment (Pisa et al. 2021) and human health (Kim et al. 2017) require to rethink strategies of crop protection. Evidence shows that simplified cropping systems entrenched in homogeneous landscapes are more sensitive to pest colonization and spread, less prone to biological control by

natural enemies (i.e. predators and parasitoids), and more frequently and intensively treated with insecticides (Larsen and Noack 2021; Gagic et al. 2021; Nicholson and Williams 2021). Simplified cropping systems are also more infested by weeds, hence more frequently and intensively treated with herbicides (Andert et al. 2016; Strehlow et al. 2020). Achieving an agriculture free of pesticides therefore requires redesigning agro-ecosystems (Deguine et al. 2017). New agro-ecosystems have to diversify by maximizing functional biodiversity in order to reduce cropping system sensitivity to pests and favour their regulation by local natural enemies (i.e. conservation biological control) (Hatt et al. 2018).

One way of reducing cropping system sensitivity to pests is through intercropping, i.e. the simultaneous cultivation of two or more crop species (or genotypes) coexisting in the field at least for a time. Increasing crop species diversity generally enhances the competition for resources, favouring weed suppression (Bedoussac et al. 2015). In this respect,

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✉ Séverin Hatt
shatt@natagriwal.be

¹ Institute of Crop Science and Resource Conservation, Agroecology and Organic Farming Group, University of Bonn, Auf Dem Hügel 6, 53121 Bonn, Germany

² Natagriwal Asbl, Gembloux Site, Passage Des Déportés 2, 5030 Gembloux, Belgium

it is especially beneficial to crops with weak competitiveness against weeds, i.e. often non-cereal crops (Gu et al. 2021). Further, diversifying crops favours the presence of non-host plants that dilute host species and create barriers between them (Andow 1991), leading to a lowered colonization and spread of insect pests (Mansion-Vaquié et al. 2020). Known as the ‘resource concentration’ hypothesis, this bottom-up effect of intercropping can be complemented by the ‘enemies’ hypothesis, i.e. the increase of biological control through the multiplication of ecological niches, the diversification of resources, and the reduction of inter- and intra-specific competition in complex agro-ecosystems (Root 1973). Evidence however shows that intercropping does not consistently provide benefits to natural enemies (Lopes et al. 2016; Rakotomalala et al. 2023).

A potential way to reduce this variability and to strengthen conservation biological control in intercropping is by implementing and managing non-crop habitats at field margins (Gurr et al. 2017). Non-crop habitats maintained over time are more stable environments for many insects in comparison to crop fields (Tooker et al. 2020), therefore represent shelters against disturbances (Gontijo 2019) and suitable overwintering sites (Pfiffner and Luka 2000). In addition, they often offer food resources through flowers whose nectar and pollen are essential, but also alternative, food for natural enemies of pests (Lu et al. 2014), and by hosting alternative prey, which are non-pest insects (Snyder 2019). Pluriannual wildflower strips sown at field margins are one of such non-crop habitats (Haaland et al. 2011; Ganser et al. 2019) and have been increasingly considered to enhance conservation biological control (Hatt et al. 2020). In a meta-analysis, Albrecht et al. (2021) reported a significant increase of 16% on average of pest control in crops adjacent to wildflower strips in comparison to crops without such strips.

The success of wildflower strips at enhancing biological control depends, at least partly, on the level of spill-over of natural enemies into the crops. Distance decay effect of wildflower strips on biological control is known (Albrecht et al. 2021). Previous studies demonstrated a positive effect of flower strips on biological control within the first 10 m but not beyond (Tschumi et al. 2015, 2016). Triggering this spill-over might benefit from the presence of flowers within field. Weeds are generally unwanted in crop fields because they compete for resources (but see Colbach et al. 2020). However, they represent important food resources for flower visiting insects (Rollin et al. 2016). Their flowers could attract natural enemies at the direct vicinity of crop plants and improve biological control of insect pests (Altieri and Nicholls 2004; Serée et al. 2023). Taking advantage of the flower resources offered by weeds should however not be at the cost of significant crop yield losses. This potential trade-off could be solved through intercropping that can control weeds. Indeed, crop diversification was proposed as an approach to maximize weed diversity (Esposito et al.

2023), which may mitigate crop yield losses through reduced weed biomass (Adeux et al. 2019). Furthermore, intercropping generally increases cropping system productivity through an improved resource use efficiency (Li et al. 2020). It enhances temporal and spatial complementarity, resource sharing and facilitation between crop partners (Brooker et al. 2015). Although it can introduce some trade-offs in the productivity of the respective crops (i.e. with one crop benefiting from the association at the cost of the other; Huss et al. 2022), intercropping allows compensation in the case one partner (partially) fails (Döring and Elsalahy 2022).

So far, the agro-ecological benefits of diversified cropping and flower-rich field margins have been studied separately; and weeds generally remain unwelcomed. The strategic integration of these diversification instruments at the agro-ecosystem level with a view on their multifunctional effects is currently missing (Hatt and Döring 2023). Through a randomized field experiment conducted over two consecutive years in organic farming conditions, the first aim of the study was to assess the effect of cropping system (intercropping versus respective pure stand crop) and field margin (wildflower strip versus crop stand) on insect pests and their natural enemies, weed biomass and productivity. Specifically, it tested the following hypotheses:

- (1) Intercropping with wildflower strips reduces insect pest infestation and strengthens biological control by enhancing the presence and predation of natural enemies
- (2) Intercropping reduces weed pressure with no effect of wildflower strips
- (3) Intercropping with wildflower strips enhances cropping system productivity

Second, with the hypothesis that intercropping maintains weed pressure at an acceptable level, the study explored whether in intercropping, flowering weeds can support natural enemies and contribute to conservation biological control.

Material and methods

Experimental set-up

A unique split-split plot field experiment was implemented to analyse the effects of crop diversification and field margin management, while considering distance-effects to this margin (Fig. 1). The experiment, conducted over two cropping seasons (2020/2021 and 2021/2022), took place in a 1.5 ha field (249 × 62 m) of the University of Bonn Teaching and Research Station for Organic Farming Wiesengut (50°47'32" N, 7°15'04" E, Hennef, Germany). The experimental station is part of a diverse landscape, comprising

crop fields, permanent pastures and semi-natural habitats (hedgerows and woodlands), along the Sieg river. The field comprised four replicated blocks, each containing two sub-blocks (36×25 m). Sub-blocks were separated by a buffer zone of 21 m sown with cereals (winter wheat *Triticum aestivum* L. (Poaceae) in 2020/2021 and spring barley *Hordeum vulgare* L. (Poaceae) in 2022). Within blocks, one of the sub-block had a wildflower strip sown at one margin (36×3 m), while the other sub-block had a cereal crop strip identical to the buffer zone instead (“control strip”) (Fig. 1). Perpendicular to each margin strip, four cropping plots (9×25 m, randomized between blocks) were cultivated under four different cropping systems: (i) a flowering crop in sole cropping, (ii) a cereal crop in sole cropping, (iii) the intercropping of both in an intermediate mixture design (i.e. 100% of the flowering crop density + 50% of the cereal crop density), (iv) the cereal crop with undersown companion plants (Fig. 1). This last treatment was however not considered in the present analysis since the undersown plants failed to establish successfully in both trial years. As for intercropping, we chose from a range of different design options (Verret et al. 2020). In a substitutive or replacement design, the plant densities of the partners in the intercropping, relative to the respective densities in the sole cropping, add up to 100%, so that total relative density is the same in both systems and diversity

effects can be disentangled from density effects. In farming practice, however, so-called intermediate designs are more common, where the total crop density in the intercrop is larger than 100% of the sole crop densities (Verret et al. 2020). In the present study, an intermediate design was followed, where one of the partners was considered as the main crop of interest for the farmer, i.e. the flowering crop as the reference system. Its density was the same in the reference sole cropping and in the intercropping.

In the first cropping season, winter faba bean (var. Arabella), winter wheat (var. Livius), and the mixed intercropping of both were sown in the respective cropping plots on 19 October 2020. Field mustard (*Sinapis arvensis* L., Brassicaceae) was cultivated as a winter cover crop in the whole field (except the wildflower strips which remained) from September 2021 to March 2022. In the second cropping season, spring breadseed poppy (var. Viola) followed faba bean, and spring barley (var. Avalon) followed wheat, in the sole cropping as well as in the intercropping plots. Breadseed poppy and barley were intercropped by alternating one row of breadseed poppy and three rows of barley (Luhmer 2021, p. 24). Breadseed poppy was sown ahead of barley (29 March, and 22 April 2022, respectively) to avoid a detrimental competition of barley on poppy seedlings (Luhmer et al. 2021). More

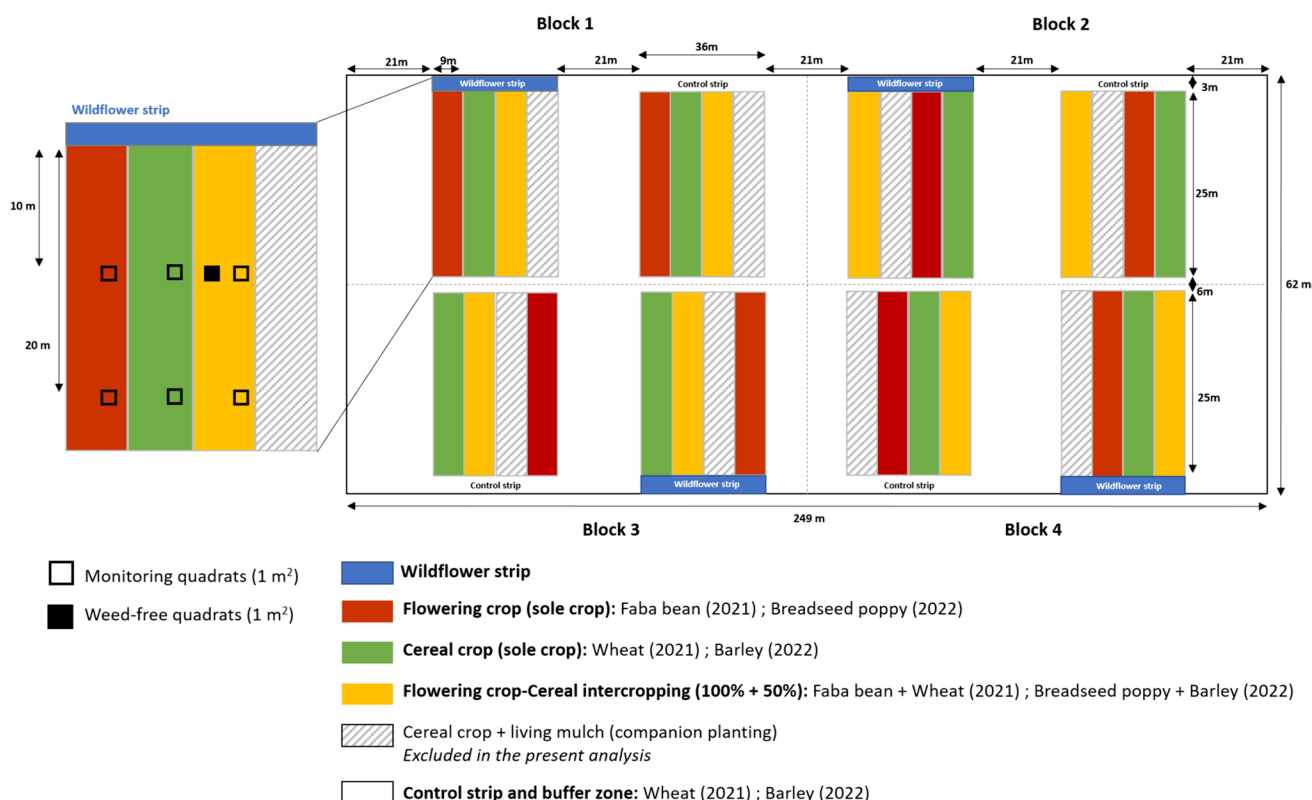


Fig. 1 Experimental design

details on the sowing protocol (sowing rate, row spacing) are provided in Table S1.

In the first cropping season, no direct (mechanical) weed management was applied after sowing. In the second season, breadseed poppy plots were hoed on 13–14 April 2022 and both barley and breadseed poppy sole cropping (but not the intercropping plots) were hoed again on 05–06 May 2022. Intercropping plots were not hoed for a second time in that season, i.e. once barley was sown, because we anticipated that the higher total crop density of the intercrop would suppress weeds more strongly than the sole crops, leaving farmers an option to reduce costs of mechanical weeding. In addition, because of this high density of sown crops, there was a risk that mechanical weeding destroys crop seedlings. Note that the experiment, following a farming systems approach, was designed to associate the diversification measures with realistic management options. The field was managed organically, and received neither pesticides nor fertilizers.

The wildflower strips were sown on 20 October 2020 with a self-composed mixture of 12 forb species (Table S2) and one grass species (*Festuca rubra* L., Poaceae). All but one species were sown at an equal weight of seeds ($2 \text{ kg} \cdot \text{ha}^{-1}$), for a total sown density of $28 \text{ kg} \cdot \text{ha}^{-1}$. The forb species were chosen in order to create a pluriannual mixture maximizing the availability of nectar for flower visitors with short mouth parts (hoverflies (Diptera: Syrphidae), lacewings (Neuroptera: Chrysopidae), ladybird beetles (Coleoptera: Coccinellidae)). Furthermore, the mixture harboured a balanced diversity of trait values for additional functional traits known to affect insect attraction (blooming start, blooming duration, flower colour, ultra-violet pattern, Table S2, Hatt et al. 2020). The wildflower strips were mown once in September 2021 and cuts were exported.

Data collection

All data were collected in permanent quadrats of 1 m^2 installed in each cropping plot at 10 m and at 20 m from the margin strip, respectively (Fig. 1).

Effect of cropping system and field margin on insects, weeds and productivity

Faba bean in 2021, and breadseed poppy in 2022, were observed to evaluate aphid (Hemiptera: Aphididae) and predator colonization rates. A crop plant was considered colonized by aphids if at least one aphid was found on this plant. Similarly, a crop plant was considered colonized by predators if at least one predatory insect was observed.

Predators considered were hoverflies (eggs, larvae, pupae), lacewings (eggs, larvae, pupae) and ladybird beetles (eggs, larvae, pupae, adults). Observations were conducted twice on faba bean (on 16 June and on 1 July 2021) and once on breadseed poppy (on 18 May 2022, when aphid population peaked). For faba bean, all crop plants per quadrat were observed (i.e. 8 ± 2 plants). The variability between quadrats is explained by a freezing event in winter 2020/2021 that affected part of the faba bean plants in the field. For breadseed poppy, 20 plants per quadrat were observed. Aphid colonization rate per quadrat was calculated by dividing the number of plants with aphids by the total number plants observed. Similarly, predator colonization rate was calculated by dividing the number of plants with predators by the total number plants observed.

Aphid predation cards were used to evaluate the potential level of predation. A card corresponded to a $5 \times 5 \text{ cm}$ sand paper (granulation: 120) on which five aphids (*Acyrtosiphon pisum* Harris, purchased to Katz Biotech AG, Germany) were evenly glued alive the day before being used in the field. A solvent-free glue was used and the cards bearing aphids were stored during the night in a cooling chamber at 4°C . In each quadrat, two cards were hung for 24 h on two different flowering crop plants. The day the cards were collected, aphid predation was inspected in the laboratory under a binocular. This procedure was repeated twice on faba bean (09–10 June and 08–09 July 2021) and conducted once on breadseed poppy (16–17 June 2022). Predation rate was calculated for each card by dividing the number of aphids missing by the number of aphids originally glued.

Crops (each sole crop, and both intercrops in the intercropping plots) and weeds were manually harvested together in all quadrats in the weeks of 30 July to 4 August 2021, and 20–27 July 2022. Crop plants and weeds were separated manually. Grain yield and dry biomass of weeds were obtained after drying samples at 105°C during 24 h.

Additional quadrats (hereafter named “weed-free quadrats”) were installed at 10 m from the managed margin to assess the impact of weed presence on crop yield (Fig. 1). In this third quadrat, all weeds were cut by hand by using electric plant shears once a month (2021: four times from 1 March to 22 June; 2022: on 12 May and 10 June). Grain yield was obtained in the same way as for the regular monitoring quadrats. Weed impact on yield was assessed in intercropping plots to evaluate if this practice allows maintaining weeds at an acceptable level.

In intercropping: effect of weed flowers on conservation biological control

If weeds can be maintained at an acceptable level through intercropping, weed flowers could be considered as a relevant functional agrobiodiversity to support natural enemies

within field towards enhancing biological control. To this aim, the cover of weed flowers was evaluated in intercropping plots by identifying all flowering weed individuals at the species level (only *Veronica* sp. were identified at the genus level) in each quadrat. Cover evaluation was done in two steps. First, abundance of flowering weeds was evaluated by counting either the number of inflorescences (for *Matricaria recutita* L. (Asteraceae) and wild poppies *Papaver rhoeas* L. (Papaveraceae)), or the number of individual plants (all the other species/genus). Second, a subset of weed individuals was randomly chosen for each species (20 individuals per species if possible) to count the number of inflorescences per plant, measure the area of inflorescences, and calculate an average value of inflorescence cover for each plant species. Finally, the inflorescence area (in cm²) per species in each sampling quadrat was estimated by multiplying the count of plant individuals by the respective value of inflorescence cover. Flowering weeds were monitored five times in faba bean-wheat intercropping (4 May, 19 May, 7 June, 25 June and 13 July 2021) and three times in breadseed poppy-barley intercropping (25 May, 13 June, and 4 July 2022).

Insects visiting weed flowers were observed in breadseed poppy-barley intercropping. Each quadrat was observed during 10 min by two observers simultaneously on 4 July 2022 between 10:00 am and 16:00 pm. Any insect which landed on a weed flower (without specifically distinguishing if it was feeding on flower resources or resting) within the quadrat was identified at the highest taxonomic level possible, and its succession of flower visitations was followed until it left the quadrat. Hence, both the abundance of individual insects and insect-flower links were recorded.

Statistical analyses

All statistical analyses were performed with R software v. 4.0 (R Core Team 2020) taking each crop-year separately.

Effect of cropping system and field margin on insects, weeds and productivity

Aphid and predator colonization rates and predation rates were analysed through linear mixed models (LMM) tested by using a type 1 analysis of variance (ANOVA, R function *anova* in the start package *base*) for each crop-year separately. Data retrieved from the two observations on faba bean (2021), as well as data obtained from the two predation cards installed in each quadrat, were averaged in the respective analyses. Normal distribution was checked visually by plotting the models' quantiles against the quantiles of a normal distribution, and the density function of models' residuals. Full models included field margin (two levels: flower strip and control strip), cropping system (two levels: intercropping and flowering crop

sole cropping), distance (two levels: 10 and 20 m) and their two-way and three-way interactions as fixed factors (R function *lme* in the package *nlme*, Pinheiro et al., 2023). Distance nested in field margin nested in block were included as random factors to integrate their dependent relationship. When distance showed no significant effect, reduced models including field margin, cropping system and their two-way interaction as fixed factors, and field margin nested in block as random factors, were also fitted. Akaike information criterion (AIC) was used to compare the full and the reduced models, and the model with the lowest AIC was retained (see Table S3 for AIC comparisons).

Weed biomass was also analysed through LMM and type 1 ANOVA for each crop-year separately. Full models were fitted with field margin, cropping system (three levels: intercropping and the two sole crops), distance, and their two-way and three-way interactions as fixed factors, and distance nested in field margin nested in blocks as random factors. Similarly as for insects, reduced models were fitted with field margin, cropping system, and their two-way interaction as fixed factors, and field margin nested in block as random factors. The model with the lowest AIC was retained (Table S3). Pairwise comparisons of means were performed on the factor cropping system by using a post-hoc test of Tukey (R function *glht* in the package *multcomp*, Hothorn et al. 2008).

Grain yield was analysed with LMM and type 1 ANOVA in a similar way than for insects. Land-use efficiency was analysed by calculating the land equivalent ratio (LER) for each sub-block at each distance (i.e. for each replicate). For a mixture of species *i* and *j*, LER is the sum of the partial land equivalent ratios (pLER) of each species, and is calculated as (Eq. 1):

$$\text{LER} = \text{pLER}_i + \text{pLER}_j = \frac{\text{yield}_i \text{ intercropping}}{\text{yield}_i \text{ sole cropping}} + \frac{\text{yield}_j \text{ intercropping}}{\text{yield}_j \text{ sole cropping}} \quad (1)$$

Effect of field margin and distance on LER was analysed using LMM and type 1 ANOVA with field margin and distance as fixed factors, and distance nested in field margin nested in blocks as random factors. In addition, a LER greater than one means that intercropping is more efficient than sole cropping for a single unit of land. Hence, *t*-tests were used to evaluate whether LER were significantly higher than 1 for each mixture, either with or without wildflower strip at margin (by pooling data at 10 and 20 m). Finally, the impact of weeds on grain yield was tested by using *t*-tests against zero on the mean relative difference of yield between the weed-free quadrats and the regular monitoring quadrats at 10 m. The relative difference of yield in percentage was calculated in each intercropping plot through (Eq. 2):

$$\frac{\text{Yield}_{10 \text{ m}} - \text{Yield}_{\text{weed free}}}{\text{Yield}_{\text{weed free}}} \times 100 \quad (2)$$

In intercropping: effect of weed flowers on conservation biological control

The impact of weed flowers on conservation biological control in intercropping was analysed in two complementary ways. The first one was through a redundancy analysis (RDA), that could however be performed only in faba bean-wheat intercropping (2021). In 2022, aphid colonization on breadseed poppy (2022) occurred before the first weed plant bloomed. The second one was by analysing interactions between flowering weeds and flower visiting insects in breadseed poppy-barley intercropping.

Redundancy analysis combines regression and principal component analysis (PCA). It is a direct extension of regression analysis to model multivariate response data (Borcard et al. 2011). It is useful here to associate the matrix of flowering weeds as explanatory variables, which comprised the mean inflorescence cover per quadrat of each flowering weed species/genus calculated over the cropping season; and the centred matrix of conservation biological control as response variables, which comprised the rates of aphid colonization, predator colonization and predation. The interaction between the two matrices was analysed by performing a forward selection of the flowering weeds that significantly ($P < 0.05$) affected the matrix of conservation biological control (R function *ordstep* in the package *vegan*, Oksanen et al. 2015); and then by introducing the weeds showing the most significant effects (i.e. the lowest P -value, or the lowest AIC in case of equal P -value; see Borcard et al. 2011, p. 176, for details) at each selection step in a redundancy analysis (RDA) using Bray–Curtis distances (R function *capscale* in the package *vegan*, Oksanen et al. 2015). The obtained ordination, as well as each of its axis, were tested with a permutation test ($n = 1000$, $P = 0.05$).

The analysis of interactions between flowering weeds and flower visiting insects in intercropping was conducted in 2022 only, with the aim of deepening our understanding of the 2021's RDA results. The abundance of insects visiting weed flowers, the abundance of hoverflies visiting weed flowers (i.e. a subset of the total insect abundance), and the number of links between hoverflies and *M. recutita* were analysed through Generalized linear mixed models (GLMM) and tested using a Wald chi-square test. Field margin, distance to the margin, and their two-way interactions were included as fixed factors. Field margin nested in blocks was included as random factors. When interaction effects were significant, subsequent analyses were conducted by fitting models with the factors separately. Poisson error distribution (log-link function) was used (function *glmer* in the package *lme4*, Bates et al. 2015). Multicollinearity was assessed with variance inflation factors (VIF) and all VIF were below 4 (*vif* function in the package *car*, Fox and Weisberg 2019). However, for the full model analysing hoverflies-*M. recutita*

links, a negative binomial distribution was used to solve the overdispersion of the residuals (R function *glmmTMB* in the package *glmmTMB*, Brooks et al. 2017) (Zuur et al. 2009).

Results

In 2021, *Centaurea cyanus* (Asteraceae) (i.e. the only annual species in the mixture, Table S2) was the only sown species that bloomed in the wildflower strips, starting flowering from the end of May. Other blooming plants were volunteer species, similar to those found in the field core (i.e. weeds). In 2022, all the species sown in the wildflower strips bloomed, the earliest to flower being *Geranium pyrenaicum* (Geraniaceae), from mid-April. Faba bean bloomed around mid-May in 2021, and breadseed poppy bloomed around mid-June in 2022.

Effect of cropping system and field margin

On insect pests, predators and predation

Acyrtosiphon pisum (Harris) and *Aphis fabae* (Scopoli) were the two aphid species observed on both faba bean and breadseed poppy, with *A. pisum* being the main aphid pest on faba bean and *A. fabae* being the main one on breadseed poppy. Aphid colonization rate was lower in intercropping than in sole cropping both on faba bean (Table 1; Fig. 2a) and on breadseed poppy (Table 1; Fig. 2b). Field margin had no effect on aphid colonization rate (Table 1). Nonetheless, an interaction effect between field margin, cropping system and distance was found on aphid colonization rate in breadseed poppy (Table 1). Analyses testing the impact of field margin in each cropping system and at each distance separately showed an effect of wildflower strips at reducing aphid colonization rate in intercropping at 10 m ($F_{1,3} = 24.8$, $P = 0.016$), but not at 20 m ($F_{1,3} = 0.27$, $P = 0.638$) and not in sole cropping (10 m: $F_{1,3} = 0.05$, $P = 0.836$; 20 m: $F_{1,3} = 0.27$, $P = 0.638$) (Fig. 3a).

Active predators observed in the field were ladybird beetle larvae and adults (mostly *Coccinella septempunctata* and *Harmonia axyridis*, but also *Propylea quatuordecimpunctata* and *Tytthaspis sedecimpunctata*), hoverfly larvae and lacewing larvae. Eggs and pupae of these predators were also observed and counted. Predator colonization rate was higher in sole cropping than in intercropping on breadseed poppy (Table 1; Fig. 2d) and predation was higher in sole cropping than in intercropping on faba bean (Table 1; Fig. 2e). Cropping systems had no effect on predator colonization rate in faba bean (Table 1; Fig. 2c) and on predation rate in breadseed poppy (Table 1; Fig. 2f). Field margin had no effect on predator colonization and on predation rates (Table 1). Nonetheless, a two-way

Table 1 Effect of field variables on aphid colonization rate, predator colonization rate, predation rate, weed biomass and grain yield in faba bean (2021) and breadseed poppy (2022). Reduced models without the factor distance were fitted if distance shows no significant effect, and the model with the lowest AIC was retained (see Table S3 for AIC comparisons)

	Faba bean (2021)			Breadseed poppy (2022)		
	<i>df</i>	<i>F</i>	<i>P</i>	<i>df</i>	<i>F</i>	<i>P</i>
<i>Aphid colonization rate</i>						
Margin type	1,3	0.006	0.944	1,3	0.72	0.459
Cropping System	1,22	6.89	0.016	1,12	36.21	< 0.001
Distance	–	–	–	1,6	1.48	0.270
Margin type x Cropping System	1,22	2.43	0.133	1,12	3.43	0.089
Margin type x Distance	–	–	–	1,6	2.31	0.180
Cropping System x Distance	–	–	–	1,12	0.86	0.373
Margin type x Cropping System x Distance	–	–	–	1,12	5.36	0.039
<i>Predator colonization rate</i>						
Margin type	1,3	0.61	0.490	1,3	0.12	0.750
Cropping System	1,22	2.65	0.118	1,22	5.17	0.033
Margin type x Cropping System	1,22	3.49	0.075	1,22	1.50	0.234
<i>Predation rate</i>						
Margin type	1,3	0.71	0.460	1,3	0.11	0.761
Cropping System	1,22	7.44	0.012	1,22	0.90	0.353
Margin type x Cropping System	1,22	4.98	0.036	1,22	2.30	0.143
<i>Weed biomass</i>						
Margin type	1,3	0.14	0.735	1,3	0.004	0.952
Cropping System	2,24	348.68	< 0.001	2,24	76.80	< 0.001
Distance	1,6	0.74	0.424	1,6	2.26	0.183
Margin type x Cropping System	2,24	1.25	0.304	2,24	1.49	0.246
Margin type x Distance	1,6	0.13	0.730	1,6	0.001	0.982
Cropping System x Distance	2,24	1.13	0.340	2,24	2.27	0.126
Margin type x Cropping System x Distance	2,24	0.74	0.490	2,24	1.99	0.158
<i>Grain yield</i>						
Field margin	1,3	0.11	0.757	1,3	0.13	0.744
Cropping System	1,12	21.2	< 0.001	1,12	4.1	0.066
Distance	1,6	0.37	0.563	1,6	0.01	0.933
Field margin x Cropping System	1,12	2.34	0.152	1,12	3.2	0.099
Field margin x Distance	1,6	0	1	1,6	0.22	0.657
Cropping System x Distance	1,12	0.35	0.565	1,12	0.28	0.606
Field margin x Cropping System x Distance	1,12	0.03	0.877	1,12	0.1	0.758

Degrees of freedom (*df*), *F*-values and *P*-values of linear mixed models tested with an analysis of variance are indicated

Significant effects ($P < 0.05$) are shown in bold

interaction of field margin with cropping system was found on predation rate in faba bean (Table 1). Analyses testing the impact of field margin on each cropping system separately showed an impact of wildflower strips at increasing predation rate in intercropped faba bean ($F_{1,7} = 6.73$, $P = 0.036$) but not in sole cropping ($F_{1,7} = 0.36$, $P = 0.57$) (Fig. 3b).

On weed biomass

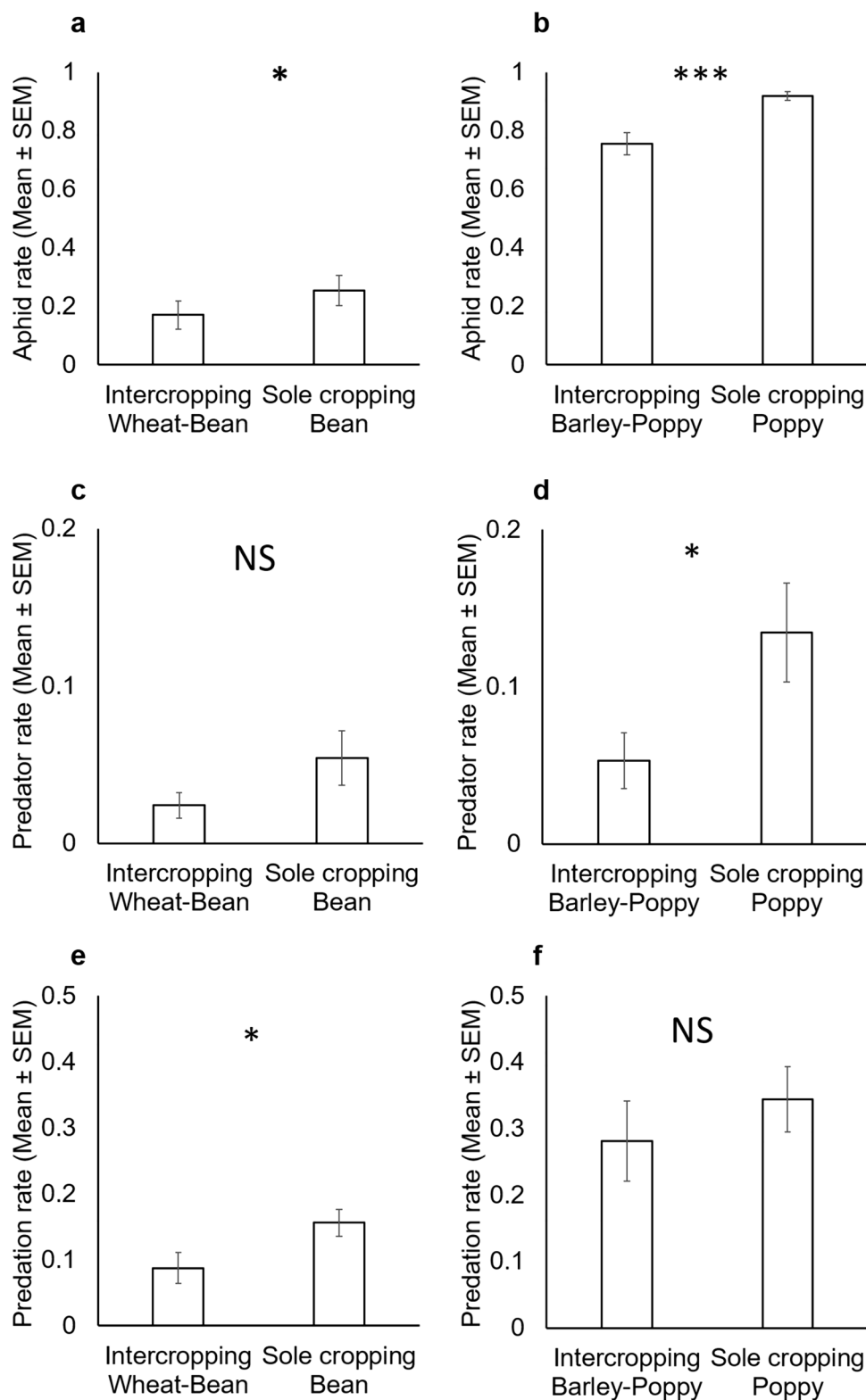
Weed biomass was consistently impacted by the cropping systems (Table 1). Weed biomass in intercropping

was lower than in sole cropping of the flowering crop, and higher than in cereal sole cropping only in the case of barley (Fig. 4). The type of margin had no impact on weed biomass (Table 1).

On productivity

Overall, faba bean yielded $222 \pm 34 \text{ kg ha}^{-1}$ (mean $\pm$ SEM) and breadseed poppy yielded $58 \pm 9 \text{ kg ha}^{-1}$ (mean $\pm$ SEM). Field margin had no impact on yield of both crops (Table 1). Faba bean yield was lower in intercropping ($125 \pm 34 \text{ kg ha}^{-1}$) than in sole cropping ($318 \pm 48 \text{ kg ha}^{-1}$)

Fig. 2 Effect of cropping system on **a–b** aphid colonization rate, **c–d** predator colonization rate, and **e–f** predation rate, on faba bean and breadseed poppy, respectively. * $P < 0.05$; *** $P < 0.001$, NS: not significant, from analysis of variance performed on linear mixed models (see Table 1 for statistical results)

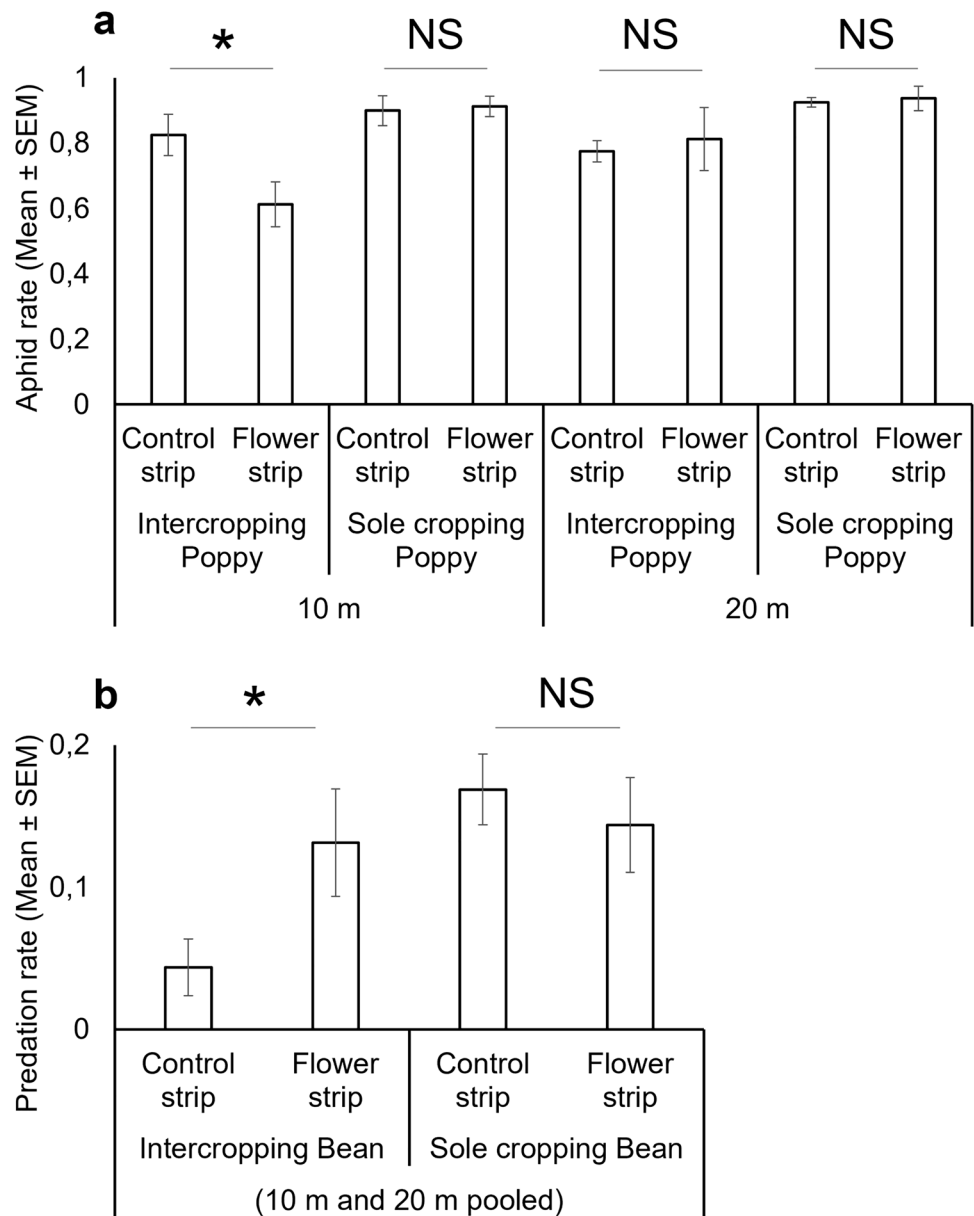


(Table 1), while cropping system had not impact on breadseed poppy yield (Table 1).

Land equivalent ratio was 1.35 ± 0.1 (mean $\pm$ SEM) for faba bean-wheat intercropping, and 1.27 ± 0.2 (mean $\pm$ SEM)

for breadseed poppy-barley intercropping. For both mixtures, LER was not different in plots with flower or control strip at margin, and at 10 m or at 20 m from this strip (Table S4). Yet, LER of faba bean-wheat intercropping was

Fig. 3 Effect of margin strip for each cropping system separately on **a** aphid colonization rate on breadseed poppy at 10 m and 20 m, and **b** predation rate on faba bean. * $P < 0.05$, NS: not significant, from analysis of variance performed on linear mixed models



the highest and significantly higher than one when associated with wildflower strips ($LER = 1.53 \pm 0.2$; $df = 7$, $t = 3.52$, $P = 0.005$; Fig. 5; Table S5).

In intercropping, the presence of weeds had no impact either on yield of faba bean ($df = 6$, $t = -0.58$, $P = 0.292$), or on yield of breadseed poppy ($df = 7$, $t = 0.18$, $P = 0.43$).

In intercropping: effect of weed flowers on conservation biological control

Fifteen weed species were observed flowering in faba bean-wheat intercropping. Among them, *M. recutita* and *P. rhoeas* were the species contributing the most to weed inflorescence cover per quadrat, with $54 \pm 5\%$ and $34 \pm 4\%$ (mean ± SEM), respectively (Table S6). *Matricaria*

recutita ($F_{1,14} = 2.23$, $P = 0.045$), and in a lesser extent *P. rhoeas* ($F_{1,13} = 2.89$, $P = 0.085$), were also the weed species which inflorescence cover affected the matrix of pest and predator colonization and predation rates ($F_{2,12} = 3.69$, $P = 0.037$; Table S7). Of the total variance, 38.1% was explained by the inflorescence cover of these two species, among which 36.1% was explained through the first axis (axis 1: $F_{1,12} = 7.0$, $P = 0.022$; axis 2: $F_{1,12} = 0.38$, $P = 0.715$). The ordination plot indicates that predation rate was positively correlated, and aphid colonization rate was negatively correlated, with the inflorescence cover of *M. recutita* flowers (Fig. S1).

In breadseed poppy-barley intercropping, 120 individual insects were observed visiting weed flowers in early July 2022. Hoverflies represented the large majority of insects

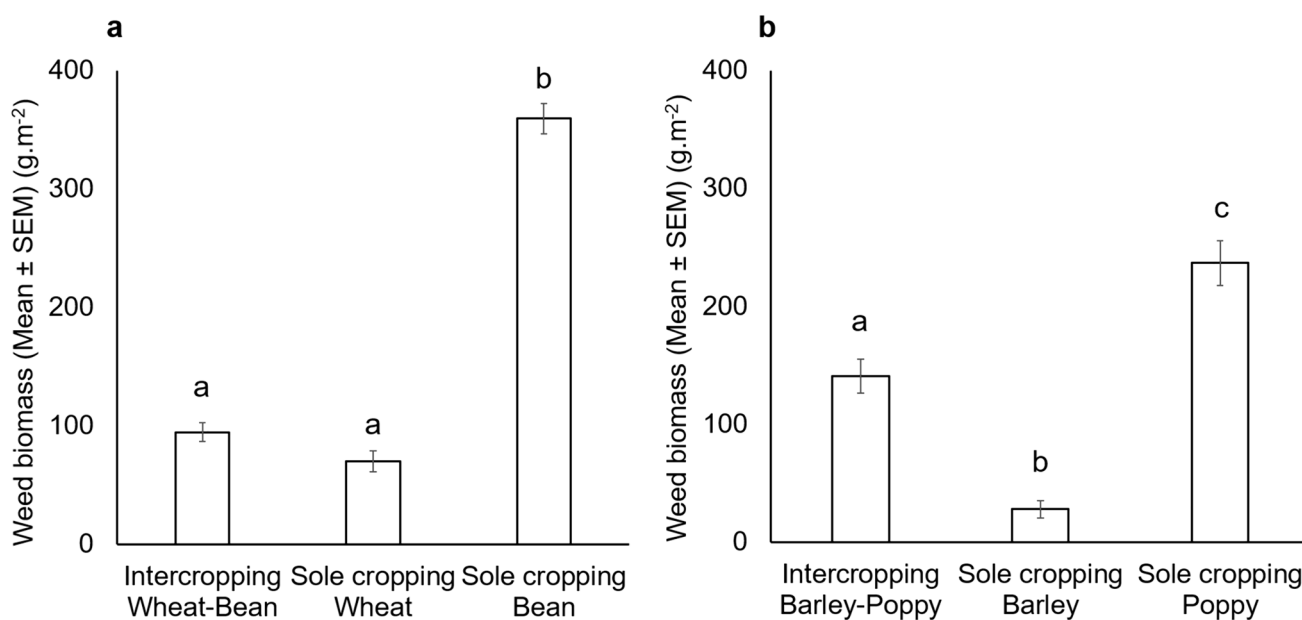


Fig. 4 Effect of cropping system on weed biomass at crop harvest in the cultivation systems involving **a** faba bean and wheat, and **b** breadseed poppy and barley. Different letters indicate the significant differ-

ences ($P < 0.05$) of means using a post-hoc Tukey test performed on linear mixed models

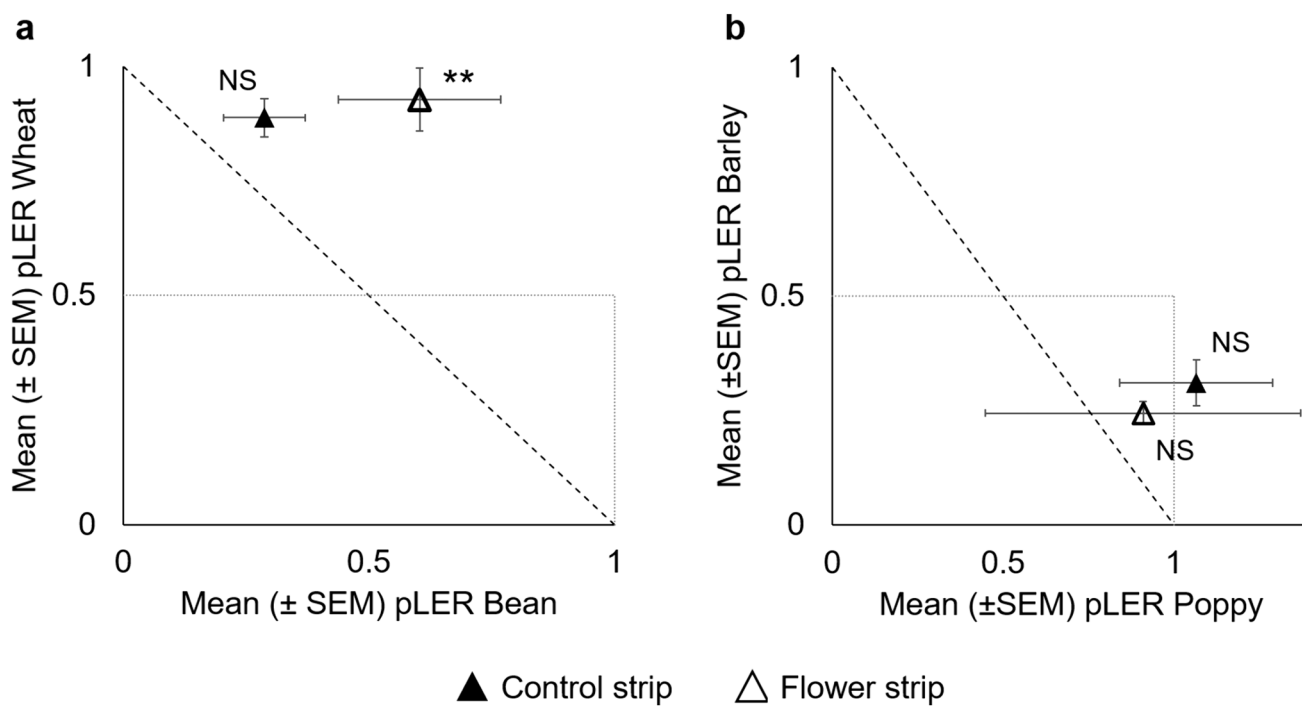


Fig. 5 Mean (± SEM) partial Land Equivalent Ratios (pLER) for **a** faba bean-wheat and **b** breadseed poppy-barley intercropping with control strip or wildflower strip at margin. The black dashed line represents a LER = 1. The grey dotted line represents the expected

respective pLER for intermediate design (mixture 1:0.5). ** $P < 0.01$, NS: not significant, from t -tests for LER > 1 (see Table S5 for statistical results)

observed (i.e. 82.5%, Fig. S2a), all but one identified as the predatory *Sphaerophoria* sp. (the remaining one was an *Eristalis* sp.). At the time of observations, inflorescence cover was dominated by *M. recutita* ($48 \pm 6\%$) and *Raphanus raphanistrum* L. ($39 \pm 6\%$), followed by *P. rhoeas* ($11 \pm 5\%$) (Table S6). Wildflower strips enhanced the total abundance of insects visiting weed flowers, and among them hoverflies, however only at 10 m from the field margin (Table 2; Fig. 6a–b). In addition, 351 insect-flower links were counted, 85% of which made by hoverflies, and 77% of all insect-flower links involved *M. recutita* (while only 7% of all links involved *R. raphanistrum*). Hoverfly-*M. recutita* links represented 66% of all insect-flower interactions (Fig. S2b). Wildflower strips marginally enhanced the total number of hoverfly-*M. recutita* links overall, and significantly increased interactions at 10 m from the margin (Table 2; Fig. 6c). The cover of *M. recutita* flowers was not affected by the type of field margin and the distance to it (Table S8).

Discussion

The present research tested the integration of diversification practices at the agro-ecosystem level to enhance the biological regulation of pests, and enhance cropping system productivity. The dual role of weeds, potentially competing with crops, but also as relevant components of functional agrobiodiversity, was analysed. The study shows that intercropping is a measure to consistently control insect pests and weeds, and enhance land-use efficiency. It demonstrates the significant—but variable—added value of associating wildflower

strips to intercropping to further enhance pest control. In addition, the study highlights that certain flowering weeds, maintained at an acceptable level through intercropping, can positively interact with wildflower strips to support natural enemies of pests and contribute to conservation biological control.

Controlling insect pests

Aphids were significantly reduced in intercropping compared to sole cropping. It is consistent with previous findings (Lopes et al. 2016) and follows the ‘resource concentration’ hypothesis (Root 1973). Aphids are known to be sensitive to the physical and chemical camouflage of their host plants and barrier effects (Ninkovic et al. 2013; Döring 2014; Mansion-Vaquié et al. 2020) that are key ‘associational resistance’ mechanisms (sensu Tahvanainen and Root 1972) characterizing intercropping systems. Predator colonization and predation were however generally lowered in intercropping compared to sole cropping. It confirms that intercropping alone may not enhance the presence of natural enemies (Lopes et al. 2016) and suggests that bottom-up effects were the primary force of aphid control.

Yet, wildflower strips further reduced aphid colonization in breadseed poppy-barley intercropping and enhanced predation in faba bean-wheat intercropping. In its seminal work proposing the ‘enemies’ hypothesis, Root (1973) highlighted the key role of non-crop flowers to support natural enemies in complex agro-ecosystems. While, modern intercropping systems tended to reduce the complexity to the sole diversity of crops (Brooker et al. 2015), the present results indicate

Table 2 Effect of field variables on the abundance of insects (all insects, and hoverflies specifically) visiting weed flowers, and the number of links between hoverflies and *Matricaria recutita* flowers, in breadseed poppy intercropping

	<i>df</i>	χ^2	<i>P</i>	<i>df</i> at 10 m	χ^2	<i>P</i>	<i>df</i> at 20 m	χ^2	<i>P</i>
<i>All insect abundance</i>									
Margin type	1	6.81	0.009	1	11.1	<0.001	1	0.17	0.68
Distance	1	0.54	0.463						
Margin type x Distance	1	4.47	0.035						
<i>Hoverfly abundance</i>									
Margin type	1	11.7	<0.001	1	13.4	<0.001	1	1.70	0.192
Distance	1	0.26	0.609						
Margin type x Distance	1	3.39	0.066						
<i>Hoverfly-M. recutita links</i>									
Margin type	1	2.93	0.087	1	35.8	<0.001	1	1.04	0.308
Distance	1	0.19	0.660						
Margin type x Distance	1	4.34	0.037						

Full models include the two factors and their interaction. As significant, or marginally significant, interaction effects are observed, subsequent models tested the effect of margin type for each distance

Degrees of freedom (*df*), χ^2 -values and *P*-values of generalised linear mixed models tested with a Wald chi-square test are indicated

Significant effects (*P* < 0.05) are showed in bold

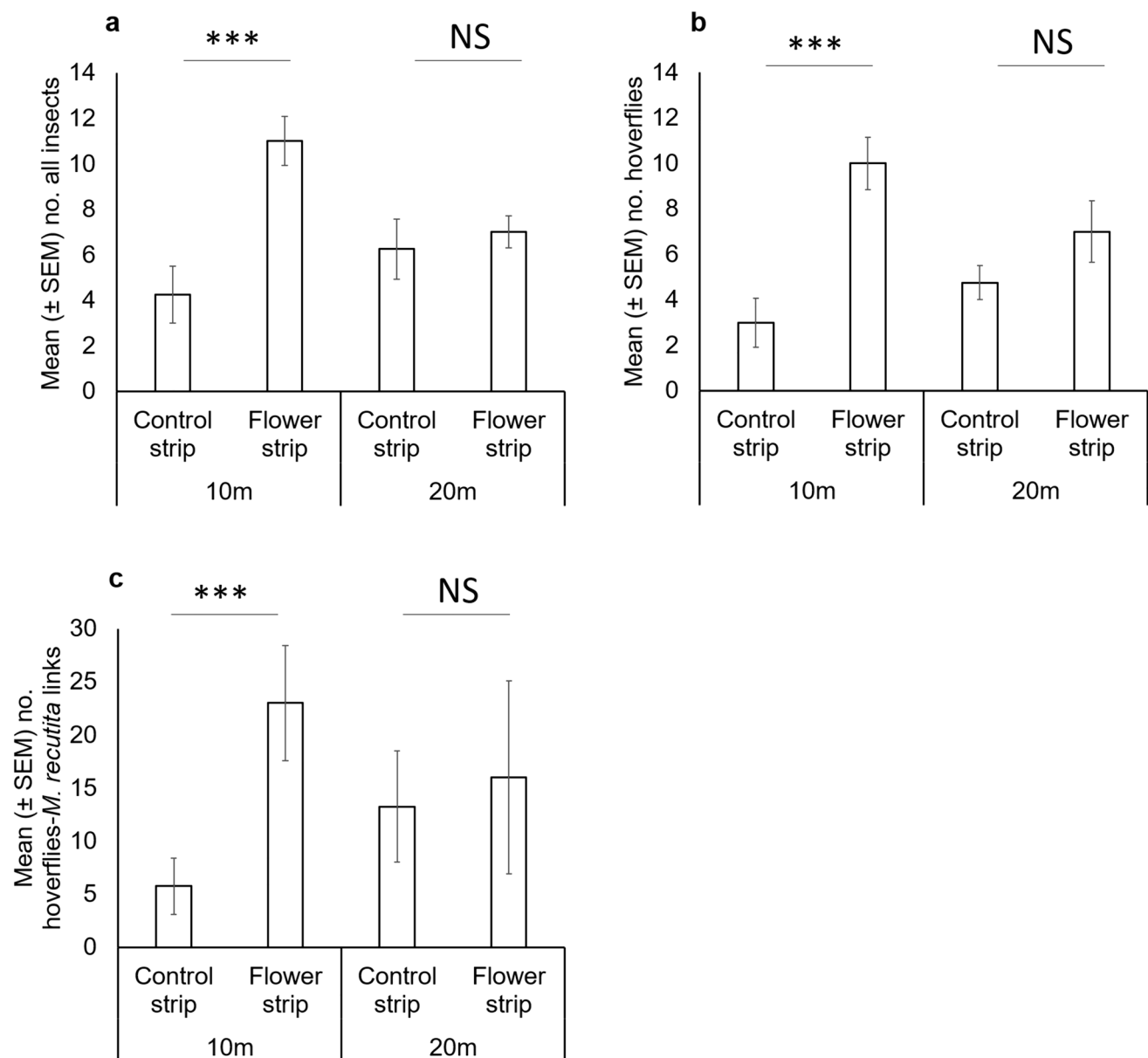


Fig. 6 Effect of margin type at 10 and 20 m in intercropping plots on **a** the abundance of all insects visiting weed flowers, **b** the abundance of hoverflies (all but one being *Sphaerophoria* sp., the remaining one being an *Eristalis* sp.) visiting weed flowers, **c** the number of links

between hoverflies and flowers of *Matricaria recutita*. *** $P < 0.001$, NS: not significant, from generalized linear mixed models and Wald chi-square tests (see Table 2 for statistical results)

that diversifying both the crop field and its margins can partially strengthen pest regulation. Interestingly, wildflower strips showed non-significant effect at enhancing biological control in sole cropping. We hypothesize, that the excess of flowering weeds in sole cropping (due to the high weed biomass in this treatment both years) diluted the offer of floral resources brought by wildflower strips. It suggests that the synergistic interaction between wildflower strips and intercropping in the regulation of insect pests depends on the ability of this last to control weeds.

Balancing weed control and conservation

Intercropping indeed reduced weed biomass by 60% over the two cropping seasons compared to sole cropping of the flowering crop, which is consistent with the meta-analysis of Gu et al. (2021). Both the effects of crop density and diversity can explain the weed suppressive effect of intercropping (Liebman and Dyck 1993). While increasing the density of sown plants would reduce the chance of weeds to grow by enlarging the space occupied by crops, increasing

plant diversity can improve the use of available resources by the crops through resource partitioning (Bedoussac et al. 2015). In the present intermediate design, these two effects cannot be separated and both of them can explain the strong suppressive effect of intercropping compared to the sole cropping of the flowering crop. When compared to the cereal sole cropping, the lower density of this strong weed competitor in intercropping can explain a lower suppression of weeds. The significant difference between intercropping and barley sole cropping is also likely to be due to the mechanical weeding performed this year with a last hoeing done relatively late in the season (i.e. early May) in sole cropping, but not in intercropping. In a pan-European study conducted in organic farming, Corre-Hellou et al. (2011) also showed that intercropping with intermediate design can perform as well as cereal sole cropping to control weed biomass in the absence of mechanical weeding.

This effective weed control resulted in the absence of significant impact of weeds on yield in intercropping. Oerke (2006) estimated that weeds can cause yield losses of 34%, and suggested that they can be managed mechanically or chemically. Following Petit et al. (2018), the present results put forward a further path based on biodiversity, namely intercropping, that can maintain weeds at an acceptable level, opening-up new agro-ecological perspectives. Indeed, our study demonstrates that certain weed species can contribute to conservation biological control, while weed flowers are more often visited by natural enemies in intercropping fields adjacent to wildflower strips. Most of previous studies reported the spill-over of natural enemies from wildflower strips to the field core without referring to weeds (e.g. Bischoff et al. 2022; Hatt et al. 2017). Serée et al. (2023) recently showed that a greater abundance of infield nectar resources provided by weeds enhanced parasitism of pollen beetle pests in oilseed rape, but no effect of field margins could be observed.

The benefits of additional infield flower resources would lie in providing natural enemies in energy, while foraging for prey to lay their eggs. Indeed, not only hoverfly and lacewing adults (which rely on flower food as diet) but also adults of ladybird beetles benefit from nectar and pollen to survive and reproduce (Hatt and Osawa 2019). Nectar within field would furthermore sustain predators between pest abundance peaks, i.e. when prey are scarce (Limburg and Rosenheim 2001), and can initiate a faster resume of oviposition once prey become available again (Wolf et al. 2018). Finally, the availability of non-prey food could trigger the spill-over of natural enemies early in the season, which is a key requirement for success of biological control on aphids (Landis and Werf 1997). The present experiment however suggests that it is more likely to be effective on winter crops, since aphids may infest spring crops before weeds start flowering.

One weed species—*M. recutita*—played a significant role. The attraction of *M. recutita* to predatory hoverflies is recognized and can be attributed to its short effective corolla depth offering easily accessible nectar to insects with short mouth parts (Van Rijn and Wäckers 2016). Other aphid predators, i.e. lacewing larvae and adults of ladybird beetles, were also observed on *M. recutita* flowers during the experiment (Fig. S3). Storkey and Westbury (2007) asked whether there is “such a thing as a ‘good weed’?”, and considered as beneficial weeds species that have high value for higher trophic groups and low competitive ability against crops. *Matricaria recutita* is classified as “with biodiversity value and intermediate competitive ability” in cereals (Storkey and Westbury 2007). Our study suggests that maintaining *M. recutita* at an acceptable level through intercropping allows considering this plant species as an ally more than a threat towards enhancing conservation biological control of aphids.

Enhancing land-use efficiency

Land equivalent ratios were consistently higher than one on average, indicating an enhanced productivity per unit of land in intercropping compared to their respective sole cropping plots. This benefit of intercropping has been repeatedly demonstrated (Li et al. 2020), and our results are no exception. Land equivalent ratio values are also in accordance with Yu et al. (2015) who modelled a LER of 1.24 for a relative density of 1.5. Interestingly, LER of faba bean-wheat intercropping was enhanced with wildflower strips at margin, thanks to an improved performance of faba bean. This beneficial effect can be attributed to the higher predation level observed on intercropped faba bean when bordered with wildflower strips. It could also be the consequence of an improved pollination (Nayak et al. 2015), which was however not measured in the present study.

Limitations and perspectives

The study analysed the complex interactions at play in a highly diversified agro-ecosystem. Evaluating the multiple performances in terms of insect pest and weed control, as well as productivity, implied to collect a wide range of different data, which was at the cost of their respective sample sizes. It is acknowledged that the robustness of the results could have benefited from multiplying insect observations on crops and weeds, and from conducting the study on multiple sites. Time-repeated counting of aphids and their natural enemies on crops could have informed on their respective dynamic and contribute to clarify the ecological mechanisms of pest control. Matching the phenology of natural enemies (flying time) and weeds (flowering time) would have required the assessment of natural enemy-weed flower interactions at different time during the cropping season.

Analysing the effects on the cereals (and not only on the flowering crops), and more generally of all treatments on all variables (e.g. weed impact on yield in sole crops), would have been useful to offer a full picture of the complex interactions at play in the system. Integrating environmental variability would have been possible by conducting the study on multiple sites.

Yet, consistent effects are observed. Intercropping consistently reduced aphid colonization and weed biomass, and consistently increased land-use efficiency. *Matricaria recutita* was a key flowering weed species, significantly attracting natural enemies in interaction with wildflower strips on the one hand, negatively correlated with aphid colonization and positively correlated with aphid predation on the other hand. The effects of wildflower strips at enhancing biological control were more variable, and when significant, the effects were in general observed at 10 m, but not at 20 m. It is consistent with the exponential decline function modelled by Albrecht et al. (2021) who showed a strong distance decay effect on biological control within the first metres from flower plantings.

Future research with further in-depth observations would be needed to move from correlation to proof of causation. They could associate other diversification practices (e.g. hedgerows, agroforestry, variety mixtures), with different crop species, in other environments, likely involving other weed and insect communities. Pest regulation is often affected by crop type and landscape context (Boetzi et al. 2020; Vogel et al. 2023; but see Albrecht et al. 2021). In addition, the evaluation of the agro-ecosystem performances would benefit from a monetary analysis (e.g. Li et al. 2021), to quantify whether the increased control of multiple pests and the enhanced land-used efficiency lead to economic benefits. Adoption of intercropping by farmers remains low (at least in Europe) and it is partly explained by a potential increase of management complexity and labour requirement (Huss et al. 2022). The present results already suggest that within field diversification through intercropping is an effective method to decrease pest colonisation and tolerate weeds, whilst maintaining productivity. Remaining weeds in intercropping turn out to be relevant functional biodiversity in interacting with wildflower strips to support natural enemies for conservation biological control.

Author contributions

Séverin Hatt and Thomas F. Döring conceived the ideas and designed methodology; Séverin Hatt collected and analysed the data, and led the writing of the manuscript; both authors contributed critically to the drafts and gave final approval for publication.

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Data availability The datasets generated and analysed during the current study are available in the Dryad repository, <https://doi.org/10.5061/dryad.w6m905qxm>

Declarations

Conflict of interest The authors declare no conflict of interest.

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