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RESEARCH ARTICLE

Agroecological farming, flowering phenology and the pollinator–herbivore–parasitoid nexus regulate non-crop plant reproduction

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Abstract

1. Agroecological farming uses crop and non-crop plant biodiversity to promote beneficial insects supplying pollination and biocontrol services to crops. Non-crop plants (sown or weeds) are integral to supporting these beneficial insect species interactions. How the uplift of biotic complexity by agroecological management (crop diversification, ecological infrastructure) influences mutualistic and antagonistic insect interactions regulating the reproduction of non-crop plants remains less understood.
2. Using a pesticide-free farm-scale (125 ha) agroecological experiment, we tested how the individual reproduction of pollinator-dependent, non-crop plant species with different flowering phenology (*Cyanus segetum*, *Centaurea jacea*) and their mutualistic (pollinator) and antagonistic (seed herbivore–parasitoid) insect interactions were affected by agroecological practices.
3. Seed set and species interactions of replicate *C. segetum* and *C. jacea* randomly introduced to field margins were correlated with floral resource heterogeneity at focal plant (e.g. flower display size), local community (floral richness/abundance driven by sown wildflower or grass margins) and local landscape (crop diversification, area of semi-natural habitat or mass flowering crops) scales.
4. At the seasonal peak of non-crop floral diversity and abundance, antagonistic interactions weakly regulated *C. segetum* seed set with gains from pollinator activity predominating. Conversely, *C. jacea*, which flowered past the peak of non-crop floral diversity/abundance, benefited from the promotion of seed herbivore parasitism and pollinator activity by the local landscape cover of semi-natural habitat and mass flowering crops.
5. *Synthesis and applications.* Agroecological management produced spatial and temporal gradients in crop and non-crop floral resources that interacted to modify pollinator or seed herbivore–parasitoid interactions and *Cyanus*

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segetum and *Centaurea jacea* seed set. The degree of phenological overlap between *C. segetum* and *C. jacea* flowering and floral resources in the local community or landscape dictated the type and level of exposure to insect interactions influencing reproduction. Design of agroecological practices to deliver pollination and biocontrol services must consider how effects will vary with species traits and the mutualistic (pollination) and antagonistic (herbivory, parasitism) interactions governing non-crop plant reproduction. Agroecological management supporting beneficial insect interactions may feedback to help restore functional non-crop plant populations and associated biodiversity, potentially reducing the frequency of management interventions (e.g. re-sowing wildflower strips).

KEYWORDS

agri-environment, ecological intensification, parasitoid, pollinator, seed herbivore, seed set, trophic interactions, wildflower strips

1 | INTRODUCTION

Conventional intensive agriculture (large-scale monocultures with intensive agrochemical inputs) homogenises landscape structure and reduces biodiversity, thereby jeopardising ecological processes that underpin agricultural productivity and resilience (Aizen et al., 2019; Dainese et al., 2019; Kovács-Hostyánszki et al., 2017; Potts et al., 2016). Mitigating the environmental crisis and safeguarding our food security and other ecosystem benefits requires a transformation of management to achieve a sustainable agriculture (Garibaldi et al., 2017; Kovács-Hostyánszki et al., 2017; Vanbergen et al., 2020). Agroecological farming is a nature-inspired approach that aims to harness functional biodiversity and ecological processes for yield assurance through spatio-temporal crop diversification, increased ecological infrastructure and reduced external inputs (Garibaldi et al., 2017; Petit et al., 2015; Vanbergen et al., 2020). Such practices elevate plant diversity and availability of habitat resources supporting beneficial biodiversity from field to landscape scales (Kovács-Hostyánszki et al., 2017; Potts et al., 2016; Steffan-Dewenter et al., 2001).

This agroecological increase in biotic heterogeneity from field to landscape scales is likely to modulate the antagonistic and mutualistic interactions that regulate plant reproduction and populations (Shackelford et al., 2013). At community levels, floral resource diversity drives adaptive foraging and colony reproduction of bees (Carvell et al., 2015; Jha & Kremen, 2013; Vaudo et al., 2016) influencing reproduction of non-crop plants inhabiting agroecosystems (Van Reeth et al., 2019; Windsor et al., 2021). Nectar diversity or amount can similarly support natural enemy lifecycles, diversity and the top-down regulation of insect herbivores (Dainese et al., 2019; Tschumi et al., 2016). Plant phenological development, for instance the flowering period, may also play a key role in shaping biotic heterogeneity that influences species interactions: a concurrent bloom

of flowering species can increase the diversity and abundance of food sources for antagonistic and mutualistic arthropods (Junker et al., 2013). Phenological succession of trophic resources may, however, play a role in sustaining insect populations over time (Memmott et al., 2010) and the temporal efficacy of ecological infrastructure should be considered in any agroecological interventions.

Greater plant diversity under agroecological management may also modify the interplay between non-crop and crop species affecting insects that use those resources (Shackelford et al., 2013). Although non-crop plants can compete with crops (Adeux et al., 2019; Colbach & Cordeau, 2018), they supply trophic resources supporting insect populations providing ecosystem services (Campos et al., 2020; Kovács-Hostyánszki et al., 2017; Monticelli et al., 2020). The complex connections between non-crop flowers and crops via multiple interactions of both abundant and rare insect species (Ebeling et al., 2012; Gorden & Adler, 2018; Sauve et al., 2016), and how this plant–insect nexus responds to agroecological management remain poorly understood (Petit et al., 2018; Van Reeth et al., 2019).

Plant reproduction also depends on soil nitrogen (N) availability and photosynthetic processes that support the physiological mechanisms (e.g. cellular redox processes) involved in pollination (e.g. meiosis, pollen self-incompatibility) and fruit or seed set (Ramirez & Herrera, 2017; Traverso et al., 2013). Individual plant quality, particularly nitrogen levels, may therefore directly enable the increase in seed production capacity and indirectly shape antagonistic and mutualistic interactions by increasing the strength or frequency of tri-trophic and plant–pollinator interactions (Monticelli, Bishop, et al., 2022; David et al., 2019).

Using a farm-scale agroecological experiment, we assessed how individual reproduction (seed set) of pollinator-dependent, non-crop plants (*Cyanus segetum* L., *Centaurea jacea* L., Asteraceae) and their antagonistic or mutualistic interactions was affected by

agroecological management modifying floral diversity and abundance. We tested the impact on seed set of individual plant quality (C/N ratio) and agroecological practices implemented at either plant community (sown wildflower or grass-legume margins) or local landscape scales (diversification and cover of mass flowering crops, semi-natural habitat area, zero tillage occurrence). We predicted elevated seed production where greater abundance and diversity of crop and non-crop floral resources correspondingly increased activity and diversity of pollinators on focal plant flowers. We also predicted that greater nectar resources by supporting adult seed herbivores/parasitoids would lead to increased larval seed herbivory and parasitism rates of larval seed herbivores. Finally, we expected that differences in plant species phenology (*C. segetum* and *C. jacea* bloom early and late in the season respectively) would dictate which management factors and floral resources interacted to affect levels of interspecific insect interactions affecting seed set.

2 | MATERIALS AND METHODS

2.1 | Experimental design

The experiment was performed (2019) at the INRAE CA-SYS platform (Bretenière, France, 47°19'06.7"N 5°04'17.6"E), an arable farm-scale system experiment (125 ha). This aims to test pesticide-free, biodiversity-based agroecological management utilising diverse spatio-temporal crop rotations (wheat, barley, corn, soybeans, peas, chickpeas, lupins, mustard, rapeseed, sunflower), tillage regimes (\pm) and planned ecological infrastructure (permanent semi-natural habitat, wildflower or grass-legume strips) (see [Appendix S1](#), [Figure S1](#); [Vanbergen et al., 2020](#); [Petit et al., 2021](#)). Sixteen plots ≥ 150 m apart were established in the centre of wildflower ($n = 10$ plots) or grass-legume ($n = 6$ plots) field margins (species composition – [Table S1](#)) across the CA-SYS platform ([Figure S2](#)). Into each plot, we randomly transplanted three triplets of *C. segetum* and *C. jacea* (nine randomly selected plants per species per plot = 288 plants), with individual plants within a triplet 50 cm apart and triplets separated by 1 m within a plot ([Figure S2](#)). No permits or special licences were required for any of the fieldwork or sampling.

2.2 | Focal plant species

Cyanus segetum (syn. *Centaurea cyanus* L.) and *Centaurea jacea* L. were selected as focal plant species because they are widely distributed in Europe, depend on pollinators for reproductive success and attract seed herbivores (Tephritidae; Diptera) and their parasitoids (Hymenoptera) ([Ouvrard et al., 2018](#); [Steffan-Dewenter et al., 2001](#)). *C. segetum* is an annual, pseudo-self-compatible, archaeophyte species flowering May–July with a segetal habit (i.e. it grows in cereal fields) and often included in wildflower seed mixtures. *C. jacea* is a self-incompatible perennial that flowers between June and October occurring in field margins and semi-natural areas. *C. segetum* seed

(<http://www.arbiotech.com>) was germinated ($22 \pm 3^\circ\text{C}$; 16-hr light; 8-hr dark) and maintained in controlled environment cabinets (4 February 2019–4 March 2019 at $8\text{--}10^\circ\text{C}$ 12hr:12hr; thereafter $15\text{--}18^\circ\text{C}$) until transplantation into field plots (11 March 2019–12 March 2019). *C. jacea* replicates were field collected (7 March 2019–13 March 2019) at the pre-reproductive stage (rosette ~ 10 mature leaves) from nearby locations (CA-SYS platform: 47°14'32.2"N 5°05'11.8"E; Dijon: 47°19'06.7"N 5°04'17.6"E; Champdôtre: 47°10'42.5"N 5°17'02.0"E) and transplanted into the plots (12 March 2019–15 March 2019) after washing their roots free of soil.

2.3 | Focal plant chemical quality

To quantify the individual capacity for reproduction (seed set) according to their uptake of soil nitrate or ammonium, we took a random sample of mature leaves (~ 5 g) prior to the onset of flowering (13 May 2019) from each *C. jacea*/*C. segetum*. After oven drying (48 hr, 80°C) and milling (diameter $\leq 80 \mu\text{m}$, re-dried 80°C , 24 hr), we used a Thermo Scientific FLASH 2000 Organic Elemental Analyzer™ to quantify the C/N content in 4–6 mg of these ground tissue samples. Sample injection and oxidation (O_2 under helium flow at 950°C) followed by reduction (Nox) and removal of excess $\text{O}_2/\text{H}_2\text{O}$ (Cu at 750°C /anhydron) yielded N_2 and CO_2 . Gas chromatography (Porapak column 40°C in stationary phase) separated and detected (catharometer) the component N, CO_2 and He. Integrated examination of signal peaks and calibration curves allowed determination of % N and % C dry weight (g).

2.4 | Mass flowering crops, non-crop vegetation and semi-natural habitat

We quantified the abundance and species richness of the non-crop (dicotyledon) plants once per month (from May to August) in sixteen $2\text{m} \times 100\text{m}$ transects along field borders centred on each focal plant plot ([Figure S2](#)). Non-crop floral species richness and floral abundance ([Tables S1](#) and [S2](#)) were recorded in six quadrats ($2\text{m} \times 50\text{cm}$) systematically placed at 20 m intervals along the transect. Flowering plant species (cumulative count) were identified ([Appendix S2](#) for keys) and the total number of inflorescences (individual flower/umbel/spike/capitulum) per quadrat was derived for all species per plot per sampling period ([Figure S2](#)).

Within a radius of 300 m of each plot, we quantified the local landscape composition (ArcGIS Pro 10.8) as: (a) mass flowering crop species richness; and the proportional area of (b) mass flowering crops and (c) semi-natural habitats (woodland, hedges, grass and wildflower strips, vegetation along pathways/tracks) ([Tables S2](#) and [S3](#)). The occurrence of tillage in the fields adjacent to the focal plant plots was pre-determined by the CA-SYS experimental design ([Table S2](#); [Figure S2](#)).

Mean non-crop floral species richness and floral abundance, the proportional area and species richness of mass flowering crops were

calculated separately for *C. segetum* and *C. jacea* to coincide with their species-specific flowering periods and represent their phenological overlap with crop and non-crop floral resources (Figure 1).

2.5 | Focal plant biomass, flower head production and seed set

After flowering (16 July 2019 for *C. segetum* and 9 September 2019 for *C. jacea*), the focal plant flower stalks were harvested and placed in muslin bags. After seed head insects emerged (below), we measured the dry weight of plant biomass (g), the number of flower heads (capitula) and the count (*n*) and mass (g) of seeds per replicate plant. A priori we expected these plant metrics to be highly correlated (Appendix S3 and Figure S4, all $p < 0.001$). Consequently, we chose seed yield (count) as a direct measure of reproductive potential that also indicated other aspects of focal plant performance.

2.6 | Pollinator visitation

Both focal plants and transects were observed (09:30–17:30, dry weather, little wind, $\geq 14^{\circ}\text{C}$) for insect pollinators (mainly Hymenoptera and Diptera, with a single Lepidopteran) fortnightly (*C. segetum*: late May to mid-July; *C. jacea*: mid-July–September). Sampling effort was standardised by observing pollinator visitation for a fixed duration of 30 min (15 min each per focal plot and transect). The order of sampling (plot + transect) on each date was randomised to avoid introducing a systematic bias due to the time of day. Pollinator species observed legitimately visiting a flower (contact with stamen/carpel, nectar or pollen feeding) were captured, killed and stored (70% ethanol) until identification (ZEISS Stemi 2000-C microscope, see Appendix S2 for standard keys, Table S4).

Observations of focal plants provided the number of pollinator individuals and species per focal individual over the season. We supplemented this with transect data (10 surveys) giving pollinator

abundance and species richness on non-focal *C. segetum* (and hybrids with horticultural varieties) or *C. jacea* during the season. This assumed that pollinators foraging on *C. segetum*/*C. jacea* in transects could have visited focal plants (c.f. directly observed interactions) and so comprised a potential pool of visitors active in the vicinity (100m) of our focal plants. Therefore, pollinator abundance and species richness were the sum of insect visits and cumulative count of different species recorded per focal plant individual and focal plant species per transect.

2.7 | Seed herbivores and parasitoids.

After a minimum of 2 months of storage ($20 \pm 3^{\circ}\text{C}$), seed herbivores (Tephritidae; Diptera) and their parasitoids (Hymenoptera) emerged within the muslin bags containing the harvested focal plant capitula. Tephritid seed herbivores and parasitoids were counted and identified using standard keys (Appendix S2) to the highest taxonomic resolution possible (Table S5) (ZEISS Stemi 2000-C). Seed herbivory rate was estimated as the proportional count of seed herbivores per total number of seeds (n/N) per plant. Parasitism rate was the proportional count of parasitoids (n/N) per total potential hosts—estimated as the sum of herbivores and parasitoids emerging per plant and assuming a 1:1 host–parasitoid relationship with no hyper-parasitism (Vanbergen et al., 2006, 2007).

2.8 | Statistical analyses

We used GLMs implemented in R (R Development Core Team, version 3.3.3). For each focal species (*C. segetum* or *C. jacea*), we analysed the response to management predictors of: (a) seed yield, (b) pollinator species richness, (c) pollinator abundance, (d) seed herbivore and (e) parasitoid abundance, and rates of (f) seed herbivory and (g) parasitism of seed herbivores. Models (a–e) were fitted using a negative binomial distribution to correct for overdispersion in count data, and spatial autocorrelation was tested using Moran's *I* (SPDEF package), while models vi–vii were fitted using a quasi-binomial distribution to account for overdispersion. Candidate predictors fitted to these models were: (a) C/N ratio of focal plant individuals; (b) non-crop floral species richness; (c) non-crop floral abundance; (d) mass flowering crop species richness; (e) proportional area of mass flowering crops; (f) proportional area of semi-natural habitat; (g) the occurrence of tillage in the adjacent field (+/-); (h) the number of flower heads per focal plant (insect models only); (i) abundance and species richness of pollinators (seed yield models only); rates of (j) seed herbivory and (k) parasitism rate (seed yield models only); and (l) seed herbivore abundance (parasitoid abundance model only). Models included statistical interactions between pollination factors (pollinator species richness \times pollinator abundance), management factors (proportion of semi-natural habitat \times proportion of co-flowering crop; non-crop floral abundance \times non-crop floral diversity) and the size of floral displays (non-crop floral abundance \times the number of flower heads per focal plant).

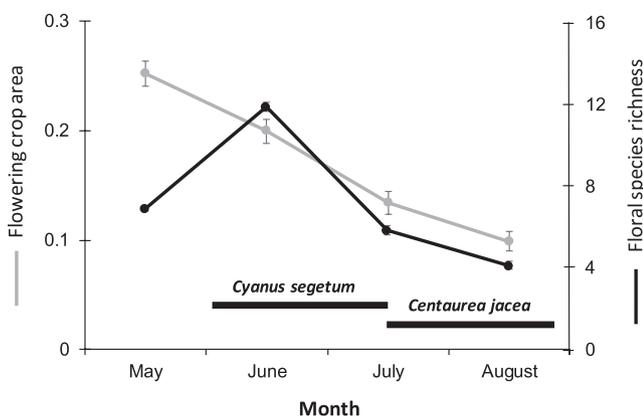


FIGURE 1 Mean (\pm SE) local floral species richness (≤ 100 m) and proportional area of flowering crops (300 m radius) in 2019 (all the plots pooled) centred on focal plant plots. Horizontal black lines indicate focal plant flowering periods.

We report the best fitting model (lowest AICc) from all subsets model comparisons performed with the 'dredge' function in the MuMIn package (Burnham & Anderson, 2002; Figure S6). For each model, explanatory power and goodness-of-fit were assessed using R^2 calculated as: $1 - (\text{residual deviance} / \text{null deviance})$, and the normality of the model residual was checked (visual quantile–quantile plot) except for binomial data since there were a lot of observations with zero prior weights. The ΔAIC of selected models was >2 points away from a null model AIC. Statistical significance of retained variables was determined by analysis of variance (ANOVA) with a χ^2 test, and we estimated and visualised marginal effects of predictors on dependent variables using the GGEFFECTS package.

3 | RESULTS

3.1 | Focal plant reproduction

To precisely align the phenology of mutualistic interactions and seed set, the analysis of floral seed set was constrained to focal plant individuals that flowered during the pollinator surveys (*C. segetum*: 114 individuals—79%; *C. jacea*: 92 individuals—64%). Overall, seed yield (mean count \pm SE) per plant individual was 288.6 ± 34.3 and 1113.2

± 211.6 for *C. segetum* and *C. jacea* respectively. There was an inverse relationship between seed yield and leaf C/N ratio prior to the onset of flowering, indicating the importance of soil N availability and individual chemical composition for reproduction (Table 1; Figure 2).

The seed yield of both species increased with pollinator abundance and decreased with the seed herbivory rate (Table 1; Figure 2). Non-crop floral abundance and species richness in the field margin interacted to facilitate a maximal seed yield for *C. segetum* plants where floral abundance was high and richness correspondingly lowest, while the interaction was not significant for *C. jacea* and seed yield was positively related to both floral abundance and richness (Table 1; Figure 2). Seed yield of *C. jacea* related negatively to the cover of semi-natural habitat (Table 1; Figure 2), whereas *C. segetum* seed yield increased with flowering crop cover where there was a correspondingly high semi-natural habitat cover (Table 1; Figure 2). The occurrence of tillage in the field adjacent to the plot elevated *C. segetum* seed yield almost fivefold, but *C. jacea* was unaffected (Table 1).

3.2 | Pollinator visitation

Thirty-eight pollinator species visited the focal native plants with 376 individuals of 26 species and 88 individuals of 24 species visiting

TABLE 1 Response of individual *Cyanus segetum* and *Centaurea jacea* seed yield to focal plant quality, insect interactions, agroecological management effects (local plant community or landscape structure) and interactions. Coefficients (β) estimated by model averaging and weighted by the selection probabilities with the best model (lowest AICc) derived from all subset comparisons ('dredge' function). Parameters not retained (–).

Predictor		Seed yield/plant individual					
		<i>C. segetum</i>			<i>C. jacea</i>		
		β	χ^2	<i>p</i>	β	χ^2	<i>p</i>
Focal plant quality	C/N ratio	–0.08	239.1	<0.001	–0.06	10.6	0.001
Mutualistic interactions	Pollinator abundance	0.1	76.2	<0.001	0.46	44.8	<0.001
	Pollinator species richness	–0.12	0.5	0.486	–	–	–
	Pollinator abundance \times Pollinator species richness	–	–	–	–	–	–
Antagonistic interactions	Herbivory rate	–2.6	4.7	0.029	–7.88	29.1	<0.001
	Parasitism rate	–	–	–	–	–	–
Agroecological management							
Local plant community ($\leq 100\text{m}$)	Floral species richness	–0.30	2.1	0.147	0.24	5.70	0.017
	Floral abundance	0.003	1.7	0.190	0.001	7.1	0.008
	Floral abundance \times Floral species richness	–0.0002	40.2	<0.001	–0.0003	3.3	0.071
Local landscape composition (300m radius)	Flowering crop species richness	–	–	–	–	–	–
	Flowering crop area	–3.6	1.4	0.236	–	–	–
	Semi-natural habitat area	6.5	19.3	<0.001	–6.1	10.7	0.001
	Flowering crop area \times Semi-natural habitat area	33.5	5.8	0.016	–	–	–
	Flowering crop area \times Flowering crop species richness	–	–	–	–	–	–
	Tillage (\pm)	1.4	18.1	<0.001	–	–	–
R^2		0.77			0.51		

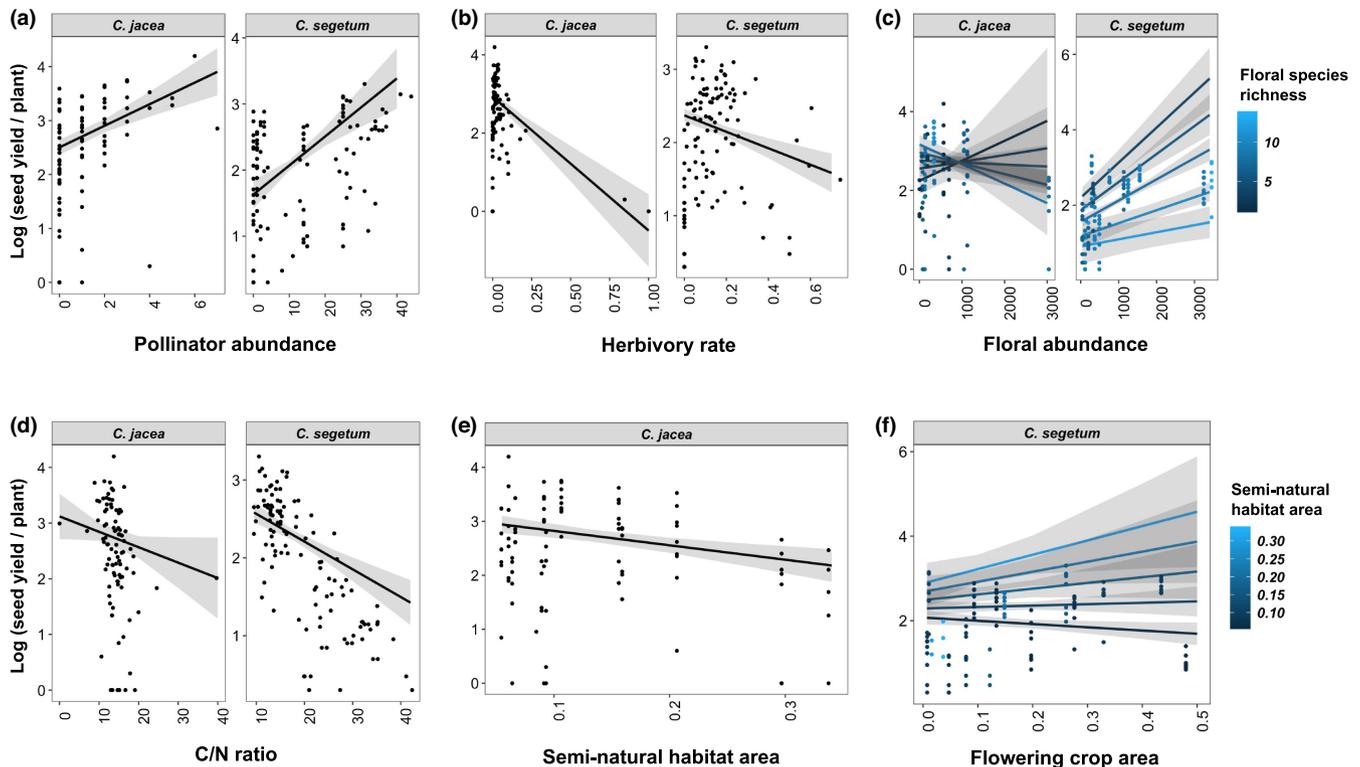


FIGURE 2 *Cyanus segetum* and *Centaurea jacea* seed yield (count) response to (a) pollinator abundance, (b) herbivory rate (n herbivores/N seeds), (c) floral species richness \times abundance in local plant community, (d) focal plant quality (C/N ratio), (e) proportional cover of semi-natural habitat and (f) proportional cover of semi-natural habitat \times proportional of flowering crop area in a 300-m radius plot. Points are raw data and lines are the predicted marginal effects (both log₁₀ transformed for visualisation on the same axis) estimated from the best subset of GLMs (AICc). Shaded area = 95% confidence interval.

C. segetum and *C. jacea* respectively (Table S4; Figure S3). *Apis mellifera* was the dominant pollinator (*C. segetum* 37.5% and *C. jacea* 33%), followed by *Lasioglossum malachurum* (15.7% and 10.2% respectively), for both plant species. The next most abundant bees were *Bombus lapidarius* (8.8%) and *Halictus simplex* group (13.2%) for *C. segetum* and *C. jacea* respectively.

The number of flower heads per focal plant related positively to pollinator abundance for both focal species and richness of *C. jacea* visitors (Table 2). The abundance of pollinators on *C. segetum* related positively to non-crop species richness and negatively to non-crop floral abundance in the border (Table 2). Greater non-crop flower richness increased and decreased richness of pollinators for *C. segetum* and *C. jacea* respectively (Table 2; Figure S5 from Appendix S4).

A significant interaction revealed that *C. segetum* and *C. jacea* received higher abundance and species richness of pollinators where there was greater cover of flowering crops, but only when the corresponding area of semi-natural habitat was very low (<10%) (Table 2; Figure 3; Figure S5). Flowering crop species richness increased the number and richness of pollinators on *C. segetum* when the cover of flowering crops was lower (<20%) (Table 2; Figure 3; Figure S5). Tillage in the adjacent field correlated with reduced species richness and numbers of pollinators on *C. segetum*, but left *C. jacea* unaffected (Table 2).

3.3 | Seed herbivore abundance and herbivory rate

At harvest, 140 (97%) *C. segetum* and 104 (72%) *C. jacea* had completed flowering, with the remainder dead or failed to bloom. *Cyanus segetum* was attacked by a single tephritid seed herbivore *Acanthiophilus helianthi* (6,765 individuals), whereas *C. jacea* was attacked by 2,327 individuals from three tephritid species: *A. helianthi* (81%), *Chaetorellia jaceae* (3.7%) and *Urophora quadrifasciata* (1.2%) (Table S5; Figure S3).

The number of flower heads predicted greater seed herbivore abundance for both focal species (Table S6 from Appendix S4), but only affected *C. segetum* seed herbivory rate (Table 3). This positive relationship between the amount of *C. segetum* flower heads and seed herbivory diminished with greater non-crop floral abundance in the field border (Table 3; Figure 3). *Cyanus segetum* seed herbivory rates related positively to the cover of flowering crops (Table 3). Greater non-crop floral abundance increased *C. segetum* seed herbivory, an effect that was enhanced with increasing flower species richness (Table 3; Figure 3). Seed herbivore abundance on *C. segetum* related positively to the species richness of flowering crops and the cover of semi-natural habitat, but negatively to the non-crop floral richness in the border (Table S6). No other parameters affected *C. jacea* herbivory (Table S6; Table 3).

TABLE 2 Response of pollinator (abundance and species richness) visiting *Cyanus segetum* and *Centaurea jacea* to agroecological management effects (local plant community or landscape structure) and interactions. Coefficients (β) estimated by model averaging and weighted by the selection probabilities with the best model (lowest AICc) derived from all subset comparisons ('dredge' function). Parameters not retained (–).

Predictor	C. segetum pollinator visitation						C. jacea pollinator visitation					
	Abundance			Species richness			Abundance			Species richness		
	β	X ²	p	β	X ²	p	β	X ²	p	β	X ²	p
Focal plant	0.0003	347.5	<0.001	–	–	–	0.004	27.9	<0.001	0.004	24.9	<0.001
Local plant community (≤100 m)												
Number of flower heads	0.84	186.2	<0.001	0.60	77.20	<0.001	–	–	–	–0.2	6.10	0.013
Floral species richness	–0.001	32.6	<0.001	–	–	–	–	–	–	0.003	1.3	0.262
Floral abundance	–0.00008	0.1	0.738	–	–	–	–	–	–	–0.0004	4.1	0.044
Floral abundance × Floral species richness	–	–	–	–	–	–	–	–	–	–	–	–
Floral abundance × Number of flower heads	–	–	–	–	–	–	–	–	–	–	–	–
Local landscape composition (300 m radius)												
Flowering crop species richness	3.1	221.4	<0.001	3.3	86.5	<0.001	1.43	0.3	0.598	1.73	0.003	0.955
Flowering crop area	19	398.4	<0.001	20.5	69.8	<0.001	19.6	8.9	0.003	23.2	7.2	0.007
Semi-natural habitat area	–3.4	132.1	<0.001	2.2	1.8	0.186	–1.6	1.0	0.315	–2	0.007	0.932
Tillage (±)	–0.9	76.4	<0.001	–0.4	11.2	<0.001	–	–	–	–	–	–
Flowering crop area × Semi-natural habitat area	–26.8	6.2	0.013	–55.7	26.7	<0.001	–128.7	8.5	0.004	–182.3	11.8	<0.001
Flowering crop area × Flowering crop species richness	–9.8	127.5	<0.001	–10.7	76.5	<0.001	–9.5	2.4	0.118	–9.5	0.7	0.401
R ²	0.90			0.81			0.35			0.39		

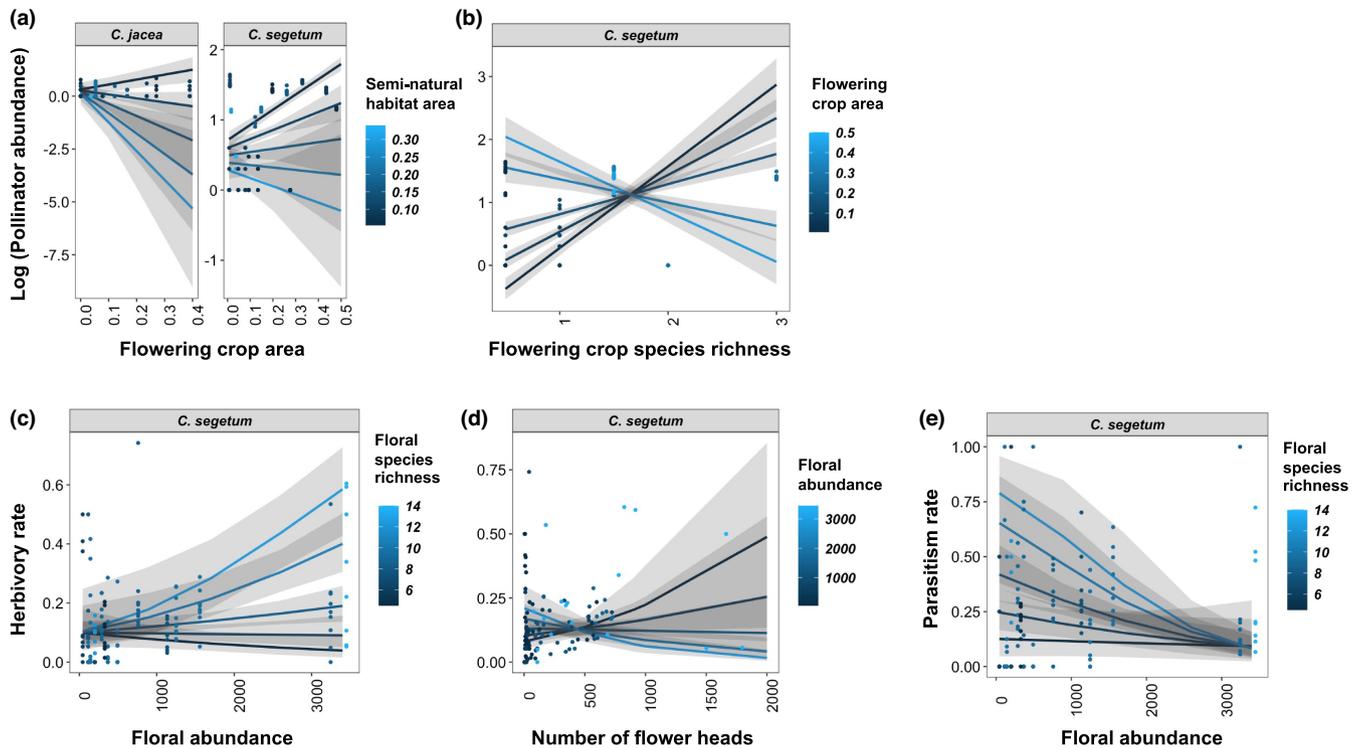


FIGURE 3 Response of mutualistic and antagonistic interactions on *Cyanus segetum* and *Centaurea jacea* to spatial biotic heterogeneity. Relationships of pollinator abundance to (a) proportional flowering crop area × proportional semi-natural habitat area (300m radius) and (b) flowering crop species richness × proportional flowering crop area. Relationships of (c) herbivory rate (n herbivores/ N seeds) and (e) parasitism rate (n parasitoids/ N potential hosts) to floral abundance × floral species richness in the margin, and (d) herbivory rate to the number of flower heads × the floral abundance in the margin. Points are raw data, and lines are the predicted marginal effects (log 10 transformed for visualisation on the same axis for pollinators) estimated from the best subset of GLMs (AICc). Shaded area = 95% confidence interval.

3.4 | Parasitoid abundance and parasitism rate

Cyanus segetum supported 3001 parasitoid individuals from 13 species, while *C. jacea* 383 parasitoid individuals from 11 species (eight species shared between both plants) (Table S5; Figure S3). Parasitism rate of *C. segetum* seed herbivores increased with the number of flower heads per plant and decreased with a greater cover of semi natural habitat, whereas parasitism of seed herbivores on *C. jacea* was increased by greater flowering crop cover (Table 3). Parasitism on *C. segetum* related negatively to non-crop floral abundance in the border, with the slope increasing with greater flower species richness (Table 3; Figure 3).

Parasitoid abundance on *C. segetum* or *C. jacea* increased with the cover of mass flowering crops and the number of flower heads per focal plant (when non-crop floral abundance was low for *C. segetum*) (Table S6; Figure S5). Flowering crop species richness and host insect abundance increased parasitoid abundance on *C. segetum* only (Table S6).

4 | DISCUSSION

Overall, pollinator abundance, but not species richness, promoted seed set of both focal plants with generalist pollinator species

dominating (>50%). Complex spatial interactions between non-crop and crop floral resources, however, modulated both seed set and pollinator visitation (Holzschuh et al., 2016; Montero-Castaño et al., 2016; Van Reeth et al., 2019). While semi-natural cover reduced *C. jacea* seed set, a combination of the highest cover of flowering crops and semi-natural habitats enhanced *C. segetum* seed production. Abundant and diverse pollinators to both focal species were facilitated by a greater extent of nearby flowering crops—although only where semi-natural habitat cover was lowest. This conditionality reflects pollinator resource partitioning or competing attraction of mass flowering crops and semi-natural habitats (Holzschuh et al., 2016; Jha & Kremen, 2013; Montero-Castaño et al., 2016) that affects seed set through the dilution of focal plant visits. This implies greater efficiency of pollinators for *C. segetum* in comparison to *C. jacea* where overall visitation rate was more important for seed production. Finally, as hypothesised, a lower C/N ratio in plant tissues indicating higher soil nutritional quality positively impacted the reproduction of both focal plant species. Floral abundance and diversity in surrounding crop fields and field margins also interacted to modify seed set and pollinator interactions. Seed set for both focal species was maximised by non-crop floral abundance, but only at the lowest non-crop plant diversity. Greater flowering crop diversity in the surrounding area facilitated a spillover of pollinators on *C. segetum*

TABLE 3 Response of seed herbivory rate (Tephritidae) and parasitism rate (Hymenoptera) on *Cyanus segetum* and *Centaurea jacea* to agroecological management effects (local plant community or landscape structure) and interactions. Coefficients (β) estimated by model averaging and weighted by the selection probabilities with the best model (lowest AICc) derived from all subset comparisons ('dredge' function). Parameters not retained (-).

Predictor	<i>C. segetum</i>						<i>C. jacea</i>					
	Herbivory rate			Parasitism rate			Herbivory rate			Parasitism rate		
	β	X ²	p	β	X ²	p	β	X ²	p	β	X ²	p
Focal plant	0.001	16.6	0.372	0.00014	169.2	<0.001	-	-	-	-	-	-
Local plant community (≤100m)												
Number of flower heads	0.0005	157.8	0.006	0.35	21.50	0.143	-	-	-	-	-	-
Floral species richness	-0.00063	257.5	<0.001	0.0003	153.6	<0.001	-	-	-	-	-	-
Floral abundance	0.0001	188.7	0.003	-0.00011	59.2	0.015	-	-	-	-	-	-
Floral abundance × Floral species richness												
Floral abundance × Number of flower heads	-7.7E-07	195.3	0.002	-4.5E-07	4.2	0.517	-	-	-	-	-	-
Local landscape composition (300m radius)												
Flowering crop species richness	-	-	-	-	-	-	-	-	-	-	-	-
Flowering crop area	1.58	245.3	<0.001	-	-	-	-1.3	67.9	0.101	4	96.3	<0.001
Semi-natural habitat area												
Tillage	-0.36	28.1	0.244	-9.13	75.8	0.006	-	-	-	-	-	-
Flowering crop area × Semi-natural habitat area	-	-	-	-	-	-	-	-	-	-	-	-
Flowering crop area × Flowering crop species richness	-	-	-	-	-	-	-	-	-	-	-	-
R ²	0.31			0.32			0.05			0.21		

at the lowest level of flowering crop cover, while non-crop floral richness attracted and floral abundance deterred pollinators. *C. segetum* visitation and seed production were therefore maximised where there were sufficient floral displays to attract the dominant generalist pollinators (Bauer et al., 2017; Fowler et al., 2016). High floral diversity, however, diluted *C. segetum* visitation, potentially due to an increase in heterospecific foraging (Jha & Kremen, 2013; Vaudo et al., 2016) that decreased conspecific pollen deposition and contributed to lower seed set (Eckert et al., 2010). These complex spatial interactions reflect the dynamic nature of pollinator foraging among floral resource patches varying in nutritional quality and quantity (Fowler et al., 2016; Jha & Kremen, 2013; Kleijn et al., 2015; Vaudo et al., 2016).

Habitat or plant diversity context modified also seed herbivory and parasitism. Seed herbivore parasitism of *C. jacea* was elevated by greater mass flowering crop cover which may have been linked to reduced herbivory pressure. For *C. segetum*, differential responses of herbivores and parasitoids to management-driven heterogeneity at different scales produced a more complex outcome (Kruess, 2003). Mass flowering crop cover increased the *C. segetum* herbivory rate (but not parasitism); while greater non-crop abundance and diversity within the field margin elevated herbivory (individual recruitment), reduced parasitism and decreased seed yield. At the scale of *C. segetum* individuals, the positive relationship between herbivory and seed availability (flower heads) was mitigated or inverted by greater non-crop floral abundance.

Different mechanisms therefore governed antagonisms and seed set of *C. segetum*. Alternative larval host individuals and species or pollen/nectar sources for foraging herbivore adults in the heterogeneous floral margins may have uplifted *C. segetum* seed herbivory (Vanbergen et al., 2006). At low level of floral diversity, higher host plant resources in the margin are not sufficiently attractive to seed herbivores and a higher number of flowering plant individuals may have diluted herbivore attack rates on the focal plants (Nitschke et al., 2017; Otway et al., 2005). Alternatively, the highest levels of floral diversity providing complementary food resources may have increased the attractiveness of the field margin to herbivores, increasing the seed herbivory rate (Vanbergen et al., 2006). Similarly, highest parasitism rate was recorded for the highest levels of floral diversity suggesting a strong attractiveness of the diverse field margin to parasitoids (Lavandero et al., 2006; Tschumi et al., 2016). Increasing the number of flowering plants may, however, have (a) diluted parasitoid attack rates on the focal plants since a greater number of herbivores was recruited compared to the parasitoids, or (b) interfered with the bouquet of visual and olfactory signals used for host location reducing parasitoid ability to oviposit in host developing on the focal plants (Gols et al., 2005; Nitschke et al., 2017; Randlkofer et al., 2010). Therefore, the greater diversity of the community floral display created costs for *C. segetum* seed yield by direct herbivore recruitment and reduced herbivore parasitism rates, alongside reproductive gains from elevated pollination arising from their foraging on nearby crop and non-crop resources.

Intrinsic focal plant phenology shaped how agroecosystem complexity affected seed production and mutualistic and antagonistic interactions. Local field management ($\leq 300\text{m}$) affected both focal plant species interactions, while only *C. segetum* insect interactions were affected by sown flower strips ($\leq 100\text{m}$ along field edges). *Cyanus segetum* is a segetal species pre-adapted to heterospecific competition for pollination services and its peak flowering coincided with a major bloom of diverse wildflowers and mass flowering crop species. Whereas *C. jacea* typically inhabits marginal habitat and was phenologically constrained to flower outside the peak of mass flowering crops (Figure 1), and so inhabited an agroecosystem relatively poor in floral resources and pollinator interactions. During *C. segetum* flowering, therefore foraging insects responded to multiple simultaneous, sometimes competing, floral signals from highly diverse crop and non-crop assemblages. In contrast, during *C. jacea* flowering, the cover of late season mass flowering crops (sunflower) and semi-natural habitat along with the size of individual floral displays solely dictated insect interactions (Fowler et al., 2016; Jha & Kremen, 2013; Mallinger et al., 2016). Such differences in phenology and community composition may therefore explain the observed patterns in seed herbivory. The greater agroecological complexity during *C. segetum* flowering may have promoted the abundance of the generalist seed herbivore (*Acanthiophilus helianthi*) able to utilise alternative hosts available in the highly diversified floral situation. By contrast, the efficacy of the specialist herbivores monophagous on *C. jacea* phenologically constrained by their host plant to operate in a lower diversity agroecosystem remained able to rely on co-evolved host-specific cues to locate them (Jonsen & Fahrig, 1997; Nitschke et al., 2017).

4.1 | Synthesis and applications.

Agroecological practices (crop diversification, reduced tillage intensity, use of agroecological infrastructure) in a zero-pesticide farmed environment interact to affect the reproduction of non-crop plants and interactions with mutualists and antagonists. The phenology of the focal plant species was key to shaping how they interacted with insects and the farmed environment (Stanley & Stout, 2014). When the floral diversity and abundance of the agroecosystem was maximal, the balance of the antagonistic interactions only weakly regulated *C. segetum* reproduction compared to the uplift in seed production associated with pollinator activity. Conversely, *C. jacea* flowered in the period characterised by fewer and less diverse floral resources and only the agroecological practices and ecological infrastructure at the farm scale promoted parasitism rate and pollinator activity which in sum increased seed yield. Species flowering phenology is thus crucial to the interplay of agroecological management with mutualistic and antagonistic interactions governing non-crop plant reproduction. It remains to be seen how these ecological interactions persist or develop as the present study was conducted in a single year and the recently established ecological infrastructure (2018) will promote a new community over time.

Overall, our models predicted (R^2) seed yield of the focal plants and variation in pollinator diversity and abundance to a higher level than rates of herbivory or parasitism (although variation in herbivore and parasitoid abundances were predicted to a similar level to pollinators). This suggests that farm management practices designed to increase beneficial insects at the farm level (here 125 ha) are likely effective in elevating pollinator biodiversity and pollination functions (Kovács-Hostyánszki et al., 2017), but that more complex effects on natural biocontrol processes may prevail, at least for tephritid seed herbivory of non-crop plants. In contrast, agricultural practices do promote other taxa (e.g. carabid beetles) in ways that deliver effective non-crop seed regulation (Carbonne et al., 2020).

Our data illustrate how agroecological management practices can modify pollination/biocontrol processes affecting seed production of non-crop plants through spatial gradients in heterospecific flower cover and diversity that affect foraging insect behaviour. How such management affects the interplay of crops and non-crop plants competing for soil resources and mutualistic services within fields remains to be established. Although *C. segetum* is an arable segetal weed that can reduce cereal and oilseed rape yields (Bellanger et al., 2012), co-occurring cereal crops do not attract or interact with pollen- or nectar-feeding insects, so the outcome for the insect-mediated reproductive outcome for *C. segetum* would completely differ where it is relatively isolated within a flower-poor cereal field. By contrast, co-occurring oilseed rape may benefit *C. segetum* seed yield due to their overlapping flowering phenology. We did not concurrently measure flowering crop performance alongside non-crop plant reproduction. However, our results may inform further tests of the hypothesis that phenological overlap is a key predictor of the relative balance of mutualistic and antagonistic interactions between co-occurring blooms of non-crop and crops within fields (cf. field edges) and their reproduction and yield outcomes.

Understanding the strength of mutualistic and antagonistic interactions affecting the reproduction of non-crop flowering plants can help to conceive agroecological systems that support plant biodiversity providing substantial floral rewards to pollinators and natural enemies (Ouvrard et al., 2018). Restoration of these plant populations, such as certain *Centaurea*, *Cyanus*, *Cirsium* spp., within ecological infrastructures will elevate functional biodiversity with potential spillover of ecosystem services to crops. Agroecological management that support beneficial insect interactions may feedback to contribute to the restoration of these high-quality plant species, potentially reducing the need for frequent management interventions for farmers (e.g. re-sowing wildflower strips) while conserving/preserving biodiversity in agricultural systems. Such knowledge can contribute to the critical scientific and policy objective of facilitating the transition to a sustainable agriculture.

AUTHORS' CONTRIBUTIONS

A.J.V., V.D. and S.C. conceived the ideas and designed the methodology; L.B.-D., M.T., E.F., E.L., A.M. and E.V. collected the data; L.S.M. and A.L. identified the insects; L.S.M. analysed the data; L.S.M. and

A.J.V. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.00000005q> (Monticelli, Labonté, et al., 2022).

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