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Wildflower plantings have mixed effects on insect herbivores and their natural enemies

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ABSTRACT

Flower strips are advocated as a strategy to promote beneficial insects as well as the services they deliver to adjacent crops. Flower strips have, however, often been developed separately for pollinators and natural enemies and, additionally, little consideration has been given to effects on insect herbivores. We sampled insect herbivores, their natural enemies and parasitism of pest eggs using vacuum sampling, sticky cards and egg cards in nine pairs of bee-attractive wildflower plantings and control field borders, as well as in adjacent tomato and watermelon crop fields in Yolo County, California 2015–2016. Control field borders had a higher total number of herbivores on sticky traps than did wildflower plantings, a pattern that was driven by more aphids, hoppers, psyllids and whiteflies, whereas wildflower plantings had more lace bugs and Lygus bugs. The total number of herbivores in the adjacent crop fields did not differ between treatments, but there were more leaf beetles near (at 10 m but not 50 m from) wildflower plantings. Control field borders had a higher total number of predators, driven by more big-eyed bugs, lady beetles and minute pirate bugs, whereas spiders were more common in wildflower plantings. The total number of predators in adjacent crop fields was, however, higher in those next to wildflower plantings, which was driven by more minute pirate bugs. Parasitoid wasps were more common in wildflower plantings and at 10 m but not 50 m into adjacent crop fields. Stink bug egg parasitism rate did not differ between treatments, either in the borders or in the crop fields. In conclusion, wildflower plantings clearly affect the insect herbivore and natural enemy community, but do so in a highly taxon-specific manner, which can lead to both positive and negative outcomes for pest control as a result.

1. Introduction

Flowering agricultural field borders are widely promoted as a strategy to mitigate threats to pollinators from agricultural intensification (Gill et al., 2016; IPBES, 2016). Flower rich field border habitats are often effective in attracting large numbers of insect pollinators relative to unenhanced field borders (Zamorano et al., 2020; Lowe et al., 2021; Carvell et al., 2022). They can also promote pollinator persistence (M'Gonigle et al., 2015) and enhance pollinators in surrounding landscapes (Jönsson et al., 2015; Bommarco et al., 2021), although their effects on pollination and crop yields are more variable (Albrecht et al., 2020; Zamorano et al., 2020; Lowe et al., 2021). Research on supplementing natural enemies' use of pollen and nectar from flower plantings has largely been developed in parallel to the literature on flower plantings for pollinators (Fiedler et al., 2008; Wratten et al., 2012) and shown potential to improve pest control in adjacent crop fields (Albrecht et al., 2020). Only recently has the potential for multifunctional habitats that benefit both pollinators and natural enemies been explored (Balzan et al., 2016; Morandin et al., 2016; Campbell et al., 2017; Sutter et al., 2018a; Grab et al., 2018). For this reason, it remains largely unclear to what extent flower plantings targeting pollinators enhance natural enemies to crop pests and pest control services.

Provision of nectar and pollen is thought to be a main mechanism by which flower plantings favor natural enemies (Heimpel and Jervis, 2005). Flower plantings might also provide natural enemies shelter and protection from disturbances such as pesticide exposure, supplement alternative prey, and offer overwintering habitat (Haaland et al., 2011; Ganser et al., 2019; Boetzl et al., 2022). The same set of mechanisms might, however, also favor insect herbivores (Lavandero et al., 2006; Wäckers et al., 2007; Sutter et al., 2018b). A further key consideration when designing flower plantings for pollinators and natural enemies is therefore their direct effects on crop pests (Sidhu and Joshi, 2016).

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Considering flower plantings in an integrated pest and pollinator management perspective (Lundin et al., 2021) will make plantings more cost effective (Morandin et al., 2016) and increase likelihood of adoption (Garbach and Long, 2017). While effects of flower plantings on individual herbivore species or groups such as leaf beetles or aphids are well documented (Tschumi et al., 2015, 2016; Cahenzli et al., 2019; Boetzl et al., 2020; Raderschall et al., 2022; Fountain, 2022), less is known about how flower plantings more broadly affect the community of herbivorous insects (but see Blaauw and Isaacs, 2015).

Measuring the abundance of insect herbivores and their natural enemies only in the flower plantings themselves and comparing them to control field borders is not sufficient for drawing clear conclusions for pest control in adjacent crop fields. This is because higher herbivore numbers in field borders could imply either herbivore spillover to the crop, or alternatively that herbivores are drawn away from the crop, thereby reducing their numbers in the crop (‘trap cropping’, Hokkanen, 1991). Moreover, providing habitat for non-crop herbivores in field borders could promote natural enemies, and thereby increase their numbers in the crop (‘banker plants’, Huang et al., 2011). Similarly, for the natural enemies, plantings that attract higher numbers in field borders often promote, but can occasionally also disrupt their spillover into adjacent crop fields (Gontijo, 2019). Assessments of the implications of flower plantings for pest control should therefore consider simultaneous effects on herbivores and their natural enemies in both the field border habitat and in adjacent crop fields.

The aim of this study was to examine how wildflower plantings designed for pollinators affect the abundances of insect herbivores and natural enemies as well as biological pest control potential measured as egg parasitism rate. For this we compared insect herbivores, their natural enemies and egg parasitism in bee-attractive wildflower plantings (Williams et al., 2015; Nicholson et al., 2020), control field borders and adjacent crop fields over two years in the northern part of the Central Valley, California, USA.

2. Materials and methods

2.1. Study design

We conducted the study from 2015 to 2016 in Yolo County California, USA. The study area is characterized by intensive agriculture. We studied nine pairs of wildflower plantings and control field borders and their adjacent fields situated next to the wildflower plantings and control field borders; four pairs in 2015 and five pairs in 2016. The four wildflower plantings studied in 2015 were maintained in the same place and restudied in 2016. The control field borders moved between years in order to match the adjacent crop with each pair, as further detailed below. The distance between wildflower plantings and their paired control field borders was a minimum of 1 km and a maximum of 7 km in order to ensure spatial independence, while still keeping both in the same overall landscape type. Sites in different pairs within a year were also at least 1 km apart. To verify that the landscape composition was similar around wildflower and control sites, we calculated the proportion of cropland in a 1 km radius around each site by interpreting the 2012 Yolo County Map from the National Aerial Imagery Program in ArcGIS 10.3 (ESRI, Redlands, CA). We found that the landscapes were dominated by cropland, and that the proportion of cropland was similar for wildflower planting sites (80%, including 11% orchard crops) and control sites (83%, including 7% orchard crops). Examples of common annual crops grown in the area are processing tomato, sunflower and wheat.

The wildflower plantings were established along crop field edges and were on average 340 m long (range: 150–640 m) and 6 m wide (range: 3–10 m). They were seeded in fall before winter rains with eleven plant species native to California: *Clarkia williamsonii* (Onagraceae), *Eschscholzia californica* (Papaveraceae), *Grindelia camporum* (Astereae), *Lupinus densiflorus* (Fabaceae), *L. succulentus*, *Monardella villosa* (Lamiaceae), *Phacelia californica* (Boraginaceae), *P. ciliata*, *P. tanacetifolia*, *Trichostema lanceolatum* (Lamiaceae) and *Trifolium fucatum* (Fabaceae). The age of the plantings in the season that they were sampled varied between one (established in the previous fall) to three years. The mixture of sown plant species provides continuous bloom from early spring to fall and all species are attractive to bees (Williams et al., 2015; Nicholson et al., 2020). We selected a matching control field border of a similar size for each wildflower planting. These control field borders were managed as per standard management chosen by the landowner, which typically included frequent mowing, herbicide spraying and/or tillage to control weeds. Vegetation cover and height was therefore generally lower in control compared to wildflower borders. We matched wildflower and control fields by crop species and, to the extent possible, crop planting date. In all but one field pair, fields adjacent wildflower plantings and control field borders were also managed by the same grower, which promoted homogeneous crop management within pairs. Our in-field sampling focused on watermelon and tomato, but because we studied perennial wildflower plantings surrounded by diverse annual crops, only seven of the nine site pairs had either tomato or watermelon adjacent and could be sampled. Thus in 2015, we sampled two pairs of watermelon fields, and in 2016 we studied four pairs of tomato fields, as well as a third pair of watermelon fields. All fields were conventionally managed.

We visited and sampled all field borders and field pairs three times each year between late May and early August (watermelon sites: June 2 – August 4; tomato sites: May 25 – August 4). The first sample coincided with crop establishment and bud formation, the second sample was conducted during crop flowering, and the final sample was taken during crop fruit maturation.

2.2. Vegetation and floral area in field borders

During each of the three visits, we identified flowering plant species and quantified their floral area in twenty randomly placed 1 m^2 quadrats along a central transect running the length of the wildflower and control field border habitats. We determined floral area using methods described in Williams et al. (2015). In each quadrat we measured the number of floral units containing open flowers separately by plant species. A floral unit was equal to an individual flower in most cases, but for Asteraceae species one inflorescence (composite flower) was counted as a floral unit. We measured the diameter for actinomorphic flowers, or length and width of zygomorphic flowers, of 5–10 flowers per plant species. From this, we calculated the average floral area per flower per plant species. The floral area per flower for each plant species was then multiplied by the average number of flowers per meter square of that plant species. In 2016 only, we also visually estimated the proportions of vegetation and bare ground cover in the wildflower and control field borders. Vegetation cover was divided into sown species (for wildflower borders), other broadleaf plants and grasses.

2.3. Pests and natural enemies

We vacuum sampled arthropods in the wildflower and control field borders using a modified leaf blower (Stihl, Norfolk, VA, USA). We took four vacuum samples each in the wildflower and control field border at each of the three visits. The vacuum was run for 30 s on two square meters of live vegetation for each sample. Arthropods were collected in one-gallon fine mesh paint strainer bags (Trimaco, Morrisville, NC, USA) placed over the intake of the vacuum. In 2015, samples were frozen at − 20 C̊ and we later separated arthropods from vegetation in the laboratory. Because separation of arthropods from vegetation in the thawed samples was time consuming, we adjusted the method in 2016 and instead put the vacuum samples in modified Berlese traps at the end of each field day. These samples were placed on plastic mesh sieves inside the traps. The modified Berlese traps had two collecting vials with ethylene alcohol (30%); one at the top of the trap for flying arthropods and one at the bottom for crawling arthropods. The traps were left at room temperature for at least 24 h. We searched through vegetation remaining on the sieve under a microscope and collected any dead arthropods before discarding the sample.

We also sampled pests and natural enemies using yellow sticky traps (76 *127 mm, BioQuip, Rancho Dominguez, CA, USA). At each of the three visits, four traps each were placed adjacent to vegetation in the wildflower and control field borders, as well as 10 m and 50 m into the adjacent crop fields, for a total of 24 sticky traps per site pair and visit. We left the traps out for a week, after which we retrieved them from the field, marked and wrapped them in plastic, and put them in a freezer for later processing. In the laboratory, we counted and identified insects and spiders on half of the trap area of each sticky trap: the two outer thirds of one side of the trap, and the center third of the other side of the trap. Only half of the area on each sticky trap was assessed due to resource constraints.

Taxonomic identifications of specimens in vacuum samples and on sticky traps followed Lundin et al. (2019) and were based on arthropod functional roles: herbivores, predators and parasitoid wasps. Identification of specimens varied from order to genus level depending on the variation in feeding habits within taxa. The most common arthropods that were not classified into any of our functional groups were Diptera, Coleoptera or Miridae specimens that had omnivorous, scavenging or unknown feeding habits. The taxonomic level and life stages that we considered for each taxon are specified in Table S1.

2.4. *Pest control experiment*

We performed a pest control experiment using stink bug (Hemiptera: Pentatomidae) eggs. We chose stink bugs because they are generalist pests of multiple crops in the study area, including tomato and watermelon (ipm.ucdavis.edu). We experimentally determined stink bug egg parasitism following established protocols (Ehler, 2000; Morandin et al., 2014). We collected adult consperse stink bugs (*Euschistus conspersus* Uhler) in spring and early summer in each year. Adults were kept in containers at ambient light and temperature in the laboratory. We fed the stink bugs fresh green beans and sunflower seeds, and provided paper towels as oviposition substrate. Egg masses produced were cut out from the towels every second or third day and put in the freezer at − 25 °C.

During the second (crop flowering, 2015) or third visit (crop fruit maturation, 2016), eight egg masses each were attached to the underside of leaves using hair clips in the wildflower and control field borders, as well as to crop leaves 10 m and 50 m into the adjacent crop fields, for a total of 48 egg masses per site pair. Egg masses were deployed later in the season in the second year because it took longer time to establish experimental stink bug colonies and rear sufficient amounts of egg masses in the laboratory. Egg masses were left in the field for 5 (2015) to 7 days (2016). They were collected into plastic bags perforated with a needle for ventilation, and left in the lab at room temperature for at least one month. Egg masses were assessed for parasitism and predation following Morandin et al., 2014. Egg predation was rare and is not considered further. We regarded eggs as parasitized if they either had a parasitoid emerge, partially emerged or if the egg had a dark black color (Ehler, 2000; Morandin et al., 2014). Parasitism rate was calculated as the number of parasitized eggs divided by the total number of eggs (excluding the eggs lost due to predation).

2.5. *Statistical analyses*

For all analyses, all samples taken among visits were aggregated for each field border habitat and for on-crop data at each field distance. We did not analyze the three visits to each site individually in order to avoid excessive zeros in data and facilitate model convergence. In comparisons of field border habitat types, we analyzed taxonomic groups that were present on at least half of the habitats ($\geq$ 9 of the 18 wildflower and control habitats) with at least 50 individuals in total (vacuum samples: 16 groups, Table 1; sticky traps: 13 groups, Table 2). In all analyses of within-field distances we used all groups that were present on at least half ($\geq$ 14) of the 28 crop-field-by-distance combinations with at least 100 individuals in total (12 taxonomic groups; Table S2) to facilitate model convergence and fulfill model assumptions. Additionally, we analyzed overall herbivore and predator densities for each sampling method in the field border habitats as well as in the adjacent crop fields.

We analyzed differences between field border habitats and between distances within crop fields in relation to adjacent border treatment using generalized mixed effects models (‘glmmTMB’). Models for differences between wildflower plantings and control field borders included the factors ‘field border habitat type’ (wildflower planting or control) and ‘year’ (2015 or 2016) as fixed effects and the field pair as random intercept. The model for egg parasitism rates additionally accounted for zero inflation in the data. Models for within-field effects included the factors ‘field border habitat type’, ‘distance’ (10 m or 50 m), their interaction ‘field border habitat type: distance’ and ‘year’ as fixed effects and site identity (individual crop field) nested in field pair as random intercept. The model for egg parasitism rates in the crop fields additionally accounted for zero inflation in the data. To account for a low number of lost samples (one vacuum sample and three sticky traps), all models except the model for egg parasitism included the number of samples as offset (log transformed to fit the residual distributions used, Table S3, Table S4). Due to limited sample size, study years were not analyzed separately and no interactions with the study year were included in the models. All results presented are thus averaged over the two years. As all but one watermelon site was sampled in the first year and all tomato sites were sampled in the second year, it was further not possible to include crop type in addition to year in the models. The study year acts as a control variable in our analyses, but we do not discuss further any significant effects of this variable.

All models were checked for the suitability of the chosen residual distributions, under- and overdispersion and zero inflation using the ‘DHARMa’ package (version: 0.4.4, Hartig, 2022) and optimized where necessary. Final models used Poisson or negative binomial residual distributions, except models for egg card parasitism rates which used a beta regression residual distribution (Table S3, Table S4). Models were tested using type 2 Wald χ^2 tests using the command ‘Anova’. All model predictions represent estimated marginal means with 95% confidence interval (CI; command ‘ggemmeans’).

All statistical analyses were performed in R 4.1.2 for Windows, using the packages ‘car’ (version: 3.0–12, Fox and Weisberg, 2019), ‘effectsize’ (version: 0.5.0.10, Ben-Shachar, Lüdecke and Makowski, 2020), ‘ggeffects’ (version: 1.1.1, Lüdecke, 2018) and ‘glmmTMB’ (version: 1.1.2.9000, Brooks et al., 2017).

3. Results

3.1. *Vegetation*

Wildflower planting habitats had an average cover of 23.8% sown forbs, 1.3% other broadleaved plants, 0.3% grasses and 21.0% bare ground. Control field borders had an average cover of 13.7% broadleaved plants, 2.7% grasses and 63.6% bare ground (remaining ground was covered with dead vegetation and residual leaf litter in both treatments). Floral area was approximately seven times higher in wildflower planting compared to control field borders (wildflower planting: 5733 cm^2, 95% CI: 3080 – 10,671 cm^2; control: 859 cm^2, 95% CI: 457 – 1615 cm^2; $\chi^2 = 64.51$, $p < 0.001$). Great Valley gumweed (*Grindelia camporum*) provided the majority of floral area in the wildflower plantings (93%) and field bindweed (*Convolvulus arvensis*) in the control field borders (90%, Table S5).

Table 1

Accumulated counts (N) and statistical test results for all taxonomic groups collected by vacuum sampling in the field border habitats in both years. Predicted values represented estimated marginal means obtained from the fitted models with 95% confidence interval (CI). $\chi 2$ = chi-square value; p = p-value; R^2_m = marginal R^2. (*) indicates $p < 0.1$; * indicates $p < 0.05$; ** indicates $p < 0.01$; *** indicates $p < 0.001$.

taxonomic group		wildflower planting		control				2015		2016				
	N_{total}	N	predicted [CI]	N	predicted [CI]	χ^2	p	N	predicted [CI]	N	predicted [CI]	χ^2	p	R^2_m
Herbivores	12432	5667	671.08 [387.27; 1162.87]	6765	690.39 [404.97; 1176.97]	0.01	0.937	7298	899.65 [506.95; 1596.52]	5134	514.99 [308.82; 858.80]	2.38	0.123	0.16
aphids (Aphidoidea)	2906	133	13.82 [5.66; 33.71]	2773	259.21 [109.80; 611.90]	26.20	**< 0.001** ***	2227	110.50 [44.12; 276.78]	679	32.41 [14.07; 74.66]	4.55	**0.033** *	0.74
butterflies & moths (Lepidoptera)	133	39	3.53 [1.51; 8.26]	94	9.42 [4.32; 20.52]	3.40	**0.065 (*)**	35	3.61 [1.48; 8.80]	98	9.20 [4.38; 19.35]	3.01	**0.083 (*)**	0.27
Calocoris bugs (*Calocoris* sp.)	11	1		10				10		1				
ebony bugs (Thyreocoridae)	10	10		0				10		0				
fruit flies (Tephritidae)	11	10		1				8		3				
grasshoppers & crickets (Orthoptera)	6	5		1				3		3				
hoppers (Auchenorrhyncha)	5089	3164	320.36 [160.31; 640.19]	1925	178.29 [93.64; 339.46]	2.39	0.122	3170	356.02 [162.76; 778.80]	1919	160.43 [81.17; 317.09]	2.86	**0.091 (*)**	0.28
lace bugs (Tingidae)	1374	1185	117.43 [27.68; 498.28]	189	8.27 [1.52; 45.07]	7.75	**0.005** **	312	30.35 [4.90; 187.99]	1062	31.99 [6.88; 148.81]	< 0.01	0.962	0.46
leaf beetles (Chrysomelidae)	333	231	25.92 [11.99; 56.04]	102	11.24 [5.12; 24.69]	2.70	0.100	183	20.88 [9.21; 47.35]	150	13.96 [6.65; 29.28]	0.62	0.431	0.18
leaf-footed bugs (Coreidae)	10	8		2				10		0				
leafminers (*Liriomyza* sp. (Agromyzidae))	151	58	6.59 [3.13; 13.91]	93	10.08 [4.92; 20.65]	0.78	0.377	82	9.62 [4.47; 20.70]	69	6.91 [3.44; 13.90]	0.47	0.492	0.06
Lygus bugs (*Lygus* sp.)	214	174	18.26 [12.26; 27.20]	40	4.08 [2.50; 6.65]	37.73	**< 0.001** ***	131	12.39 [7.49; 20.47]	83	6.01 [3.73; 9.71]	5.47	**0.019** *	0.47
psyllids (Psyllidae)	791	19	1.56 [0.69; 3.55]	772	64.62 [33.14; 125.99]	252.32	**< 0.001** ***	458	14.74 [5.54; 39.23]	333	6.85 [2.62; 17.89]	1.57	0.210	0.47
scale insects (Coccoidea)	25	0		25				0		25				
seed bugs (Lygaeidae)	801	519	61.96 [27.86; 137.79]	282	29.63 [13.59; 64.61]	1.97	0.161	398	51.81 [22.48; 119.40]	403	35.43 [16.80; 74.75]	0.52	0.473	0.17
stink bugs (Pentatomidae)	115	75	7.87 [4.52; 13.69]	40	4.26 [2.34; 7.76]	2.67	0.102	39	4.68 [2.50; 8.76]	76	7.17 [4.23; 12.18]	1.27	0.260	0.11
vinegar flies (Drosophilidae)	6	6		0				6		0				
weevils (Curculionidea)	19	13		6				3		16				
whiteflies (Aleyrodidae)	427	17	1.57 [0.51; 4.82]	410	47.79 [19.22; 118.83]	23.50	**< 0.001** ***	213	6.33 [2.11; 18.99]	214	11.84 [4.65; 30.14]	0.80	0.372	0.75
Predators	2702	1056	111.99 [83.43; 150.32]	1646	172.97 [128.68; 232.49]	7.30	**0.007** **	1663	201.23 [141.69; 285.79]	1039	96.26 [69.76; 132.84]	11.22	**< 0.001** ***	0.46
assassin bugs (Reduviidae)	46	36		10				31		15				
big-eyed bugs (*Geocoris* spp.)	360	97	9.89 [5.34; 18.33]	263	27.90 [15.48; 50.28]	6.89	**0.009** **	240	26.77 [14.37; 49.88]	120	10.31 [5.75; 18.49]	5.83	**0.016** *	0.40
damsel bugs (Nabidae)	12	4		8				6		6				
ground beetles (Carabidae)	4	1		3				2		2				
hoverflies (Syrphidae)	9	4		5				2		7				
lacewings (Chrysopidae)	28	21		7				15		13				
lady beetles (Coccinellidae)	52	5	0.55 [0.18; 1.68]	47	5.26 [2.79; 9.91]	14.52	**< 0.001** ***	23	1.78 [0.74; 4.26]	29	1.64 [0.73; 3.70]	0.02	0.880	0.44
mantids (Mantodea)	1	0		1				1		0				
minute pirate bugs (Anthocoridae)	1146	263	21.86 [11.53; 41.45]	883	74.16 [39.82; 138.13]	23.14	**< 0.001** ***	702	60.50 [26.19; 139.75]	444	26.80 [12.52; 57.38]	2.44	0.119	0.40
rove beetles (Staphylinidae)	5	1		4				5		0				
soft-winged flower beetles (Melyridae)	172	129		43				136		36				
spiders (Araneae)	867	495	54.35 [41.50; 71.17]	372	41.23 [30.70; 55.37]	2.30	0.129	500	61.01 [45.58; 81.66]	367	36.73 [27.89; 48.36]	7.66	**0.006** **	0.22
Parasitoid wasps (Parasitica)	3139	1714	186.64 [108.66; 320.57]	1425	143.07 [83.65; 244.69]	0.57	0.451	2111	262.35 [148.63; 463.09]	1028	101.78 [61.07; 169.64]	7.14	**0.008** **	0.34

Table 2

Accumulated counts (N) for all taxonomic groups collected with sticky traps in the field border habitats in both years. Predicted values represented estimated marginal means obtained from the fitted models (see text) with 95% confidence interval (CI). χ2 = chi-square value; p = p-value; R2m = marginal R2. (*) indicates $p < 0.1$; * indicates $p < 0.05$; ** indicates $p < 0.01$; *** indicates $p < 0.001$.

taxonomic group		wildflower planting		control				2015		2016				
	N_{total}	N	predicted [CI]	N	predicted [CI]	χ^2	p	N	predicted [CI]	N	predicted [CI]	χ^2	p	R^2_m
Herbivores	7150	1816	183.49 [129.50; 259.99]	5334	530.34 [375.97; 748.09]	71.03	**< 0.001** ***	4694	461.51 [287.44; 741.01]	2456	210.86 [137.84; 322.55]	7.08	**0.008** **	0.65
aphids (Aphidoidea)	2357	343	35.12 [21.33; 57.82]	2014	196.05 [121.82; 315.52]	49.10	**< 0.001** ***	1560	120.20 [65.95; 219.07]	797	57.28 [33.02; 99.36]	3.89	**0.048** *	0.67
butterflies & moths (Lepidoptera)	171	76	5.80 [3.65; 9.21]	95	7.27 [4.64; 11.40]	2.16	0.141	30	3.56 [1.83; 6.92]	141	11.86 [7.03; 20.00]	9.50	**0.002** **	0.24
fruit flies (Tephritidae)	5	0		5				3		2				
hoppers (Auchenorrhyncha)	1394	393	36.47 [25.78; 51.59]	1001	101.88 [73.03; 142.15]	21.27	**< 0.001** ***	1031	119.32 [84.17; 169.15]	363	31.14 [22.36; 43.36]	36.32	**< 0.001** ***	0.70
lace bugs (Tingidae)	105	101		4				6		99				
leaf beetles (Chrysomelidae)	136	67	7.54 [4.69; 12.12]	69	7.61 [4.77; 12.15]	< 0.01	0.978	67	8.36 [5.12; 13.65]	69	6.87 [4.37; 10.80]	0.40	0.527	0.01
leafminers (Liriomyza (Agromyzidae))	871	259	18.13 [8.80; 37.35]	612	66.41 [32.45; 135.93]	11.78	**< 0.001** ***	559	55.32 [21.81; 140.28]	312	21.77 [10.21; 46.42]	2.75	**0.097 (*)**	0.43
Lygus bugs (*Lygus* sp.)	67	57	5.47 [2.18; 13.75]	10	0.91 [0.28; 2.93]	6.72	**0.010** **	51	4.60 [1.70; 12.42]	16	1.08 [0.37; 3.21]	4.58	**0.032** *	0.45
psyllids (Psyllidae)	434	137	15.20 [9.54; 24.21]	297	30.82 [19.26; 49.34]	7.00	**0.008** **	211	24.36 [14.34; 41.37]	223	19.23 [11.49; 32.21]	0.47	0.492	0.18
scale insects (Coccoidea)	7	4		3				0		7				
scarab beetles (Scarabaeidae)	5	1		4				3		2				
seed bugs (Lygaeidae)	483	182	20.52 [9.92; 42.46]	301	33.11 [16.24; 67.48]	1.03	0.310	252	29.76 [13.93; 63.57]	231	22.83 [11.54; 45.16]	0.31	0.576	0.08
stink bugs (Pentatomidae)	3	2		1				1		2				
weevils (Curculionidea)	14	0		14				13		1				
whiteflies (Aleyrodidae)	1098	194	13.40 [5.68; 31.62]	904	49.03 [21.23; 113.25]	20.56	**< 0.001** ***	907	40.36 [12.42; 131.17]	191	16.28 [5.74; 46.15]	1.57	0.211	0.31
Predators	591	260	24.75 [17.17; 35.69]	331	35.82 [25.36; 50.60]	3.70	**0.054 (*)**	385	44.40 [29.09; 67.79]	206	19.97 [13.51; 29.51]	9.06	**0.003** **	0.29
beeflies (Bombyliidae)	1	1		0				1		0				
big-eyed bugs (*Geocoris* spp.)	62	6	0.59 [0.22; 1.56]	56	5.75 [3.60; 9.19]	20.91	**< 0.001** ***	44	3.32 [1.79; 6.19]	18	1.02 [0.47; 2.18]	8.86	**0.003** **	0.53
dragonflies & damselflies (Odonata)	4	0		4				0		4				
ground beetles (Carabidae)	3	0		3				0		3				
hoverflies (Syrphidae)	28	4		24				2		26				
lacewings (Chrysopidae)	7	5		2				3		4				
lady beetles (Coccinellidae)	43	11		32				19		24				
minute pirate bugs (Anthocoridae)	178	43	3.53 [2.17; 5.72]	135	11.30 [7.59; 16.81]	41.49	**< 0.001** ***	142	14.48 [8.68; 24.14]	36	2.75 [1.52; 4.97]	21.76	**< 0.001** ***	0.51
predatory stink bugs (Pentatomidae)	1	1		0				1		0				
rove beetles (Staphylinidae)	26	10		16				8		18				
soft-winged flower beetles (Melyridae)	170	133		37				144		26				
spiders (Araneae)	68	46	4.68 [2.99; 7.35]	22	2.18 [1.26; 3.77]	6.45	**0.011** *	21	2.34 [1.30; 4.19]	47	4.37 [2.78; 6.88]	3.56	**0.059 (*)**	0.15
Parasitoid wasps (Parasitica)	10184	6398	682.74 [449.22; 1037.67]	3786	404.01 [264.03; 618.18]	4.47	**0.034** *	4676	505.80 [310.38; 824.26]	5508	545.34 [354.70; 838.42]	0.06	0.802	0.20

3.2. Arthropods in field borders

In vacuum samples, the total number of herbivores did not differ between treatments (Fig. 1a, Table 1). Among the herbivore groups that were sufficiently abundant in vacuum samples to analyze individually, there were more aphids, psyllids and whiteflies in control field borders, and there also tended to be more butterflies and moths, while there were more lace bugs and Lygus bugs in wildflower plantings (Fig. 1a, Table 1). On sticky traps, more herbivores were found in control field borders compared to wildflower plantings (Fig. 1a, Table 2). Among the herbivore groups that were sufficiently abundant on sticky traps to analyze individually, there were more aphids, hoppers, leafminers, psyllids and whiteflies in control field borders while there were more Lygus bugs in wildflower plantings (Fig. 1a, Table 2).

In vacuum samples, the total number of predators was higher in control field borders while the number of parasitoid wasps did not differ between treatments (Fig. 1b, Table 1). Among the predator groups that were sufficiently abundant in vacuum samples to analyze individually, there were more big-eyed bugs, lady beetles and minute pirate bugs in control field borders (Fig. 1b, Table 1). On sticky traps, the total number of predators tended to be higher in control field borders while the number of parasitoid wasps was higher in wildflower plantings (Fig. 1b, Table 2). Among the predator groups that were sufficiently abundant on sticky traps to analyze individually, there were more big-eyed bugs and minute pirate bugs in control field borders, while there were more spiders in wildflower plantings (Fig. 1b, Table 2).

3.3. Arthropods in the crop

The total number of herbivores in crop fields declined with distance to field border but did not differ between treatments (Fig. 2a, Table 3). Among the herbivore groups that were sufficiently present to analyze individually, there were more leaf beetles in crop fields next to wildflower plantings but only at 10 m and not at 50 m into the crop (Fig. 2h). There were more butterflies and moths in crop fields next to control field borders (Fig. 2f), and more psyllids in crop fields next to wildflower plantings (Fig. 2l, Table 3).

The total number of predators was higher in crop fields next to wildflower plantings irrespective of distance to field border (Fig. 2b, Table 3). Among the predator groups that were sufficiently present to analyze individually, minute pirate bug densities were higher next to wildflower plantings (Fig. 2k).

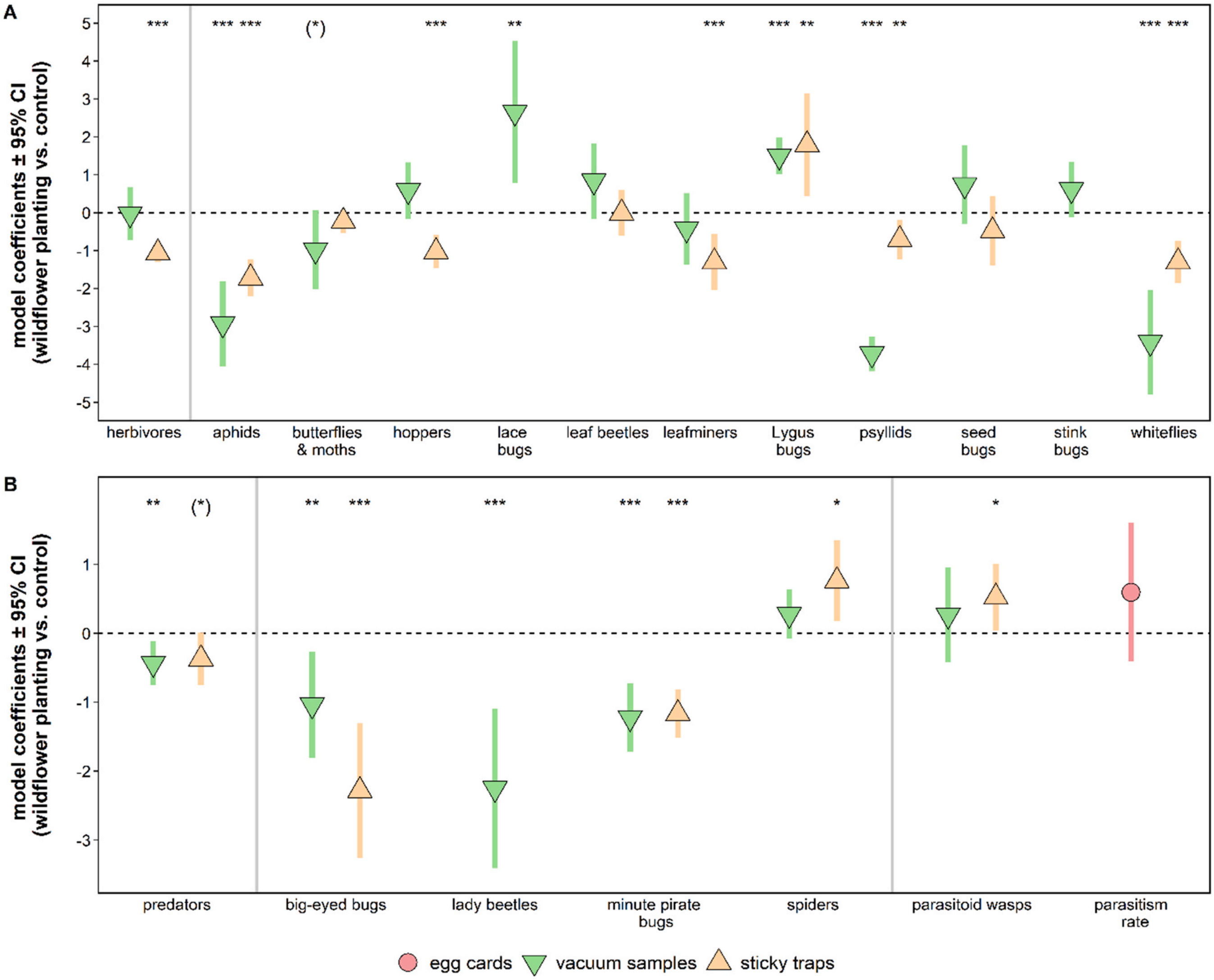

Fig. 1. Model coefficients for the wildflower planting compared with control field border (positive values indicate the response is higher in the wildflower planting than in the control field border) for insect herbivores (a) and arthropod predators, parasitoid wasps and egg parasitism (b). (*) indicates $p < 0.1$; * indicates $p < 0.05$; * * indicates $p < 0.01$; * ** indicates $p < 0.001$. Colors / symbols indicate different methods (see legend). For statistics, unstandardized model estimates and scientific names for all groups see Tables 1–2.

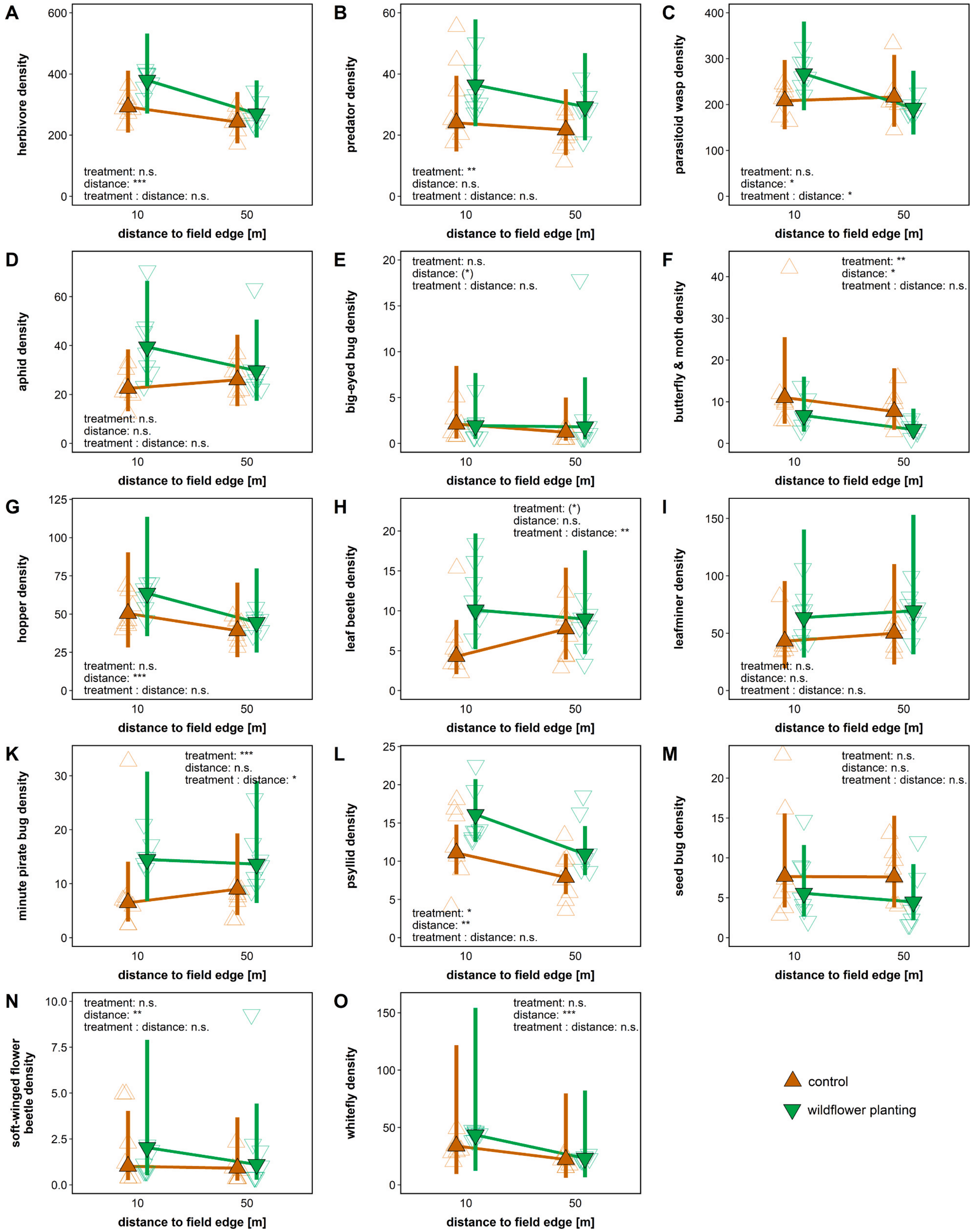

Fig. 2. Predicted densities of arthropod groups in crop fields adjacent wildflower and control field borders; (a) all herbivores, (b) all predators, (c) parasitoid wasps, (d) aphids, (e) big-eyed bugs, (f) butterflies and moths, (g) hoppers, (h) leaf beetles, (i) leafminers, (k) minute pirate bugs, (l) psyllid bugs, (m) seed bugs, (n) soft-winged flower beetles and (o) whiteflies (estimated marginal means with 95% confidence interval). Open symbols represent partial residuals. Colors / symbols indicate different adjacent border treatments (green: wildflower planting; brown: control border; see legend). n.s. indicates $p > 0.1$, (*) indicates $p < 0.1$; * indicates $p < 0.05$; * * indicates $p < 0.01$; * ** indicates $p < 0.001$. For statistics and scientific names for all groups see Table 3.

Table 3
Model results for the different responses (herbivores total and seven herbivore groups, predators total and three predator groups, parasitoid wasps and parasitism rate) within the crop fields adjacent to two different field border habitats (wildflower planting or control) at different within-field distances (10 m or 50 m) and in the two years obtained from type II Wald χ^2 tests. χ^2 = chi-square value; p = p-value; R^2_m = marginal R^2. (*) indicates $p < 0.1$; * indicates $p < 0.05$; ** indicates $p < 0.01$; *** indicates $p < 0.001$. Accumulated counts (N) can be found in Table S2.

	border treatment		distance		treatment: distance		year		
response	χ^2	p	χ^2	p	χ^2	p	χ^2	p	R^2_m
Herbivores	1.20	0.274	15.92	**< 0.001** ***	1.38	0.240	14.54	**< 0.001** ***	0.54
aphids (Aphidoidea)	2.37	0.124	0.25	0.620	1.99	0.159	4.86	**0.028** *	0.23
butterflies & moths (Lepidoptera)	6.67	**0.010** **	4.10	**0.043** *	0.44	0.509	1.13	0.287	0.24
hoppers (Auchenorrhyncha)	1.17	0.279	21.72	**< 0.001** ***	0.55	0.458	15.45	**< 0.001** ***	0.57
leaf beetles (Chrysomelidae)	3.15	**0.076 (*)**	1.12	0.290	7.78	**0.005** **	11.22	**< 0.001** ***	0.35
leafminers (*Liriomyza* sp. (Agromyzidae))	1.58	0.209	0.65	0.421	0.04	0.840	5.19	**0.023** *	0.34
psyllids (Psyllidae)	5.92	**0.015** *	9.65	**0.002** **	0.04	0.839	38.53	**< 0.001** ***	0.24
seed bugs (Lygaeidae)	1.28	0.258	0.13	0.716	0.14	0.708	8.82	**0.003** **	0.21
whiteflies (Aleyrodidae)	0.16	0.691	35.99	**< 0.001** ***	1.40	0.237	0.60	0.440	0.09
Predators	9.61	**0.002** **	2.19	0.138	0.23	0.63	29.66	**< 0.001** ***	0.66
big-eyed bugs (*Geocoris spp.*)	0.06	0.800	3.25	**0.071 (*)**	1.78	0.182	8.62	**< 0.001*****	0.37
minute pirate bugs (Anthocoridae)	38.43	**< 0.001** ***	0.68	0.411	4.10	**0.043** *	16.14	**< 0.001** ***	0.61
soft-winged flower beetles (Melyridae)	0.30	0.586	7.02	**0.008** **	0.95	0.330	9.71	**0.002** **	0.28
Parasitoid wasps (Parasitica)	0.35	0.557	4.04	**0.044** *	6.22	**0.013** *	6.61	**0.010** *	0.39
Egg card parasitism rate	0.218	0.640	0.925	0.336	1.47	0.225	0.30	0.584	0.33

The total number of parasitioid wasps was higher in crop fields next to wildflower plantings, but only at 10 m and not at 50 m into the crop (Fig. 2c, Table 3).

3.4. Egg parasitism

Stink bug egg parasitism rate did not differ between treatment or study years, either in the borders (treatment: $\chi^2 = 1.35$, $p = 0.246$, wildflower planting: 0.26, 95% CI: 0.14–0.43, control: 0.16, 95% CI: 0.07–0.33, Fig. 1b; year: $\chi^2 = 0.01$, $p = 0.992$, 2015: 0.20, 95% CI: 0.08–0.43, 2016: 0.20, 95% CI 0.11–0.34) or in the crop fields (Fig. S1, Table 3).

4. Discussion

Wildflower plantings along field borders affected herbivore and natural enemy communities in a highly taxon-specific manner. In addition, wildflower plantings in several cases increased or decreased the abundance of a taxon in the border habitat, but had no effect or even an opposite effect in the adjacent crop field. Flower plantings have been shown to have similarly variable effects on pollinators between the border and adjacent crop habitat. In that case, plantings consistently enhance pollinator diversity in the border habitat but not in the adjacent crop fields, and thus do not generally increase crop pollination and yield (Zamorano et al., 2020). Our study illustrates that positive effects of flower plantings on pest control (Albrecht et al., 2020) are not universal across cropping systems, and that effects could additionally vary depending on the taxon considered within a single cropping system. In adjacent crop fields, effects of wildflower plantings on predators and parasitoid wasps were mostly positive, but egg parasitism was not affected and impacts on herbivores were variable. Further research is thus needed on how to achieve pest control benefits from flower plantings through a more consistent reduction of herbivore population sizes in adjacent crop fields, in turn reducing crop damage and increasing crop yield.

Control field borders had a higher total number of herbivores on sticky traps compared with those at wildflower plantings, a pattern which was driven by related groups of aphids, hoppers, psyllids and whiteflies in the hemipteran suborders Auchenorrhyncha and Sternorrhyncha. On the other hand, lace bugs and Lygus bugs in the hemipteran suborder Heteroptera were more abundant in the wildflower plantings. Differences in the vegetation composition and structure of the two field border habitats might explain these results. Higher grass cover in control field borders might have favored Auchenorrhyncha and Sternorrhyncha, which contain many grass-feeding species (Huusela-Veistola et al., 2016). In contrast, wildflower plantings favored Heteroptera, which contains many forb-feeding species (Huusela-Veistola et al., 2016). Lace bugs are minor pests on shrubs and trees that were not found in the adjacent crops, while Lygus bugs are important pests in several field crops (ipm.ucanr.edu). Wildflower plantings have previously been shown to harbor more Lygus bugs than control field borders (McCabe et al., 2017; Grab et al., 2018); however, those studies were in a different climatic region and landscape context. Lygus bug numbers were low in adjacent watermelon and tomato fields compared to borders irrespective of treatment and while more abundant in crop fields next to wildflower plantings, their densities were too low to be analyzed statistically. These patterns suggest multiple potential strategies for managing Lygus, for example by excluding preferred host species from planting designs. Alternatively wildflower plantings could be approached like a trap crop to retain and distract Lygus from adjacent crops (Godfrey and Leigh, 1994; Shelton and Badenes-Perez, 2006). Such a strategy could, however, require mowing to limit buildup of Lygus bug populations, which tradeoff against other goals of the planting, such as provision of continuous floral resources for beneficial arthropods throughout the season.

The total number of herbivores in adjacent tomato and watermelon fields declined with distance to field border but did not differ between treatments. Certain taxa were, however, more abundant in fields adjacent wildflower plantings and other taxa were more abundant in fields adjacent control field borders. We found more leaf beetles (at 10 m but not 50 m from) and psyllids (all distances) near wildflower plantings. Leaf beetles include several important pest species such as flea beetles (Alticinae) and cucumber beetles (*Acalymma trivittatum* and *Diabrotica undecimpunctata undecimpunctata*). Although cucumber beetles in watermelon can be managed using insecticides, the net effect on crop yield of doing so could be negative because of reduced flower visitation by wild bees (Pecenka et al., 2021). The greater number of psyllids in the crop fields next to wildflower plantings despite there being fewer psyllids in the wildflower plantings compared to control field borders further illustrates complexities of managing organism spillover between border plantings and crop fields. Differences in psyllid abundance might have been caused by control field borders effectively working as a trap that reduced their numbers in the adjacent fields, or by wildflower plantings providing resources and facilitating spillover of only a subset of psyllid species to adjacent crop fields. In contrast butterflies and moths, which also include important regional crop pests (ipm.ucanr.edu), were more common in crop fields next to control borders. Butterflies and moths tended to be more common in vacuum samples in control field borders, so perhaps control field borders provide more suitable habitat compared to wildflower plantings for butterflies and moths, which subsequently lead to spillover and increase their abundance in adjacent fields. Our results highlight the need for future studies that identify herbivore groups to pest and non-pest species in order to better understand organism spillover between field border and crop habitats. More generally, our work illustrates the tight coupling between management of pollinators and pests. Integrated management of pests and pollinators for this reason holds promise for achieving both crop pollination and pest control goals (Lundin et al., 2021).

The higher number of predators in control field borders in vacuum samples were driven by big-eyed bugs, lady beetles and minute pirate bugs, which might have been attracted to the higher numbers of prey such as aphids, psyllids and whiteflies (Flint and Dreistadt, 1998). Ladybeetles for example, often show an aggregational response to aphid densities (Schellhorn and Andow, 2005). Spiders were the only predator group that was more common in wildflower plantings, on the sticky traps. This might have been due to a more suitable vegetation structure and microclimate provided by the sown forb species (Sunderland and Samu, 2000), and is in line with findings that flower strips promote spider activity density (Raderschall et al., 2022). In addition, crab spiders, which were observed on flowers in wildflower plantings (O. Lundin, pers. obs.), likely benefitted from the increased densities of flowers and associated flower visiting insects on which these spiders feed (Dukas and Morse, 2003). In line with earlier findings (see e.g., Gurr et al., 2017), parasitoid wasps were more common in wildflower plantings on sticky traps even though several groups of herbivores on which they might depend were more common in control field borders. Additional nectar resources provided by the sown forbs likely attracted parasitoid wasps and augmented their numbers (Jervis and Heimpel 2005). Indeed, Great Valley gumweed (*Grindelia camporum*), which provided the majority of floral area in the wildflower planting over the summer, is an attractive plant for parasitoid wasps (Lundin et al., 2019). More generally, in field borders where we sampled arthropods using both vacuum samples and sticky traps, results varied slightly depending on sampling method. This is likely because sampling method efficiency depends on focal taxon, e.g., sticky traps being more effective than vacuum sampling for parasitoid wasps.

In adjacent crop fields, predators were more common next to wildflower plantings irrespective of distance into the field, a result which was driven by minute pirate bugs. When taken together with our data from the borders themselves, we speculate that in crop fields next to control field borders, these predators are retained in borders due to the higher availability of preferred prey. Prey availability in the wildflower borders was lower and minute pirate bugs might more often have hunted for prey in crop fields, while still benefiting from alternative food in the wildflower plantings in the form of pollen and nectar (Flint and Dreistadt, 1998). Parasitoid wasp numbers were also higher in adjacent crop fields next to wildflower plantings but only at 10 m, indicating that these natural enemies are exported into the fields, but only relatively short distances. This result could be explained by spillover from wildflower plantings to crop field edges or higher prey presence in crop field edges near wildflower plantings, and is in line with the finding that benefits of wildflower plantings quickly decay from field borders towards centers (Albrecht et al., 2020). We found no effect of wildflower plantings on pest control measured as stink bug egg parasitism in either borders or adjacent crop fields, despite parasitoid wasps being more common in wildflower plantings and at 10 m into adjacent crop fields. This might be because the egg parasitoids of consperse stink bugs, which we did not sample specifically, did not benefit from the wildflower plantings and might require nectar through more open and shallow flowers (Ehler, 2000; Pease and Zalom, 2010; Morandin et al., 2014). Our use of frozen egg masses might also have led to an underestimation of egg parasitism and partial masking of differences in egg parasitism between treatments, as they probably only are attractive to parasitoids for a few days in the field before they desiccate (Morandin et al., 2014).

Our study was limited by the reality of rotational cropping patterns in the study region. Despite careful planning, fields adjacent the borders were planted both to watermelon and tomato, and sample sizes were too low to split data between the two crops. Moreover, crop identity and study year were related - all tomato fields and only one watermelon field pair were sampled in the second year – meaning that year and crop effects could not be teased apart. The limited sample sizes and combined analysis of watermelon and tomato fields limited our ability to detect effects of the border treatment on the adjacent crop field, and further inquiry would be needed to identify crop-specific effects. Variation in the age of the wildflower plantings from one to three years and differences in crop management practices such as insecticide use, which we did not record but aimed to control for by standardizing the grower within each wildflower-control site pair, could have affected our results as well. A further limitation is that classification of arthropods into desired (e.g., predators) and undesired groups (e.g., herbivores) is not straightforward. For example, whether individuals within a herbivore group are damaging, neutral or even beneficial (as an alternative prey species) often depends on a combination of herbivore and crop identity (Saunders et al., 2016). Identifying all arthropods to species might have partly overcome this limitation, but was not feasible given the substantial taxonomic expertise needed. Furthermore, for closely related species of some groups (e.g., Homoptera) no keys exist for immature stages.

In summary, our evaluation of wildflower plantings that have been shown to be highly attractive for pollinators (Nicholson et al., 2020) showed variable effects on different groups of arthropod herbivores, predators and parasitoid wasps. There was some evidence for positive effects of wildflower plantings on spillover of important predators and parasitoid wasps, but this did not lead to lower overall herbivore numbers or increased egg parasitism on the adjacent crop. There is thus scope to increase the multifunctionality of the plantings, notably by including plant species with flower morphologies that can provide accessible nectar and pollen to predators and parasitoid wasps, while not benefiting herbivore species of concern (Lundin et al., 2019). Wildflower plantings require time and money to establish, and sometimes they also take agricultural land out of production. With this in mind, further research on how wildflower plantings can be tailored to provide multiple benefits, while limiting their liabilities, will improve the outcome of their cost-benefit analysis and contribute more integrated strategies for pest and pollinator management.

Declaration of Competing Interest

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

Data Availability

Data will be made available on request.

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Author’s contribution

OL, KLW and NMW designed the study, OL collected data, FAB analyzed data, and OL and FAB wrote the first draft of the manuscript. All authors interpreted the results, revised the manuscript and gave final approval for publication.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2023.108587.

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