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# The success of a habitat specialist biological control agent in the face of disturbance

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## Abstract

Natural enemies that can use multiple habitats are thought to better withstand disturbances in agricultural systems than natural enemies that are habitat specialists. This is because habitat generalists have populations in multiple habitats that can serve as sources of immigrants into an agricultural crop following a disturbance. In contrast, the dynamics of habitat specialists are tightly coupled with those of one agricultural crop. Nonetheless, some habitat specialists are successful in highly disturbed environments. To test how the magnitude of within-field disturbance affects biological control agents, we conducted a large-scale field manipulation in alfalfa fields and monitored the response of pea aphids, habitat-generalist predators, a habitat-specialist parasitoid (*Aphidius ervi*), and hyperparasitoids of *A. ervi*. The manipulation involved three treatments: harvesting normally (intermediate disturbance); spraying insecticide immediately after harvesting (high disturbance); and harvesting in strips (low disturbance). As a group, the habitat-generalist predator species showed a range of responses to disturbances, from no response to decreases in abundance in the high-disturbance treatment, indicating differences in their response to the density of pea aphids following disturbances. Surprisingly, percentage parasitism by the habitat-specialist parasitoid was little affected by experimental disturbance manipulations. Furthermore, two of the four hyperparasitoids of *A. ervi* were negatively affected by the magnitude of disturbance, suggesting that disturbance could have an indirect positive effect on *A. ervi*. These results suggest that a habitat specialist can overcome the detrimental effects of disturbances without using alternative habitats. In addition, disturbance can sometimes benefit biological control agents by disproportionally negatively affecting their enemies from the fourth trophic level.

**KEYWORDS**
*Acyrthosiphon pisum*, alfalfa crop system, *Aphidius ervi*, hyperparasitoids, parasitoids, strip harvesting

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## INTRODUCTION

Environmental constancy is generally regarded as favoring the evolution of ecological specialization (Futuyma & Moreno, 1988, p. 212), with disturbances conversely favoring generalization. This is because if disturbances remove some resources, a generalist species has other potential resources to maintain its population. The expectation that generalist species are better able to survive disturbances explains the growing number of studies, showing that species requiring specialized habitats are the most sensitive to anthropogenic disturbances (Clavel et al., 2011). Many agricultural systems are highly disturbed by harvesting and other management activities (Tooker et al., 2020). This has led to the presumption that generalist natural enemies of agricultural pests have advantages over specialists in highly disturbed agroecosystems (Doutt & DeBach, 1964; Gámez-Virués et al., 2015). For crops that experience regular disturbances from harvesting or insecticide application, for example, surrounding undisturbed areas act as a source for generalist natural enemies that can rapidly return to fields following disturbances to the control pest populations (Landis et al., 2000; Redlich et al., 2018; Thies & Tscharntke, 1999).

Generalization and specialization can be discussed in many ways, but one that is especially useful for understanding biological control agents in agricultural systems is their use of habitats, including different crops and noncrop areas. Biological control agents that are habitat generalists feed either on a variety of prey species or on prey species that are themselves generalists. Therefore, control agents that are habitat generalists may have multiple source populations in the landscape (Lami et al., 2020; Martin et al., 2019). In contrast, biological control agents that are habitat specialists are restricted in their distribution (Lami et al., 2020). For example, parasitoids that feed on a host confined predominantly to a single crop species would be a habitat specialist. This potentially makes habitat specialists particularly sensitive to disturbances to the crop harboring their target pest. Diet specialization is another way to classify natural enemies, but diet specialization gives little direct information about the potential importance of habitats outside a disturbed crop for successful pest control; for example, a diet specialist parasitoid that parasitizes a single host would still be able to use a variety of habitats if its host is a generalist that feeds on many crop types, and perhaps natural vegetation.

Biological control agents may also differ in how they are directly or indirectly affected by the within-field disturbance itself (Tooker et al., 2020). For example, if natural enemies have a relatively immobile life stage, such as larval lady beetles or parasitoid larvae within wingless hosts, then insecticide application or harvesting could lead to high mortality. Disturbances could also have indirect effects on natural enemy populations by reducing pest densities. If natural enemies show positive prey density-dependent immigration, then their populations will remain low until pest populations have started to recover from the disturbance. In contrast, if immigration is high even at low pest density, a natural enemy could impose control before pest densities reached high levels (Costamagna et al., 2015; Ives & Settle, 1997). Furthermore, natural enemies with short generation times could reproduce within fields following disturbances, providing subsequent control of pests. Thus, the effects of disturbance on biological control depend not only on the size of source populations of control agents and their immigration into disturbed fields, but also on the dynamics of the control agents within fields following disturbances.

Finally, natural enemies may have natural enemies of their own, and therefore, it is necessary to consider the effects of disturbances not only on pests and control agents but also on the natural enemies of the control agents (Schellhorn et al., 2015). Many parasitoid biological control agents, for example, are themselves parasitized by hyperparasitoids. Hyperparasitoids have similar life-history traits to primary parasitoids, but hyperparasitoids often attack a wider range of parasitoid species (host generalists). Therefore, they might use habitats differently from biological control agents (Rand et al., 2012). Furthermore, many hyperparasitoids have a longer developmental time than the primary parasitoids they attack, and increases in their population are further delayed by the time it takes their host (parasitoid) population to build in a field following a disturbance. Therefore, hyperparasitoids are likely to respond differently to disturbance events than the parasitoids they attack.

To investigate the effects of within-field disturbances on biological control agents, we focused on natural enemies of pea aphids (*Acyrthosiphon pisum*), a pest of alfalfa (lucerne). We designed a whole-field experiment to examine the response of the alfalfa community to different levels of disturbance by increasing or decreasing the magnitude of disturbance at harvesting. The experimental manipulation involved three treatments: harvesting normally (intermediate disturbance), spraying insecticide immediately after harvesting (high disturbance), and harvesting in strips (low disturbance). At our study site, pea aphids are attacked by a range of predators including lady beetles, damsel bugs, and minute pirate bugs, in addition to the parasitoid wasp *Aphidius ervi* (Braconidae). *Aphidius ervi* is attacked by four common species of hyperparasitoids, which can play an important role in biological control systems (Schooler et al., 1996; Schooler et al., 2011; Tougeron & Tena, 2019) and potentially

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**TABLE 1** Landscape sources of natural enemies in the region surrounding the study site in Dane County, Wisconsin

| Variable or organism | Alfalfa | Soybean | Maize |
|---|---|---|---|
| Proportion of farmland | 20% | 15% | 36% |
| Fields sampled per year | 10 | 5 | 5 |
| Years sampled | 5 | 5 | 5 |
| *Coccinella septempunctata* | 0.28 ± 0.09 | 1.70 ± 1.19 | 0.27 ± 0.12 |
| *Harmonia axyridis* | 0.13 ± 0.04 | 7.69 ± 3.43 | 0.64 ± 0.26 |
| *Coleomegilla maculata* | 0.09 ± 0.02 | 0.28 ± 0.12 | 0.88 ± 0.37 |
| Pirate bugs | 1.75 ± 0.40 | 1.65 ± 1.04 | 0.40 ± 0.19 |
| Damsel bugs | 1.28 ± 0.38 | 0.21 ± 0.14 | 0.05 ± 0.01 |
| Adult *Aphidius ervi* | 1.11 ± 0.02 | 0 | 0 |

*Note*: Natural enemies were sampled twice (alfalfa) or once (soybean and maize) a week during the months of the summer, 2013–2017. In alfalfa, natural enemies were sampled with a sweep net, and in soybean and maize, natural enemies were visually counted per plant. Densities of natural enemies are standardized approximately to 10 $m^2$ (±SE).

reduce the effectiveness of *A. ervi*. Finally, alfalfa is a perennial crop that is harvested three to four times over the summer, and these harvests are disturbance events that kill a large proportion of aphids and natural enemies. We assessed response not only of the pea aphid population and their natural enemies to the experimental disturbance manipulation but also of the growth of alfalfa, since data on habitat manipulation for the first trophic level (crop) are often lacking (Gurr et al., 2000).

## MATERIALS AND METHODS

### Study system and organisms

The study was conducted in the Arlington Agricultural Research Station, Dane County, Wisconsin, USA. The agricultural (nonurban) areas in Dane County are dominated by three crop types—maize, soybean, and alfalfa—together amounting to about 70% of the landscape (Wisconsin Agricultural Statistics, 2005–2006) (Table 1). The pea aphid system in alfalfa is particularly well suited to manipulative within-field experiments owing to the short generation times of aphids and the variety of different natural enemies. Alfalfa is grown for several years as a perennial and is harvested three to four times during the growing season in southern Wisconsin. Because alfalfa makes up roughly 20% of areal crop coverage around the study site (Table 1), it represents a major habitat for both pea aphids and their natural enemies.

The pea aphid is originally an old-world species that was introduced into North America in the 19th century (Mackauer & Kambhampati, 1986). During the summer, reproduction is asexual, and development takes about 7 days (Hutchison & Hogg, 1984; Hutchison & Hogg, 1985). *Aphidius ervi* is the dominant parasitoid attacking pea aphids in alfalfa, making up >99% of primary parasitism. It was introduced into the United States as a biological control agent in the 1960s, and it has now spread over much of North America (Mackauer & Kambhampati, 1986). *Aphidius ervi* parasitize aphids by laying a single egg through its exoskeleton, and the larva develops in the aphid and pupates within the mummy (the skeletonized aphid). The total time between oviposition and emergence is roughly 14 days (Meisner et al., 2014).

At our study site, *A. ervi* is attacked by four common hymenopteran hyperparasitoids (Schooler et al., 1996): two species of pteromalids, *Asaphes suspensus* and *Pachyneuron altiscutum*; one megaspilid, *Dendrocerus carpenteri*; and one figitid, *Alloxysta victrix*. The first three are ectoparasitoids, attacking *A. ervi* in the mummy stage, and their development takes about 3 weeks. *Alloxysta victrix* is a larval endoparasitoid that attacks still-living aphids and takes about 2 weeks to develop (Sullivan, 1972).

Predatory natural enemies include lady beetles (Coleoptera: Coccinellidae), mainly *Coccinella septempunctata*, *Harmonia axyridis*, and *Coleomegilla maculata*, which can not only be considered as aphid specialists but are also known to feed on a variety of other food items including pollen and fungal spores (Koch, 2003; Lundgren & Wiedenmann, 2004; Triltsch, 1999). In addition, the generalist damsel bugs (Heteroptera: Nabidae) and minute pirate bugs (Heteroptera: Anthocoridae) are also important natural enemies of pea aphids. All of these predators can also prey on parasitized aphids, and even hyperparasitized aphids, especially by the endohyperparasitoid. Although other predators occur, they either are uncommon (lacewings and syrphid flies) or are likely to be unaffected by both the manipulations and the density of aphids within fields (carabids; Snyder & Ives, 2001).

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## Characterizing the natural enemies in the landscape context

To characterize the natural enemies that feed on pea aphids in alfalfa according to their habitat specialization, we used a large dataset collected at the Arlington Agricultural Research Station. This dataset contains collections of natural enemies from five maize fields, five soybean fields, and 10 alfalfa fields from 2013 to 2017. Each field was sampled throughout the summer, once a week for maize and soybean, and twice a week for alfalfa. For maize and soybean, insects were counted on individual plants, and for alfalfa, sweep nets were used. To determine habitat use, the mean abundance for each of the three species of lady beetles, damsel bugs, minute pirate bugs, and the parasitoid *A. ervi* was calculated for each of the crops.

## Within-field disturbance experiment

The disturbance experiment was conducted during the summer of 2001. The experiment was run in three fields of 3.2, 3.5, and 7.5 ha that were located between 0.6 and 3.7 km apart. Each field was divided into three equal sections to which one of the following treatments was applied: control, insecticide, or strip. In the control, alfalfa was harvested normally. In the insecticide treatment, the plot was harvested normally, and then, the permethrin insecticide Pounce 32 EC (0.584 L/ha) was applied. In the strip treatment, strips of alfalfa were left uncut during the normal harvesting event. These uncut strips were harvested 2 weeks later, when the cut parts of the plot had already regrown. This represents a lower degree of disturbance to the arthropods, because they can survive in the uncut strips and immigrate into the cut strips after they have started to regrow. In the first round of harvesting, the uncut strips were meant to be 5 m wide. This was mechanically hard to execute, which resulted in uneven strips, some thinner than the desired 5 m. In the second and third harvesting events, the strips were made to be the width of the harvester (7.3 m), so the cut and uncut strips were of the same width.

Insects were sampled with sweep nets from 17 May (Day 0) to 22 September 2001 (Day 128). Samples were taken once or twice a week depending on weather conditions (rain sometimes prevented sampling) and alfalfa height. Immediately after harvest, the alfalfa was too short for sampling, except for the uncut parts of the strip treatment. Ten samples were taken in each treatment/field on every sampling date. All samples were taken at least 5 m away from the field edge. The number of sweeps per sample changed according to aphid abundance: At the extreme low aphid abundance, 40 sweeps were taken (which resulted in 400 sweeps per treatment/field), while at the extreme high abundance (more than 50 aphids per sweep), only one sweep was taken per sample (10 sweeps per treatment/field). In order to measure parasitism directly, aphids from the sweep samples were returned to the laboratory. Fifty adults (and fourth instars if 50 adults were not obtained) were dissected from every treatment/field on every sampling event to count second- and third-instar parasitoid larvae. Finally, three 3-min sets of visual searches were conducted to assess *A. ervi* mummy abundance; searches were conducted by walking slowly through the field and recording visible mummies. All mummies were collected and reared in the laboratory in petri dishes to estimate hyperparasitism rate.

Östman and Ives (2003, figure 4) present additional data from this experiment for potato leafhoppers.

## Cages

To understand the importance of immigration on the within-field insect communities after disturbance events, we used 12 cages in one of the fields to block immigration. Four cages were placed in each treatment 8 days after harvesting in the second cycle (early July) and were left until the next harvesting event (early August). In the strip treatment, the uncut areas were harvested a week after cages were set, and cages were removed and returned once harvesting was over. Cages were $2 \times 2 \times 2$ m made with $0.5 \times 0.5$ mm mesh netting ($32 \times 32$ mesh Lumite screen, BioQuip, Gardena, California, USA; catalogue number 1412C) covering all sides but the bottom. We established sham control cages (hereafter "shams") 2 m from each cage, where the shams consisted of $2 \times 2$ m areas sampled in the same way as the cages. Aphids, mummies, and predators were counted by visually scanning 100 stems in each cage and sham on the same day as the sampling of the large-scale experiment.

## Alfalfa quality

To assess the effect of treatment on alfalfa quality, samples of alfalfa height and weight were taken on 26 July, just before the third harvesting event. In each treatment/field, a Hula-Hoop was thrown eight times. For each throw, six stems touching the hoop roughly evenly spaced around the hoop were selected. Stems were selected from the base in order to prevent bias toward selecting tall stems. Stems were cut at the base, and their height was measured. Cut stems were taken to the laboratory

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and dried at 60°C, and six of the stems from each treatment/field were chosen randomly and weighed. Alfalfa quality was similarly measured in the cages.

## Statistical analyses

To analyze the response of pea aphids and different natural enemies to the disturbance manipulations, we used a mixed model with the structure of a classical repeated-measures ANOVA model (Gurevitch & Chester Jr., 1986):

$$\text{Transformed } x(t) \sim \text{treatment} + \text{field} + \text{day} + \varepsilon(t).$$

Here, $x(t)$ is the dependent variable of interest, which is appropriately transformed. The independent variable treatment (insecticide, strip, or control) is a fixed effect, and both field (three levels) and day of sampling (25 levels) are fixed effects to account for the repeated measures of our data. The effects of harvesting on $x(t)$ are absorbed by the variable for day of sample, because all harvests occur on the same day. Residuals $\varepsilon(t)$ are assumed to follow a first-order autoregressive process, AR(1), to account for temporal autocorrelation in the same section (treatment/field). In the strip treatment, only the samples from the parts of the field that were harvested at the same time as the other treatments (cut) were used for analysis. This was done so that the statistical comparisons are not the result of differing height and maturity of the alfalfa. For analyses of count data, it is necessary to account for heteroskedasticity, because low counts will necessarily have associated high variance. To account for this heteroskedasticity, either dependent variables can be suitably transformed (e.g., Larsen & Marx, 1981), or a general linear model (GLM) framework can be used (McCullagh & Nelder, 1989). Our model necessarily incorporates temporal autocorrelation, which presents challenges for GLM analyses. Therefore, we transform dependent variables to account for heteroskedasticity, which for our purpose of testing the significance of independent variables will often perform better than a GLM approach (Ives, 2015; Warton et al., 2016).

We analyzed the following dependent variables: pea aphid abundance, damsel bug abundance, minute pirate bug abundance, abundance of the three adult lady beetle species separately, adult *A. ervi* abundance, percentage parasitism of pea aphids from dissections, and percentage hyperparasitism from collected *A. ervi* mummies (dead or empty mummies were not counted) for each of the hyperparasitoid species. Abundance data were transformed as $\log[x(t) + x_{\min}]$, where $x_{\min}$ is the lowest nonzero value observed in a field sample. For percentage parasitism and hyperparasitism data, only values of >2 aphids/mummies were included in the analysis, and percentage data were arcsine-square-root-transformed. We used the Benjamini–Hochberg adjustment for multiple comparisons to account for the number of separate analyses of the seven dependent variables. We analyzed the effect of treatment on alfalfa height and dry mass using linear mixed models with field as a random effect. A linear model fit with generalized least squares was used to analyze the cage data from one field, with day of sampling as a factor fixed effect and including autocorrelated residuals of lag 1. Data on alfalfa height and dry mass from the cages/shams were analyzed using a linear model. The package nlme (Pinheiro et al., 2017) in R version 3.6.2 (R Core Team, 2013) was used for data analyses, and ggplot2 (Wickham, 2016) was used for figures.

# RESULTS

## Habitat-generalist and habitat-specialist natural enemies

All of the predatory natural enemies (lady beetles, damsel bugs, and minute pirate bugs) were found in maize, soybean, and alfalfa (Table 1). We classified all of these predators as habitat generalists in this system, because following a disturbance in alfalfa, they can immigrate from different habitats, which account for 71% of the agricultural landscape. As expected, the parasitoid *A. ervi* was only found in alfalfa, and therefore, we classify *A. ervi* as a habitat specialist. Over many years, we have found aphids parasitized by *A. ervi* in isolated areas other than alfalfa, such as on clover in roadside ditches, and *A. ervi* will attack pea aphids in pea and bean crops. Nonetheless, these habitats are rare compared with alfalfa, which makes up 20% of the farmland.

## Disturbance experiment

Pea aphid abundance varied across the season and was depressed in each harvesting event. Furthermore, abundance was consistently lower in the insecticide treatment than in the control and strip treatments (Figure 1a, Table 2). Excluding the uncut strips in the strip treatment, the abundance of all predators was depressed by harvesting, but predators differed in their responses to the magnitude of the experimental disturbance manipulation. The numbers of lady beetle adults were generally low, with *H. axyridis*, *Coc. septempunctata*, and *Col. maculata* being the most abundant species. The abundance of *H. axyridis* and *Col. maculata* was lower in the insecticide treatment than in the other two treatments,

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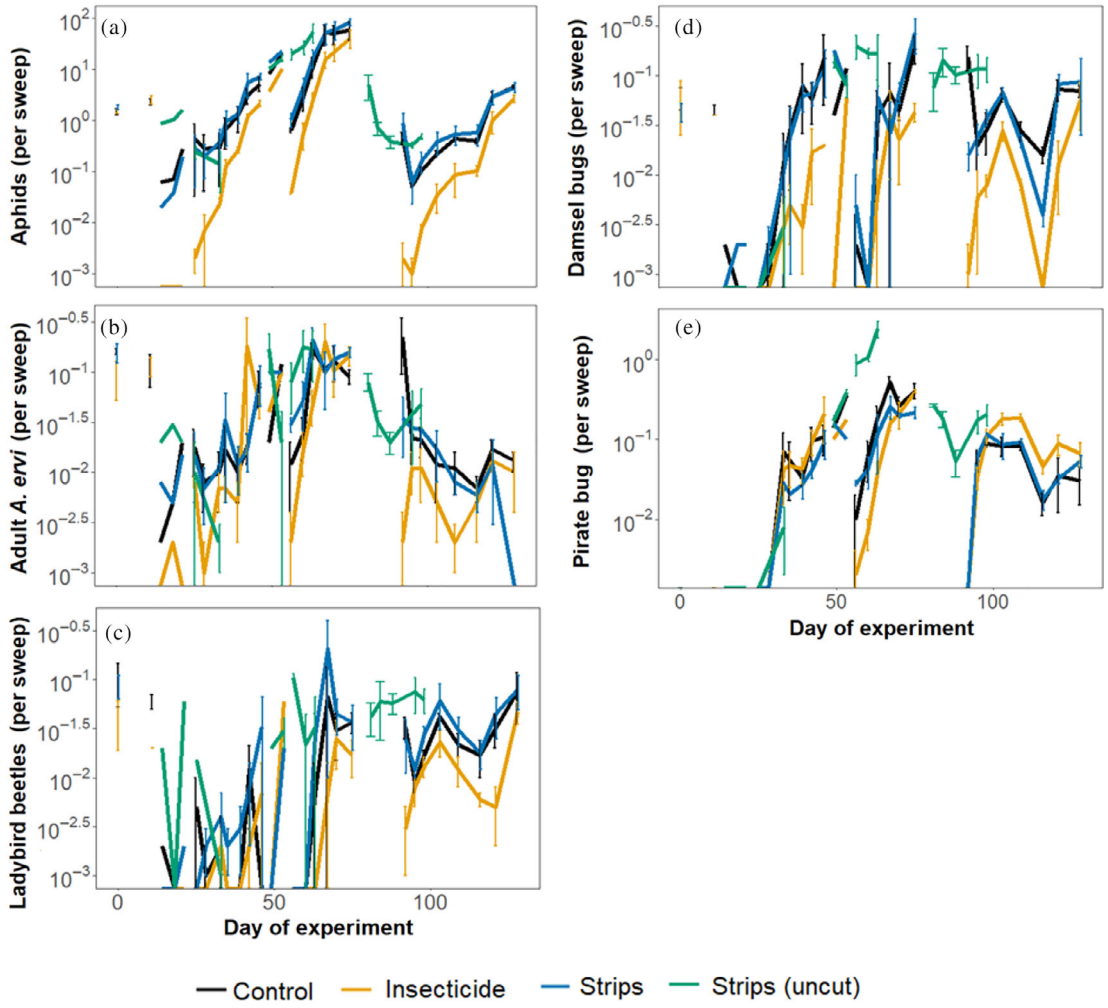


**FIGURE 1** For the three fields, the mean ± SE per sweep of (a) log pea aphids, (b) log adult *Aphidius ervi*, (c) log lady beetles (the three species combined), (d) log damsel bugs, and (e) log pirate bugs. Day 0 was 17 May 2001, and lines are interrupted at harvesting events. Data on aphids and damsel bugs from this experiment are also presented in figure 4 of Östman and Ives (2003)

and no difference was found between control and strip treatments (Figure 1c). Damsel bug abundance was lower in the insecticide than in the other treatments (Figure 1d). *Coccinella septempunctata* and minute pirate bug abundance was not affected by treatment (Figure 1e).

The adult *A. ervi* abundance was decreased in the insecticide relative to other treatments (Figure 1b). Nonetheless, the parasitism rate of pea aphids by *A. ervi* was not significantly affected by the treatments (Figures 2a and 3b). The most abundant species of hyperparasitoid was *Al. victrix* (197 individuals), followed by *P. altiscutum*, *As. suspensus*, and *D. carpenteri* (56, 47, and 25 individuals, respectively). Percentage hyperparasitism by *Al. victrix* and *As. suspensus* was higher in the strip treatment than in the other treatments and did not differ between control and insecticide treatments (Figures 2b and 3c). Hyperparasitism by *P. altiscutum* and *D. carpenteri* was similar in the different treatments. Higher hyperparasitism rates generally coincided with greater abundance of parasitoid hosts, as measured by the number of mummies in the different treatments (Figure 2c).

## Cages

We used cages to stop the movement of insects into fields following harvesting. Pea aphid abundance was higher in the cages than the control shams in the insecticide treatment, while no difference was found in the control treatment (Figure 4a–c) (cages–shams: insecticide: $F = 27.95$, $p < 0.0001$; control: $F = 1.394$, $p = 0.244$). In the strip treatment, aphid numbers were higher in the cages at the beginning of the harvesting cycle and collapsed after harvesting, but there was no overall difference between cages and control shams ($F = 3.153$, $p = 0.084$).

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**TABLE 2** Results of generalized least squares models for seven dependent variables regressed on treatments (insecticide, control, and strip—only the cut parts) with day as sampling as a factor fixed effect

| Organism | Model | *F* | *t* | *p* |
|---|---|---|---|---|
| Pea aphids | Mean/plant = 7.93 ± 19.73, ρ = 0.658 | 12.33 | | <0.0001* |
| | Strips–control | | 0.321 | 0.747 |
| | Strips–insecticide | | 4.452 | <0.0001* |
| | Control–insecticide | | 4.130 | 0.0001* |
| *Coccinella septempunctata* | Mean/plant = 0.004 ± 0.007, ρ = 0.0016 | 1.105 | | 0.3335 |
| *Harmonia axyridis* | Mean/plant = 0.008 ± 0.02, ρ = 0.1691 | 6.366 | | 0.0021 |
| | Strips–control | | 0.661 | 0.508 |
| | Strips–insecticide | | 3.367 | 0.0009* |
| | Control–insecticide | | 2.705 | 0.0075* |
| *Coleomegilla maculata* | Mean/plant = 0.007 ± 0.03, ρ = 0.146 | 8.593 | | 0.0003* |
| | Strips–control | | 1.939 | 0.053 |
| | Strips–insecticide | | 4.142 | 0.0001* |
| | Control–insecticide | | 2.203 | 0.028* |
| Pirate bugs | Mean/plant = 0.08 ± 0.11, ρ = 0.276 | 0.667 | | 0.667 |
| Damsel bugs | Mean/plant = 0.04 ± 0.06, ρ = 0.118 | 20.90 | | <0.0001* |
| | Strips–control | | −0.087 | 0.930 |
| | Strips–insecticide | | 5.556 | <0.0001* |
| | Control–insecticide | | 5.643 | <0.0001* |
| Adult *Aphidius ervi* | Mean/plant = 0.05 ± 0.076, ρ = −0.0144 | 7.487 | | 0.0007* |
| | Strips–control | | −0.802 | 0.423 |
| | Strips–insecticide | | 2.877 | 0.0045* |
| | Control–insecticide | | 3.679 | 0.0003* |
| Parasitism and hyperparasitism (%) | | | | |
| *A. ervi* | Mean/plant = 19.61 ± 24.84, ρ = 0.179 | 1.216 | | 0.298 |
| *Alloxysta victrix* | Mean/plant = 6.69 ± 11.53, ρ = 0.038 | 3.729 | | 0.0304* |
| | Strips–control | | 2.934 | 0.0049* |
| | Strips–insecticide | | 2.453 | 0.0174* |
| | Control–insecticide | | 0.187 | 0.852 |
| *Asaphes suspensus* | Mean/plant = 0.725 ± 3.22, ρ = −0.077 | 3.280 | | 0.0452* |
| | Strips–control | | 2.503 | 0.0153* |
| | Strips–insecticide | | 2.415 | 0.0191* |
| | Control–insecticide | | 0.513 | 0.609 |
| *Dendrocerus carpenteri* | Mean/plant = 0.6 ± 2.98, ρ = 0.569 | 0.543 | | 0.583 |
| *Pachyneuron altiscutum* | Mean/plant = 1.35 ± 4.49, ρ = 0.360 | 0.045 | | 0.955 |

*Note*: The residual variation is assumed to be autocorrelated with lag-1 autocorrelation coefficient ρ. For percentage parasitism and hyperparasitism, only samples with >2 aphids/mummies were analyzed. Asterisks denote statistically significant results after a Benjamini–Hochberg *p* value adjustment for multiple comparisons.

Parasitized aphid numbers (mummies) only differed between cages and shams in the insecticide treatment and were higher in the shams (Figure 4d–f) (cages–shams: insecticide: $F = 15.66$, $p < 0.0001$; control: $F = 2.598$, $p = 0.114$; and strip: $F = 1.619$, $p = 0.211$). Predator numbers were very low in both cages and shams (a total of 37 individuals from all predatory beetles and bugs) and were therefore not analyzed. The low numbers of predators in the cages can be attributed to the small size of the cages relative to the movement of predators and to the method of sampling (counting individuals on alfalfa stems).

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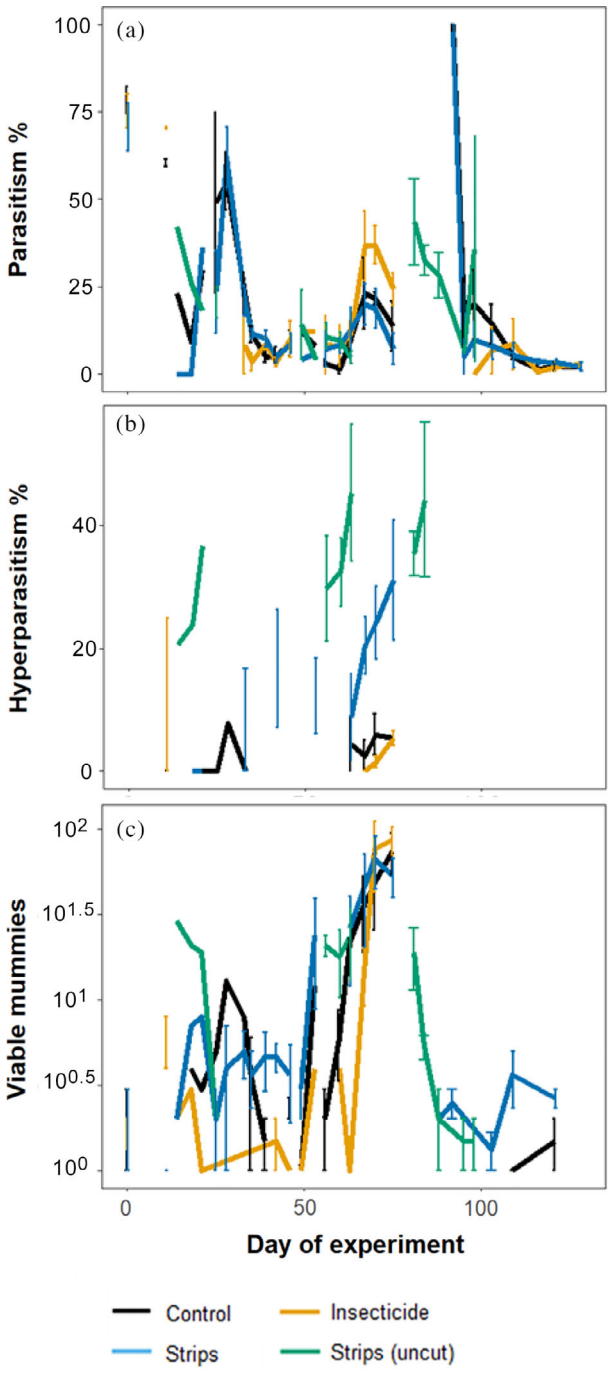


**FIGURE 2** Mean ± SE of (a) percentage parasitism of pea aphids by *Aphidius ervi*, (b) percentage hyperparasitism of pea aphid, and (c) log viable mummies collected for the hyperparasitism estimate. In the case of hyperparasitism, samples in which >2 mummies were viable are shown. Day 0 was 17 May 2001, and lines are interrupted at harvesting events

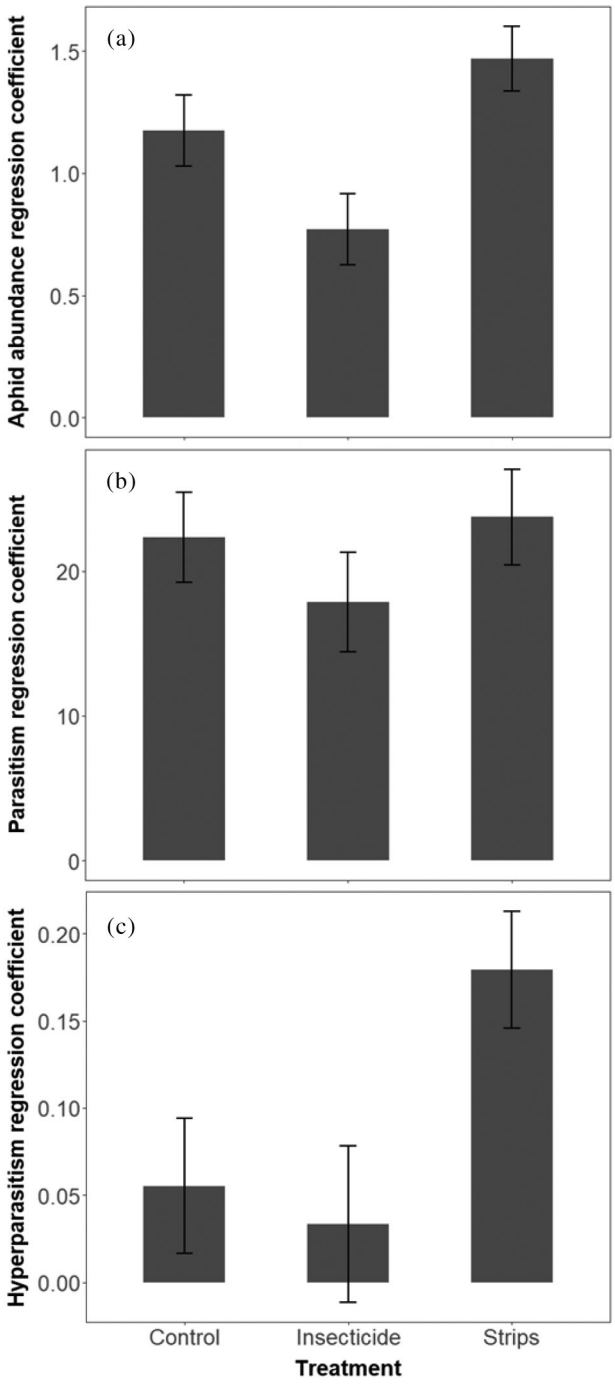


**FIGURE 3** Regression coefficients and corresponding SEs are displayed for the abundance of (a) pea aphid, (b) parasitism of aphids by *Aphidius ervi*, and (c) hyperparasitism of aphids, in the different treatments

## Alfalfa quality

Alfalfa dry mass and height varied among treatments. Stem dry mass was greater on average in the insecticide treatment, but did not differ between control and strip treatments (strip–control: df = 67, $t = -1.547$, $p = 0.126$; strip–insecticide: df = 67, $t = -5.551$, $p < 0.0001$; and control–insecticide: df = 67, $t = -4.003$, $p < 0.001$). Stem height had a similar response: Alfalfa was highest in the insecticide treatment and lowest in the strip treatment (strip–control: df = 211, $t = -4.553$, $p < 0.0001$; strip–insecticide:

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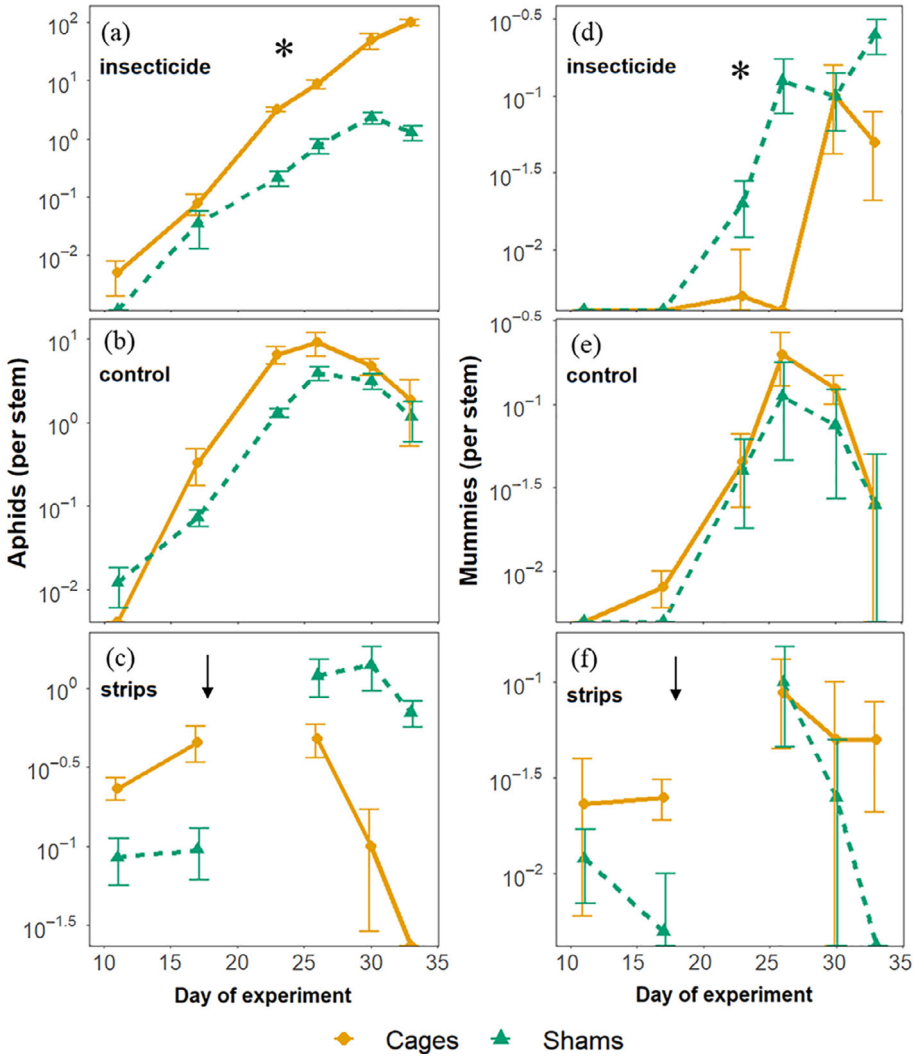


**FIGURE 4** Abundance of aphids (a–c) and parasitism by *Aphidius ervi* (d–f) in (a, d) insecticide, (b, e) control, and (c, f) strip treatments in cages and shams. Arrows mark the harvest of uncut parts in the strip treatment (c, f). Asterisks indicate significant differences between cages and shams ($P < 0.05$)

df = 211, $t = -10.856$, $p < 0.0001$; and control–insecticide: df = 211, $t = -6.303$, $p < 0.0001$).

Comparing the cages with shams, alfalfa dry mass was similar in the control and strip treatment, but was higher in the shams than in the cages in the insecticide treatment (cages–shams: insecticide: $t = -3.948$, $p = 0.0075$; control: $t = -1.933$, $p = 0.101$; and strips: $t = -2.213$, $p = 0.068$). Alfalfa was higher in the shams than in the cages in the strip treatment and similar in the other treatments (cages–shams: insecticide: $t = 0.107$, $p = 0.919$; control: $t = -0.011$, $p = 0.991$; and strips: $t = -4.44$, $p = 0.0043$).

## DISCUSSION

We investigated how habitat-generalist and habitat-specialist natural enemies of pea aphids respond to the magnitude of disturbances within alfalfa fields. Some, but not all, of the habitat generalists responded to disturbance manipulations, which could be explained by their direct responses to pea aphid densities. Parasitism by the habitat-specialist parasitoid was not directly affected by the experimental disturbance manipulations. Furthermore, the parasitoid could indirectly benefit from disturbances that occur under normal harvesting practices because it reduced overall hyperparasitism rates.

### Habitat generalists

In our 5-year dataset (Table 1), all predatory species were common in the three dominant crops in the landscape: alfalfa, maize, and soybean. Thus, all of the studied predators are habitat generalists in the surrounding

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landscape. Furthermore, all the predators are unlikely to be able to complete development from egg to adult in alfalfa fields, because time intervals between harvesting are the same or shorter than their developmental time (Arbab et al., 2016; Cocuzza et al., 1997; Katsarou et al., 2005; Lamana & Miller, 1998; Obrycki & Tauber, 1978). Therefore, not only do habitats outside alfalfa fields provide a source for predators, the populations of predators could not be supported by alfalfa alone. Thus, alfalfa is likely a population sink for the habitat generalists.

The abundance of all predators followed the abundance of pea aphids after harvesting events (Figure 1). This shows that they immigrate in response to pea aphid density, as shown by previous studies (Harmon et al., 2009; Molleman et al., 2016). Most of the predators were also affected by the manipulation. The effect of the insecticide treatment on pea aphids was greater than the strip treatment, and *H. axyridis*, *Col. maculata*, and damsel bugs also showed decreases in abundance in the insecticide treatment. This sensitivity to disturbance and pea aphid abundance could be a detriment to biological control, because early immigration of natural enemies can stop incipient pest outbreaks before they occur (Costamagna et al., 2015; Ives & Settle, 1997).

## Habitat specialist

As shown by the long-term data (Table 1), *A. ervi* is a habitat specialist at our field site, especially compared with the predators of pea aphid. Nevertheless, we do not have data on all of the landscape, but only on the 70% that is agricultural. Therefore, it is possible that other agricultural or natural areas could provide a source for *A. ervi*. Nonetheless, the abundance of alfalfa, and the ubiquity of pea aphids in alfalfa, suggests that the vast majority of the *A. ervi* population occurs in alfalfa.

In the experiment, *A. ervi* parasitism rates were similar across treatments and showed no strong response to aphid density. This is consistent with laboratory experiments in which *A. ervi* parasitism is only weakly dependent on the number of aphids per stem (Ives et al., 1999). This density-independent response does not necessarily mean that the population of *A. ervi* was unaffected by disturbance treatments, and indeed, differences were found in the abundance of adult parasitoids. Nonetheless, *A. ervi* appears to forage very successfully at low pea aphid density. This is particularly important, because attacking pea aphids relatively early in a harvesting cycle is needed to ensure successful development before the next harvest. The development time of *A. ervi*, from attack to adult emergence, is roughly 2 weeks (Meisner et al., 2014), and the time between harvesting is generally 4–6 weeks. If most parasitism occurred within 2 weeks of the next harvest, most parasitoids would be killed in the harvesting event.

Results from the cages and shams that we set up following the second harvest support the importance of *A. ervi* adult movement in explaining the lack of response of parasitism to treatments (Figure 4d). The high numbers of parasitized aphids in the shams after insecticide application is a reflection of a rise in *A. ervi* mummies across all sampled fields in the second cycle in this treatment (Figure 2a). In contrast, parasitism was much lower in the cages for the insecticide treatment. The high densities of pea aphids in the cages of the insecticide treatment emphasize the strong role of parasitoid and predator immigration, and subsequent top-down control of pea aphids (Ives et al., 2020; Snyder & Ives, 2001). In the strip treatment, however, after harvesting the initially uncut alfalfa, control of pea aphids was stronger in the cages than in the shams (Figure 4b,c). This might have been caused by greater survival of parasitoids and the resulting higher parasitism rate.

## Indirect effects of disturbance on *A. ervi* from hyperparasitoids and predators

In contrast to *A. ervi*, two of its common hyperparasitoids were affected by the experimental harvesting manipulation, especially benefitting from survival in uncut strips in the strip treatment. This is consistent with the field observation that hyperparasitoids of pea aphids do not survive well when the interval between harvest is short (Schooler et al., 2011). In contrast to *A. ervi*, Schooler et al. (1996) showed that the hyperparasitoids have a density-dependent response to parasitized pea aphids at the scale of fields, leading to density-dependent hyperparasitism rates. Although the hyperparasitoids can immigrate into fields as parasitized aphid numbers rise (Schooler et al., 1996), their life history reduces the survival of their larvae. Since alfalfa is harvested every 4–6 weeks, and *A. ervi* takes about 2 weeks to develop, the number of parasitized aphids and mummies available for hyperparasitoids is generally greatest toward the end of a harvesting cycle (Figure 2b). Because the hyperparasitoids have development times of 2–3 weeks, most of the hyperparasitoid larvae cannot finish their development before the next harvesting, making the alfalfa a sink habitat. In this system, they must be habitat generalists and use other crops and host species (consistent with literature knowledge to these species being feeding generalists; Ferrer-Suay et al., 2012; Noyes, 2003). In addition to the effects of hyperparasitoids, disturbance lowers the abundance of predators, and that can lower intraguild

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predation. All predators studied here can feed on parasitized aphids, and some may occasionally feed on mummies. By lowering predator abundance, disturbance lowers the chances of a parasitized mummy being eaten, and therefore also may indirectly benefit *A. ervi*.

## Effects of disturbance on the crop

Alfalfa quality, as measured by height and dry mass, was highest in the insecticide treatment, as expected by the lower densities of pea aphids in the insecticide treatment (Figure 1a). The reduction in pea aphid density, and possibly leafhopper density (Östman & Ives, 2003), by insecticides very early in the harvesting cycle had the largest effect on alfalfa growth. While we do not advocate for the prophylactic application of insecticide after harvesting, the efficacy of our insecticide treatments argues for the importance of controlling alfalfa pests very early in the harvesting cycle. The results for alfalfa quality in our cage–sham experiment strengthen these observations.

# CONCLUSIONS

Our results highlight the importance of life history and behavioral adaptations of natural enemies to handle within-field disturbance. Although the habitat-specialist parasitoid, *A. ervi*, uses a smaller part of the landscape compared with the habitat generalists and thus is unlikely to be affected by habitat diversity, it nonetheless can immigrate into disturbed fields from other alfalfa fields. Therefore, surrounding alfalfa fields have the same buffering effect against disturbance for the habitat specialist as other crops do for the habitat generalists. For agricultural management, if the timing of harvesting or insecticide disturbances in alfalfa fields were asynchronous among alfalfa fields, this could increase biological control. In contrast, the synchronous harvesting of alfalfa could lead to "resource discontinuity" (Iuliano & Gratton, 2020; Schellhorn et al., 2015). This is particularly important for specialized natural enemies such as parasitoids that can escape disturbance only to a field from the same crop type (Tscharntke et al., 2016).

The ability of *A. ervi* to immigrate into alfalfa fields from other alfalfa fields following disturbances, however, is only one of the life history and behavioral characteristics that allows them to exert biological control in disturbed alfalfa fields. *Aphidius ervi* succeeds also because they are well adapted to disturbances: They are very effective at finding aphids at low densities and therefore achieve high parasitism rates soon after harvesting. Their density-independent parasitism means that they start to exert control at low densities to possibly prevent incipient outbreaks. Furthermore, their short generation time allows them to recruit another generation before the next harvesting disturbance. Finally, primary parasitoids may even benefit from disturbance, which has a disproportionately negative effect on their hyperparasitoids and some of their intraguild predators. Thus, to understand how habitat-specialist biological control agents can be effective, it is important to understand their life history and behavioral characteristics that make them successful in their specialist habitat.

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## CONFLICT OF INTEREST

The authors declare no conflict of interest.

## AUTHOR CONTRIBUTIONS

Anthony R. Ives designed and executed the study. Anthony R. Ives and Miriam Kishinevsky conducted the analyses. Anthony R. Ives and Miriam Kishinevsky led the writing of the manuscript. All authors gave final approval for publication.

## DATA AVAILABILITY STATEMENT

Data (Kishinevsky & Ives, 2022) are available from Dryad: https://doi.org/10.5061/dryad.41ns1rng4

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