

REPORT

Biodiversity and biocontrol: emergent impacts of a multi-enemy assemblage on pest suppression and crop yield in an agroecosystem

Bradley J. Cardinale*,
Chad T. Harvey¹, Kevin Gross²
and Anthony R. Ives³

Department of Zoology,
University of Wisconsin-
Madison, Madison,
WI 53706, USA

¹*ctharvey@wisc.edu*

²*kgross@wisc.edu*

³*arives@wisc.edu*

*Correspondence: E-mail:

bjcardinale@wisc.edu

Abstract

The suppression of agricultural pests has often been proposed as an important service of natural enemy diversity, but few experiments have tested this assertion. In this study we present empirical evidence that increasing the richness of a particular guild of natural enemies can reduce the density of a widespread group of herbivorous pests and, in turn, increase the yield of an economically important crop. We performed an experiment in large field enclosures where we manipulated the presence/absence of three of the most important natural enemies (the coccinellid beetle *Harmonia axyridis*, the damsel bug *Nabis* sp., and the parasitic wasp *Aphidius ervi*) of pea aphids (*Acyrtosiphon pisum*) that feed on alfalfa (*Medicago sativa*). When all three enemy species were together, the population density of the pea aphid was suppressed more than could be predicted from the summed impact of each enemy species alone. As crop yield was negatively related to pea aphid density, there was a concomitant non-additive increase in the production of alfalfa in enclosures containing the more diverse enemy guild. This trophic cascade appeared to be influenced by an indirect interaction involving a second herbivore inhabiting the system – the cowpea aphid, *Aphis craccivora*. Data suggest that high relative densities of cowpea aphids inhibited parasitism of pea aphids by the specialist parasitoid, *A. ervi*. Therefore, when natural enemies were together and densities of cowpea aphids were reduced by generalist predators, parasitism of pea aphids increased. This interaction modification is similar to other types of indirect interactions among enemy species (e.g. predator–predator facilitation) that can enhance the suppression of agricultural pests. Results of our study, and those of others performed in agroecosystems, complement the broader debate over how biodiversity influences ecosystem functioning by specifically focusing on systems that produce goods of immediate relevance to human society.

Keywords

Acyrtosiphon, alfalfa, *Aphidius*, aphids, ecosystem functioning, *Harmonia*, *Nabis*, parasitoids, predators.

Ecology Letters (2003) 6: 857–865

INTRODUCTION

Pest suppression has been highlighted as a potentially important ecosystem service of biodiversity (Way & Heong 1994; Mooney *et al.* 1995; Swift *et al.* 1996; Schlapfer *et al.* 1999; Wilby & Thomas 2002). Despite this, experimental studies examining the impact of predators, parasitoids and pathogens on insect pests have historically focused on only one enemy species, or have considered different enemies only one at a time. Three avenues of research are stimulating greater interest in the role of natural enemy diversity *per se*.

First, there is a long-standing, but unresolved, debate among biocontrol experts over whether introduction of multiple natural enemies leads to more efficient pest suppression than the release of single enemy species (Hassell & Waage 1984; Kakehashi *et al.* 1984; Hassell & May 1986; Hochberg 1996; Denoth *et al.* 2002). Second, it is thought that many modern agricultural practices – including the simplification of habitat complexity, intense fertilization and insecticide use – may be compromising biological control by reducing the variety of enemies that are available to attack pests (Andow 1991; Kruess & Tscharntke 1994; Hawkins *et al.* 1999; Thies

& Tscharrntke 1999; Benton *et al.* 2003). Third, a growing body of research has begun to outline the variety of non-additive interactions among natural enemy species that may cause diverse enemy guilds to have 'emergent' impacts on their prey/host populations (see Rosenheim 1998; Sih *et al.* 1998 for reviews). As agroecosystems become increasingly characterized by the spread and homogenization of insect pests, experimental studies of multi-enemy impacts on pest species will be the key to understanding the role that natural enemy diversity plays in biological control.

Here we report the results of a study that examined how the species richness of natural enemies in an agricultural ecosystem influenced the population size of a widespread insect pest (the pea aphid, *Acyrtosiphon pisum*) and, in turn, the yield of an economically important crop (alfalfa, *Medicago sativa*). Our study was motivated by three observations:

- (1) While high fecundity and rapid development contribute to pea aphids being economically important pests of alfalfa in many parts of the United States, pea aphids in the midwest rarely reach densities that cause crop damage or require insecticide use (Hutchinson & Hogg 1984).
- (2) That pea aphids are not a significant pest of alfalfa in the midwest is, at least in part, because of a diverse guild of natural enemies that attack the aphids and maintain their densities below economically damaging levels (Losey *et al.* 1997; Ives *et al.* 1999; Harmon *et al.* 2000; Rauwald & Ives 2002; Snyder & Ives 2003).
- (3) In our study system, natural enemy richness tends to 'track' aphid population dynamics, with aphid populations declining when natural enemy richness is high (see Fig. 1, for example). Yet, because of the anticipated correlation between enemy richness and total enemy abundance (Fig. 1 inset), it is unknown whether declining aphid densities are influenced in any way by enemy diversity.

These three observations led us to hypothesize that natural enemy species richness plays a role in the biological control of aphid pests of alfalfa, and that this might have cascading effects on crop yield. To test this hypothesis, we performed a field experiment in which we used large enclosures to manipulate the presence/absence of three of the most important natural enemies of aphids in alfalfa. We then examined whether more diverse guilds of enemies suppressed aphid populations to a greater extent than single enemy species and, if so, whether suppression was additive (proportional to individual enemy effects) or non-additive (greater or less than expected from the individual enemy effects). Our results suggest that all three natural enemies together reduce pea aphids to a greater extent than is predicted from the effects of each natural enemy alone, and that greater pest suppression enhances crop yield.

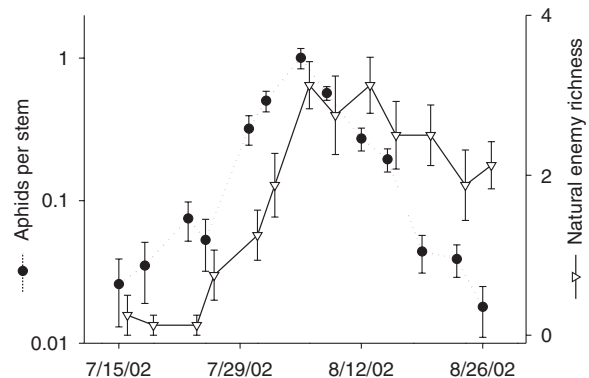
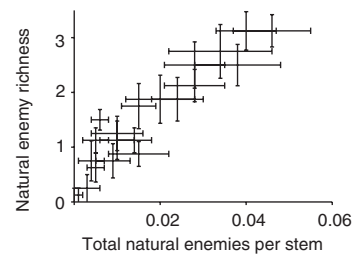


Figure 1 Correlations between aphid density and natural enemy diversity in alfalfa. Data are the mean \pm 1 SE of $n = 8$, 3×3 m permanent reference plots established in an alfalfa field at the Arlington Research Station, University of Wisconsin. Plots were monitored over a single harvesting cycle in the summer of 2002. The density of the pea aphid, *Acyrtosiphon pisum*, and the richness and abundance of natural enemies in a plot were determined by counting individuals on 100 stems of alfalfa selected equally from each of four 2.25 m^2 subplots. The main figure illustrates the temporal association between aphid population size and natural enemy species richness (average number of taxa per plot). The inset shows the anticipated correlation between natural enemy richness and total enemy abundance ($r = 0.94$, $P < 0.01$).

METHODS

Study system

We performed the experiment at the University of Wisconsin's Arlington Research Farm in south central Wisconsin. One of the most abundant herbivores in alfalfa is the pea aphid, *Acyrtosiphon pisum* Harris (Homoptera: Aphididae). *Acyrtosiphon pisum* is a phloem feeder on a variety of legumes. In Wisconsin, its primary host plants include alfalfa, peas and clover. During summer, *A. pisum* reproduces asexually with parthenogenic females producing up to six nymphs per day (Hutchinson & Hogg 1985). Development time from first instar to reproductive adult can be as little as 5 days under favourable climatic conditions (Hutchinson & Hogg 1984, 1985).

A variety of natural enemies impose biocontrol on *A. pisum* in this system (Ives *et al.* 1999; Harmon *et al.* 2000;

Rauwald & Ives 2002; Snyder & Ives 2003). Three of these, *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae), *Nabis* sp. (Hemiptera: Nabidae), and *Aphidius ervi* Haliday (Hymenoptera: Braconidae) are consistently among the most abundant enemies at our research site. *Harmonia axyridis*, the multicoloured Asian lady beetle, was introduced into the United States from China as a biocontrol agent. It is a generalist predator that feeds on several types of aphids, and on other herbivores, predators and conspecifics (LaMana & Miller 1996; Snyder *et al.* 2000). The damsel bug *Nabis* sp. is another generalist predator that uses its piercing-sucking mouthparts to attack a variety of soft-bodied insects (Lattin 1989; Snyder & Ives 2003). *Aphidius ervi* is a specialist parasitoid that was released into North America in the 1960s to control *A. pisum* (Gonzalez *et al.* 1978; Mackauer & Kambhampati 1986). Female wasps deposit a single egg into an early instar aphid (Ives *et al.* 1999). After hatching, the *A. ervi* larva develops within the aphid host for approximately 8 days, after which the host attaches itself to a leaf on the alfalfa plant and the larva pupates within the host exoskeleton to form a sclerotized 'mummy'. *Acyrtosiphon pisum* is the only common host of *A. ervi* in alfalfa fields of Wisconsin.

Experimental design

Experimental units for this study were 16, $2 \times 2 \times 2$ m cages, covered on all sides but the bottom with size 32×32 Lumite mesh screening (catalogue number 1412C; Bioquip, Gardena, CA, USA). These enclosures represent the largest spatial scale at which we can practically manipulate and replicate natural enemy assemblages in this system. Cages were set up on 5 September 2002, 9 days after the alfalfa field was harvested. Bottom edges of each cage were sealed with a 10 cm berm of soil to block movement of arthropods into or out of cages.

After cages were set up, we removed foliar arthropods by sweeping each cage four times with a D-vac suction sampler (D-vac Company, Ventura, CA, USA). We then searched the cages and removed all additional animals that could be found. To eliminate ground predators, such as carabid beetles that prey not only on aphids but potentially on other natural enemies (Snyder & Ives 2001), we placed pitfall traps into two corners of each cage. Monitoring of these traps twice weekly indicated that 94% of the ground predators were captured and removed from the cages within the first 3 days of the experiment.

On 6 September, all cages were inoculated with 25 adult *A. pisum* that had been collected from the surrounding alfalfa field. We randomly assigned each cage to one of five treatments: (1) control: no natural enemies added, (2) plus *H. axyridis*, (3) plus *Nabis* sp., (4) plus *A. ervi*, (5) plus all three natural enemy species. Treatments 1–4 were replicated in

three cages each while treatment 5 was replicated in four. We used an additive series design to manipulate natural enemy densities, which results in the more diverse enemy assemblage (treatment 5) having the summed number of enemies in less diverse assemblages (treatments 2–4). The strength of this design is that enemy density and diversity are intentionally confounded so that one can statistically establish departures from the expectation of independent, additive species effects (Sih *et al.* 1998). Thus, the design not only mimics the natural correlation between total enemy abundance and diversity in alfalfa fields (Fig. 1), it also allows us to determine whether enemy diversity has an effect exceeding that anticipated from higher enemy abundance in diverse assemblages. A further benefit of the additive series design is that intra- and interspecific interactions are less likely to be confounded across levels of diversity – a problem that can hinder interpretation of treatment effects in the more widely used replacement-series design where the density of each species is inversely proportional to richness (Connolly 1988; Snaydon 1991; Jolliffe 2000).

One limitation of the additive series experimental design is that nonlinear prey population growth and/or nonlinear functional responses of natural enemies potentially limit conclusions to the specific densities used in an experiment (Sih *et al.* 1998). Given this, we were careful to use densities of natural enemies that were comparable with the average density each species attains in the field over the course of a summer growing season (see Results). Nine *H. axyridis* were added to treatments 2 and 5, and to treatments 3 and 5 we added 18 *Nabis* sp. using animals collected from the field. Manipulations of *A. ervi* were more involved because of the complex life cycle of the species. Dissections of 50 adult *A. pisum* collected from the alfalfa field 1 day prior to the start of the study (5 September) indicated that 18% of aphids were already parasitized by *A. ervi*. Thus, the inoculation of aphids to the cages resulted in the addition of four to five parasitoids per cage. To further ensure successful establishment of the parasitoid in the appropriate treatments, we added five aphid mummies (containing the pupating parasitoid) that had been reared in laboratory cultures to cages of treatments 4 and 5. To reduce the density of *A. ervi* in cages to which it was not assigned (treatments 1–3), we performed two minute visual scans of the vegetation twice weekly and removed all mummies. This successfully held parasitism to negligible levels (<1% of the aphid population parasitized) in treatments 1–3 (see Results).

Non-focal taxa

To maintain homogeneity within treatments, we monitored for and removed non-focal taxa weekly by performing two minute visual scans in the cages. Initial removal of animals was quite effective as we never found any non-focal enemy

species, and only rarely found non-focal herbivores in the cage enclosures (median = 0, maximum = 2 per cage over all monitoring dates). The single exception to this was the cowpea aphid, *Aphis craccivora* Koch, which is a herbivore pest of alfalfa that is widely distributed across North America. At our research site, *A. craccivora* is typically rare throughout the alfalfa growing season, but it does periodically increase to notable densities. During the first 5 days of our study, we noted small numbers of these aphids on isolated stems of alfalfa in the cages. We removed these aphids initially, but after noticing more following day 5, we ceased any effort to control the species and decided to include *A. craccivora* as a component of the herbivore guild (see 'Data analyses' below).

Final measurements

This study lasted for 31 days, which is typical of the time interval between alfalfa harvests in Wisconsin. On the final date of the experiment (7 October), the densities of the herbivores *A. pisum* and *A. craccivora* were determined by counting the number of each aphid species on 50 or 100 stems of alfalfa selected from four 1 m² subplots in each cage (fewer stems were counted in cages where densities were high). We also recorded the number of *A. pisum* mummies to determine the final density of the parasitoid, *A. ervi*. Final densities of *H. axyridis* and *Nabis* sp. were determined by sampling vegetation in the cages twice with a D-vac suction sampler, followed by visual scans for any remaining enemies. We then collected two to three subsamples of alfalfa from each cage to estimate crop yield. A 0.21-m diameter hoop was tossed into one of four randomly chosen 1 m² subplots of a cage, and alfalfa within the hoop was harvested at the base of the stems. The vegetation was dried and weighed, and subsamples were averaged to determine yield per m² in each cage.

Data analyses

Because our experiment used an additive-series design in which the initial number of natural enemies in the more diverse assemblage (treatment 5) was the sum of enemies in less diverse assemblages (treatments 2–4), our analyses were specifically designed to test for an effect of natural enemy richness that deviated from the summed effect of individual enemy species—that is, a non-additive effect. There were three dependent variables: (1) *A. pisum* density [\log_{10} (no. stem⁻¹)], (2) *A. craccivora* density [\log_{10} (no. stem⁻¹)], and (3) alfalfa yield (g m⁻²). We used factorial ANOVA (v. 8.0, SAS 1996) to model each dependent variable as a function of the main effects of *H. axyridis*, *Nabis* sp., and *A. ervi*, with a term for their interaction. The density of *A. craccivora* [\log_{10} (no. stem⁻¹)] was used as a covariate in the model of *A. pisum*

density because *A. craccivora* densities were not initially standardized across treatments. In these analyses, the interaction term provides the test for additivity of natural enemy effects. A nonsignificant interaction indicates that the dependent variable could be predicted from the summed effects of enemies when alone. A significant interaction indicates that increasing the richness of natural enemies led to a change in the response variable that was greater/less than expected from the summed impact of the individual enemy species.

RESULTS

Treatments

Figure 2 shows the natural enemy assemblages in the five treatments on the final date of the study. The final densities of *H. axyridis* and *Nabis* sp. did not differ between treatment 5 (plus all enemies) and their respective single-species treatments (*H. axyridis*: $t = 0.17$, $P = 0.87$, *Nabis*: $t = -0.08$, $P = 0.94$). To compare the final density of *A. ervi* among treatments, we used the ratio [mummies stem⁻¹/(mummies + *A. pisum* stem⁻¹)] as a measure of the

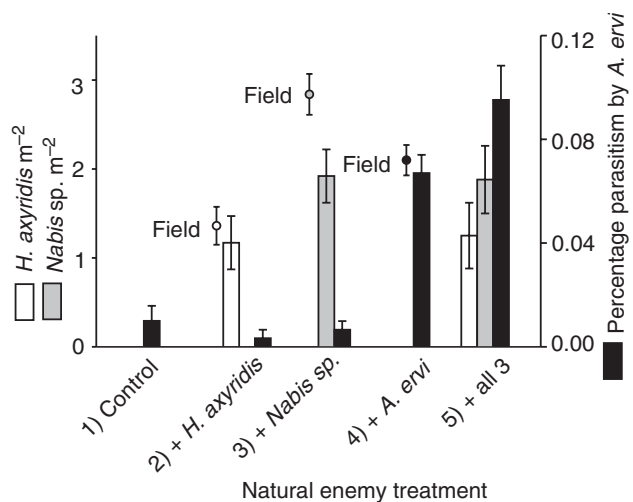


Figure 2 Natural enemies in the treatments on the final date of the study. The densities of *Harmonia axyridis* and *Nabis* sp. are based on the final numbers of individuals captured per cage. Parasitism by *Aphidius ervi* is compared among treatments with the ratio [mummies stem⁻¹/(mummies + *Acyrtosiphon pisum* stem⁻¹)]. Bars are the mean \pm 1 SE of $n = 3$ cages for treatments 1–4, and $n = 4$ cages for treatment 5. For comparison, data points give the naturally occurring densities of enemies in the alfalfa field. Data for *H. axyridis* and *Nabis* sp. are the mean density \pm 1 SE in sweep net samples collected from a known area on 19 dates throughout the alfalfa growing season (10 June to 28 August 2002). Data for *A. ervi* are from stem counts of alfalfa in the $n = 8$ reference plots described in Fig. 1.

final proportion of the *A. pisum* population that was parasitized by *A. ervi*. This ratio underestimates absolute levels of parasitism because mummies only represent the pupal stage of the parasitoid life cycle. It is, however, a relative measure of parasitism useful for comparing treatments. We successfully reduced the number of *A. ervi* in treatments 1–3 where the final proportional parasitism was only $0.008 \pm \text{SD } 0.007$. This represents nearly a 90% reduction in parasitism relative to treatments 4 and 5 where *A. pisum* mummies were not removed from the enclosures. The final proportion of *A. pisum* parasitized by *A. ervi* was higher in treatment 5 than in treatment 4 ($t = 1.90$, $P = 0.06$ for arcsine square root transformed data; Fig. 2). For all three enemy species, estimates of final density in the enclosures were at, or slightly below, the mean field densities observed over the course of the alfalfa growing season. Thus, densities manipulated in the enclosures were comparable with what occurs naturally in this system.

Aphid densities

There was a significant three-way interaction among natural enemy species indicating they had a non-additive effect on the final densities of *A. pisum* ($F_{1,10} = 7.97$, $P = 0.02$; Table 1a). None of the single-species treatments (treatments 2–4) had

A. pisum densities that differed from controls (all $P > 0.20$, post-hoc Dunnett's t -tests). Yet, the density of *A. pisum* was reduced by an average 64% in treatment 5 relative to all other cages (Fig. 3a). The final density of *A. pisum* was independent of the density of *A. craccivora*, which was used as a covariate in the analysis (Table 1a). In contrast to the effect of enemies on *A. pisum*, there was no significant interaction among natural enemies on the final densities *A. craccivora* (Table 1b). Of the three enemy species, only *H. axyridis* had a significant effect on *A. craccivora* (Table 1b), with mean densities of this aphid being reduced to <10% of the controls (Fig. 3b).

Crop yield

Alfalfa crop yield appeared to be strongly influenced by herbivory from *A. pisum*, but not by *A. craccivora*. Evidence for this comes from a multiple regression of yield against the final densities of both herbivores. Yield did not vary with the final \log_{10} density of *A. craccivora* among enclosures ($F_{1,13} = 0.73$, $P = 0.41$). However, variation in \log_{10} density of *A. pisum* explained a significant 34% of the variation in crop yield, which decreased by 87 g m^{-2} for each 10-fold increase in *A. pisum* density (Fig. 4a).

Analysing yield as a function of the factorial combination of natural enemies revealed significant main effects of *Nabis*

Table 1 Effects of three natural enemies (*Harmonia axyridis*, *Nabis* sp., and *Aphidius ervi*) on (a) final densities of pea aphids, (b) final densities of cowpea aphid, and (c,d) alfalfa crop yield

Natural enemy	d.f.	F-value	$P > F$
(a) Log_{10} (<i>A. pisum</i> stem ⁻¹)			
<i>H. axyridis</i>	10	4.90	0.05
<i>Nabis</i> sp.	10	2.30	0.16
<i>A. ervi</i>	10	0.03	0.87
<i>H. axyridis</i> × <i>Nabis</i> sp. × <i>A. ervi</i>	10	7.97	0.02
Covariate			
Log_{10} (<i>A. craccivora</i> stem ⁻¹)	10	1.03	0.33
(b) Log_{10} (<i>A. craccivora</i> stem ⁻¹)			
<i>H. axyridis</i>	11	15.62	<0.01
<i>Nabis</i> sp.	11	0.72	0.41
<i>A. ervi</i>	11	0.22	0.65
<i>H. axyridis</i> × <i>Nabis</i> sp. × <i>A. ervi</i>	11	0.19	0.67
(c) Alfalfa yield (g m^{-2})			
<i>H. axyridis</i>	11	3.92	0.07
<i>Nabis</i> sp.	11	17.89	<0.01
<i>A. ervi</i>	11	7.71	0.02
<i>H. axyridis</i> × <i>Nabis</i> sp. × <i>A. ervi</i>	11	1.83	0.20
(d) Alfalfa yield (g m^{-2})			
<i>H. axyridis</i> (no. cage ⁻¹)	8	0.07	0.80
<i>Nabis</i> sp. (no. cage ⁻¹)	8	0.00	0.96
<i>A. ervi</i> (proportion parasitism)	8	0.18	0.68
<i>H. axyridis</i> × <i>Nabis</i> sp.	8	10.97	0.01
<i>H. axyridis</i> × <i>A. ervi</i>	8	0.00	0.99
<i>Nabis</i> sp. × <i>A. ervi</i>	8	9.93	0.01
<i>H. axyridis</i> × <i>Nabis</i> sp. × <i>A. ervi</i>	8	12.48	<0.01

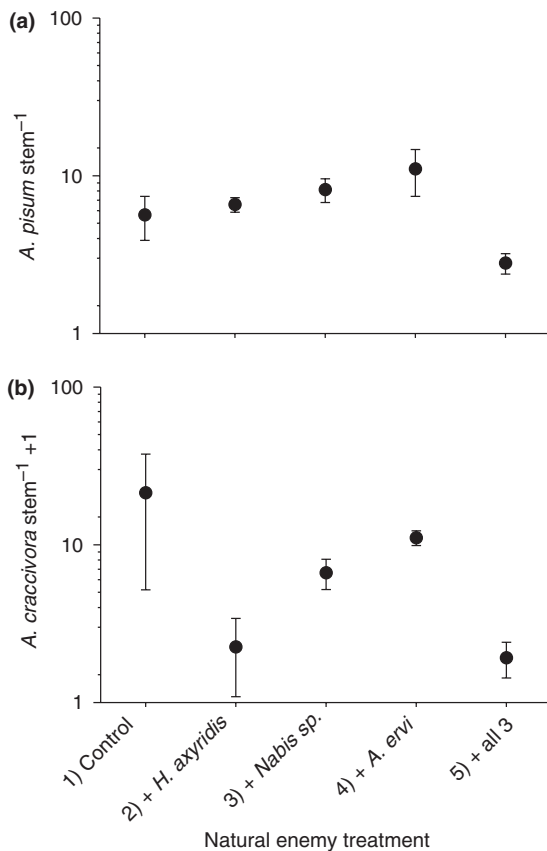


Figure 3 The mean density \pm 1 SE of (a) the pea aphid and (b) the cowpea aphid in natural enemy treatments on the final date of the study. Corresponding statistical analyses of treatment effects are given in Table 1(a,b).

sp. and *A. ervi* (Table 1c). However, the three-way interaction among the natural enemies was not significant. As this factorial analysis uses only the presence/absence of natural enemies and does not account for variation in natural enemy densities within treatments (Fig. 2), we modelled yield as a function of the final densities of each enemy species in the enclosures. This second analysis suggested a three-way interaction among natural enemies and a non-additive increase in crop yield (Table 1d). Post-hoc comparisons indicated that none of the single-species treatments (treatments 2–4) had crop yields different from the controls (all $P > 0.20$, Dunnett's *t*-tests). Yet, yield was increased by an average 51% in treatment 5 relative to all other cages (Fig. 4b).

DISCUSSION

In this study, we found that when all three enemy species were together, the population density of the pea aphid, *A. pisum*, was suppressed more than predicted from the

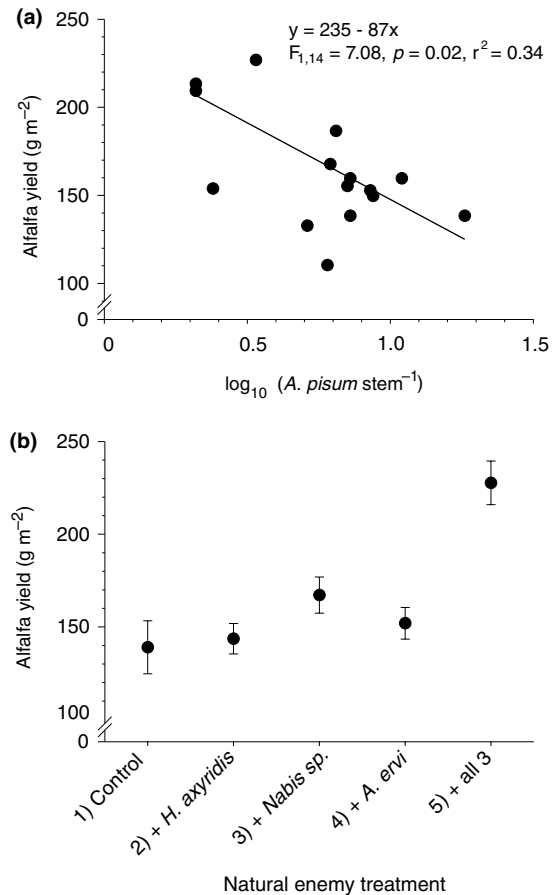
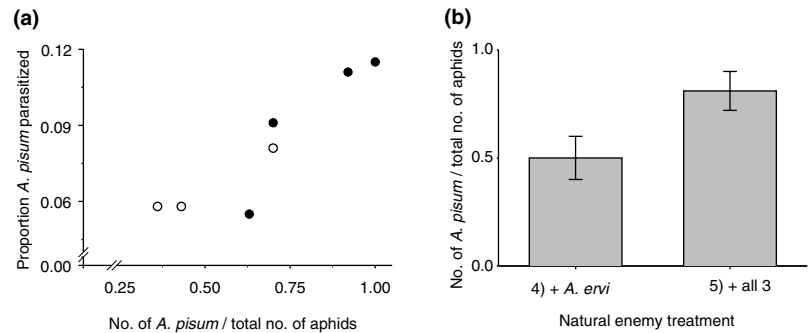


Figure 4 (a) The relationship between alfalfa yield and the final density of pea aphids in the 16 cages. (b) The mean \pm 1 SE of alfalfa yield in natural enemy treatments on the final date of the study. Corresponding statistical analyses of treatment effects on alfalfa yield are given in Table 1(c,d).

summed impact of each enemy species alone. The yield of alfalfa was inversely proportional to *A. pisum* density and, as a result, the non-additive suppression of *A. pisum* in enclosures containing the more diverse guild of enemy species led to increased alfalfa yield. Thus, we conclude that in this system there was a synergistic effect among natural enemies that resulted in more efficient biocontrol with cascading effects on crop production.

One potential explanation for the synergism among enemy species involves an interaction modification (*sensu* Sih *et al.* 1998) in which the density of the herbivore, *A. craccivora*, influenced the direct effect of the specialist parasitoid, *A. ervi*, on the pea aphid, *A. pisum*. Two observations underlie this hypothesis. First, there was a strong positive correlation between the abundance of *A. pisum* relative to *A. craccivora* in enclosures and the proportion of *A. pisum* that was parasitized by *A. ervi*

Figure 5 (a) The correlation between the proportional abundance of pea aphids in a cage and the proportion of pea aphids parasitized by *A. ervi*. Open circles are for treatment 4: plus *A. ervi*, filled circles are for treatment 5: plus all three enemy species. (b) The proportional abundance of pea aphids in treatments 4 and 5. Data are the mean \pm 1 SE.



($r = 0.93$, $P < 0.01$ for Pearson correlation between arcsine square root transformed data; Fig. 5a). Second, *A. pisum* represented a greater proportion of the total aphid abundance in treatment 5 (plus all three natural enemies) than in treatment 4 (plus *A. ervi*; $t = 2.22$, d.f. = 5, $P = 0.04$ for t -test comparing arcsine square root transformed data; Fig. 5b). The trend in Fig. 5b probably resulted because *H. axyridis* reduced the density of *A. craccivora*, but did not impact densities of *A. pisum* (see Fig. 3a,b and Table 1a,b). Taken together, these two observations suggest that when natural enemy species were together in the same enclosure, *H. axyridis* reduced the density of *A. craccivora*, thereby increasing the susceptibility of *A. pisum* to parasitism by *A. ervi*. Greater parasitism reduced *A. pisum* density and, in turn, led to higher alfalfa yield. The potential for this indirect interaction to explain the results of this study hinges on two assumptions. First, the efficiency of the parasitoid *A. ervi* was sensitive to the relative abundance of its host. We have no direct evidence to support this; however, it is a reasonable assumption given that attack rates of natural enemies are known to decrease when a high relative abundance of non-target herbivores alters encounter rates, either by changing the distribution of a target species or by reducing the search efficiency of an enemy (Bergeson & Messina 1998; Vet 2001; Symondson *et al.* 2002). The second assumption is that *A. pisum* had a larger per capita impact on alfalfa yield than *A. craccivora*. This possibility was directly supported by analyses showing that alfalfa yield was inversely related to final densities of *A. pisum*, but was not related to densities of *A. craccivora*.

An increased probability of non-additive interactions is potentially an important mechanism by which species diversity influences the rate of consumption of shared resources (Bertness 1998; Sih *et al.* 1998; Stachowicz 2001; Cardinale *et al.* 2002). The indirect interaction we propose as an explanation for our results is complementary to other forms of non-additive interaction, such as predator–predator facilitation (Losey & Denno 1998, 1999), that can enhance the suppression of agricultural pests. There are, however, a number of studies demonstrating antagonistic

interactions among enemy species that could reduce the efficiency of biological control. For example, intraguild predation and interference competition can reduce the impact of enemy species and, in turn, cause a multi-enemy guild to have less than additive effects on a prey/host population (Polis *et al.* 1989; Rosenheim *et al.* 1993; Ferguson & Stiling 1996; Holt & Polis 1997; Brodeur & Rosenheim 2000). In cases where antagonistic interactions are particularly strong, a multi-enemy assemblage could even exert less biocontrol than would be imposed by a single enemy species (for example, Snyder & Ives 2001). Given the potentially contrasting interactions among enemy species, the net impact of enemy diversity on biocontrol will ultimately depend on how diversity shifts the balance of positive and negative interactions among enemy species (Symondson *et al.* 2002).

The study of multiple enemy effects has a history that has remained largely distinct from the ongoing debate over how biodiversity affects the ‘functioning’ of ecosystems. While the former body of research has focused mostly on the role of non-additive species interactions in prey consumption, the latter has focused almost exclusively on additive mechanisms by which species richness influences resource consumption, with emphasis on terrestrial herbaceous communities (see Loreau *et al.* 2001). These additive mechanisms, including resource partitioning (Tilman *et al.* 1997; Hooper 1998) and ‘sampling effects’ (also called ‘selection-probability’, or ‘lottery’ effects; Huston 1997; Denoth *et al.* 2002), will almost certainly act in concert with non-additive species interactions to influence resource consumption by any guild of organisms. Therefore, the convergence of interests between these historically distinct lines of study represents an opportunity to better understand how variance in traits within any group of consumers might impact the use of shared resources. Combining insights from studies of natural enemy diversity with those from the broader diversity–function debate has much potential to further our understanding of the ecological consequences of diversity loss – particularly in human-dominated systems where extinction and invasion are the norm.

ACKNOWLEDGMENTS

This work was supported by a grant from the National Science Foundation to A.R.I. (DEB-0108300). We thank A. Forbes, M. Helmus, K. Guslick, R. Jameson, S. Langley and C. Williams for their assistance with field work, D. Mueller and the staff of the Arlington Research Farm for logistical support.

REFERENCES

- Andow, D.A. (1991). Vegetational diversity and arthropod population response. *Ann. Rev. Entomol.*, 36, 561–586.
- Benton, T.G., Vickery, J.A. & Wilson, J.D. (2003). Farmland biodiversity: is habitat heterogeneity the key? *Trends Ecol. Evol.*, 18, 182–188.
- Bergeson, E. & Messina, F.J. (1998). Effect of a co-occurring aphid on the susceptibility of the Russian wheat aphid to lacewing predators. *Entomol. Exp. Appl.*, 87, 103–108.
- Bertness, M.D. (1998). Searching for the role of positive interactions in plant communities. *Trends Ecol. Evol.*, 13, 133–134.
- Brodeur, J. & Rosenheim, J.A. (2000). Intraguild interactions in aphid parasitoids. *Entomol. Exp. Appl.*, 97, 93–108.
- Cardinale, B.J., Palmer, M.A. & Collins, S.L. (2002). Species diversity increases ecosystem functioning through interspecific facilitation. *Nature*, 415, 426–429.
- Connolly, J. (1988). What is wrong with replacement series. *Trends Ecol. Evol.*, 3, 24–26.
- Denoth, M., Frid, L. & Myers, J.H. (2002). Multiple agents in biological control: improving the odds? *Biol. Control*, 24, 20–30.
- Ferguson, K.I. & Stiling, P. (1996). Non-additive effects of multiple natural enemies on aphid populations. *Oecologia*, 108, 375–379.
- Gonzalez, D., White, W., Hall, J. & Dickson, R.C. (1978). Geographical distribution of Aphidae (Hym.) imported to California for biological control of *Acyrtosiphon kondoi* and *Acyrtosiphon pisum* (Hom.: Aphididae). *Entomophaga*, 23, 239–248.
- Harmon, J.P., Ives, A.R., Losey, J.E., Olson, A.C. & Rauwald, K.S. (2000). *Colemegeilla maculata* (Coleoptera: Coccinellidae) predation on pea aphids promoted by proximity to dandelions. *Oecologia*, 125, 543–548.
- Hassell, M.P. & May, R.M. (1986). Generalist and specialist natural enemies in insect predator prey interactions. *J. Anim. Ecol.*, 55, 923–940.
- Hassell, M.P. & Waage, J.K. (1984). Host–parasitoid population interactions. *Ann. Rev. Entomol.*, 29, 89–114.
- Hawkins, B.A., Mills, N.J., Jervis, M.A. & Price, P.W. (1999). Is the biological control of insects a natural phenomenon? *Oikos*, 86, 493–506.
- Hochberg, M.E. (1996). Consequences for host population levels of increasing natural enemy species richness in classical biological control. *Am. Nat.*, 147, 307–318.
- Holt, R.D. & Polis, G.A. (1997). A theoretical framework for intraguild predation. *Am. Nat.*, 149, 745–764.
- Hooper, D. (1998). The role of complementarity and competition in ecosystem responses to variation in plant diversity. *Ecology*, 79, 704–719.
- Huston, M. (1997). Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia*, 110, 449–460.
- Hutchinson, W.D. & Hogg, D.B. (1984). Demographic statistics for the pea aphid (Homoptera: Aphididae) in Wisconsin and a comparison with other populations. *Env. Ent.*, 13, 1173–1181.
- Hutchinson, W.D. & Hogg, D.B. (1985). Time-specific life tables for the pea aphids, *Acyrtosiphon pisum* (Harris), on alfalfa. *Res. Pop. Ecol.*, 27, 231–253.
- Ives, A.R., Schooler, S.S., Jagar, V.J., Knuteson, S.E., Grbic, M. & Settle, W.H. (1999). Variability and parasitoid foraging efficiency: a case study of pea aphids and *Abidius ervi*. *Am. Nat.*, 154, 652–673.
- Jolliffe, P.A. (2000). The replacement series. *J. Ecol.*, 88, 371–385.
- Takehashi, N., Suzuki, Y. & Iwasa, Y. (1984). Niche overlap of parasitoids in host parasitoid systems – its consequence to single versus multiple introduction controversy in biological control. *J. Appl. Ecol.*, 21, 115–131.
- Kruess, A. & Tscharntke, T. (1994). Habitat fragmentation, species loss, and biological-control. *Science*, 264, 1581–1584.
- LaMana, M.L. & Miller, J.C. (1996). Field observations on *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) in Oregon. *Biol. Control*, 6, 232–237.
- Lattin, J.D. (1989). Bionomics of the Nabidae. *Ann. Rev. Entomol.*, 34, 383–400.
- Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A. et al. (2001). Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science*, 294, 804–808.
- Losey, J.E. & Denno, R.F. (1998). Positive predator–predator interactions: enhanced predation rates and synergistic suppression of aphid populations. *Ecology*, 79, 2143–2152.
- Losey, J.E. & Denno, R.F. (1999). Factors facilitating synergistic predation: the central role of synchrony. *Ecol. Appl.*, 9, 378–386.
- Losey, J.E., Ives, A.R., Harmon, J., Ballantyne, F. & Brown, C. (1997). A polymorphism maintained by opposite patterns of parasitism and predation. *Nature*, 388, 269–272.
- Mackauer, M. & Kambhampati, S. (1986). Structural changes in the parasite guild attacking the pea aphid in North America. In: *Ecology of Aphidophaga* (ed. Hodek, I.). Academia, Prague, pp. 347–356.
- Mooney, H.A., Lubchenco, J., Dirzo, R. & Sala, O.E. (1995). Biodiversity and ecosystem functioning: basic principles. In: *Global Biodiversity Assessment* (ed. Heywood, V.H.). Cambridge University Press, Cambridge, pp. 275–325.
- Polis, G.A., Myers, C.A. & Holt, R.D. (1989). The ecology and evolution of intraguild predation – potential competitors that eat each other. *Ann. Rev. Ecol. Syst.*, 20, 297–330.
- Rauwald, K.S. & Ives, A.R. (2002). Biological control in disturbed agricultural systems and the rapid re-establishment of parasitoid populations. *Ecol. Appl.*, 11, 1224–1234.
- Rosenheim, J.A. (1998). Higher-order predators and the regulation of insect herbivore populations. *Ann. Rev. Entomol.*, 43, 421–447.
- Rosenheim, J.A., Wilhoit, L.R. & Armer, C.A. (1993). Influence of intraguild predation among generalist insect predators on the suppression of an herbivore population. *Oecologia*, 96, 439–449.
- SAS (1996). *Statistical Analysis System. Version 8.0 for Windows*. SAS Institute, Cary, NC, USA.
- Schlapfer, F., Schmid, B. & Seidl, L. (1999). Expert estimates about effects of biodiversity on ecosystem processes and services. *Oikos*, 84, 346–352.
- Sih, A., Englund, G. & Wooster, D. (1998). Emergent impacts of multiple predators on prey. *Trends Ecol. Evol.*, 13, 350–355.

- Snaydon, R.W. (1991). Replacement or additive designs for competition studies. *J. Appl. Ecol.*, 28, 930–946.
- Snyder, W.E. & Ives, A.R. (2001). Generalist predators disrupt biological control by a specialist parasitoid. *Ecology*, 82, 705–716.
- Snyder, W.E. & Ives, A.R. (2003). Interactions between specialist and generalist natural enemies: parasitoids, predators, and pea aphid biocontrol. *Ecology*, 84, 91–107.
- Snyder, W.E., Joseph, S.B., Preziosi, R.F. & Moore, A.J. (2000). Nutritional benefits of cannibalism for the lady beetle *Harmonia axyridis* (Coleoptera: Coccinellidae) when prey quality is poor. *Env. Ent.*, 29, 1173–1179.
- Stachowicz, J.J. (2001). Mutualism, facilitation, and the structure of ecological communities. *Bioscience*, 51, 235–246.
- Swift, M.J., Vandermeer, J., Ramakrishnan, P.S., Anderson, J.M., Ong, C.K. & Hawkins, B.A. (1996). Biodiversity and agroecosystem function. In: *Functional Roles of Biodiversity: A Global Perspective* (eds Mooney, H.A., Cushman, J.H., Medina, E., Sala, O.E. & Schulze, E.D.). Wiley, New York, NY, pp. 261–297.
- Symondson, W.O.C., Sunderland, K.D. & Greenstone, M.H. (2002). Can generalist predators be effective biocontrol agents? *Ann. Rev. Entomol.*, 47, 561–594.
- Thies, C. & Tscharntke, T. (1999). Landscape structure and biological control in agroecosystems. *Science*, 285, 893–895.
- Tilman, D., Lehman, D. & Thompson, K. (1997). Plant diversity and ecosystem productivity: theoretical considerations. *Proc. Nat. Acad. Sci.*, 94, 1857–1861.
- Vet, L.E.M. (2001) Parasitoid searching efficiency links behaviour to population processes. *Appl. Ent. Zool.*, 36, 399–408.
- Way, M.J. & Heong, K.L. (1994). The role of biodiversity in the dynamics and management of insect pests of tropical irrigated rice – a review. *Bull. Entomol. Res.*, 84, 567–587.
- Wilby, A. & Thomas, M.B. (2002). Natural enemy diversity and pest control: patterns of pest emergence with agricultural intensification. *Ecol. Lett.*, 5, 353–360.

Editor, Leon Blaustein

Manuscript received 13 May 2003

First decision made 12 June 2003

Manuscript accepted 2 July 2003