

Reciprocal effects of host plant and natural enemy diversity on herbivore suppression: an empirical study of a model tritrophic system

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Many theoretical and empirical studies have shown that species diversity in a trophic level can impact the capture of limited resources in ways that cascade up or down a food web. Only recently, however, have ecologists begun to consider how diversity at multiple trophic levels might act in concert to have opposing or reinforcing effects on resource use. Here, we report the results of an empirical study of a model, tritrophic food web in which we manipulated the diversity of host plant species (*Medicago sativa*, *Trifolium pratense* and *Vicia faba*) and natural enemy species (*Harmonia axyridis*, *Coleomegilla maculata* and *Nabis* sp.) of a widespread herbivorous pest (the pea aphid, *Acyrtosiphon pisum*) in laboratory microcosms. We found that increasing natural enemy richness from one to three species increased the proportion of aphids consumed by 0.14. This effect of enemy diversity was due to facilitative interactions and/or a reduction in intraspecific competition in the more diverse assemblages. We also found an independent and additive main effect of host plant richness, with the proportion of aphids consumed by natural enemies decreasing by 0.14 in plant polycultures. A reduction in predator efficiency on a single host plant, *Vicia faba*, appeared to be responsible for this plant diversity effect. Aphid population sizes were, therefore, simultaneously determined by a top-down effect of natural enemy diversity, and an opposing bottom-up effect of host plant diversity that modified enemy–prey interactions. These results suggest that population sizes in nature, and biotic controls over insect pests, are influenced by species diversity at multiple trophic levels.

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Habitat loss, the spread of exotic species, and over-exploitation of resources have all contributed to unprecedented losses in global species diversity over the past century (Vitousek et al. 1997, Sala et al. 2000). Of the potential ecological consequences of species loss, communities with lower biodiversity are thought to be less efficient at capturing limited resources, which might lead to decreased rates of primary and secondary production (Naem 2002). Primary and secondary production underlie many of the goods and services that ecosystems provide to society. Indeed, the production of crops and fisheries, the fertility of agricultural soils, and the suppression of pest species all depend on

how efficiently groups of consumers capture their resources and transform them into biomass (Chapin et al. 1998). Therefore, understanding when and why alterations to species diversity affect rates of resource capture remains one of the fundamental challenges in ecology.

Prior empirical and theoretical studies asking whether biodiversity influences the efficiency of resource capture have approached the question from one of two different perspectives. The first has been a ‘top-down’ perspective that focuses on how the diversity of organisms within a trophic level affects the sum of resources captured and consumed by that trophic level. This is the perspective

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taken by studies having investigated whether plant diversity influences the uptake of mineral nutrients (Hooper 1998, Hector et al. 1999, Tilman et al. 2001), whether the diversity of invertebrate consumers regulates algal and detrital processing in aquatic systems (Jonsson and Malmqvist 2000, Norberg 2000, Cardinale et al. 2002), and whether natural enemy richness affects the suppression of agricultural pests (Sih et al. 1998, Wilby and Thomas 2002, Cardinale et al. 2003a).

A complementary view is the 'bottom-up' perspective, which has focused on how diversity within a trophic level can influence the sum capture and consumption of resources at higher trophic levels. Perhaps the best known example of this perspective is the "enemies hypothesis" proposed by Root (1973) to explain how host plant diversity might influence natural enemy-victim interactions. A number of studies have tested this hypothesis empirically and, while the evidence is not conclusive, studies have found that the attack rate of predators and parasitoids is often a function of the host plant diversity of their victims (Evans 1976, Kaiser 1983, Kareiva 1987, Russell 1989, Andow 1991, Weisser 1995, Gingras and Boivin 2002, Benton et al. 2003, Hoddle 2003).

While studies stemming from the top-down and bottom-up perspectives have illustrated that diversity in a trophic level can affect resource capture in ways that cascade up or down a food web, seldom have these effects of diversity been studied in concert. This is unfortunate given that the efficiency of resource use in real food webs is likely to be influenced by diversity at multiple trophic levels, and perhaps by interactions between trophic levels. A limited but growing number of studies suggest that diversity among trophic levels can act in concert to have opposing, or reinforcing influences on resource use in ways that can be either additive or non-additive (Price et al. 1980, Holt and Loreau 2002, Raffaelli et al. 2002, Giller et al. 2004). There is, therefore, a growing sentiment among ecologists that studies of biodiversity and ecosystem functioning need to incorporate more natural trophic structures when attempting to understand the role of diversity in food web dynamics.

Here we report the results of an empirical study in which we used a model tritrophic food web to simultaneously examine the top-down and bottom-up effects of diversity on resource capture. Our study focused on a system of three plant species (*Medicago sativa*, *Trifolium pratense* and *Vicia faba*) that are hosts to a widespread herbivorous pest (the pea aphid, *Acyrtosiphon pisum*) that was subjected to predation by three of its most common natural enemies (*Harmonia axyridis*, *Coleomegilla maculata* and *Nabis* sp.). Using this model experimental system, we simultaneously manipulated species richness of natural enemies in host plant mono- and polycultures, allowing us to examine how diversity at the

bottom and top trophic levels act in concert to influence consumption of the aphid resource.

Methods

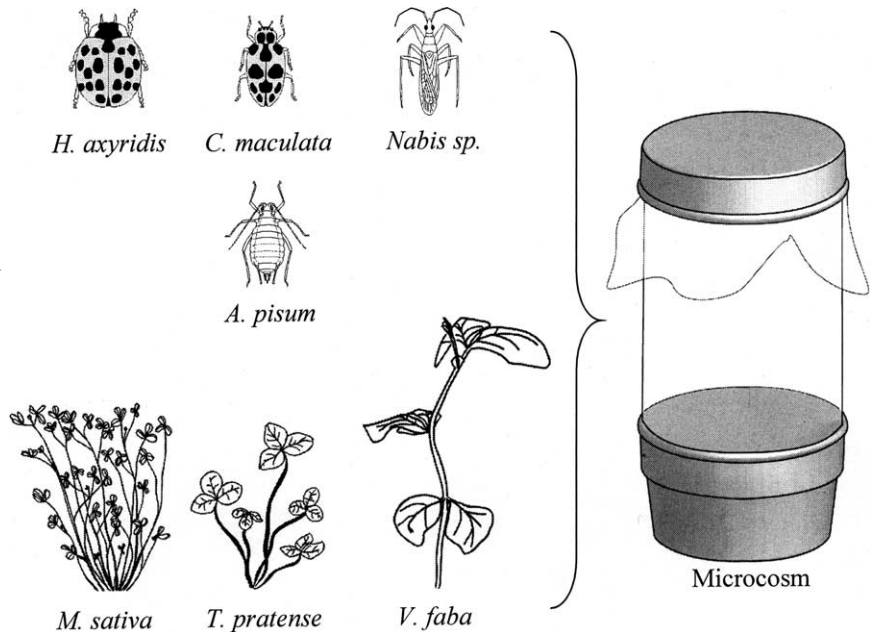
Study system

The three host plant species used in this study – alfalfa (*Medicago sativa*), red clover (*Trifolium pratense*) and fava bean (*Vicia faba*) – have nearly worldwide distributions and represent some of the most commercially important forage crops for livestock (Kay 1979, Bajaj 1990, Hagen and Hamrick 1998). The herbivore and focal resource in this study was the pea aphid, *Acyrtosiphon pisum* (Homoptera: Aphididae). The pea aphid is an Old World species that is now a frequent agricultural pest in many parts of the United States, as well as other countries (Philip and Mengersen 1989). A variety of natural enemies control pea aphid densities in the midwestern US, generally keeping population sizes below economically damaging thresholds (Hutchinson and Hogg 1984). The three natural enemies used in this study, the multicolored Asian ladybeetle (*Harmonia axyridis*, Coleoptera: Coccinellidae), the damselbug (*Nabis* sp., Heteroptera: Nabidae), and the pink spotted ladybeetle (*Coleomegilla maculata*, Coleoptera: Coccinellidae) are dominant species in the natural enemy assemblages of agroecosystems in Wisconsin, as well as other parts of the USA (Snyder and Ives 2003). All three predators are known to play an important role in the suppression of pea aphids in our study systems (Cardinale et al. 2003a, Ostman and Ives 2003, Snyder and Ives 2003). *H. axyridis* was specifically introduced to the USA from China as a biocontrol agent of aphids. It is a generalist predator that feeds on many types of aphids as well as other enemies and conspecifics (LaMana and Miller 1996). *Coleomegilla maculata* is more omnivorous, consuming a diversity of resources from aphids to pollen (Hodek and Honek 1996, Harmon et al. 2000). *Nabis* sp. will attack a variety of prey, but generally exhibits a preference for aphids (Flinn et al. 1985).

Experimental design

Our experiment was performed in a greenhouse at the University of Wisconsin-Madison. The experimental units were microcosms containing host plants grown in 20 cm diameter × 13 cm deep pots that were enclosed in 40 cm tall mylar shields capped with mesh (Fig. 1). In these microcosms, we simultaneously manipulated host plant and natural enemy richness. Treatment combinations included the three host plant monocultures plus a three plant polyculture. These four host plant treatments were crossed with four natural enemy treatments in which microcosms were stocked with each of the natural

Fig. 1. The model tritrophic system used in this experiment. Microcosms consisted of a 20 cm diameter \times 13 cm deep pots enclosed in 40 cm tall mylar shields capped with mesh. Microcosms contained either host plants (*Medicago sativa*, *Trifolium pratense* and *Vicia faba*) in monoculture or in a three species polyculture. All microcosms were inoculated with 25 adults of the herbivorous pea aphid (*Acyrtosiphon pisum*). One or three species of natural enemy of the pea aphid (*Harmonia axyridis*, *Coleomegilla maculata* and *Nabis* sp.) were then introduced.



enemy species alone, or with all three enemies together. Natural enemies were collected from agricultural fields at the University of Wisconsin's Arlington Research Station and were held in the laboratory until use.

Species richness of both plants and enemies was manipulated as a replacement series design in which the total density in a trophic level, $D_{tot}=3$, was held constant across levels of richness in that trophic level, $S=1$ or 3. This design results in the density of any given species, D_i , decreasing with increasing S ($D_i = D_{tot}/S$), which contrasts with the additive series experimental design where the more diverse assemblages have the summed number of organisms in less diverse assemblages. The relative merits of the replacement and additive series designs have been discussed at length (Connolly 1988, Jolliffe 2000), and each has strengths and limitations. We chose to manipulate species richness as a replacement series because at the small scale of this experiment, both plants and natural enemies are likely to be strong competitors; thus, holding densities constant was a logical choice.

Each of the 16 host plant \times enemy treatment combinations was replicated in three temporal blocks of the experiment run on separate dates. The first two blocks consisted of three replicates of each treatment combination, while the final block was partially replicated with 2–3 microcosms for each combination (fewer replicates were run for combinations containing *C. maculata* due to difficulty in finding this species at the time this block was run). In all, there were 48 microcosms in the first two blocks, 27 in the third block, and a total of 8–9 replicates per host plant \times enemy combination over the course of the experiment. At the beginning of a block, each microcosm was randomly assigned a treatment

combination. We then added 25 third to fifth instar (adult) pea aphids that had been reared in laboratory cultures to each microcosm. Aphids were given 10 h to distribute themselves on host plants, after which natural enemies were added to the microcosms and allowed to forage for 30 h (\pm SD=53 min). During this foraging period, microcosms were exposed to ambient light (\sim 16:8 day/night) and temperature.

Data analyses

After the foraging period, natural enemies were removed from the microcosms, and the number of adult aphids remaining was counted. Prior to any analyses of data, we excluded 19 of 123 microcosms from the study because (a) natural enemies had escaped or died during the experimental period, (b) plants were contaminated with herbivores other than the pea aphid, or (c) there was substantial reproduction by adult pea aphids during the feeding period (we used an arbitrary cutoff of >30 , 1st–2nd instar aphids). Our final analyses were, therefore, based on data from 104 microcosms in which there were no readily apparent confounding factors that might influence rates of predation.

Using this dataset, we addressed three different questions. First, we asked whether the effect of natural enemy richness differed among the four host plant treatments and, if not, did richness have any main effect when averaged over all treatments. Using a mixed model Anova (SAS 1996), we modeled the proportion of aphids consumed in a microcosm (arcsin square root transformed) as a function of natural enemy richness (1 or 3 species), host plant treatment (alfalfa, red clover, fava

bean or polycultures), and a term for their interaction. The potential temporal variation among experimental blocks was accounted for by including blocking in the model as a random effect (Littell et al. 1996). We then determined whether the effect of enemy richness on aphid consumption differed from zero in any of the four host plant treatments using estimate statements that essentially generate t-tests after accounting for the random block effect (Littell et al. 1996).

Second, we asked whether the effect of host plant richness differed among the four natural enemy treatments and, if not, whether host plant richness had any main effect when averaged across the enemy treatments. With analyses identical to those described above, aphid consumption was modeled as a function of host plant richness (1 or 3 species), natural enemy treatment (*C. maculata*, *H. axyridis*, *Nabis* sp. and the 3 enemies together), and a term for the richness \times natural enemy interaction. We then determined whether the effect of host plant richness on aphid consumption differed from zero in any of the individual natural enemy treatments as above.

Finally, we asked whether natural enemy and host plant richness interacted to influence aphid consumption. To address this question we used a third mixed model Anova to test the interaction term for natural enemy richness (1 or 3 species) \times host plant richness (1 or 3 species).

Results

Top-down effects of diversity

The effect of natural enemy richness on aphid consumption did not differ among the four host plant environments ($F_{3,96} = 1.31$, $P = 0.28$ for the richness \times host plant interaction). There was, however, a significant main effect of natural enemy richness when averaged over all plant treatments ($F_{1,96} = 5.64$, $P = 0.02$, Fig. 2A). The proportion of aphids consumed was $0.60 (\pm \text{sd} = 0.03, N = 78)$ in microcosms containing a single enemy species, and increased by 0.14 in microcosms containing all three species (mean = 0.74 ± 0.04 , $N = 26$). This main effect of natural enemy richness appeared to result primarily from dynamics on fava bean. Post-hoc contrasts indicated that the mean proportion of aphids consumed increased by 0.31 as enemy richness increased from one to three species in fava bean ($t = 2.63$, $P = 0.01$, Fig. 2D). The slopes relating aphid consumption to enemy richness were not different from zero in monocultures of alfalfa ($t = -0.17$, $P = 0.87$, Fig. 2B), red clover ($t = 1.06$, $P = 0.29$, Fig. 2C), or in polycultures ($t = 1.25$, $P = 0.22$, Fig. 2E).

The main effect of enemy richness on aphid consumption appeared to result from the relatively poor performance of two enemy species, *Nabis* sp. and *C. maculata*,

when each taxon was the sole predator in a microcosm (Fig. 2A). Both species had notably low consumption in plant polycultures (Fig. 2E) and comparably low consumption in fava bean (Fig. 2D). These trends suggest that the low efficiency of the two natural enemies on fava bean were responsible for the main effect of natural enemy richness on aphid consumption (Fig. 2A). The proportion of aphids consumed by *H. axyridis* was also reduced in fava bean (Fig. 2D), indicating this host plant was a poor environment for all natural enemy species. However, consumption of aphids by *H. axyridis* was quite similar among the other host plant treatments (compare Fig. 2A, C, E) and was typically equal to, or exceeded consumption in microcosms having the three enemy species together.

Bottom-up effects of diversity

The effect of host plant richness on aphid consumption did not differ among the four natural enemy treatments ($F_{3,96} = 1.71$, $P = 0.17$ for the plant richness \times enemy interaction). There was, however, a significant main effect of host plant richness averaged over all enemy treatments ($F_{1,96} = 17.58$, $P < 0.01$, Fig. 2F). The mean proportion of pea aphids consumed was $0.67 (\pm \text{sd} = 0.03, N = 79)$ for the host plant monocultures, but declined by 0.14 in microcosms containing host plants in polyculture (mean = 0.53 ± 0.06 , $N = 25$, Fig. 2B). Post hoc contrasts indicated that the proportion of aphids consumed decreased with host plant richness by 0.27 when microcosms contained *C. maculata* ($t = -1.78$, $P = 0.08$, Fig. 2G), by 0.42 when microcosms contained *Nabis* sp. ($t = -2.44$, $P = 0.02$, Fig. 2I), and by 0.15 for microcosms containing all three natural enemies ($t = -2.99$, $P < 0.01$, Fig. 2J). For the *H. axyridis* treatment, slopes relating aphid consumption to host plant richness were not different from zero ($t = -0.78$, $P = 0.44$, Fig. 2H).

The negative relationship between host plant richness and aphid consumption was largely influenced by the relatively poor performance of natural enemies when on fava beans (Fig. 2F). The proportion of aphids consumed in fava bean monocultures (0.50 ± 0.05 , $N = 26$) was 0.26 lower than in monocultures of either alfalfa (0.76 ± 0.04 , $N = 24$) or red clover (0.76 ± 0.04 , $N = 29$). However, on average, aphid consumption in monocultures of fava bean did not differ from that in polycultures (0.53 ± 0.06 , $N = 25$).

Test for interactive effects of diversity

Despite significant main effects of both natural enemy and host plant richness on aphid consumption, there was no interactive effect of diversity at the two trophic levels ($F_{1,100} = 0.01$, $P = 0.92$). Thus, the consumption of pea

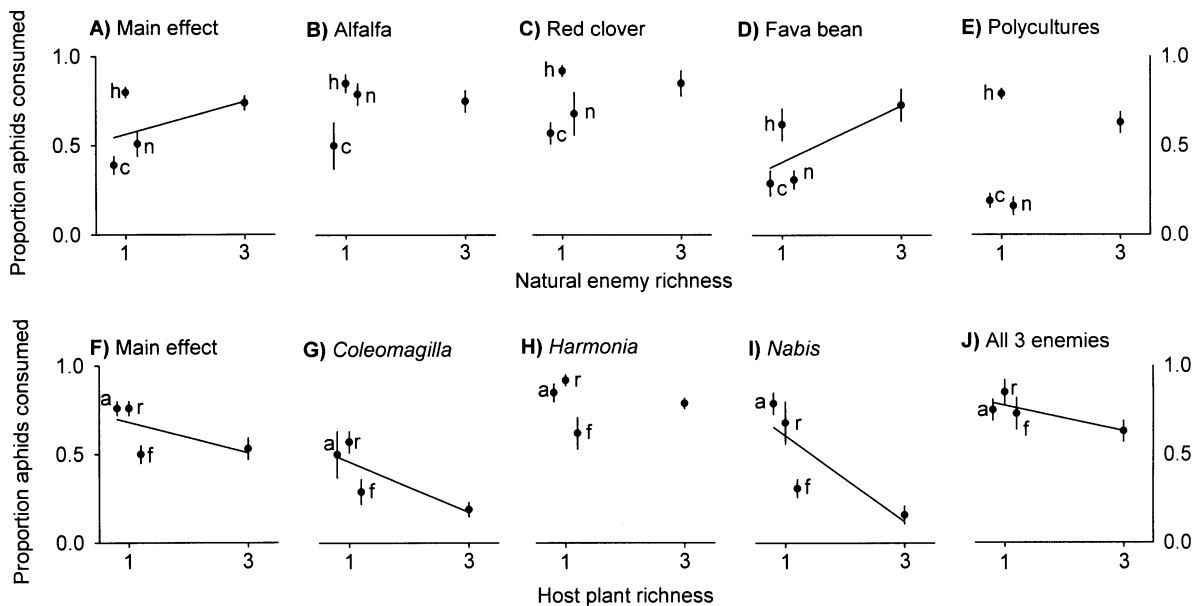


Fig. 2. The effects of natural enemy richness (A–E) and host-plant richness (F–J) on the consumption of pea aphids. The main effect of natural enemy richness averaged over all plant treatments is given in (A), with the diversity effect shown separately for each of the four host plant treatments in (B–E). Letters next to data points designate the single enemy species when alone: c = *Coleomagilla maculata*, h = *Harmonia axyridis*, n = *Nabis* sp. The main effect of host plant richness is then shown in (F), with the effect illustrated for each of the natural enemy treatments in (G–J). Letters designate plant monocultures: a = alfalfa, f = fava bean, r = red clover. All data points are the mean \pm 1 se.

aphids increased with natural enemy richness in a manner that was parallel between host plant mono- and polycultures (Fig. 3). The lack of an interaction was due to a simultaneous decrease in predation for the one enemy and three enemy species treatments in plant polycultures. Declines in the mean of the one enemy treatment were strongly influenced by reduced efficiency of both *Nabis* sp. and *C. maculata* in polycultures (Fig. 2E).

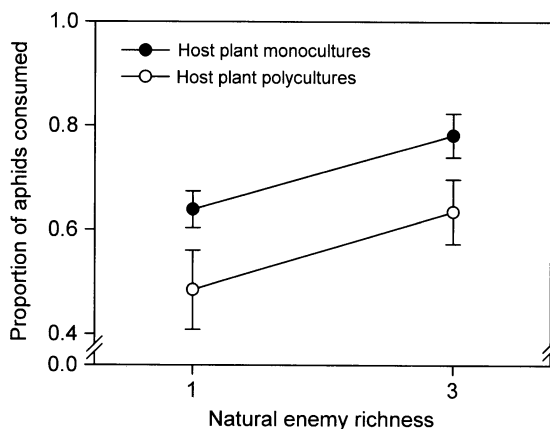


Fig. 3. The main effect of natural enemy species richness on aphid consumption in host plant monocultures and polycultures. Data points are the mean \pm 1 se of the treatments.

Discussion

A growing body of research suggests that species diversity within a trophic level can have effects on resource capture that cascade up or down a food web (reviewed by Root 1973, Russell 1989, Andow 1991, Sih et al. 1998, Tilman 1999, Naeem 2002). This study complements past research by showing that the capture and consumption of prey from a given trophic level are simultaneously influenced by species diversity at lower and higher trophic levels. We found that predation on pea aphids was affected not only by a top-down effect of natural enemy diversity, but also by a bottom-up effect of host plant diversity that modified aphid–enemy interactions. These two effects were additive and opposing. Increasing host plant richness decreased consumption of aphids by approximately the same amount that enemy richness increased consumption. Such results suggest that species population sizes in food webs may be a function of biodiversity operating antagonistically across alternating trophic levels.

Our finding that natural enemy diversity reduced pea aphid densities is consistent with a number of theoretical and empirical studies showing that multi-enemy assemblages sometimes exert stronger biocontrol over insect pests than single enemy species (Losey and Denno 1998, Sih et al. 1998, Wilby and Thomas 2002, Cardinale et al. 2003b, Snyder and Ives 2003). Given that we held natural enemy abundance constant across levels of species richness, the main effect of natural enemy

diversity on aphid population size can only be explained by greater per capita rates of consumption when enemies were in the more diverse assemblages. We can think of two alternative explanations for this result: either intraspecific competition was reduced in high diversity treatments (Jonsson and Malmqvist 2000), or consumption rates were enhanced by interspecific interactions among natural enemies (Losey and Denno 1998, Sih et al. 1998, Wilby and Thomas 2002, Cardinale et al. 2003b). For the first of these explanations, the absence of conspecific competitors in the high diversity treatment (which had only one individual of each species) may have led to greater per capita predation. The potential for intraspecific competition to change with diversity is an inherent property of the replacement series experimental design. This property is viewed by some as a flaw (Connolly 1988, Jolliffe 2000); however, the replacement series mimics many natural scenarios where the total abundance of a guild of organisms is limited regardless of whether there is one or many species in the system. Given this, if feeding rates of individual predators were constrained by interactions with conspecifics, then a release from intraspecific competition in more diverse assemblages could have increased per capita predation rate on pea aphids.

In the experiment reported here, a reduction in intraspecific competition could produce the diversity effect in one of two ways. First, if predation by *Nabis* sp. and *C. maculata* when alone were constrained by intraspecific competition, then per capita consumption of one or both species could have increased in the absence of conspecifics in more diverse enemy assemblages. Alternatively, if *H. axyridis* consumed enough aphids in their single species treatment that they were limited by food availability (as seems plausible given the high proportion of prey consumed by this taxon, Fig. 2), then a single adult *H. axyridis* might consume as many aphids in the three enemy species treatment as did three adults in the single enemy treatment. Note that, if correct, the positive relationship between natural enemy diversity and aphid consumption would have resulted solely from the enhanced performance of *H. axyridis* in the more diverse assemblage. This is similar to, but not mechanistically the same as, the 'sampling effect' of diversity where the single most efficient species dominates resource capture when alone or in a diverse assemblage (Huston 1997, Loreau et al. 2001).

The alternative explanation for the effect of natural enemy diversity on aphid consumption observed in our experiments is that enemy species could have exhibited positive interspecific interactions, such as those that result from predator–predator facilitation or indirect interactions (Losey and Denno 1998, Sih et al. 1998, Wilby and Thomas 2002, Cardinale et al. 2003b). Unfortunately, because positive species interactions are expected to produce patterns identical to those predicted

from reduced intraspecific competition, we cannot distinguish these two possible explanations in this study.

In addition to the main effect of natural enemy richness, host plant richness had a direct effect on aphid consumption with the proportion of aphids consumed decreasing by 0.14 in systems having more host plant species. This result is consistent with numerous studies showing that the efficiency of natural enemies is often lower in more diverse plant assemblages (Evans 1976, Kaiser 1983, Andow and Risch 1985, Russell 1989, Weisser 1995, Gingras and Boivin 2002, Hoddle 2003). Such patterns are generally attributed to predator or parasitoid search images being inhibited in structurally complex habitats (Kareiva 1987). However, this seems an unlikely explanation for the results of our study given that the main effect of host plant richness appeared to result from low efficiency of predators on fava beans (Fig. 2F), the most architecturally simple of the host plants studied. We suspect, therefore, that factors other than predator search efficiency played a role in generating the effect of host plant diversity. One factor that may have been important is the escape response of the pea aphid. Pea aphids use tactile and visual cues to detect natural enemies and then 'drop' from plants to escape (Losey and Denno 1998). If pea aphids were better at detecting and escaping enemies on structurally simple host plants, then the inclusion of fava bean in a more diverse host plant assemblage might have served as a 'refuge' that decreased the impact of enemies on their prey.

Several studies have suggested that the effect of diversity at one trophic level may depend on diversity in another trophic level (van der Heijden et al. 1998, Klironomos et al. 2000, Naeem et al. 2000). This has led to the prediction that trophic interactions will generate nonadditive effects of diversity among trophic levels (Holt and Loreau 2002). Contrary to this prediction, we found that the effects of host plant and enemy richness on aphid consumption were additive. This was true in spite of clear evidence of an interaction between the first trophic level (host plants) and the third trophic level (natural enemies). Indeed, the effect of natural enemy diversity on aphid consumption clearly depended on which host plant species were in the system (Fig. 2B–G), and the effect of host plant diversity on the aphid–enemy interaction clearly depended on which enemy species occupied the system (Fig. 2G–J). Although the effects of diversity at the two trophic levels were additive, it is interesting to note that they were opposing. Aphid consumption was negatively influenced by host plant richness by approximately the same magnitude that consumption was positively influenced by natural enemy richness (Fig. 3). These results suggest that, under some circumstances, the simultaneous loss of diversity from two different trophic levels might not lead to any notable change in the fluxes of energy or matter through a food

web. Because reductions in plant diversity and natural enemy diversity are often concurrent – particularly in highly simplified agricultural systems (Andow 1991, Benton et al. 2003) – determining whether diversity at various trophic levels general act in an antagonistic or reinforcing manner is an important challenge for future research.

The use of model food webs in research has historically proven useful for testing and refining ecological hypotheses. However, extrapolating from work performed in microcosms and mesocosms to natural systems is problematic for a wide variety of reasons (Carpenter 1999). Given this, several limitations of our study are apparent. Not only did the small spatial scale preclude any of the potentially important effects that dispersal can exert over resource capture (Cardinale et al. 2003b, Symstad et al. 2003), the short time scale ignored reproduction and, thus, the numerical responses of populations that can be important aspects of diversity effects (Frost et al. 1995). In spite of these limitations, our study offers some insight into the role that species diversity plays in the localized, short term process of resource capture. Aphids and their natural enemies occupy only one plant at a time such that instantaneous rates of predation are inherently defined on small spatial and short temporal scales. Therefore, results of this study indicate that the probability of an aphid being eaten increases with the diversity of predators in the immediate environment, but decreases as the diversity of adjacent plants increases.

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