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Authors

Cardinale, Bradley J
Weis, J J
Forbes, A E
et al.

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Biodiversity as both a cause and consequence of resource availability: a study of reciprocal causality in a predator–prey system

BRADLEY J. CARDINALE^{*†}, JEROME J. WEIS^{*†}, ANDY E. FORBES[†],
KELLEY J. TILMON^{†‡} and ANTHONY R. IVES[†]

^{*}University of California-Santa Barbara, Department of Ecology, Evolution & Marine Biology, Santa Barbara, CA 93106, USA; [†]University of Wisconsin-Madison, Department of Zoology, Madison, WI 53706, USA; and [‡]South Dakota State University, Plant Sciences Department, Brookings, SD 57007, USA

Summary

1. One of the oldest questions in ecology is how species diversity in any given trophic level is related to the availability of essential resources that limit biomass (e.g. water, nutrients, light or prey). Researchers have tried to understand this relationship by focusing either on how diversity is influenced by the availability of resources, or alternatively, how resource abundance is influenced by species diversity. These contrasting perspectives have led to a seeming paradox ‘... is species diversity the cause or the consequence of resources that limit community biomass?’

2. Here we present results of an experiment that show it is possible for species diversity and resource density to exhibit reciprocal causal relationships in the same ecological system. Using a guild of ladybeetle predators and their aphid prey, we manipulated the number of predator species in field enclosures to examine how predator diversity impacts prey population size. At the same time, we manipulated the abundance of aphid prey in discrete habitat patches within each enclosure to determine how smaller-scale spatial variation in resource abundance affects the number of co-occurring predator species.

3. We found that the number of ladybeetle species added to enclosures had a significant impact on aphid population dynamics because interference competition among the predators reduced per capita rates of predation and, in turn, the overall efficiency of the predator guild. At the same time, spatial variation in aphid abundance among smaller habitat patches generated variation in the observed richness of ladybeetles because more species occurred in patches where predators aggregated in response to high aphid density.

4. The results of our experiment demonstrate that it is possible for species diversity to simultaneously be a cause and a consequence of resource density in the same ecological system, and they shed light on how this might occur for groups of mobile consumers that exhibit rapid responses to spatial and temporal variation in their prey.

Key-words: ecosystem functioning, nonadditive interaction, predation, productivity, species richness.

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Introduction

It has long been recognized that the number of species in a community is linked to the availability of resources

that limit the production of community biomass (Darwin 1859). Historically, studies have tried to understand this relationship by focusing on species diversity as a response variable, asking how the richness of species within and among trophic levels varies across experimental or geographical gradients of resource supply (reviewed by Rosenzweig & Abramsky 1993; Abrams 1995; Waide *et al.* 1999; Mittelbach *et al.* 2001). Over the past decade, an alternative perspective has emerged in which diversity is viewed as an

Correspondence: Dr Bradley J. Cardinale, University of California-Santa Barbara, Department of Ecology, Evolution & Marine Biology, Santa Barbara, CA 93106, USA. Tel.: 805 893 4157; Fax: 805 893 4157; E-mail: cardinale@lifesci.ucsb.edu

independent variable that regulates how efficiently groups of organisms capture and convert available resources into new biomass (reviewed by Tilman 1999; Loreau *et al.* 2001; Naeem 2002; Hooper *et al.* 2005). These contrasting perspectives have engendered a lively debate about whether species diversity is the cause or the consequence of resource densities that limit the production of biomass (Grime 1997; Huston 1997; Fridley 2001; Loreau *et al.* 2001; Schmid 2002; Worm & Duffy 2003).

As researchers have tried to resolve these contrasting perspectives, new ideas have been formulated to explain how species diversity might simultaneously be a cause and a consequence of resource density. For example, several authors have converged on a similar hypothesis that spatial variation in the availability of key resources might drive variation in species diversity across sites while, at the same time, the diversity of species at any given site influences how efficiently available resources are captured and converted into biomass (Loreau *et al.* 2001; Schmid 2002; Worm & Duffy 2003). If correct, this idea could help resolve a seeming paradox by suggesting that species diversity and resource density exhibit reciprocal causal relationships, but the dependent and independent variables change as a function of spatial scale. Although this hypothesis has begun to take heuristic form, we are not aware of any study that has examined how species diversity and resource density might exhibit bidirectional causality in the same ecological system, or even demonstrated that reciprocal causal relationships are theoretically or empirically possible.

Here we report the results of a mesocosm study that illustrates how species diversity of a group of mobile consumers might respond to the availability of resources at one spatial scale, while species diversity at a different spatial scale controls how efficiently resources are consumed. Our research focused on a system of predatory ladybeetles and their primary resource, the pea aphid *Acyrtosiphon pisum* Harris. Our interest in reciprocal relationships between predator diversity and prey density was motivated by previous work in fields of alfalfa *Medicago sativa* L. In this system, predator diversity is strongly correlated with aphid density (Cardinale *et al.* 2003), which can vary by several orders of magnitude among fields (Gross, Ives & Nordheim 2005). This variation occurs because alfalfa is harvested three to four times per summer with 3–5 weeks between cuts. At harvest, pea aphid density is reduced by 100–1000 ×, but populations increase rapidly afterwards (Hutchison & Hogg 1985; Rauwald & Ives 2001). Because harvesting is asynchronous among fields there is considerable spatial variation in aphid density at any given time. Like most aphid predators, ladybeetles are highly mobile, and as they fly among fields in search of prey they aggregate in areas of high aphid abundance (Ives, Kareiva & Perry 1993). Within days, aggregation can lead to a strong association between aphid density and total predator abundance

and, because predator abundance and diversity are also correlated, there is a corresponding association between aphid density and predator diversity (Cardinale *et al.* 2003).

While the observations described above lead us to suspect that spatial variation in aphid density is an important determinant of variation in predator diversity, there is also reason to believe that predator diversity in the regional colonist pool (i.e. the number of species able to colonize any given field) influences how efficiently predator assemblages control aphid populations. We have documented several types of nonadditive interaction among natural enemy species in this system (Snyder & Ives 2001; Cardinale *et al.* 2003), which can cause predator assemblages to impact aphid populations in a manner that is disproportionate to the total abundance of predators. We have become increasingly interested in such interactions because in the mid-western USA where our work is performed, the richness and composition of predators have been altered by species invasions. For example, ladybeetles are the most common generalist predators in our system (Snyder & Ives 2003). Of the four to six native species, *Coleomegilla maculata* Timberlake is the only one that remains common. The guild is now dominated by *Harmonia axyridis* Pallas and *Coccinella septempunctata* L., both of which were intentionally introduced into agricultural systems for aphid biocontrol (Angalet, Tropp & Eggert 1979; Koch 2003). Growing evidence suggests that native ladybeetle species are being displaced by antagonistic interactions with their introduced counterparts (Alyokhin & Sewell 2004; Snyder, Clevenger & Eigenbrode 2004).

Taken collectively, our observations led us to hypothesize that predator diversity in this system is both a cause and a consequence of aphid density. At the larger scale where invasions and/or extinctions have altered the number and composition of species in the predator colonist pool, ladybeetle diversity may act as an independent variable that influences the efficiency of aphid biocontrol. Yet, at the smaller scale where predators aggregate in fields with high aphid density, predator diversity may be the dependent variable that responds to spatial variation in prey availability among fields. Ideally, we would test this hypothesis by manipulating aphid density and predator diversity at the 'landscape' scale where predators move among multiple fields. But of course, this is not possible, and we must settle for more limited insights that come from smaller scale models of this system. With this in mind, we set up a mesocosm experiment that attempted to capture certain key features of this system. Using a split-plot experimental design, we simultaneously manipulated predator diversity and aphid density in thirty 8-m³ field enclosures. Within each enclosure, we varied the initial density of pea aphids in 1 m² patches of alfalfa. These patches were separated by physical barriers that could only be crossed by flying adult ladybeetles, which allowed us to assess how predator

abundance and diversity respond to spatial variation in prey density at the scale of a patch. At the same time, we varied the number of species of ladybeetles that were added to the enclosures. By measuring the population growth rate of pea aphids in a cage, we determined how ladybeetle diversity impacted rates of predation at the scale of the whole enclosure. The mesocosms are only a caricature of this system, and important biological details are clearly simplified. Even so, the results are useful because they demonstrate that it is possible for species diversity to be both a cause and a consequence of resource density in the same ecological system, and they shed light on how this might occur for groups of mobile consumers.

Materials and methods

STUDY SYSTEM

The experiment was performed at the University of Wisconsin's Arlington Research Farm in south-central Wisconsin where pea aphids *A. pisum* are the dominant herbivore in alfalfa. During the summer, *A. pisum* reproduces asexually with parthenogenic females birthing up to six nymphs per day. The nymphs can develop into two morphological forms – alate or apterous. Apterous individuals have limited mobility and spend their life on a small number of adjacent plants. Development time from first instar to reproductive adult can be as little as 5 days under favourable climatic conditions (Hutchinson & Hogg 1984).

Pea aphid populations are controlled by a suite of natural enemies at our field sites, including fungal pathogens, parasitic wasps, and generalist predators (Snyder & Ives 2003). Probably the most important of the predators are ladybeetles, of which, the guild is composed primarily of three species – *Harmonia axyridis*, *Coccinella septempunctata* and *Coleomegilla maculata*. *H. axyridis*, the multicoloured Asian ladybeetle, was introduced into the United States from China in the 1980s as a biocontrol agent of aphids (Koch 2003). *C. septempunctata*, the seven-spotted ladybeetle, was introduced from Europe in the 1960s to control *A. pisum* (Angalet *et al.* 1979). *Co. maculata*, the pink spotted ladybeetle, is a native of North America.

Experimental units for the study consisted of thirty $2 \times 2 \times 2$ m cages covered on all sides but the bottom with 530 μ m mesh screening (32×32 Lumite, Bioquip, Gardena, CA, USA, catalogue number 1412C). Bottom edges were sealed with a 10 cm berme of soil to prevent arthropods from moving into or out of cages. All arthropods were initially removed by sweeping each cage twice with a D-vac suction sampler (D-vac Company, Ventura, CA 93002, USA). Following this, two researchers searched for and removed any additional animals that could be found. Cages were then subdivided into four 1-m² patches of alfalfa. One patch was designated as the observation area while the others were randomly assigned to three levels of initial pea

aphid density (7, 70 or 700 aphids m⁻²). Apterous aphids that had been cultured in a greenhouse were added to patches on 11 June, 2004. To ensure aphid abundances were not compromised by movement, patches were separated with a 30 cm high plastic fence that was coated with a lubricant (Fluon, ASAHI Glass Company, Tokyo) and sealed at the bottom. The fence successfully prevented migration of aphids with < 0.001% of the populations found moving among patches on any date. However, we will show that the predatory ladybeetles were not inhibited from flying among patches to find their prey.

PREDATOR DIVERSITY

After giving aphids 24 h to establish on plants, enclosures were randomly assigned to one of five predator treatments: (1) no predator control; (2) + *C. septempunctata*; (3) + *Co. maculata*; (4) + *H. axyridis*; or (5) + all three species together. Each treatment was replicated in six cages for a total of 30 enclosures. We used an additive design to manipulate predator densities where $n = 20$ individuals of the appropriate species were stocked in treatments 2–4, and $n = 60$ individuals (20 per species) were stocked in treatment 5 (densities that are well within the known range for this system, Harmon *et al.* 2000; Cardinale *et al.* 2003; Snyder *et al.* 2003). Advantages and disadvantages of the additive design and its counterparts (e.g. the replacement or substitutive design where total density is held constant) have been detailed elsewhere (Connolly 1988; Jolliffe 2000; Goldberg & Scheiner 2001). We chose the additive design over others because by intentionally confounding predator diversity and density, one can statistically partition the effects of predators into two components: one that is proportional to total predator abundance assuming species have independent effects on prey, and a second that is disproportionate to total predator abundance. The latter indicates a change in the per capita rates of predation by one or more predator species when together in the same system.

DEPENDENT VARIABLES

The experiment ran from 11 to 29 June 2004. On days 1, 3, 4, 6, 11, 14 and 18 we counted the number of pea aphids on 10–25 stems of alfalfa in each of the 1-m² patches of alfalfa in every cage (fewer stems were counted when abundance exceeded 100 per stem). The abundance of predator species in each patch was then determined by recording the number of individuals observed during a standardized 1 min visual scan. We have found that timed counts are the most reliable means of non-destructive sampling for mobile invertebrates.

On day 5 we measured rates of predator migration between patches in the six enclosures assigned to treatment 5 by recording all ladybeetles flying into or out of each patch over a 1-h period. On the final day of the experiment, we collected all predators that could be

found in the enclosures to verify integrity of the treatments. Mean proportional recovery was 0.57 ($\pm$ SD = 0.19), and final abundances were not different between treatment 5 and each of the respective single species treatments ($t = -0.19$, d.f. = 10, $P = 0.85$ for *C. septempunctata*, $t = -0.92$, d.f. = 10, $P = 0.38$ for *Co. maculata*, $t = -1.62$, d.f. = 10, $P = 0.14$ for *H. axyridis*). These results indicate that manipulations of predator richness remained intact, and that the additive design of the experiment was maintained over the duration of the experiment.

DATA ANALYSES

We first used a repeated measures ANOVA to test for differences in the mean density of aphids among predator treatments. Following this, we used a general linear model to assess whether the three predator species together influenced aphid population growth in a manner that deviated from the expectation of independent effects (i.e. proportional to the performance of each predator species when alone):

$$y_{t+1} = b_0 + b_1 y_t + b_2 P_1 + b_3 P_2 + b_4 P_3 + b_5 \phi + \epsilon \quad \text{eqn 1}$$

where y_t is aphid abundance at time t ($\ln[\text{no. stem}^{-1}]$), P_i is the presence/absence of *C. septempunctata*, *Co. maculata* or *H. axyridis* from the predator treatment, ϕ is the nonadditive effect of the three predator species when placed together in the same enclosure, and ϵ is the residual error. If b_5 is different from zero, this indicates that the per capita effect of one or more ladybeetle species was reduced ($b_5 < 0$) or enhanced ($b_5 > 0$) in the three predator species treatment.

The second question we asked is whether spatial variation in aphid density among patches influenced the observed diversity of ladybeetles at the scale of a patch. To address this question we focused on treatment 5, which had all three predator species together. The analyses proceeded in three steps. First, for each sampling date we used ANOVA to compare the mean density of aphids (no. per stem) among patches to determine if the initial resource gradient was still intact. Second, for dates where the gradient in aphid density was intact, we used a mixed model ANOVA with experimental unit included as a random effect to examine the response of predator richness to log-transformed aphid density (no. stem $^{-1}$) in a patch. Third, to determine whether variation in predator richness among patches could be explained simply by differences in predator abundance among patches, we used a Poisson regression to model the number of individuals of each predator species in a patch, N , as

$$N = \exp[b_0 + b_1 X_1 + \dots + b_3 X_3 + b_4 X_1^* X_3 + \dots + b_6 X_2^* X_3 + \epsilon] \quad \text{eqn 2}$$

where X_1 = aphid abundance, X_2 = predator species, and X_3 = day of the experiment. We used information

criteria to select the most parsimonious model (Johnson & Omland 2004), and then used the maximum likelihood parameter estimates from the most parsimonious model to calculate the probability of there being ≥ 1 individual of each species in a patch (which is e^{-N}). By combining these probabilities for all three species as Bernoulli trials, we obtained the number of predator species that would be expected to occur in a patch based simply on how total predator abundance varied with aphid density. The expected values were bootstrapped to obtain 95% confidence intervals. Note that this analysis is similar to using rarefaction to compare levels of richness among sites that differ in total abundance, except that the Poisson regression specifically accounts for the response of each individual predator species.

LABORATORY EXPERIMENT

One limitation of our field experiment is that the additive experimental design, where the more diverse predator assemblages have a greater total number of predators, cannot distinguish between per capita rates of predation being altered by interspecific interactions vs. nonlinear functional responses of predators and prey to total predator density (Sih, Englund & Wooster 1998). This limitation can only be overcome with supplemental experiments that explicitly examine the nature of species interactions. Therefore, to aid interpretation of our field experiment, we performed a greenhouse experiment in which we examined the short-term foraging behaviour of predators on individual plants of alfalfa when each predator species was alone versus when it was placed together with the other two species. Experimental units contained a single host plant of alfalfa grown in a 10-cm diameter $\times$ 15-cm deep pot enclosed in 40-cm tall Mylar tubes capped with mesh (as shown in Fig. 1 of Aquilino, Cardinale & Ives 2005). Twenty-five adult *A. pisum* were added to the microcosms and allowed to colonize plants for 1 h. One individual of each predator was then introduced into the microcosms alone ($n = 10$ replicates), or in combination with the other two species ($n = 10$ replicates). We recorded the vertical and horizontal location of each predator on the plant every minute for a period of 30 min, and tallied the total number of aphids consumed over this period.

Results

Repeated measures ANOVA confirmed there were significant differences in aphid density among enclosures stocked with differing numbers of ladybeetle species ($F_{2,30} = 13.87$, $P < 0.01$). When alone, each predator species reduced aphid density relative to control enclosures that had no predators (Fig. 1a, $P < 0.05$ for all F -tests comparing means). Yet, when all three predator species were together in the same enclosure, aphid densities were reduced less than would be expected from

Fig. 1. Lady beetle diversity as a cause of aphid density. (a) Aphid density at the scale of whole enclosures as a function of predator treatment (mean $\pm$ 1 SEM). When alone, each predator species significantly reduced aphid density relative to controls ($P < 0.05$ for all F -tests comparing means, H = *Harmonia axyridis*, Co = *Coleomegilla maculata*, and C = *Coccinella septempunctata*). However, when predator species were together in a three-species cage, observed aphid densities (Obs) were higher than expected (Exp) from a multiplicative risk model of independent predator effects (Sih *et al.* 1998). (b) The multipredator interaction term (dots, solid line) $\pm$ 95% confidence intervals computed independently for each day (dashed lines). This term is less than zero on all but one date of the study, which indicates that some form of interference among the predators reduced the ability of the predator assemblage to control aphid population growth. (c) Foraging location of predators on individual plants of alfalfa. Solid symbols = species when alone, open symbols = species when together, bars = 25th and 75th percentiles (∇ = *C. septempunctata*; $\square$ = *H. axyridis*; $\circ$ = *Co. maculata*), grey dots show location of aphids. (d) Consumption of aphids by each predator species when alone vs. together (mean $\pm$ 1 SEM). Connected bars are not different ($P > 0.05$ for t -tests).

the effects of each predator species when alone (compare Obs with Exp, Fig. 1a). Indeed, the multipredator interaction term (coefficient b_5 of eqn 1) was significantly less than zero on all but one date of the study (Fig. 1b), indicating that the effect of the three predator species when together was less than that expected from independent, additive effects. This suggests that when predator species were placed together in the same system, some form of antagonistic interaction reduced per capita predation efficiency and limited the ability of the predator guild to control aphid populations.

To investigate the nature of this interaction further, we performed a laboratory experiment in which we documented the foraging behaviour of predators on individual alfalfa plants when species were alone or together. When predator species were alone, each species foraged near the top and centre of plants where aphids tended to cluster (presumably to feed on new foliage, Fig. 1c). When predator species were together on the same plant, foraging *H. axyridis* and *Co. maculata* were displaced towards the plant margins, resulting in lower rates of predation by both species ($t = 2.87$, d.f. = 10, $P = 0.01$ and $t = 2.40$, d.f. = 10, $P = 0.03$, respectively, Fig. 1d). These results suggest that *C. septempunctata* is behaviourally dominant over *Co. maculata* and *H. axyridis*, and that interference com-

petition may explain the nonadditive, antagonistic interaction among lady beetle species observed in the field experiment.

The second question we asked is whether variation in aphid density among patches influenced the observed diversity of lady beetle species. Within 24 h of adding predators to the cages, there was a positive relationship between observed predator richness and aphid density in a patch (Fig. 2a). By day 3 this positive relationship was statistically significant, and it persisted through day 6. By day 11 of the experiment, predators had reduced aphid densities to low levels across patches, which resulted in there being no significant variation in aphid density within enclosures during the latter portion of the experiment. From these results, we conclude that within a matter of days, predators had distributed themselves among patches in such a way that predator diversity was an increasing function of aphid density.

A potential explanation for the positive relationship between predator diversity and aphid density is that as predators aggregated in areas with high aphid density, a higher abundance of predators led to a greater probability that any given species would be observed in a fixed sampling effort. The potential for this mechanism to explain patterns in our study is clear from Fig. 2(b), which shows that predator richness in a patch was a

Fig. 2. Ladybeetle diversity as a consequence of aphid density. (a) Richness of predators in a patch as a function of variation in aphid abundance (dark symbols = mean $\pm$ 95% CI for patches initialized with different aphid densities). The solid line gives the best fit from a mixed model ANOVA with experimental unit included as a random effect (slopes $\pm$ 95% CIs are given at right). Grey symbols give the mean $\pm$ bootstrapped 95% CI of richness predicted from a Poisson regression of predator abundance (see Table 1). (b) Observed predator richness in a patch as a function of total predator abundance (mean $\pm$ 1 SEM for each patch averaged across all dates). (c) Rates of immigration to/emigration from patches for predator species combined (main) or individually (insets).

monotonically increasing function of total predator abundance. To test this hypothesis explicitly, we used a Poisson regression to calculate levels of predator richness that would be expected based simply on how predator abundance covaried with aphid density (see eqn 2, Materials and methods). Parameter estimates for the most parsimonious Poisson regression (Table 1) indicate that: (1) predator abundance in patches differed among the three predator species (*C. septempunctata* > *Co. maculata* > *H. axyridis*); (2) predator abundance in a patch increased with aphid abundance in that patch; but (3) this response varied among dates. Using these parameter estimates to calculate expected predator richness, we found that observed levels of richness were no different than those predicted from variation in predator abundance alone (compare black/grey symbols, Fig. 2a). This result indicates that variation in predator diversity among patches can be explained simply by the accumulation of individuals of each predator species in patches with high aphid density.

Why did predators accumulate in patches with high aphid density? Predator movement on day 5 of the experiment suggests that predator emigration from a patch decreased as aphid abundance increased ($E = 1.01 - 0.44 \ln[\text{aphids st}^{-1}]$, $F_{1,16} = 8.23$, $P = 0.01$), but rates of immigration into a patch were independent of aphid density ($I = 2.47 + 0.02 \ln[\text{aphids st}^{-1}]$,

$F_{1,16} = 0.02$, $P = 0.88$) (Fig. 2c). These results argue that ladybeetles did not differentiate among patches when searching for aphid prey, but upon finding a patch with high aphid abundance they tended to remain there for longer periods of time.

Discussion

This experiment has illustrated two causal links between predator diversity and the density of prey operating at the same time in the same system. We found that as predator richness was increased, fewer aphids were consumed than would be expected from the independent effects of each predator species, apparently because interference competition among ladybeetle species limited the efficiency of the predator assemblage. At the same time, we found that variation in initial aphid abundance among patches generated variation in the number of observed ladybeetle species in the patches. This occurred because predators aggregated in areas of high aphid density, and more predator species were observed in a fixed sampling effort wherever there was greater total predator abundance. Thus, the number of predator species in an enclosure was a cause of variation in resource density among enclosures, but predator diversity in a patch was a consequence of spatial variation in resource density within enclosures.

Table 1. Maximum Likelihood estimates for a Poisson regression predicting predator abundance in patches (eqn 2 in text)

Parameter	Estimate	SE	95% Confidence limits		χ^2	Pr > χ^2
Intercept	−1.24	0.35	−1.94	−0.55	12.30	< 0.01
Aphid density	0.29	0.12	0.06	0.53	5.82	0.02
Predator species						
<i>C. septempunctata</i>	2.39	0.33	1.74	3.04	52.27	< 0.01
<i>Co. maculata</i>	1.82	0.34	1.16	2.49	28.67	< 0.01
<i>H. axyridis</i>	0.00	0.00	0.00	0.00		
Time						
Day 1	−1.71	0.35	−2.39	−1.02	23.66	< 0.01
Day 3	−0.14	0.23	−0.59	0.31	0.38	0.54
Day 4	−0.09	0.23	−0.54	0.35	0.17	0.68
Day 6	0.00	0.00	0.00	0.00		
Aphid density × time						
Day 1	−0.02	0.21	−0.44	0.40	0.01	0.92
Day 3	0.24	0.15	−0.07	0.54	2.35	0.13
Day 4	0.51	0.17	0.18	0.84	9.11	< 0.01
Day 6	0.00	0.00	0.00	0.00		

Estimates are reported relative to the last level of each variable.

WHAT'S NEW, WHAT'S NOT?

The different mechanisms operating to produce the results of our study are in no way new or unique. In fact, there is a long history of work that has demonstrated how mobile species tend to aggregate in response to the availability of their resource (a subset of reviews includes Pyke, Pulliam & Charnov 1977; Sutherland 1983; Kacelnik, Krebs & Bernstein 1992; Kennedy & Gray 1993), and that species diversity is intimately linked to community abundance (see Bunge & Fitzpatrick 1993; Gotelli & Colwell 2001; Loreau 2004). Likewise, there is a considerable body of research that has demonstrated how nonadditive interactions among a variety of predator species can alter the total efficiency of predator assemblages (Morin 1995; Rosenheim *et al.* 1995; Peckarsky & McIntosh 1998; Sih *et al.* 1998; Snyder *et al.* 2003; Finke & Denno 2004; many others). However, it is worth noting that these mechanisms have generally been studied in isolation. Indeed, theoretical and empirical research on predator–prey dynamics has tended to focus either on how predator diversity responds to prey availability, or separately, how multipredator interactions control prey populations. This is very similar to plant ecologists who have tended to focus either on how the diversity of primary producers changes across gradients in resource availability that limit community biomass (reviewed by Abrams 1995; Mittelbach *et al.* 2001; reviewed by Rosenzweig & Abramsky 1993; Waide *et al.* 1999), or separately, how producer diversity regulates the uptake and conversion of resources into biomass at a given location (reviewed by Tilman 1999; Loreau *et al.* 2001; Naeem 2002; Hooper *et al.* 2005). What is novel about our study is that it suggests both perspectives can simultaneously be true in the same ecological system. As far as we are aware, ours is the first study to demonstrate it is possible for species diversity and resource density to exhibit reciprocal

causal relationships at the same time in the same system. These results lend credence to the idea that diversity in a given community may be both a cause and a consequence of resource densities that constrain biomass (Loreau *et al.* 2001; Schmid 2002; Worm & Duffy 2003).

EFFECTS OF PREDATOR DIVERSITY OR DENSITY?

Ives, Cardinale & Snyder (2005) recently summarized the ways consumer diversity can influence resource density, emphasizing mechanisms can be proportional to species abundances (i.e. ‘additive’ where per capita efficiency is fixed), or disproportionate to species abundances (i.e. ‘nonadditive’ where the presence of one consumer influences the per capita efficiency of another). Analyses of our field experiment indicated that the effects of the predator assemblage on aphid density were clearly disproportionate to total predator abundance. However, it was not possible to tell from this experiment whether such effects were a result of nonlinear functional responses, or alternatively, if they were a consequence of nonadditive interactions among predator species. Because our experiment was not performed at multiple predator densities, we cannot eliminate the possibility of nonlinear functional responses. However, our laboratory study does suggest that the antagonistic interactions observed in the field experiment resulted, at least in part, from behavioural dominance by *C. septempunctata* and interference competition that caused the other two predator species to feed less efficiently when they were in a more diverse assemblage (Fig. 1c,d). It is unclear whether this type of interaction is a generality for our system. We have previously documented both antagonistic (Snyder & Ives 2001) as well as synergistic (Cardinale *et al.* 2003) interactions among different natural enemies, and we do not know what the net balance of these interactions is in the full assemblage. However, it is clear that the

efficiency of pea aphid biocontrol in this system is often a function of nonadditive interactions among predators, parasitoids and pathogens, as appears to be true in other systems (Morin 1995; Rosenheim *et al.* 1995; Losey & Denno 1998; Peckarsky & McIntosh 1998; Sih *et al.* 1998; Snyder *et al.* 2003; Finke & Denno 2004).

ALTERNATIVE MECHANISMS

One limitation of our study is that we focused on just one potential mechanism by which species diversity and resource density might exhibit reciprocal causal relationships. We specifically chose to manipulate aphid density at the smaller scale of a patch and predator diversity at the larger scale of whole enclosures because this situation best simulates how we think mobile predators respond to variation in aphid density among fields in our system. While the potential scales of causality in our experimental design were predetermined by our experience in this system, one can certainly envision other ways that reciprocal causality might operate. For example, when organisms are sessile, long-lived, or have very limited dispersal abilities, it could make more sense for species richness to vary locally within sites, but resource density to differ across sites. Furthermore, there is no reason to focus narrowly on how causal associations change as a function of spatial scale. It seems quite plausible that the direction of causality could just as easily change across temporal scales where resource availability might drive consumer diversity during one period in time (say, for example, the early stages of succession, or during part of a consumer–resource cycle), and diversity dictate resource use during a different period in time. As we move towards a synthetic understanding of the bi-directional relationship between species diversity and resource density, a challenge is to catalogue the variety of ways that causality might change across spatial and temporal scales.

A COMMENT ON SCALE

Obviously, if it were possible, we would have preferred to do our experiment at a much larger spatial scale that incorporated movement of predator species across numerous fields. However, as that scenario is experimentally intractable, our next best option was to simulate some of the key features of this system in controlled mesocosms. In lieu of fruitless arguments about the utility of model systems in ecological research, we simply acknowledge that these mesocosms oversimplify important biological details (e.g. landscape complexity, connectivity, the scales of dispersal, etc.), and this makes any extrapolation of results to larger-scale dynamics tenuous at best. With this caveat in mind, we do think the experiment sheds light on how predator diversity and prey density might exhibit bi-directional relationships at a larger scale if, in fact, they do. Only three things were required to produce reciprocal cau-

salinity in our study. The first was spatial variation in the density of a shared resource. The second was consumers independently aggregating in areas of high resource density. The last was predator species interacting in ways that influence each others per capita efficiency. For systems where all three of these conditions are simultaneously met, our study suggests that it is possible for species diversity to be both a dependent and independent variable at different spatial scales.

Our experiment was shorter than the generation time of the interacting predator species; thus, it offers no information on how these interactions might influence long-term dynamics in this system. The study is, however, representative of dynamics that occur within a typical harvesting cycle. Alfalfa is harvested every 3–5 weeks. Because the time from egg to reproducing adult is generally greater than the time between harvests (Giles *et al.* 2002; Lanzoni *et al.* 2004), ladybeetles must immigrate into fields of alfalfa from elsewhere. As predators aggregate in response to growing aphid populations, aphids can be driven back to near-zero densities in a matter of days (Ives *et al.* 1993; Cardinale *et al.* 2003; Snyder *et al.* 2003). This is not unlike our experiment where large initial differences in aphid density among plots were homogenized quickly as predators aggregated into areas of high resource density. Still, our results are probably best viewed as a case study of diversity–resource relationships in a system where resource and consumer dynamics are ephemeral due to frequent disturbances.

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