LETTER

Niche saturation reveals resource partitioning among consumers

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Abstract

More diverse communities of consumers typically use more resources, which often is attributed to resource partitioning. However, experimentally demonstrating this role of resource partitioning in diverse communities has been difficult. We used an experimental response-surface design, varying intra- and interspecific consumer densities, to compare patterns of resource exploitation between simple and diverse communities of aphid predators. With increasing density, each single consumer species rapidly plateaued in its ability to extract more resources. This suggests intraspecific competition for a subset of the resource pool, a hallmark of resource partitioning. In contrast, more diverse-predator communities achieved greater overall resource depletion. By statistically fitting mechanistic models to the data, we demonstrated that resource partitioning rather than facilitation provides the better explanation for the observed differences in resource use between simple and diverse communities. This model-fitting approach also allowed us to quantify overlap in resource use by different consumer species.

INTRODUCTION

Interest in the niche has recently been reawakened as ecologists have begun to examine the relationship between biodiversity and community-wide resource use (Hooper *et al.* 2005). These studies have generally found, across a broad range of community types and trophic levels, that resource extraction grows more complete when more consumer species are present (Cardinale *et al.* 2006). This pattern is generally attributed to complementary patterns of resource use among constituent species (i.e. resource partitioning): because species utilize different subsets of the total resource pool, overall resource use is greatest when many species are present together. However, this mechanism explaining greater resource use by diverse communities has proven surprisingly difficult to demonstrate (Hille Ris Lambers *et al.* 2004; Kahmen *et al.* 2006; Cardinale *et al.* 2007). Indeed, there has been much debate as to whether greater resource extraction among diverse communities results from resource partitioning at all, or rather from the greater likelihood of including particularly efficient species at higher diversity levels, that is, the sampling effect (Tilman 1997; Loreau & Hector 2001; Petchey 2003; Ives *et al.* 2005).

Furthermore, facilitation in which the presence of other consumers increases the resource extraction efficiency of each consumer is yet another possible explanation for greater resource extraction by diverse communities (Losey & Denno 1998; Cardinale *et al.* 2002). The central difficulty in demonstrating resource partitioning is that resource-use differences among species are confounded with other species-specific attributes such as size, growth rate and foraging style. This makes it difficult to isolate any effects of resource-use differences among species as a driver of the improved performance of diverse communities (Finke & Snyder 2008).

To overcome these difficulties, a variety of approaches have been attempted. In rare cases species' resource-use breadth is a plastic trait that can be manipulated independently of species identity and richness, and so this relationship can be directly tested (e.g. Finke & Snyder 2008). Generally speaking, however, differences in resource use among species are rigid, and indirect tests must be used. Perhaps the most common approach is to measure a variety of species traits and then look for relationships between differences in particular traits and the likelihood of species filling unique functional roles (e.g. Silvertown *et al.* 1999).

Similarly, species may be lumped into 'functional groups' where species within a grouping are thought, based on a researcher's prior knowledge of the system, to be more similar to one another than those outside the group. Then, functional diversity is compared with species richness as a predictor of ecosystem function (e.g. Tilman *et al.* 1997; Kahmen *et al.* 2006; Wojdak & Mittelbach 2007; Schmitz 2007, 2008). However, correlations between particular collections of traits and overall resource use do not necessarily imply a causative relationship, and functional groupings defined by researchers sometimes perform no better than randomly constructed groupings of species (Petchey & Gaston 2006; Wright *et al.* 2006).

In this study, we approach this problem by conducting experiments across a range of consumer densities, varying numbers of both intraspecific and interspecific consumers. Our consumers were a guild of aphid predators, and two aphid species were their shared resource. If consumer species differ in the subset of the prey resource that they use, then we would predict that any single-consumer species would plateau in total resource use with increasing density. This occurs as a species fully exploits the subset of resources available to it. In contrast, diverse communities of consumers, each with a different feeding niche, in aggregate have access to a larger total pool of resources. Thus, diverse groups of consumers will be capable of driving resources to lower levels than even very high densities of single consumers.

In addition to resource partitioning, facilitation could also explain the pattern of increased resource extraction by more diverse-consumer communities if consumers increase each others' feeding rates (Losey & Denno 1998; Cardinale *et al.* 2002). However, an important difference between facilitation and resource partitioning is that while both will increase the aggregate consumption rate of diverse-consumer communities relative to single species communities, only resource partitioning will be associated with saturation and a plateauing of consumption by single consumers. To distinguish between these mechanisms, and to quantify their effects on consumption, we fit models of resource partitioning and facilitation to our experimental data on aphids and their predators, allowing a statistical adjudication between them. Our results strongly support resource partitioning as the explanation for increased prey consumption by diverse-consumer communities. We then use models to quantify the degree of resource-use overlap among predators.

METHODS

Natural history

The experiments reported here were conducted within a well-studied community of insect predators common on *Brassica oleracea* plants in Washington, USA, infested with the aphids *Myzus persicae* and *Brevicoryne brassicae*. In this community, overall consumption of aphid herbivores dramatically increases when more predator species are present (Snyder *et al.* 2006, 2008; Straub & Snyder 2008). Dominant predator species include the sit-and-wait predatory bug *Nabis alternatus*, the actively searching predatory lady beetles *Hippodamia convergens* and *Coccinella septempunctata*, and the endoparasitoid wasp *Diaeretiella rapae* (Snyder *et al.* 2006). In addition to differences in hunting style, the predators encompass a broad range of body sizes and tend to forage in different locations on the plant (Straub & Snyder 2006, 2008). Differences along each of these three trait axes have been proposed to foster complementary effects on shared prey, and thus a positive relationship between diversity and resource consumption (Ives *et al.* 2005; Wilby *et al.* 2005; Casula *et al.* 2006; Schmitz 2007). Nonetheless, some species are significantly more effective/voracious predators than are others, making it difficult to entirely exclude species identity (sampling) effects (Snyder *et al.* 2006; Straub & Snyder 2006). Also, we have been unable to conclusively link differences among species in particular traits to the very effective aphid control typical of diverse communities, or to quantify the degree of non-overlap in resource use, if any, among community members (Straub & Snyder 2008). Although intraguild predation occurs among several community members (Straub & Snyder 2006; Snyder *et al.* 2006) and has the potential to weaken any benefits of predator diversity for stronger herbivore suppression (e.g. Finke & Denno 2004), our finding of consistently positive diversity effects suggests a relatively minor role for intraguild predation in this system. The work reported here expands upon our earlier findings by delineating the maximum proportion of the aphid population subject to attack by each predator species, and by multiple predator species, as a means to define niche breadth and overlap among these consumers.

Experimental design

Our experimental units were $2 \times 2 \times 2$-m field cages, covered with fine mesh and constructed as previously described (Snyder *et al.* 2006). Each cage enclosed eight aphid-infested *B. oleracea* plants; we established predator treatments and then tracked resulting effects on aphid densities (described in Methodological details of the field experiment below). We manipulated predators within a response-surface design to achieve a fully factorial cross of consumer diversity (each of the four predator species in separate monocultures vs. a diverse mix of all four species) and total consumer density (2, 4, 8, 16 or 32 predators per cage; Table 1). That is, each level of predator density included each predator species in replicate monocultures,

Table 1 The design of the field experiment. Predator diversity (one or four species) was manipulated across five levels of predator density (2, 4, 8, 16 or 32 individuals per cage)

	Predator species composition					
	Ø	*Coccinella*	*Diaeretiella*	*Hippodamia*	*Nabis*	Diverse (4 spp.)
Predator density	0	2	2	2	2	
		4	4	4	4	1 + 1 + 1 + 1 = 4
		8	8	8	8	2 + 2 + 2 + 2 = 8
		16	16	16	16	4 + 4 + 4 + 4 = 16
		32	32	32	32	8 + 8 + 8 + 8 = 32

The experiment also included no-predator controls (Ø), resulting in 25 unique treatment combinations, each of which was replicated at least twice in each of 2 Trials separated in time. Each row represents a substitutive design; for example, at a density of four the diverse community included 1 individual of each of the four species. Shading indicates an additive design across that density.

and also a diverse composition including all species (Table 1; except at a total density of 2, where, for obvious reasons, we could not include a diverse mix of all four species together). These predator densities were *c.* 0, 0.25, 0.5, 1, 2 and 4× local mean open-field density of these predators on *B. oleracea* plants that year (S.A. Steffan, T.D. Northfield, G.B. Snyder and W.E. Snyder, unpublished data), and each species composition was replicated twice at each density level. The experiment also included no-predator controls, with three replicates of this treatment in Trial 1 and five replicates in Trial 2. This experiment was itself repeated, for a total of 104 replicate arenas (field cages) across the two trials [five diversity levels × five density levels × two replicates × two trials + eight controls − four (diverse-predator treatments at the density of two, with two replicates × two trials) = 104].

Additive designs, typical of multi-predator studies, sum monoculture predator densities in diverse treatments. Such designs hold constant densities of each species, and thus intraspecific competition, across diversity levels (Sih *et al.* 1998). This allows the complete isolation of interspecific interactions, but as a tradeoff total consumer density co-varies with diversity (Ives *et al.* 2005). In contrast, biodiversity-ecosystem function studies typically utilize substitutive designs, wherein the total number of individuals is kept constant as species richness is varied (Hooper *et al.* 2005). This eliminates density as a confounding difference across diversity treatments, but with the tradeoff that intraspecific interference is necessarily diluted at higher diversity levels (Connolly 1988). In our field experiments, nested within our response-surface design were a series of both additive and substitutive manipula-

tions of species richness, at varying total predator densities (Table 1). This 'response-surface' design sacrifices replication of particular treatment combinations for knowledge of effects across a broader range of treatment levels (predator densities in this case; Inouye 2001; Gotelli & Ellison 2004; Paini *et al.* 2008), and was constructed to include multiple levels of substitutive and additive manipulations of consumer species richness within a single experiment (Sih *et al.* 1998; Griffiths *et al.* 2008). This allowed us to take advantage of the strengths of both types of diversity manipulation simultaneously. First, within the substitutive portions of the design we could trace patterns of resource consumption across densities for both single- and multi-species consumer communities, as is typically performed at a single density within biodiversity-ecosystem function studies. In addition, we could concurrently utilize the additive portions of the design to evaluate predator-predator interactions to test for facilitation. In predator–prey studies these evaluations are typically conducted across single low density–low diversity, high density–high diversity pairings, but here could be conducted across a broad range of consumer densities.

Evaluating resource partitioning and facilitation

As an initial test for an interactive effect of predator diversity and density on aphid consumption, we conducted a multi-factorial ANOVA including the terms Block, Predator density, Predator diversity and all interactions among these terms. For this analysis we did not include the single-species treatments at densities of 2, because there were no corresponding diverse (four species) treatments. The ANOVA

was conducted on log-transformed data to reduce heteroscedacity, in SYSTAT (SPSS 2004). To evaluate the importance of resource partitioning and facilitation in the relationship between consumer (predator) diversity and resource (prey) extraction, we fit a model describing concurrent effects of facilitation and resource partitioning to the consumer density-resource extraction data. We then removed either resource partitioning or facilitation from the model and refit the reduced model to the data. Statistical comparison between the fits of the full model and the two reduced models then indicates which mechanism fits the data better.

There are many candidate models that could be derived to include resource partitioning and facilitation. We selected a basic model that contains the key contrast between these mechanisms: resource partitioning leads to a plateauing of resource use by any single-consumer species, whereas facilitation does not. The full model with both resource partitioning and facilitation is

$$Y = m_b \bigg(p_0 + p_1 e^{-a_1 x_1} + p_2 e^{-a_2 x_2} + p_3 e^{-a_3 x_3} + p_4 e^{-a_4 x_4}$$

$$+ p_5 e^{-(a_1 + a_5 J)x_1 - (a_2 + a_5 J)x_2 - (a_3 + a_5 J)x_3 - (a_4 + a_5 J)x_4} \bigg) + \varepsilon \quad (1)$$

Here, Y is the density of prey at the end of an experiment that contains density x_i of consumer species i. The parameters p_1, p_2, p_3 and p_4 represent the proportion of the resource (prey) available solely to predators 1, 2, 3 and 4, respectively, p_5 is the proportion available to all predators and p_0 is attacked by none. Parameters a_1, a_2, a_3 and a_4 describe the rate at which predators 1, 2, 3 and 4 consume resources available to them. We assume that the proportion of available prey escaping consumption by a single predator species i, $e^{-a_i x_i}$, is a negative exponential that accounts for decreases in prey density caused by consumption (i.e. prey cannot be eaten more than once). Here, we build on the models presented in Casula *et al.* (2006), where parameters $p_i e^{-a_i x_i}$ for i = 1, 2, 3 and 4 are equivalent to $(1 - p'_i)$ in the Casula *et al.* model of complementarity (i.e. resource partitioning). When there are multiple predators, of the subset of prey consumed by all predators, the proportion that escapes is obtained by multiplying the proportions escaping each predator; for example, $e^{-a_i x_i} e^{-a_j x_j} = e^{-a_i x_i - a_j x_j}$ (Sih *et al.* 1998). We incorporate facilitation by assuming that in the presence of other predator species, the consumption rate of predator i on shared prey resources increases from a_i to $(a_i + a_5)$; in eqn 1, the parameter J is an indicator variable, such that J = 1 for the diverse treatment and J = 0 for the single-species treatments. Note that this formulation assumes that facilitation increases the attack rates of all predators by the same amount a_5; while this might not be the case, the experimental design in which there are either

single species or all species makes it impossible to investigate differences in facilitation among separate species. We fit data from each of the two experimental trials simultaneously, and because the trials started with different initial prey densities, final densities also differed. The parameter m_b shows the final density of prey (in the no-predator controls) or estimated final density of prey had predation not occurred (in the predator treatments), with a different value estimated for each trial (b = 1 and 2). Finally, the parameter ϵ is the error term, assumed to be normally distributed with mean zero and variance proportional to the expected number of prey in a treatment, $\sigma^2 \overline{Y}_{trt}$; in other words, we fit the model with nonlinear weighted regression with weights $1/\overline{Y}_{trt}$. We selected this error structure empirically to homogenize variances (Fig. S1; Table S1); this error structure could be generated by several processes, including sampling error and demographic stochasticity. Each model was fit to the untransformed data in all treatments/blocks simultaneously to use all data and to use the most information possible to parameterize the models.

We removed resource partitioning from the model by setting $p_1 = p_2 = p_3 = p_4 = 0$ and refit the reduced model to evaluate the null hypothesis that resource partitioning was not capable of explaining patterns in the data (i.e. that removing resource partitioning did not affect the fit of the model to the data). We then conducted a likelihood ratio test to compare the models with and without resource partitioning to statistically test the null hypothesis that resource partitioning was unimportant (Judge *et al.* 1985). Under the null hypothesis that resource partitioning is not important, twice the difference in log-likelihoods between the full and reduced models is chi-square value distributed with 4 d.f. (the difference in the number of parameters between models). Similarly, we tested the importance of facilitation using the reduced model without facilitation by setting $a_5 = 0$ in eqn 1.

Evaluating niche overlap

In addition to comparing resource partitioning and facilitation, we assessed the degree of resource partitioning using three models that assume either no niche overlap, complete overlap or intermediate overlap. We started with the model including only resource partitioning without facilitation by setting $a_5 = 0$ in eqn 1 to present

$$Y = m_b \bigg(p_0 + p_1 e^{-a_1 x_1} + p_2 e^{-a_2 x_2} + p_3 e^{-a_3 x_3} + p_4 e^{-a_4 x_4}$$

$$+ p_5 e^{-a_1 x_1 - a_2 x_2 - a_3 x_3 - a_4 x_4} \bigg) + \varepsilon. \quad (2)$$

The model with no niche overlap was constructed by setting $p_5 = 0$, thus removing any overlap between predator species. We then used a likelihood ratio test to compare

this reduced model to the resource partitioning model (eqn 2); if the models are statistically significantly different, then we would conclude that predators share resources in common. The model with complete niche overlap among predators was constructed by setting $p_1 = p_2 = p_3 = p_4 = 0$, so that a fraction p_5 of resources were available to all predators, and p_0 were available to none. If the models are statistically significantly different, then we would conclude that there is resource partitioning with some resources used exclusively by different species.

This analysis of resource overlap statistically evaluates the two extremes of no resource overlap among species or complete overlap. If both of these extremes are statistically rejected, then we conclude that there is partial overlap among species. We did not conduct a specific test for sampling (species identity) effects, because this was unnecessary in our analyses. A sampling effect occurs when there are predators with unequal effect sizes in the community, and diverse communities exhibit improved performance purely because more diverse than single-species communities include the particularly effective predator. However, in our analyses a sampling effect mechanism that completely explains higher consumption in the diverse-consumer treatment corresponds to the model with no resource overlap; in this model, the most efficient consumer present in the diverse-consumer treatment could potentially explain any increase in consumption above the average observed in the single-consumer treatments (Ives *et al.* 2005). Therefore, a statistical rejection of the no-overlap model would demonstrate that resource partitioning rather than the sampling effect mechanism better explains the effects of predator diversity in the data.

Methodological details of the field experiment

The experiments were conducted at the Washington State University research station in Othello, WA. The first trial was initiated 20 June, and the second trial 25 July, 2007. Each cage housed eight *B. oleracea* plants, transplanted from the greenhouse 4 weeks after planting (as in Snyder *et al.* 2006). Aphids were released onto plants 24 h later. In the first trial, 10 aphids per species per plant were released (i.e. 80 aphids per species and 160 aphids total, per cage). In the second trial, anticipating more rapid aphid population growth typical of mid-summer and seeking to achieve similar aphid densities to Trial 1, we released five aphids per species per plant (i.e. 40 aphids per species and 80 aphids total per cage). The aphids were reared on *B. oleracea* plants in field cages prior to use in the experiments. Aphids were allowed 24 h to acclimate to the plants, after which their densities were censused by counting all aphids on four randomly selected plants per cage.

After the initial aphid count, predators were released into each cage with density and species composition determined by treatment (Table 1). True predators were collected from surrounding vegetation using a D-vac suction sampler (Rincon Vitova, Ventura, CA, USA), sexed and released into cages to establish an even (1 : 1 male–female) sex ratio for all species. The parasitoid *D. rapae* was reared in field cages, using both aphid species on *B. oleracea* plants. Four weeks after predator release, aphids were again sampled by counting all aphids and predators on four randomly selected plants per cage. At this time parasitoids were in their second generation and at the pupal (mummy) stage, when the wasps are most easily counted and wasp pupae were counted concurrent with the aphid count. The experiment was then terminated by destructively sampling all plants in each cage and hand-collecting predators. The length of the experiments also allowed sufficient time for true predators to reproduce, and for some young produced *in situ* to nearly reach the adult stage (Snyder *et al.* 2006).

RESULTS

The simple ANOVA analysis indicated that aphid control was strengthened by both increasing predator density and diversity (main effect of predator density: $F = 5.899$, d.f. = 3, 64, $P = 0.001$; main effect of predator diversity: $F = 38.713$, d.f. = 1, 64, $P < 0.001$; Table 2), and that the magnitude of the diversity effect increased with increasing predator density (predator density × diversity interaction: $F = 3.57$, d.f. = 3,64, $P = 0.019$; Table 2).

Resource partitioning vs. facilitation

Initial aphid densities were 31% higher in Trial 1 (20.62 ± 0.58 per plant) than in Trial 2 (15.74 ± 0.57 per plant). All predator species substantially depressed aphid densities (Fig. 1). Furthermore, the diverse-predator community reduced prey densities more than any single-species treatment, especially at high predator densities (Fig. 1). In

Table 2 Three-way ANOVA testing the effects of predator diversity (Diversity), predator density (Density) and trial date (Trial), as well as all interactive effects, on final aphid density

Source	d.f.	MS	*F*-ratio	*P*-value
Diversity	1	2.411	38.713	<0.001
Density	3	0.367	5.899	0.001
Trial	1	7.231	116.109	<0.001
Diversity × density	3	0.222	3.57	0.019
Diversity × trial	1	0.257	4.126	0.046
Density × trial	3	0.01	0.16	0.923
Diversity × density × trial	3	0.019	0.308	0.819
Error	64	0.062		
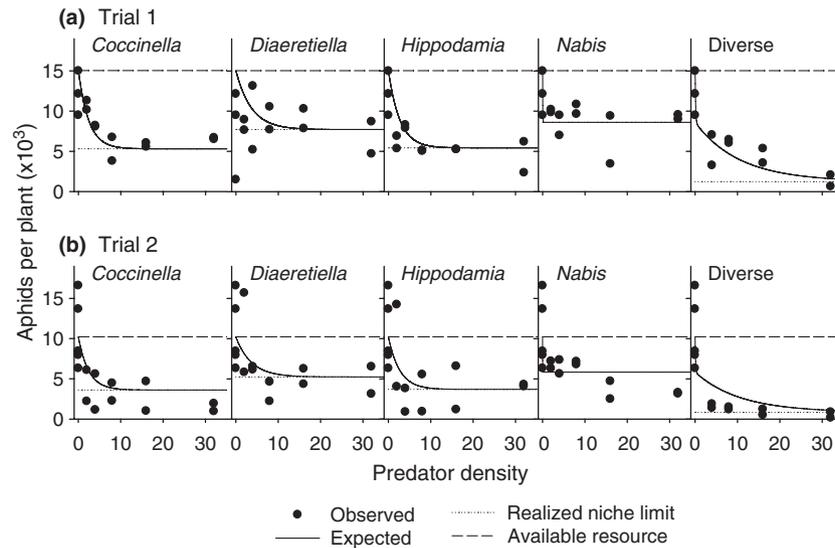
Figure 1 Final aphid densities in (a) Trial 1 and (b) Trial 2 across six initial predator density levels for one of four single-predator species or a diverse mix of all four predator species. The two experimental trials shared identical designs, although initial aphid densities were higher in Trial 1 than 2. Nonlinear weighted least-squares regression was used to fit a model (eqn 2) describing resource partitioning between predators, assuming degree of partitioning and overlap between predator species. We show the fits of this model to the data because it was the most parsimonious (i.e. it did not differ statistically from the model with both resource partitioning and facilitation, eqn 1). Predator compositions: in monoculture, the lady beetles *Coccinella septempunctata* (*Coccinella*) and *Hippodamia convergens* (*Hippodamia*), the parasitoid *Diaeretiella rapae* (*Diaeretiella*) and the predatory bug *Nabis alternatus* (*Nabis*); or, all four of these species in polyculture (Diverse).

Table 3 Log-likelihood (LL) values and likelihood ratio tests evaluating the effects of facilitation, resource partitioning and niche overlap on the fits of a model predicting prey consumption by a community of aphid predators

Model (equation no.)	LL	χ^2-value	d.f.	*P*-value
Resource partitioning and facilitation evaluation				
Full facilitation and resource partitioning (eqn 1)	−500.81			
Resource partitioning removed ($p_1 = p_2 = p_3 = p_4 = 0$)	−514.94	28.2561	5	<0.0001
Facilitation removed ($p_5 = 0$; eqn 2)	−501.4	1.1754	1	0.2784
Niche overlap evaluation				
Full resource partitioning model (eqn 2)	−501.4			
Niche complementarity removed ($p_1 = p_2 = p_3 = p_4 = 0$)	−518.74	34.6924	4	<0.0001
Niche overlap removed ($p_5 = 0$)	−512.48	22.1558	1	<0.0001

The full model used in the first set of comparisons (*Resource partitioning and facilitation evaluation*) combines facilitation and resource partitioning. Because there was no effect of removing facilitation in the *Resource partitioning and facilitation evaluation tests*, we used the 'facilitation removed' model as the full model for evaluation of the effects of resource partitioning, overlap and complementarity (*Niche overlap evaluation*). Therefore, the 'resource partitioning removed' model in the *Resource partitioning and facilitation evaluation tests* included facilitation, whereas the 'niche complementarity removed' model in the *Niche overlap evaluation* did not.

our statistical comparison between resource partitioning and facilitation as mechanisms explaining higher consumption in diverse-predator treatments, the removal of resource partitioning significantly reduced the fit of the model (Table 3). Conversely, removing facilitation from the model provided no significant change in fit (Table 3), indicating that facilitation does not play an important role in explaining the observed data.

The pattern in the data responsible for the difference in model fits between resource partitioning and facilitation

models is the observed plateauing of consumption on prey at high initial predator densities in the single-predator vs. diverse-predator treatments (Fig. 2). For the model with resource partitioning alone (Fig. 2a,b), the model fits for single species plateaued at high initial predator density. In contrast, the facilitation model could not show this pattern, because the facilitation hypothesis assumes that all prey are vulnerable to all predators; only the effectiveness (consumption rates) of the predators increase in diverse-predator treatments. While obtaining this statistical
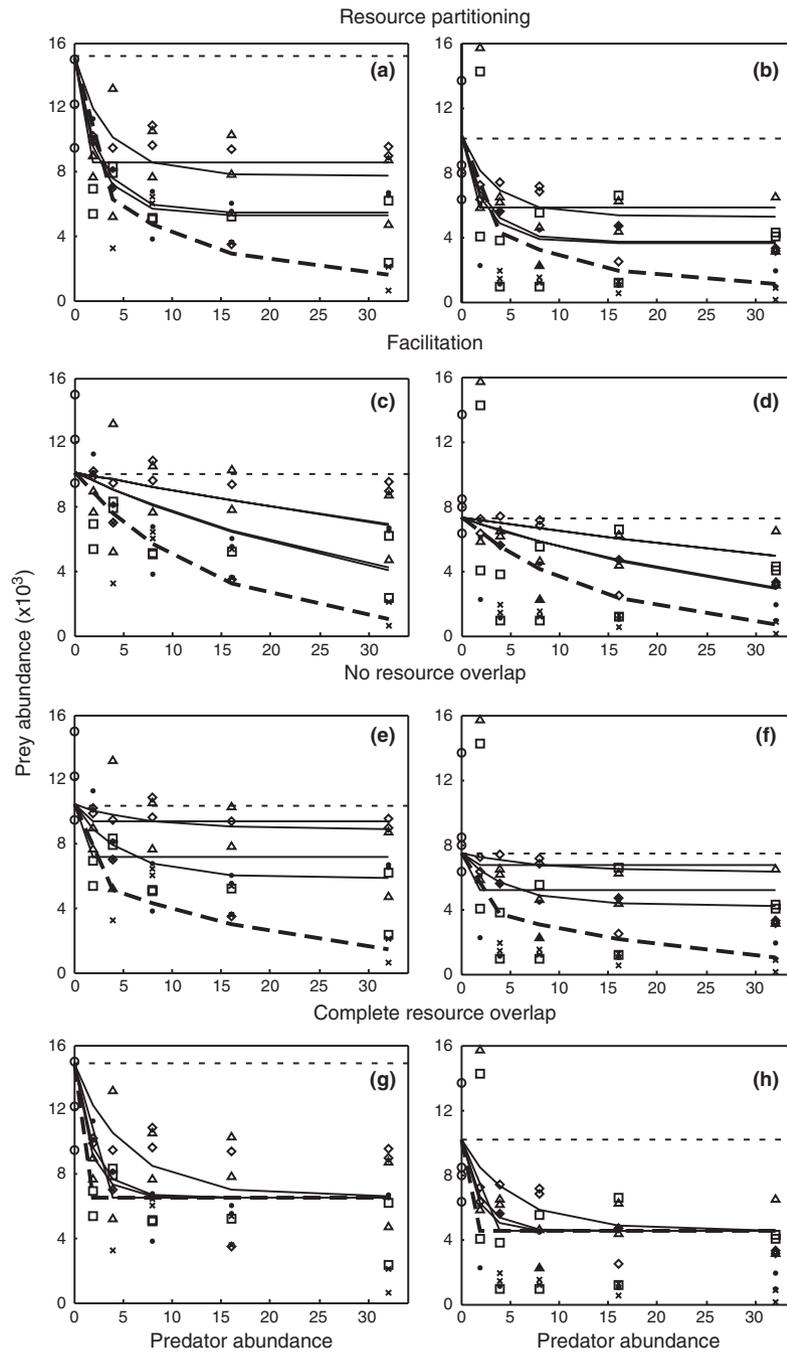
Figure 2 Final aphid densities in (a, c, e, g) Trial 1 and (b, d, f, h) Trial 2 across six initial predator density levels for one of four single-predator species (open circles, *Coccinella septempunctata*; triangles, *Hippodamia convergens*; dots, *Diaeretiella rapae*; diamonds, *Nabis alternatus*) or a diverse mix of all four predator species (×'s). The two experimental trials shared identical designs, although initial aphid densities were higher in Trial 1 than 2. Nonlinear weighted least-squares regression was used to fit models (eqns 1 and 2) describing resource partitioning between predators (a, b: resource partitioning), facilitation between predators (c, d: facilitation), no niche overlap between predators (e, f: no resource overlap) and complete niche overlap between predators (g, h: complete resource overlap). The fits of the models to the data (Table 3) determine the ability of resource partitioning vs. facilitation to explain the data (a, b vs. c, d) and whether resource partitioning is intermediate (a, b) between no resource overlap (e, f) and complete resource overlap (g, h). The solid lines show the fits of the respective models to the single-predator treatments, and the thick dashed line shows the fit of the model to the diverse-predator treatment. The thin dashed line represents the predicted number of prey remaining when no predators are present.

comparison required us to specify explicit models of resource partitioning and facilitation, the qualitative patterns characteristic of resource partitioning are observable in the data. Therefore, we would likely obtain the same results using other models of resource partitioning and facilitation.

Niche overlap

To assess the degree of resource overlap, we compared models with no, complete or the full model with intermediate overlap (eqn 2). Both the no- and complete-overlap models were statistically rejected in favour of the model with intermediate overlap (Table 3). From the model estimates, 43% (p_5 from eqn 2) of the prey population was shared by the four predators, and two of the predators were able to consume > 60% of the prey population (*C. septempunctata*: 65% = $p_5 + p_1$ and *H. convergens*: 0.64 = $p_5 + p_3$) (Fig. 3). These patterns are observable in the data (Fig. 1), which show plateauing in the single-predator treatments at sufficiently low resource levels that some resource overlap must occur; if resource overlap did not occur, then on average the four single-predator treatments would have to plateau above 75% of the control (no predator) treatments. For example, if four equally effective
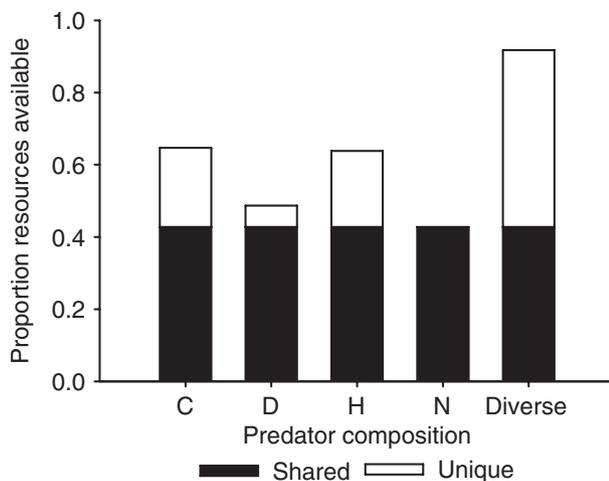
Figure 3 Estimated proportion of the aphid population (resources) available to the lady beetles *Coccinella septempunctata* (C) and *Hippodamia convergens* (H), the parasitoid *Diaeretiella rapae* (D), and the predatory bug *Nabis alternatus* (N), and a polyculture mix of all four of these species (diverse). Proportion estimates presented are the maximum likelihood estimates for the p_i values in eqn 2. The proportion of resources shared by all four species (shared; p_5 from eqn 2) is shown in black, while the proportion of the resources available solely to a single-predator species (unique; p_1, p_2, p_3 or p_4, from eqn 2) is presented in white.

predators did not share any portion of the aphid resource, the maximum consumption of each would be 25% of the resource, such that all of the resource would be consumed only when all four predators were present (25% + 25% + 25% + 25% = 1). Furthermore, the rejection of the no-overlap model eliminates the sampling effect as the sole explanation for the higher consumption rates in the diverse-predator treatments.

Effects on predators

Densities of true predators and parasitoids were not significantly impacted by predator diversity or density treatments in either Trial 1 or 2 (Fig. S2; Table S2).

DISCUSSION

We found clear evidence that the impacts of multiple predator species exceeded what any single-predator species could exert. Therefore, we can reject the sampling effect in favour of resource partitioning as the main explanation for the higher consumption in the diverse-predator community. For all single-species treatments, depletion of the aphid–prey resource rapidly plateaued with increasing predator density, such that increasing the density of any single species to *c.* 4× typical field density did not lead to a consistent further drop in aphid densities (Fig. 1). The response was quite different for the diverse-predator community, where aphid depletion plateaued at aphid densities lower than could be achieved by even the single most effective predator species (Fig. 1). Thus, it was impossible for the inclusion of any single-predator species to explain the very efficient resource extraction typical of diverse communities.

The resource–depletion curves were consistent with resource-niche partitioning among species, but inconsistent with interspecific facilitation. We used a combination of nonlinear models and likelihood ratio tests to compare the fit of the data first to a model including both resource partitioning and facilitation, and then to reduced models excluding either of these two processes. There was no statistically significant difference in fit between the model including both processes and that including resource partitioning alone, whereas the model including only facilitation produced a significantly poorer fit to the data. The reason for the varying performances of these models is straightforward: only resource partitioning could produce the plateau in resource use by single species that was apparent in the data (Fig. 1). While the model including only facilitation reproduced the high resource extraction by the diverse community, it could not reproduce the resource-niche saturation observed for single species. Having concluded that resource partitioning explains the data better

than facilitation, we performed statistical comparisons among models containing no, complete, or intermediate overlap in resource use. Both the no-overlap and complete-overlap models of resource use were rejected in favour of the intermediate resource overlap model, with this model estimating that a subset of prey resources was used by single species and 43% of resources shared by predator species (Table 3, Fig. 3).

Previous work in this and similar predator–prey systems suggests that at least two processes, interspecific partitioning of foraging space and intraspecific interference competition, may contribute to the resource partitioning that we observed. We showed previously that different members of the aphid-predator community forage on different parts of *B. oleracea* leaves (Straub & Snyder 2008), establishing the possibility of resource partitioning through the subdivision of foraging space. We suspect that this is the main form of resource partitioning underlying our experimental results. Even though the experiment was performed with two aphid species, we do not think that different predators partitioned resources by prey species. The two aphid species inhabit spatially distinct niches, with *M. persicae* occurring primarily on lower, older leaves and *B. brassicae* occurring primarily on newer apical leaves (Snyder *et al.* 2008). However, these differences in prey-feeding behaviour do not appear to further accentuate leaf-scale differences in predator foraging behaviour, because predators do not differ in their preference for one aphid over the other and diversity effects are not strengthened in communities containing two vs. one aphid species (Snyder *et al.* 2008).

A second possible mechanism explaining resource partitioning is intraspecific interference. In our predator–prey system, intraspecific interference is most likely to be manifested through territoriality and/or cannibalism (or its avoidance). Of our community members, lady beetles and aphid parasitoids have been shown to fastidiously avoid foraging where other conspecifics have already visited, because of high risks of cannibalism to any young left in these patches (Doumbia *et al.* 1998; Raymond 2000; Nakashima *et al.* 2004; Rutledge *et al.* 2008). Avoidance of conspecifics appears generally to be based on chemical cues, with predators often better attuned to detecting conspecific than heterospecific chemical traces (Höller & Hörmann 1993). Intraspecific avoidance would generate resource partitioning because areas on plants that are visited by an individual predator would then be avoided by subsequent conspecifics, generating a refuge that remains until the chemical cues break down. In this case, predators would be limited by the number of plants where conspecific, but not heterospecific predators had recently foraged. Therefore, we would expect prey depletion to saturate at lower predator densities in single-species communities than in the diverse communities, due to reduced predator foraging in communities with higher conspecific densities. Although this might play a small role in explaining our results, we suspect that it is at most minor. Any chemical cues generating intraspecific avoidance will likely break down rapidly in comparison to the duration of the experiment, because previous studies that have detected these effects were conducted over much shorter time scales (e.g. Doumbia *et al.* 1998; Rutledge *et al.* 2008) or have shown that chemical signals quickly disappear (Nakashima *et al.* 2004). Furthermore, one predator (*Nabis alternatus*) showed clear resource-use saturation (Fig. 1) even though there is no evidence that it avoids areas that have been visited by conspecifics.

Previous studies on the relationship between consumer diversity and consumption (or, more generally, diversity and productivity) have asked whether the effects of consumers in diverse treatments are additive or non-additive in comparison to the effects of consumers in single-species treatments (e.g. Cardinale *et al.* 2006, 2007; Schmitz 2007; Wojdak & Mittelbach 2007; Griffiths *et al.* 2008; Griffin *et al.* 2008). Because we have used a mechanistic approach and fit explicit models to the data, we do not need to address this question to identify resource partitioning as the best explanation for our experimental results. Nonetheless, the fitted model can provide insight into the pattern of additivity/sub-additivity in our resource-use data. For the subsets of prey that are used exclusively by separate species, the effects of diversity will be strictly additive. For example, for consumer species i and j that have exclusive subsets p_i and p_j of resources, the combined consumption of these resources in the two-consumer community is additive, $p_i(1 - e^{-a_i x_i}) + p_j(1 - e^{-a_j x_j})$. This is because resources accessible to predator i are inaccessible to predator j, and vice versa (see also Casula *et al.* 2006). However, for the subset of p_{ij} resources shared by both consumers, the combined consumption of resources is multiplicative, $p_{ij}(1 - e^{-a_i x_i} e^{-a_j x_j})$, which is sub-additive. Here, sub-additivity arises from competition between predators i and j for the subset of resources that they share in common (see also Sih *et al.* 1998). Thus, rather than asking only whether consumer effects are additive or not, our more-mechanistic approach attempts to parse out the processes underlying the observed effects of diversity.

There have been numerous recent attempts to demonstrate resource partitioning as a mechanism underlying diversity effects on productivity and resource consumption (Tilman 1997; Tilman *et al.* 1997; Loreau & Hector 2001; Chase & Leibold 2003; Hooper *et al.* 2005; Cardinale *et al.* 2006; Stachowicz *et al.* 2007; Wojdak & Mittelbach 2007; Finke & Snyder 2008). Our approach employed a stepwise increase in consumer density to fully saturate resource niches. This allowed us to demonstrate that no single-consumer species, even at high density, was capable of

driving resources to as low a level as could be achieved by a diverse mix of consumers – the hallmark of resource partitioning. This approach provides an experimentally and statistically rigorous test for resource partitioning, eliminating the key concern of critics of purely trait-based approaches to niche definition (e.g. Strong *et al.* 1979; Simberloff & Boecklen 1981; Lewin 1983). Our approach may be broadly useful for defining the breadth and overlap of resource-use differences among species.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 Residual error plotted against expected values for the best fit model (incomplete resource partitioning; eqn 2 in text), fit with non-weighted least squares (a), and weighted least squares (b).

Figure S2 Natural enemies recovered at the end of the experiment, divided by the number originally released, summed for true predators in (a) Block 1 and (c) Block 2, and for pupae of the parasitoid *D. rapae* in (b) Block 1 and (d) Block 2.

Table S1 Log-likelihood (LL) and Akaike information criterion (AIC) values for the models presented in the text, fit to the data, using least squares (LS) and weighted least squares (weighted LS).

Table S2 Three-way ANOVA of the final densities of (a) true predators and (b) the aphid parasitoid *D. rapae*.

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