SPECIES DIVERSITY MODULATES PREDATION

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Abstract. Predation occurs in a context defined by both prey and non-prey species. At present it is largely unknown how species diversity in general, and species that are not included in a predator's diet in particular, modify predator–prey interactions.

Therefore we studied how both the density and diversity of non-prey species modified predation rates in experimental microcosms. We found that even a low density of a single non-prey species depressed the asymptote of a predator's functional response. Increases in the density and diversity of non-prey species further reduced predation rates to very low levels. Controls showed that this diversity effect was not due to the identity of any of the non-prey species. Our results establish that both the density and diversity of species outside a predator's diet can significantly weaken the strength of predator–prey interactions. These results have major implications for ecological theory on species interactions in simple vs. complex communities. We discuss our findings in terms of the relationship between diversity and stability.

Key words: biodiversity; functional response; interaction modification; microcosms; non-prey species; *Paramecium aurelia*; predator–prey model; predatory flatworm; *Stenostomum virginianum*.

INTRODUCTION

A predator's intake rate as a function of prey density is known as its functional response (Solomon 1949, Holling 1959). This relationship is an important component of community and food web models that are central to theoretical ecology and its applications in conservation biology, fisheries management, and biological control. However, experimental studies of functional responses are usually carried out in simplified systems in which predators only encounter a single prey species (e.g., Hassell 1978, Gross et al. 1993). Much of the structural complexity and diversity of non-prey species in the food web are often excluded from experimental set ups, even though these may have substantial effects on a predator's ability to locate and pursue prey in nature. Nearly all functional responses published in the literature suffer from this simplification. As a result, much of current predator–prey theory may contribute more to understanding trophic interactions in relatively contrived laboratory settings than give insight into predation and food web dynamics in realistic natural environments.

Naturally, there is good reason to exclude much of the complexity observed in the real world when modeling or performing experiments. Most of the non-prey species in a food web are irrelevant to particular predator–prey interactions. However, for each specific predator, a

subset of species will modify its interaction with any given prey. This may occur for a variety of reasons. Some non-prey species provide structural complexity that allows prey to avoid and evade predators more easily (Mayer et al. 2001, Grabowski 2004). Other species provide a masking background in terms of infochemical cues or a cryptic background in terms of visual cues that make prey less detectable (Wootton 1992, Vos et al. 2001). Some non-prey may be similar to prey in one or more aspects of their shapes, colors, sounds, or odors, and these similarities may cause confusion in predators. All of the above effects force predators to spend increasing amounts of time on information processing as the diversity of “relevant” non-prey and the ratio of such non-prey to prey in the environment increase (Vos et al. 2001).

These kinds of effects are a form of interaction modification (Abrams 1983, Wootton 1993), where one species alters the interaction between individuals of two other species. There is a growing recognition that interaction modifications are likely to be important in nature (e.g., Anholt and Werner 1995, 1998, Peckarsky and McIntosh 1998, Cardinale et al. 2003, Palomo et al. 2003). However, few studies have started to address consequences of interaction modifications in communities caused by species diversity (but see Vos et al. 2001, Thébault and Loreau 2006).

Empirical studies across many taxa (Drutz 1976, Kareiva 1985, Stachowicz and Hay 1999, Mayer et al. 2001, Vos et al. 2001, Grabowski 2004, van Veen et al. 2005) show that a non-prey species may interfere with the foraging behavior of predators and parasitoids and

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thus influence rates of predation or parasitism. However, we are not aware of any study that systematically investigates the effects of non-prey density and diversity on functional responses. Many such studies are needed to test whether simple functional responses can be extrapolated to natural settings in which many non-prey species exist.

In this study, we experimentally investigated whether and how non-prey species modify consumption rates of a predator. We first observed the functional response of the predatory flatworm *Stenostomum virginianum* (hereafter referred to as predator or *Stenostomum*) on its ciliate prey *Paramecium aurelia* (hereafter prey or *Paramecium*) in the absence and presence of a single non-prey species. *Stenostomum* usually detects potential prey from a very short distance and may “try” to test its suitability (M. Vos, *personal observation*). Prey and non-prey species are mainly distinguished on the basis of their size. This experimental system is thus especially suited as a model for predation under gape limitation, an important factor in many aquatic predator–prey systems. However, it is also a model in the wider sense for any system in which the predator or parasitoid needs to spend some time distinguishing between prey and non-prey.

In the second experiment, we measured whether an increasing density and diversity of non-prey reduced predation rates. We also tested whether species identity effects occurred, with some non-prey species having stronger effects on predation than others, or whether diversity itself modified the interaction. Answering these questions is important for obtaining a reference to how the shapes of functional responses could differ in simple vs. more diverse communities. This is crucial to our ability to predict the dynamics and functioning of complex ecological systems.

MATERIALS AND METHODS

The experimental system: predator, prey, and non-prey

The predatory flatworm *Stenostomum* (Rhabdocoela, Turbellaria) is a benthic omnivore that has been cultured asexually in Pyrex crystallizing dishes with 300 mL of NAYA mineral water (Mirabel, Quebec, Canada) and autoclaved wheat grains since we isolated it from sediments of a freshwater pond on the University of Victoria (UVic) campus in 2002. In our cultures, the flatworms fed on bacteria and small flagellates. The prey in our experiments was the holotrich ciliate *Paramecium*, also isolated from a UVic pond. Three other species, having sizes that make them inedible for this gape-limited predator were used in the experiment: the hypotrich ciliate *Euplotes aediculatus*; (originally obtained from K. Wiackowski), the ciliate *Spirostomum ambiguum*, and the bdelloid rotifer *Philodina roseola*, both obtained from Sciento (Manchester, UK). The non-prey are hereafter referred to as *Euplotes*, *Spirostomum*, and *Philodina*. All prey and non-prey were cultured in 100–200 mL of medium, which was prepared

by filtering 1.5 crushed pellets (~0.7 g each; Nr. 13-2360, Carolina Biological Supply Company, Burlington, North Carolina, USA) through double-layered No. 4 coffee filters and dissolved in 2.0 L of NAYA water. One wheat grain was added to the medium, which was then autoclaved before inoculation. We subcultured all species every 3–5 weeks. All cultures were kept and the experiments were conducted at a laboratory temperature of ~21°C.

We used freezer-killed *Stenostomum* to induce a morphological defense in *Euplotes* 24 hours prior to each experiment. The procedure involved exposing 4 mL of dense *Euplotes* culture to 600 µL of *Stenostomum* kairomone (250 individuals/mL, stored in 1.5 mL Eppendorf tubes at –20°C), which caused *Euplotes* to increase in body width to an inedible size. Before the start of each trial, we photographed 20–50 *Euplotes* and measured the maximum body width using Image Pro Plus software to check whether they were too large to be ingested by *Stenostomum* (i.e., >80 µm; Altwegg et al. 2006).

Experiment 1: functional response with one non-prey species

We compared functional responses of the predator on *Paramecium* prey in the presence or absence of non-prey *Euplotes* (Fig. 1). We set densities of *Paramecium* at 40, 60, 80, 100, 120, 140, 160, and 200 individuals per 900 µL of medium, with or without 60 induced *Euplotes* (101.5 ± 11.9 µm; mean body width $\pm$ SD, $n = 104$). We randomly assigned treatment combinations of predator density, prey density, and presence or absence of non-prey species to individual wells in 24-well tissue culture plates (Costar, Corning, Corning, New York, USA). To introduce them into wells, all organisms were individually pipetted and counted under a dissecting microscope (Leica MZ8). We washed and then pipetted 16 predators into each well in order to obtain mean predation rates. This was intended to even out variation among predators. As some predators stuck to the pipette tips, the actual number of predators per well in this experiment varied, and predation rates are therefore given as number of prey ingested per predator. The mean length of *Stenostomum* was 505.2 ± 144 µm ($n = 79$). The feeding experiment was stopped after four hours by the addition of two drops of acid Lugol's solution (5%; Sherr and Sherr 1993). For each well, the remaining prey as well as predators and non-prey were counted. Replication resulted in 8 *Paramecium* densities $\times$ 2 *Euplotes* treatments (absence/presence) $\times$ 6 replicates of each = 96 data points.

In order to determine the shape of the predator's functional response on prey with or without one non-prey species, we performed nonlinear curve fitting of Holling Type II and Type III functional response models to our data. We fit separate functional responses in the presence and absence of non-prey, as well as a single functional response which ignored the presence or

FIG. 1. Number of *Paramecium* eaten per predator in four hours (mean $\pm$ SE; $n = 6$ replicates) in relation to prey density. The experiment was conducted in the medium described in *Materials and methods*, but without the wheat grain. Open circles and solid squares denote the presence or absence of 60 non-prey *Euplotes* per well. The solid line (without non-prey) and the dashed line (with non-prey) are best-fit Type III functional response models.

absence of non-prey. We also examined both model types with the addition of an intercept to account for possible systematic counting error, cell death, or reproduction during the experiment.

We fit the following functional response models to the data:

$$\text{Type II)} \quad y(X) = \frac{aX}{1 + abX} \quad (1a)$$

$$\text{Type II with intercept)} \quad y(X) = c + \frac{aX}{1 + abX} \quad (1b)$$

$$\text{Type III)} \quad y(X) = \frac{aX^2}{1 + abX^2} \quad (2a)$$

$$\text{Type III with intercept)} \quad y(X) = c + \frac{aX^2}{1 + abX^2} \quad (2b)$$

where y represents ingestion rate, X is prey density, a is attack rate, b is handling time, and c is intercept. Because each of the six replicates of all treatments was conducted on a different day, we tested for the effect of blocks by using nonlinear mixed effects models (Pinheiro and Bates 2000). Prey density was treated as a fixed effect and blocks as random effects. We chose the best model based on the smallest Akaike's Information Criterion (AIC) and log-likelihood values (Burnham and Anderson 2002). Statistical analyses were performed in R software, version 2.2.1 (R Development Core Team 2005). The calculated measure for the functional response's contribution to stability was the range of prey densities for which the Type III functional response showed positive density-dependent predation. This stabilizing part of the functional response is equivalent to the part of the curve describing the predation risk per prey that has a positive slope, i.e., $[y(X)/X]' > 0$, which requires $y'(X) > y(X)/X$ (Oaten and Murdoch 1975). We only compared the ranges of prey densities for which

the curves were stabilizing after having determined by AIC that two separate models for the data with and without non-prey were better supported than a single model for these data combined. If predators spend time on non-prey this could cause estimates of the attack rate to decrease and of the handling time to increase. Such changes would result in lowering both the initial slope and the asymptote of the functional response on prey in the presence of non-prey. In the case of Type III functional responses, this would entail an increase in the range of prey densities for which the curve is stabilizing.

Experiment 2: non-prey species diversity, density, and identity

In the second experiment we used single *Stenostomum* feeding on *Paramecium* in 800 μL of NAYA water in the presence or absence of *Philodina*, *Spirostomum*, induced *Euplotes* ($102.0 \pm 13.1 \mu\text{m}$; mean $\pm$ SD, $n = 358$), and their combinations. Using a single predator per well avoided any potential confounding effect of predator interference. We observed *Stenostomum* feeding on either 60 or 90 *Paramecium* alone, with one non-prey (30 *Euplotes*), with two non-prey (30 *Euplotes* + 30 *Philodina*), and with three non-prey (30 *Euplotes* + 30 *Philodina* + 30 *Spirostomum*). Here the density of non-prey species (0–90) increased together with their diversity (Fig. 2, data from two and three non-prey treatments were also used in Fig. 3).

To separate the effect of density and diversity per se, we included treatments of a single *Stenostomum* feeding on 60 *Paramecium* in the presence of non-prey monocultures: either 30, 60, or 90 *Euplotes*; 30, 60, or 90 *Philodina*; or 90 individuals of *Spirostomum* (see Fig. 3). This allowed us to compare, for example, the effect 90 individuals of a single non-prey species to 90 non-prey individuals consisting of a mixture of three non-prey species (30 of each). We were also able to compare

FIG. 2. The effect of diversity and density of non-prey species on the predator's feeding rate. The bars represent a single *Stenostomum* feeding on either 60 or 90 of the prey *Paramecium* per 800 µL of NAYA mineral water in the presence or absence of non-prey species. Sets of bars, left to right, represent *Stenostomum* with the prey *Paramecium* and no non-prey, one non-prey (30 *Euplotes*), two non-prey species (30 *Euplotes* and 30 *Philodina*), and three non-prey species (30 *Euplotes* + 30 *Philodina* + 30 *Spirostomum*). Data are means + SE of eight replicates.

the relative effect of each non-prey species (species identity).

In order to check whether non-prey species were indeed not consumed by *Stenostomum*, we incubated two densities (30 or 60 individuals per 800 µL) of each non-prey species with and without one *Stenostomum* predator. We also incubated 60 or 90 *Paramecium* alone to estimate the accuracy of our pipetting and counting and to control for other factors such as prey reproduction.

All experimental organisms were individually pipetted and counted. Treatments were randomly distributed over 24-well tissue culture plates and replicated in time using an incomplete random block design. The experiment was replicated eight times, except the single *Stenostomum* + 60 *Paramecium* + 90 *Spirostomum* treatment, for which $n = 6$. We stopped the experiment after four hours by adding two drops of acid Lugol's solution (5%) and counted the fixed individuals of all species. The analysis was performed in R software, version 2.2.1, using multiple regression.

We estimated that *Stenostomum* had a density of about one predator per 6 mL in UVic ponds. This estimate for the mean is lower, but not orders of magnitude lower, than the density of one predator per 0.8 mL we used in experiment 2. In a pond studied by Finlay and Esteban (1998), ciliates ranged in density from 0–3466 individuals per mL. In a lake study, protozoans ranged in density from 7.11 to 97.5 per mL (Gomes and Godinho 2003). In the latter data set, *Paramecium* comprised 7% of the total density and 39%

of the protozoan community biomass on the bottom of the lake. Based on size, two protozoan species in that lake would have been inedible to a specialist predator of small *P. aurelia*. One of these, *Spirostomum*, can comprise 18% of the total bottom-dwelling protozoan biomass. Rotifers may further contribute to the number of relevant non-prey species (Finlay and Esteban 1998).

RESULTS

Functional responses in the presence and absence of one non-prey species

The functional response of *Stenostomum* feeding on *Paramecium* is best described by two sigmoid (Type III) curves, in the presence and absence of non-prey *Euplotes* (Fig. 1, Table 1). The model where both treatments were described by one single Type III functional response was not supported. Type II responses were unsatisfactory because the estimated handling times were all negative. Positive handling times were only possible if we included an intercept in the model. This model was, however, not supported by AIC and log likelihood, and Type III models always gave a better fit to the data (Table 1). Neither the blocks in the nonlinear mixed effects models nor the addition of an intercept for the Type III model improved the fit.

We observed a consistent effect of the presence of non-prey species on the functional response of the predator. The ingestion rate of prey was lower in the treatments with induced non-prey *Euplotes*, and the effect was more pronounced at high prey densities (Fig. 1). Two separate Type III responses were best

FIG. 3. The effect of diversity, density, and species identity of non-prey species on the predator's feeding rate. A single *Stenostomum* predator was feeding on 60 *Paramecium* prey in 800 µL of NAYA water in the presence of non-prey species: bars for species combinations represent 30 *Euplotes* + 30 *Philodina* (total non-prey density 60) and 30 *Euplotes* + 30 *Philodina* + 30 *Spirostomum* (total non-prey density 90). Data are means + SE of eight replicates and of six replicates for the *Spirostomum* monoculture data.

TABLE 1. Information statistic summary for the fit of seven functional response models describing per capita ingestion of *Paramecium* prey by *Stenostomum*, as a function of prey density in 900- μ L wells, over four hours.

Model	Mixed effects	Non-prey effect	K	Log likelihood	AIC	Akaike weight
Type III	no	yes	4	-172.43	352.86	0.999
Type III	no	no	2	-185.70	375.40	<0.001
Type III	yes	yes	12	-172.43	368.86	<0.001
Type III	yes	no	6	-185.70	383.40	<0.001
Type III + intercept	yes	yes	14	-172.33	372.66	<0.001
Type III + intercept	yes	no	12	-185.64	395.28	<0.001
Type II + intercept	yes	yes	20	-173.01	386.01	<0.001

Notes: The best model is in bold font. K is the number of model parameters.

supported and showed that the stabilizing prey density range widened from 0–147 to 0–181 prey per 900 μ L in the treatment with non-prey *Euplotes*.

Non-prey species diversity, density, and identity

The predator had a higher overall consumption rate at a density of 90 prey per 800 μ L than at a density of 60 ($P < 0.001$ for *Paramecium* density; Table 2, Fig. 2). According to the analysis, the predator consumed 3.06 more prey individuals in four hours when an additional 30 *Paramecium* prey were added. This effect of prey density gradually disappeared when non-prey density and diversity increased (Fig. 2).

Each non-prey species in the experiment caused a significant reduction in the predator's consumption rate, both at 60 and 90 prey per 800 μ L ($P = 0.002$ for *Euplotes*, $P < 0.001$ for *Philodina*, and $P < 0.001$ for *Spirostomum*). The magnitude of reduction in predation rate was similar for all three non-prey species. Addition of 30 *Euplotes*, *Philodina*, or *Spirostomum* non-prey reduced the predator's consumption by 1.29, 0.99, and 1.17 prey individuals, respectively (Table 2). Therefore, non-prey species identity was not an important factor in our experiment. The diversity of non-prey per se had the strongest effect ($P < 0.001$), as an equivalent addition of 30 individuals of different species reduced the predator's consumption by 1.92 prey individuals.

Control treatments

When incubating 30 or 60 *Paramecium* for four hours without predators we lost, on average, 2.13 or 2.75 individuals, respectively. In both control treatments this

mean was strongly affected by two extreme data points. Without these, there was a difference of +0.33 individuals from the original 30, and of -0.17 individuals from the original 60 individuals. We believe the extreme points are true outliers, as we could reliably and consistently measure low predation rates of about 0.5 prey per predator per well per four hours (e.g., Fig. 1). There was no difference in the number of non-prey retrieved from wells with or without a predator, which shows that non-prey were indeed not eaten (t tests, $n = 7$, $P = 0.66$ for *Euplotes*, $P = 0.94$ for *Philodina*, $P = 0.92$ for *Spirostomum*).

DISCUSSION

Many models in food web and community ecology incorporate ecological realism by using nonlinear functional responses (e.g., Rosenzweig 1973, Williams and Martinez 2000, Brose et al. 2003, 2006, Kondoh 2006 and references therein). An assumption of these models is that per capita predation rates depend only on the densities of prey species. However, this assumption is probably rarely met in natural communities, where predator and prey populations are never isolated from the diversity and complexity of their biotic surroundings. Many other species directly or indirectly interact with predators or prey, and these complex linkages may strongly affect the process of predation (Peacor and Werner 2004).

We observed *Stenostomum* preying on *Paramecium* with a Type III functional response (see also Altwegg et al. 2006). We showed that a single non-prey species can substantially modify this interaction. The presence of a

TABLE 2. Results of multiple regression analysis of the effects of non-prey species on the predator's prey consumption rate ($n = 8$ replicate trials with one predator for all treatments, not including the *Spirostomum* monoculture; for treatment with *Spirostomum*, $n = 6$ replicate trials with one predator, i.e., the *Spirostomum* monoculture).

Effects	df	SS	F value	P	Consumption rate per 30 additional prey or non-prey
<i>Paramecium</i> prey density	1	189.96	14.839	<0.001	3.06
<i>Euplotes</i> non-prey density	1	126.11	9.851	0.002	-1.29
<i>Philodina</i> non-prey density	1	228.60	17.858	<0.001	-0.99
<i>Spirostomum</i> non-prey density	1	295.05	23.049	<0.001	-1.17
Non-prey diversity	1	152.86	11.942	<0.001	-1.92
Residuals	112	1433.73			

Note: Coefficients of prey and non-prey densities were multiplied by 30 individuals.

relatively low density of *Euplotes* non-prey decreased the predator's functional response. Non-prey species additionally caused the Type III functional response to be density-dependent over a wider range of prey densities. Through this effect, the presence of non-prey may contribute to the stability of the predator-prey interaction. The observed change in the shape of the functional response was most likely caused by predators spending some time trying to capture non-prey individuals. Consequently, they would have had less time to search for and handle their prey. The results lend support to the "wasted-time" hypothesis for predation in more diverse communities (Vos et al. 2001). A more complete explanation of the shape of the predator's functional response, based on another data set, will be presented elsewhere. These data, however, still indicate that the basic shape is a sigmoid Type III functional response.

The results from our second experiment establish that interaction modification is not necessarily a matter of only one species affecting the interaction between two others. These results clearly show that several non-prey species, or such non-prey diversity per se, may modify the interaction between a predator and its prey. The non-prey diversity range, over which strong effects of diversity itself occur, may greatly differ among systems, with some species or taxonomic groups being more sensitive than others. Differential sensitivities to diversity can be important within the context of both conservation- and invasion ecology. Spending considerable time on non-prey can weaken and stabilize predator-prey interactions that would otherwise be unstable. The effect may either be complete stabilization or a damping of predator-prey population cycles (McCann et al. 1998, Vos et al. 2001, van Veen et al. 2005). The results presented here pertain to a specific system in the laboratory. If our results are general, as suggested by laboratory as well as field data on bacteria, leaf beetles, parasitoids, and fish, that have all been shown to waste time on non-prey (Drutz 1976, Kareiva 1985, Stachowicz and Hay 1999, Mayer et al. 2001, Vos et al. 2001, Grabowski 2004, van Veen et al. 2005), this could have far-reaching consequences for ecological theory on the functioning of complex ecological systems.

We found that non-prey diversity and non-prey density both reduced the predators' feeding rate in our experiments. Our analysis allowed us to tease apart their relative contributions and showed a surprisingly strong effect of diversity itself. This result indicates that a predator needs to spend more time to discriminate between prey and non-prey items when non-prey are more diverse. In our experiment, no single non-prey species was particularly hard to deal with (Fig. 3, Table 2). We can therefore rule out the possibility that the very strong effect on predation rate in the high diversity treatment was caused by non-prey species identity. Although the three non-prey species were very different in shape, they were similar in terms of being too large to be ingested by the gape-limited predator. When a

predator has different recognition or handling times on different non-prey, species identity effects would be expected.

Non-prey species can modify predator-prey interactions by masking prey, diluting prey concentrations, or confusing predators (Vos et al. 2001). Our results suggest how species diversity itself could contribute to the stability of diverse communities. Diversity-modified predation is an ecological mechanism that could cause a prevalence of weak and moderate interaction strengths in natural systems (see McCann et al. 1998). Ecological mechanisms that explain how diversity itself affects coexistence in natural communities have largely been lacking in the long-standing debate about diversity-stability relations (McCann 2000, Vos et al. 2001, Brose et al. 2003, Kondoh 2006). Recognizing that the diversity of species that seem to be unconnected to certain predator and prey species could promote the persistence of the community as a whole, has important implications for the conservation of diverse ecosystems and for the development of strategies to effectively manage biodiversity. We further conclude that one of the new challenges emerging from our study is to pay more attention to which seemingly irrelevant species are in fact part of the community context that determines predation rates and the strength of food web links in nature.

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