

REPORT

Consumer effects decline with prey diversity

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Abstract

While consumer species diversity is known to influence the capture of limited resources, little is known about how prey diversity impacts the transfer of energy and matter among trophic levels. Here, we perform a meta-analysis of experiments that have examined the impact of grazers on the biomass of periphytic algae to test the hypothesis that the magnitude of consumer (grazer) effects on prey (algae) depends on the species diversity of the prey assemblage. The analysis reveals that consumer effects tend to decrease as the diversity of a prey assemblage increases. This trend is robust for several different, yet complementary indices of grazer effect size and algal diversity. The trend also remains significant after statistically controlling for a variety of factors that can covary with prey diversity among studies. We discuss several possible mechanisms for the documented pattern, such as diversity enhancing the probability of inedibility and of positive interactions.

Keywords

Biodiversity, ecosystem functioning, grazing, meta-analysis, periphyton, resistance, trophic structure.

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INTRODUCTION

There has been much recent interest in how loss of species diversity from communities might impact the efficiency of resource use in food webs (Tilman 1999; Loreau *et al.* 2001; Naeem 2002). Studies having addressed this topic have generally focussed on how diversity at a particular trophic level affects the consumption of resources at some lower trophic level ('top-down' effects of consumer diversity). Theory suggests that groups of consumers characterized by higher diversity will have increased efficiency of resource use (Holt & Loreau 2001; Duffy 2002), and this prediction has received limited experimental support (Norberg 2000; Duffy *et al.* 2003).

Compared with studies having addressed the role of consumer diversity in food web dynamics, little attention has been paid to the influence of prey diversity on the transfer of biomass among adjacent trophic levels. This is despite the fact that prey diversity might be expected to decrease the effectiveness of trophic interactions via several plausible mechanisms (Duffy 2002). For example, increased prey diversity inherently corresponds to greater variation in prey traits that might increase the chance that non-edible or unpalatable species are present at high diversity (Duffy 2002). Alternatively, because the probability of synergistic species interactions increases with diversity, prey

assemblages with more species may exhibit greater resistance to, or faster recovery from consumption. Indeed, associational resistance against consumers has been observed in terrestrial plant assemblages (Hambäck *et al.* 2000) and marine coastal assemblages (Wahl & Hay 1995). Such mechanisms could be further augmented by niche partitioning among species that allow diverse prey communities to recover more quickly from the impacts of consumers.

In spite of the potentially important influence of prey diversity on the strength of trophic interactions, only two experimental manipulations of prey diversity have been recently published. Steiner (2001) found that increased phytoplankton species richness resulted in lower total consumption by zooplankton, a pattern that was modified by the identity of the consumer species. Yoshida *et al.* (2003) manipulated clonal diversity of a single algal species and found that intraspecific variation had a strong impact on consumer–prey dynamics. Despite being convincing examples that prey diversity can impact food web dynamics, both studies were performed in laboratory microcosms with communities of relatively low diversity. Thus, the role of prey diversity in trophic interactions under more natural conditions remains open for debate.

Here, we present results from meta-analyses of 172 experiments that manipulated the presence of invertebrate or vertebrate grazers while also measuring the magnitude of

grazer effects on algal biomass, and the diversity of algal assemblages. The analysis reveals a strong decrease in the magnitude of consumer effects with increasing diversity of an algal assemblage. As algal diversity was not manipulated in these experiments, we give much attention to possible confounding factors that might generate a negative relationship between grazer effect and prey diversity. A key strength of this meta-analysis is that it includes studies spanning a large range of prey diversity and a variety of ecosystems, while utilizing naturally co-occurring species. As such, it offers insight that complements more controlled, but less realistic, theoretical and experimental studies of the role prey diversity plays in food webs.

METHODS

Selection of studies

The effect of consumers on freshwater and marine periphyton has been addressed in numerous experimental studies (see reviews by Feminella & Hawkins 1995; Steinman 1996; Hillebrand 2002). Taking advantage of this body of work, we assembled data from field and laboratory experiments that directly manipulated consumer presence (excluding studies that used predators to reduce grazer density). A total of 172 experiments, derived from 35 publications, included values for species richness (S) and/or Shannon's index of diversity (H') of algae in ungrazed periphyton assemblages (Appendix 1). We used the mean of these indices in the consumer-free treatments of each study as the measure of prey diversity in our analyses. We used both S and H' in our analyses as these two measures potentially give complementary information. The number of species gives a direct estimate of the number of traits (e.g. edibility) present (Loreau *et al.* 2001), but is subject to changes in taxonomy and effort in sampling and analysis. H' is more robust against sampling effort, and including it in our analyses also allows us to discuss how species evenness potentially augments the richness of algal traits.

The effect of invertebrate or vertebrate consumers on periphyton biomass in the 172 experiments was characterized using two complementary indices. First, the absolute effect of grazers on algal biomass was measured as Hedges' d , which is the standardized difference between mean algal biomass in ungrazed controls and grazed treatments (Gurevitch & Hedges 1993). Secondly, the relative effect of consumers was measured as the log response ratio (LRR), which is the natural log transformed ratio of mean algal biomass in ungrazed controls relative to grazed treatments (Hedges *et al.* 1999). For each measure, increasingly negative values correspond to a greater fraction of algal biomass consumed. While Hedges' d and LRR describe slightly

different aspects of herbivory (absolute vs. relative impacts), the metrics were moderately correlated for the experiments considered here ($r = 0.57$, $P < 0.001$, $n = 152$). Nonetheless, following the recommendations of Lajeunesse & Forbes (2003), we considered both measures of grazer impact in our analyses to preclude the possibility that observed patterns might result from the unique statistical properties of any given metric.

Meta-analyses

Sampling variances are available for both Hedges' d and LRR , which allowed us to conduct weighted meta-analyses where each experiment-wise effect size was weighted by the inverse of its variance (Gurevitch & Hedges 1993; Hedges *et al.* 1999; Rosenberg *et al.* 2000). Weighted regression meta-analyses were used to test for significant relationships between the indices describing grazer effect size and those describing algal diversity (Rosenberg *et al.* 2000). Mixed models were employed so as to avoid some of the rigid assumptions of comparable fixed effects models (Gurevitch & Hedges 1993).

Of the 172 experiments included in the dataset, 51 manipulated some other factor in addition to grazing (typically nutrient or light availability, indicated in Appendix 1). To assess whether these additional treatments had any influence over conclusions from our first set of analyses, we repeated the procedures above using only those experiments in which grazer presence was the sole variable manipulated. Degrees of freedom for the meta-analyses differed, partly because some studies reported only S or H' but not both, and partly because some studies did not report the data needed to calculate Hedges' d .

Confounding factors

Algal species richness was neither controlled nor directly manipulated in any of the studies included in our meta-analyses. Therefore, one concern is that a relationship between algal diversity and grazer effect size could emerge not because of any direct effect of prey diversity on consumers, but rather, because of the influence of some third, confounding factor that is associated with prey diversity. Obviously, it is impossible to account for the wide variety of factors that might be associated with prey diversity, and that might also influence grazing rates among the large number of studies included in our analyses. Therefore, our conclusions are inherently limited in scope. However, we were able to obtain data on a number of key factors known to influence the effect of grazers on periphyton biomass (see reviews by Feminella & Hawkins 1995; Steinman 1996; Hillebrand 2002), which we attempted to account for as potentially confounding factors.

Three categorical variables were included in these analyses: habitat (lotic, lentic, coastal), experiment type (aquaria, channels, enclosure and exclosure), grazer type (crustaceans, gastropods, insects, vertebrates, other monospecific grazers and diverse grazer assemblages). The number of studies in each category varied, as summarized in Appendix 2a. Six continuous variables were also considered: experimental duration (days), year of study (which may reflect changes in algal taxonomy over time), geographic location of study (longitude, latitude), total consumer biomass (\log g dry weight m^{-2}), and total algal biomass. Algal biomass was obtained from the ungrazed control treatments; however, because biomass was reported in a variety of units (chlorophyll, biovolume, dry mass, etc.), we standardized each measure as a proportion of the mean of that measure across all studies. This derived measure also helped reduce the confounding of algal biomass with the effect size.

Of the 172 experiments included in our meta-analyses, 87 reported information on the 10 factors listed above (Appendix 2b), and only these studies are considered here. Within these 87 studies, several of the quantitative factors exhibited weak to moderate correlations with each other, or with one or both measures of algal diversity. Such correlations pose a problem in most statistical analyses because multi-collinearity among explanatory variables can lead to unreliable estimates of effect sizes (Philippi 1993). Given this, we subjected the set of eight quantitative variables (including S and H') to a Principle Components Analysis (PCA) in order to separate and condense variables into orthogonal (that is, independent) components (SYSTAT v. 9, using a quartimax rotation to maximize separation). The PCA was successful in separating variables into six principal components, with each PC being interpreted uniquely (Appendix 3). PC1 represented the year and geographic location of the studies, PC2 was a vector of algal species richness, PC3 uniquely described the duration of studies, PC4 was a vector of Shannon's diversity index, PC5 and PC6 represented grazer and algal biomass, respectively.

We then modelled consumer effect size (either Hedges' d or LRR) as a function of the six principal components and three categorical variables (habitat, experiment type and grazer type) using a mixed model ANOVA (SAS v 8.02). To assess the importance of algal diversity as an explanatory variable of grazer effect size, we used an information-theoretic approach to judge the relative likelihood of models with and without algal diversity terms included (Burnham & Anderson 2002; Johnson & Omland 2004). We began by running the unconstrained models containing all nine explanatory variables to determine the Akaike Information Criteria (AIC), and then re-ran nested models with the vectors of algal diversity eliminated (PC2, PC4, or both) to

determine the change in AIC values. The difference in values of AIC between each model i and the 'best' model having the lowest AIC, Δ_i , was then used to calculate the likelihood of each model as $\exp(-1/2\Delta_i)$ (Burnham & Anderson 2002). When normalized across all models to sum to 1, this relative likelihood is called the *Akaike weight*, which can be interpreted as 'the probability that model i is the best model for the observed data, given the candidate set of models' (Johnson & Omland 2004). Thus, we used the *Akaike weights* to assess the weight of evidence supporting models with and without algal diversity included as an explanatory variable. It should be noted that while these analyses evaluate the likelihood that algal diversity explains a portion of grazer effect size after considering the potentially confounding factors, they do not elaborate on the importance of the confounding factors themselves. Given this, and given that our interest here is specific to assessing the role of algal diversity, we do not discuss the potentially important effects of the other factors included in the model.

RESULTS

Our meta-analyses revealed that consumer effect sizes were significantly reduced at higher prey diversity (Table 1); thus, grazer effects on algal biomass tended to decrease as algal diversity increased (Fig. 1). This decrease in consumer effect size was evident for both the relative (Hedges' d) and the absolute (LRR) measure of consumer effects on prey biomass. Moreover, the decrease in consumer effect size was evident for both diversity measures, H' and S (Fig. 1), although the relation between S and effect sizes had a flatter slope compared with the relation between H' and effect sizes. This likely reflects the broader range of richness than H' . Visual inspection of the data revealed that two studies had unusually high H' and, therefore, potentially high influence on the results. However, excluding these two experiments did not alter the conclusion that grazer effect sizes significantly decreased with increasing algal diversity ($P < 0.003$). Results of the analyses were also not altered, qualitatively or quantitatively, by confining the dataset to experiments that only manipulated presence/absence of grazers (Table 1). Thus, patterns were comparable for studies that varied grazers in combination with other treatments.

Using a mixed model ANOVA, consumer effect size was modelled as a function of nine explanatory factors (Table 2). Several of the explanatory factors were significant in the model; however, our focus here is on PC2 (algal richness) and PC4 (Shannon diversity), which are the two variables relevant to our hypothesis that grazer effect size relates to algal diversity. To assess the importance of algal diversity as an explanatory variable of grazer effect size, we used an information-theoretic approach to compare the likelihood

Table 1 Results of weighted meta-analysis of consumer effects on periphyton biomass. The table gives the heterogeneity in consumer effects explained by prey diversity (Q_{regr}) compared with the residual heterogeneity (Q_{res}) as well as the intercept and slope of the weighted regression (\pm standard error). Prey diversity was measured either as species richness (S) or as Shannon's diversity index (H'). The analyses were conducted for all experiments (all data) or for experiments manipulating only consumer presence (restricted). k : number of experiments; P : significance level

Measure	Effect size	k	Q_{regr}	Q_{res}	P	Intercept	Slope
All data							
S	Hedges d'	131	9.57	192.49	0.002	-2.56 (0.34)	0.04 (0.01)
	LRR	133	20.94	132.19	<0.001	-1.79 (0.19)	0.03 (0.01)
H'	Hedges d'	126	12.02	210.84	<0.001	-3.08 (0.41)	0.68 (0.20)
	LRR	128	15.68	127.20	<0.001	-1.76 (0.21)	0.42 (0.11)
Restricted							
log S	Hedges d'	83	7.33	114.15	0.006	-2.74 (0.41)	0.05 (0.02)
	LRR	85	12.67	99.41	<0.001	-1.73 (0.21)	0.03 (0.01)
H'	Hedges d'	81	6.30	137.53	0.012	-3.13 (0.51)	0.63 (0.25)
	LRR	83	11.80	89.16	<0.001	-1.83 (0.25)	0.42 (0.12)

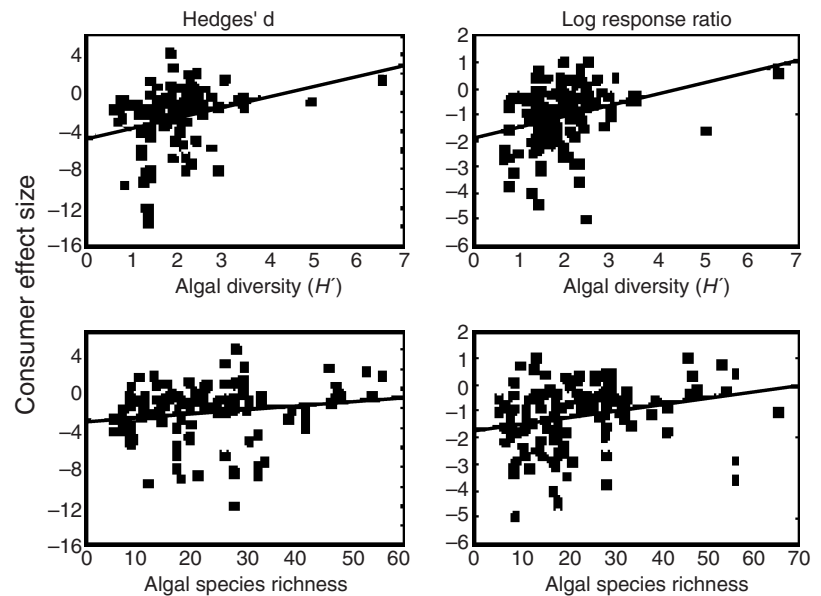


Figure 1 Consumer effect size vs. prey diversity. Effect sizes are Hedges' d (left column) or log response ratio (right column), diversity is represented by Shannon's diversity index (first panel) or species richness (second panel).

of models with and without two algal diversity terms included (see Methods). For both measures of grazer impact (Hedges' d and LRR), unconstrained models containing all terms (including both PC2 and PC4) had the lowest values of the Akaike Information Criterion (AIC). Removing PC2 or PC4 individually led to relatively large increases in AIC, and removing the two in combination led to even higher values (see Table 2, note that models with $\Delta_i > 4$ are generally thought to be inferior explanations for the data, Burnham & Anderson 2002). These results suggest that models without algal diversity included were less likely explanations of grazer effect size. Just how unlikely can be quantified as the Akaike weight, which uses deviations in AIC values to assess the relative weight of evidence in

support of each model (Burnham & Anderson 2002; Johnson & Omland 2004). Of the models considered, the probability of the unconstrained model being the best explanation of grazer effect size was 0.94 for Hedges' d and >0.99 for LRR . The probability of the alternative models, which excluded PC2, PC4, or both was always <0.05 (Table 2). These results indicate two things. First, after considering the potentially confounding factors included in the analyses, exclusion of algal diversity as an explanatory variable leads to highly improbable explanations of grazer impact. Secondly, algal richness (PC2) and Shannon diversity (PC4) appear to explain unique fractions of grazer effect size, suggesting that different aspects of prey diversity operate simultaneously to mediate grazer impact.

Table 2 Grazer effect size, measured as either log RR or Hedges' d , modelled as a function of nine explanatory variables. PC1–PC6 are the factor scores of a Principle Components Analysis, PCA, used to separate quantitative variables into orthogonal components. Each PC can be interpreted uniquely (see Appendix 3). Of particular relevance here are PC2 and PC4, which represent vectors of algal species richness (S) and Shannon diversity (H'), respectively. We begin with the unconstrained models (all nine variables included) and give parameter estimates, F -values and levels of significance for each variable. We then constrain the model by eliminating PC2, PC4, or both principle components. The difference in values of the Akaike Information Criterion (AIC) between each model i and the 'best' model having the lowest AIC, Δ_i , was used to calculate the Akaike weight, w_i . The Akaike weight is the probability that model i is the best explanation of the dependent variable given the candidate set of models (see Burnham & Anderson 2002; Johnson and Omland, in press). Models are ranked in order of the weight of evidence supporting them

Dependent	Explanatory	B (\pm SE)	df	F	P	AIC	Δ_i	w_i	
Hedges' d	Intercept	-8.76 (2.77)							
	PC1: Location/time	1.77 (1.31)	1	1.83	0.1807				
	PC2: Algal richness	1.94 (0.87)	1	5.00	0.0289				
	PC3: Study duration	-1.48 (1.86)	1	0.63	0.4287				
	PC4: Algal diversity	1.60 (0.56)	1	8.20	0.0057				
	PC5: Grazer biomass	0.02 (0.58)	1	0.00	0.9771				
	PC6: Algal biomass	-0.89 (0.44)	1	4.13	0.0463				
	Habitat type		2	0.70	0.4064				
	Consumer group		2	2.95	0.0595				
	Experimental unit		2	1.46	0.2320				
	Unconstrained model (all nine variables)			63			321.4	0.00	0.948
	With PC2 eliminated			64			327.8	6.40	0.039
	With PC4 eliminated			64			329.9	8.50	0.014
	With PC2 & PC4 eliminated			65			347.4	26.00	0.000
Log RR	Intercept	1.91 (2.05)							
	PC1: Location/Time	1.23 (0.42)	1	8.70	0.0043				
	PC2: Algal richness	1.22 (0.27)	1	20.00	<0.0001				
	PC3: Study duration	-0.27 (0.59)	1	0.22	0.6424				
	PC4: Algal diversity	0.70 (0.19)	1	13.86	0.0004				
	PC5: Grazer biomass	-0.27 (0.18)	1	2.29	0.1342				
	PC6: Algal biomass	-0.54 (0.15)	1	13.90	0.0004				
	Habitat type		2	21.94	<0.0001				
	Consumer group		2	6.72	0.0021				
	Experimental unit		2	14.87	<0.0001				
	Unconstrained model (all nine variables)			74			214.9	0.00	0.996
	With PC4 eliminated			75			226.3	11.40	0.003
	With PC2 eliminated			75			232.1	17.20	0.000
	With PC2 & PC4 eliminated			76			263.2	48.30	0.000

DISCUSSION

Our analyses indicate that periphyton assemblages characterized by higher species diversity are less prone to consumption by grazers. This conclusion was robust after accounting for several potentially important covariates of prey diversity that might mediate grazer impact, and was consistent for two different measures of consumer impact and prey diversity. This study is the first to show that diverse prey assemblages are generally less vulnerable to consumption across broad ranges of species diversity and a variety of community types.

Several aspects of our work complement prior studies that have manipulated, or controlled the diversity of prey species (Steiner 2001; Duffy *et al.* 2003; Yoshida *et al.* 2003).

First, the range of diversity included in our analyses (richness up to 65 taxa, H' up to 7) is much higher than typically manipulated in controlled experiments. Indeed, studies to date have considered only a few prey species or clones at a time (Duffy *et al.* 2003; Yoshida *et al.* 2003, but see Steiner 2001). Secondly, the prey assemblages considered in our meta-analyses consisted of naturally co-occurring species; experimental studies, however, generally consider randomly assembled species combined from some larger species pool, which may result in experimental artefacts (Huston 1997; Fukami *et al.* 2001). Thirdly, the studies used in our analyses encompass experiments performed in a variety of habitat types, having used a number of different experimental units, under varying abiotic and biotic conditions. Given this, the observation

that consumer effect size decreases with increasing prey diversity appears to be general.

While the generality of results is a key strength of our meta-analyses, our study simultaneously bears the risk of oversimplification. As diversity was not directly manipulated in any of the experiments we considered, it is certainly possible that confounding factors could have led to non-causal associations between prey diversity and consumer effect size. In an effort to address this possibility, we modelled consumer effect size as a function of both prey diversity and a variety of additional factors that are known to account for a large proportion of the variation of grazer effects on periphyton (algal biomass, grazer biomass, experiment duration, habitat type, experiment type, grazer type, and location – see Feminella & Hawkins 1995; Steinman 1996; Hillebrand 2002). This approach supported patterns documented in the meta-analysis. Excluding either S or H' from models containing all explanatory factors led to highly improbable explanations of grazer impact. Models that simultaneously excluded both S and H' were even more unlikely explanations of the data, suggesting that both S and H' have unique explanatory power. This suggests that consumer effects were altered not only by the number of prey taxa present but also by the evenness (more embodied in H') of the prey assemblage (discussed more below). We cannot exclude the possibility there were other important factors not included in our analysis; however, the consistency of results across aquatic ecosystems, consumer groups, and experimental designs makes this seem unlikely. Therefore, we tentatively conclude that consumer effect size decreases as a function of increasing prey diversity.

We can think of at least three non-mutually exclusive mechanisms that might generate a negative relationship between consumer effect size and prey diversity. First, more diverse prey assemblages have a higher chance of containing less edible species (Duffy 2002). Grazers of periphyton differ in their ability to ingest and assimilate various growth forms of algae (Steinman 1996). Algae growing close to the substratum are typically less available to large grazers that scrape or 'mow' the periphyton, whereas large algae may exhibit a size refuge from smaller grazers. Moreover, several types of algal species are less digestible because of gelatinous structures (Sommer 1997) or chemical compounds (Jüttner 2001). The presence of non-edible prey is generally expected to reduce the efficiency of consumer-prey interactions (Grover 1995; Leibold *et al.* 1997; Persson *et al.* 2001; Steiner 2003).

Secondly, higher prey diversity could maximize the utilization of limiting resources in a way that increases recovery of periphyton from the impacts of grazing. Benthic grazers not only consume algal biomass, but indirectly alter the availability of resources such as light and nutrients that stimulate algal population growth (Steinman 1996;

Hillebrand & Kahlert 2001). Periphyton assemblages characterized by higher diversity could utilize these resources more fully – either because diverse communities are more likely to contain fast growing or highly efficient species, or because diverse communities contain taxa that use resources in complementary ways. Under either scenario, one would expect higher levels of algal biomass in ungrazed patches and faster rates of recovery in grazed patches, resulting in greater similarity between grazed and ungrazed treatments.

Thirdly, positive species interactions such as facilitation are often stronger and more likely to be expressed in diverse assemblages (Vandermeer 1989; Mulder *et al.* 2001; Cardinale *et al.* 2002). Positive interactions could, in turn, speed recovery from consumer impacts in more diverse prey assemblages. Various forms of positive interaction among benthic producer species have been demonstrated experimentally; most occur when algae retard flow or induce turbulence near a substrate in ways that enhance the capture of resources or facilitate colonization of other species (Stevenson & Glover 1993; Escartin & Aubrey 1995; Dodds & Biggs 2002). We do not know of any studies that have assessed whether such forms of facilitation are more likely to occur in more diverse vs. less diverse algal assemblages. However, this possibility warrants attention given the growing recognition that positive interactions are more pervasive than previously thought (Bruno *et al.* 2003).

The unique contributions of S and H' in explaining consumer effect size (see Table 2) suggests that several of the mechanisms discussed above may operate simultaneously. The unique contribution of S as an explanatory variable strengthens the idea that the simple presence/absence of different biological traits among species comprising a prey assemblage (e.g. edibility or resource use) can influence consumer effect size. At the same time, the apparently unique contribution of H' as an explanatory variable suggests that the relative contributions of each species to total community biomass or abundance (i.e. evenness) affects consumer effect size. We can think of two potential mechanisms for the importance of evenness. First, the positive interactions outlined above may gain importance when many species contribute significantly to the total community. Secondly, high dominance of single species (=low evenness) may be related to high grazing susceptibility. Hillebrand *et al.* (2000) showed that nutrient additions increased the dominance of single algal species, which however were highly prone to grazing.

A considerable body of evidence has suggested that consumer diversity has a strong impact on resource utilization in food webs. Our study indicates that prey diversity also influences the transfer of energy and matter among trophic levels, and does so in ways that may oppose the influence of consumer diversity. Net diversity effects

may thus depend on trophic structure (Worm & Duffy 2003). Given this, the efficiency of consumer–prey interactions in real food webs is almost certainly a function of species diversity at both trophic levels, which may act in concert to produce additive or non-additive fluxes. Studies that seek to relate biodiversity to various aspects of community ‘function’ will, therefore, need to incorporate more natural trophic structures when attempting to understand the importance of biodiversity in food web dynamics.

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Appendix 1 List of studies used for this meta-analysis with authors and reference, the habitat, consumer group and experimental unit used for the experiment, the substratum employed, any further treatments in addition to grazer manipulation, and the number of experiments obtained from each study

Authors	Reference	Habitat	Consumer	Exp. units	Sub.	Other treatments	# Exp
Abe <i>et al.</i> 2001	Arch Hydrobiol 150: 581–595	lotic	Fish	aquaria	hard	none	1
Carpenter 1981	J Mar Res 39: 749–765	coastal	Echinodermata	enclosures	hard	none	2
De Nicola <i>et al.</i> 1990	Freshw Biol 23: 475–489	lotic	Gastropoda	channels	hard	none	3
Hagerthey <i>et al.</i> 2002	Mar Ecol Progr Ser 245: 47–59	coastal	Gastropoda	aquaria	sediment	none/fertilized	4/4
Hill & Knight 1987	Ecology 68: 1955–1965	lotic	Ephemeroptera	channels	hard	none	3
Hillebrand & Kahlert 2001	Limnol Oceanogr 46: 1881–1898	coastal	natural mix	enclosures	hard	none/fertilized	11/11
Hillebrand <i>et al.</i> 2000	Mar Ecol Progr Ser 204: 27–38	coastal	natural mix	enclosures	hard	none/fertilized	6/3
Hillebrand <i>et al.</i> 2004	Oikos, in press	lentic	Gastropoda	aquaria	hard	none/irradiance	4/2
Holomuzki & Hemphill 1996	Am Midl Nat 136: 315–327	lotic	Gastropoda	enclosures	hard	none	3
Huchette <i>et al.</i> 2000	Aquaculture 186: 45–60	lotic	Fish	enclosures	hard	none	1
Hunter & Russel-Hunter 1983	Ecology 64: 761–769	coastal	Gastropoda	enclosures	hard	none	1
Hunter 1980	Hydrobiologia 63: 251–259	lentic	Gastropoda	enclosures	hard	none	1
Jernakoff & Nielsen 1997	Aquat Bot 56: 183–202	coastal	Gastropoda	enclosures	plant	none	6
Kehde & Wilhm 1972	Am Midl Nat 87: 8–24	lotic	Gastropoda	channels	hard	none	1
Lamberti & Resh 1983	Ecology 64: 1124–1135	lotic	Trichoptera	enclosures	hard	none	1
Lowe & Hunter 1988	J N Am Benthol Soc 7: 29–36	lentic	Gastropoda	enclosures	hard	none	2
Marks & Lowe 1989	Hydrobiologia 185: 9–17	lentic	Gastropoda	enclosures	hard	none/fertilized	1/1
McClatchie <i>et al.</i> 1982	N Z J Mar Freshw Res 16: 299–309	coastal	Gastropoda	enclosures	sediment	none	2
McCormick & Stevenson 1989	J North Am Benthol Soc 8: 162–172	lotic	Gastropoda	enclosures	hard	none/fertilized	4/8
Mulholland <i>et al.</i> 1991	Ecology 72: 966–982	lotic	Gastropoda	channels	hard	none/fertilized	1/1
Munoz <i>et al.</i> 2000	Arch Hydrobiol 148: 517–532	lotic	Gastropoda	channels	hard	none	5
Nicotri 1977	Ecology 58: 1020–1032	coastal	Gastropoda	enclosures	hard	none	4
Peterson & Boulton 1999	Oecologia 118: 340–352	lotic	Amphibia	enclosures	hard	none	2
Poff & Ward 1995	Oikos 72: 179–188	lotic	Trichoptera	enclosures	hard	none	2
Pringle 1996	Freshw Biol 35: 125–140	lentic	Decapoda	naturally	hard	none/irradiance	2/1
Smith <i>et al.</i> 1996	Mar Ecol Progr Ser 145:53–61	coastal	Annelida	non-availab. enclosures	sediment	none	4
Sommer 1999	Ecol Lett 2: 65–69	coastal	Gastropoda	aquaria	hard	none	16
Sommer 2000	Oecologia 122: 284–287	coastal	Isopoda	aquaria	hard	none	10
Steinman <i>et al.</i> 1989	J Phycol 25: 478–485	lotic	Gastropoda	channels	hard	none/irradiance	1/2
Sumner & McIntire 1982	Arch Hydrobiol 193: 135–157	lotic	Gastropoda	channels	hard	none/irradiance/ fertilized	1/1/1
Swamikannu & Hoagland 1989	Can J Fish Aquat Sci 46: 1698–1704	lentic	Gastropoda	enclosures	hard	none	3
Underwood & Thomas 1990	Freshw Biol 23: 505–522	lentic	Gastropoda	aquaria	plant	none	4
Underwood <i>et al.</i> 1992	Oecologia 91: 587–595	lentic	Gastropoda	enclosures	plant	none	3
Wellnitz <i>et al.</i> 1996	J North Am Benthol Soc 15: 496–507	lotic	Ephemeroptera	channels	hard	none/irradiance	2/4
Worm <i>et al.</i> in prep.	See Appendix 1 in Hillebrand 2002, J North Am Benthol Soc 21: 349–369	coastal	natural mix	enclosures	hard	none/fertilized	4/12
SUM Studies: 35						SUM experiments:	172

Appendix 2 Distribution of number of experiments k on different levels of four categorical variables. The number of studies are generally higher for log RR as a response variable because the calculation of Hedges' d requires more information. The levels are given for habitat (coastal, lentic, lotic), consumer (crustacean, diverse, gastropods, insects, vertebrates, other), experimental units (aquaria, channels, enclosures, exclosures) and substrate (hard, sediment, plant)

(a) Distribution of all 172 experiments

	Habitat			Consumer						Experimental unit				Substrate		
	Coa	Len	Lot	Cru	Div	Gas	Ins	Ver	Oth	Aqu	Cha	Enc	Exc	Hard	Sed	Plant
Hedges	73	35	44	15	56	59	14	5	3	35	22	36	59	128	12	12
Log RR	86	38	48	22	56	71	14	5	4	47	26	40	59	145	14	13

(b) After running the PCA, there were $k = 87$ studies remaining in the dataset. These were distributed as follows among the categorical variables

	Habitat			Consumer				Experimental unit			Substrate		
	Coa	Len	Lot	Cru	Div	Gas	Aqu	Enc	Exc	Hard	Sed	Plant	
Hedges	44	19	12	10	40	25	20	12	43	67	8	0	
Log RR	54	21	12	16	40	31	30	14	43	79	8	0	

Appendix 3 Factor loadings of a Principle Components Analysis, PCA, used to separate and condense eight explanatory variables into orthogonal (independent, uncorrelated) components (using SYSTAT v. 9). A quartimax rotation was used to maximize separation of variables

Variable	PC1	PC2	PC3	PC4	PC5	PC6
S	0.06	0.95	0.07	0.11	0.24	-0.04
H	0.04	0.11	0.02	0.97	0.17	0.11
Year	-0.86	-0.3	-0.08	-0.06	0.25	0.12
Log10 grazer biomass	-0.17	0.28	0.02	0.2	0.92	0.05
Study duration	0.05	0.07	0.98	0.02	0.01	0.16
Latitude	-0.96	0.14	0.09	-0.16	-0.14	-0.06
Longitude	-0.95	0.03	-0.07	0.15	0.08	-0.08
Log10 algal biomass	0.04	-0.04	0.17	0.11	0.04	0.98
Per cent variance explained	32.41	13.88	12.72	13.23	12.69	12.74
Cumulative per cent variance explained	32.41	46.29	59.01	72.24	84.93	97.67
Interpretation of vector	Location/ time	Algal richness	Study duration	Algal diversity	Grazer biomass	Algal biomass