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LETTER

Prey diversity is associated with weaker consumer effects in a meta-analysis of benthic marine experiments

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Abstract

A rapidly accumulating body of research has shown that species diversity consistently affects the functioning of ecosystems. The incorporation of trophic complexity and the extension of this research to larger scales and natural ranges in species diversity remain as important challenges for understanding the true magnitude of these effects in natural systems. Here, we test whether the diversity of prey communities affects the magnitude of aggregate consumer effects. We conducted a meta-analysis of 57 consumer removal field experiments from a range of intertidal and subtidal hard substrate marine communities. We found that the richness of the prey community was the strongest predictor of the magnitude of consumer effects while controlling for habitat type, taxonomic composition, and other variables. Consumer removal increased aggregate prey abundance on average by 1200% at the lower limit of prey diversity (two species), but only 200% at the upper limit of 37 species. Importantly, compositional change was substantial at both high and low prey diversity, suggesting predation intensity did not vary with prey richness. Rather diverse prey communities appear to be more capable of maintaining abundance via compensatory responses, by containing prey species that are resistant to (or tolerant of) predators. These results suggest that the effects of species diversity on trophic interactions may scale consistently from small-scale manipulations to cross-community comparisons.

Keywords

Biodiversity, coral reef, ecosystem function, horizontal diversity, intertidal, kelp forest, subtidal, top-down control, trophic cascade.

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INTRODUCTION

Human alteration of the diversity and composition of ecological communities (Wilcove *et al.* 1998; Sala & Knowlton 2006) has prompted ecologists to ask how the number of species in an ecosystem affects aggregate ecosystem properties (Kinzig *et al.* 2002; Loreau *et al.* 2002). A large number of experiments over the past 15 years have experimentally manipulated the species richness of a community and measured community-level responses, typically those related to the magnitude and stability of resource production and consumption (Cardinale *et al.* 2006a; Stachowicz *et al.* 2007). On average, these experiments have shown a positive effect of species richness on ecosystem function, but experimental polycultures on average tend to perform no better than the best-performing

monoculture (Cardinale *et al.* 2006a). Limitations of these experiments include the relatively small spatial and temporal scale of the manipulations, and the often small number of species or few levels of species richness represented (Srivastava & Vellend 2005). There is some evidence that the effects of diversity may be more apparent over larger spatial or temporal scales that are more inclusive of the heterogeneity of natural communities (Tilman *et al.* 2001; Cardinale *et al.* 2007; Stachowicz *et al.* 2008a,b). In addition, the majority of experiments have focused on processes occurring at a single trophic level, but a full understanding of the effects of changing species richness will include effects on trophic interactions (Duffy *et al.* 2007).

Experimental manipulations of species diversity can be complemented by examining how ecosystem processes vary among communities that differ naturally in species richness.

This kind of comparative data must be interpreted cautiously due to the many factors that covary with species diversity (Levine 2000; Foster *et al.* 2002) and the potentially complex causal relationships between species diversity and other community processes (Schmid 2002; Worm & Duffy 2003; Cardinale *et al.* 2006b; Gross & Cardinale 2007; Hughes *et al.* 2007). Nonetheless the patterns that emerge in cross-community comparisons can add context at scales that are usually experimentally unobtainable, and understanding the causes of large scale patterns can be aided by combining insights from multiple experimental studies with statistical models that attempt to isolate interacting processes across studies (e.g. Hillebrand & Cardinale 2004, Grace *et al.* 2007; Vila *et al.* 2007). Here, we use this approach to investigate the relationship between the diversity of sessile prey in benthic marine communities and the effect of consumers on aggregate prey abundance as quantified in experimental manipulations.

Benthic marine communities are known to exhibit strong top-down effects on both prey abundance (Shurin *et al.* 2002) and prey coexistence via tradeoffs between consumer resistance and competitive ability, particularly among sessile species (Paine 1966, 2002; Lubchenco 1978; Hay 1981). For ecological communities in general there are several hypothesized mechanisms by which prey diversity could limit consumer effects, any of which may apply to benthic marine communities. Large differences in consumer resistance among species could mean that more diverse prey communities are more likely to contain a species resistant to any specific consumer (reviewed in Duffy *et al.* 2007). Furthermore, if consumer effects are spatially heterogeneous (e.g. Navarrete 1996) and consumer-susceptible species tend to be more productive (e.g. Lubchenco 1978), the presence of a range of species along the consumer resistance-productivity axis could result in complementarity over space and therefore greater prey productivity over the full community. Consumer-resistant species could also provide an associational refuge for consumer-susceptible species (Stachowicz 2001), and specialized consumers may forage less efficiently in diverse prey communities (Duffy *et al.* 2007). Finally, diverse prey communities could even increase consumer pressure by providing a varied diet that increases consumer growth rate (reviewed in Duffy *et al.* 2007). Experimental manipulations of prey diversity designed to test these hypotheses are relatively few. Some studies have shown a negative effect of prey diversity on consumer effects that is likely related to variation in consumer resistance (Steiner 2001; Duffy *et al.* 2005), but not all experiments have seen such an effect (Fox 2004; Gamfeldt *et al.* 2005; Wojdak 2005). In addition, a meta-analysis of experiments in aquatic periphyton communities showed that the magnitude of consumer effects was smaller in communities with greater algal diversity (Hillebrand & Cardinale 2004). Testing this

hypothesis over a broader variety of aquatic ecosystems, we use a meta-analytic approach to ask whether the magnitude of top-down effects quantified in consumer removal experiments from a range of marine hard substrate communities is negatively related to prey diversity. We also examine whether the effect of predation varies consistently as a function of habitat type, prey type, latitude and other variables. We chose sessile, hard substrate prey communities because the literature is replete with consumer manipulations in these systems, and because the environmental and taxonomic similarity among these systems allows us to make interpretable comparisons over a nonetheless broad range of conditions. These comparisons should provide insight into key processes for communities dominated by sessile prey in general, such as terrestrial plants.

METHODS – DATA COLLECTION AND EXTRACTION

We performed a comprehensive literature search for studies in hard substrate marine communities that contain both a consumer removal experiment and thorough reporting of the species richness of the sessile prey community. We searched the databases Web of Science, BIOSIS Previews, and Aquatic Sciences and Fisheries Abstracts using the search phrase: [(herbiv* or predat* or consum* or graz*) and (remov* or manipulat* or exclu* or cage) and (intertidal or subtidal or 'rocky shore' or 'rocky reef' or 'hard bottom' or 'hard substrate' or fouling or 'marine benthic' or epibenthic or macroalga* or seaweed or kelp or barnacle or limpet or chiton or urchin)]. From the search results, we selected papers that met the following criteria. First, the study was performed in an intertidal or subtidal hard substrate system. These included the rocky intertidal, subtidal rock walls, kelp forests, other subtidal algal communities including coral reef communities, and communities on artificial substrates in bays/estuaries. Communities on artificial substrate were only included if the focal community was analogous to a naturally occurring community and if benthic consumers had access to the substrate. Second, the authors experimentally excluded either the entire consumer community or the presumed dominant consumers, and reported some measure of prey abundance in removal and control treatments. Third, the authors comprehensively reported the species richness of the prey community in their study system. This typically took the form of either a list of all the species commonly encountered in the system, or survey data for the system. From this data, we calculated a single species richness number for the prey community that represented the total number of reasonably abundant species that could potentially colonize an experimental plot. When abundance data were presented, we used species present at > 1% total abundance to calculate species richness. If species were

reported in a list, but some species were noted to be rarely encountered, we did not include those species in the count. Using these criteria, we attempted to quantify how many species were present that could play a role in sustaining community production under consumer pressure. We took care to only include studies that made a demonstrable effort to report the full membership of the prey community.

These search criteria yielded a total of 49 studies from which data were extracted (Table S1). If a study performed experiments in multiple habitats that varied in species richness (e.g. different tidal zones), these experiments were recorded separately and possible non-independence of the data was accounted for as described below. These considerations yielded a total of 57 separate data entries. We calculated the effect of consumers as $\log_{10}(P_r/P_c)$, where P_r is total prey abundance in the consumer removals and P_c is total prey abundance in controls with consumers present. We will refer to this quantity as the log response ratio or the effect size of the consumer manipulation. We preferred total prey biomass when present as a measure of abundance (14 instances), but total cover (40 instances) or density (3 instances) were used as alternates. Numbers were taken from tables or from figures using ImageJ (Rasband 1997–2009). When multiple experiments were performed in the same prey community under different conditions (e.g. small patches cleared vs. large patches cleared), we calculated a log response ratio for each experiment separately and used the average log response ratio for the study. We recorded the following data for covariates in our analysis: response variable type (biomass/cover/density), length of experiment (in months), number of replicates, consumer taxa present (echinoderm/mollusc/crustacean/vertebrate), consumer taxonomic richness (one vs. multiple phyla, including echinoderms, molluscs, arthropods (crustaceans), chordates (vertebrates)), consumer feeding niche (herbivore/carnivore/omnivore), prey type (invertebrate/algae/mixture), latitude, habitat type (high intertidal/mid intertidal/low intertidal/kelp forest/coral reef/other subtidal). In some cases, a subset of the total sessile community was the focus of the experiment, e.g. the authors studied the response of an intertidal algal community to gastropod consumers while barnacles were present in the background. In these cases, we recorded species richness and experimental response of the focal community, and we recorded that the prey community was a subset of the full sessile community using a community subset variable (yes/no). Although approximately two-thirds of the studies included data on consumer density in control plots, we chose not to use consumer density as a covariate. We made this decision because nearly all variation in consumer density was due to whether small gastropods were the primary consumers, as opposed to chitons, urchins, or fish. Small gastropods such as littorines and limpets are typically present at $\sim 2000 \text{ m}^{-2}$, while

urchins may be present at $\sim 5 \text{ m}^{-2}$ and have an equivalent impact on the prey community. We therefore do not think consumer density would accurately reflect potential consumer impact.

A majority of the studies in our dataset reported some information on the relative abundance of species or functional groups in the two treatments, allowing us to examine whether richness of the prey community or consumer effect size was correlated with compositional change. However, few studies reported individual abundances for all species, and when species were lumped into functional groups those groups were not consistent across studies. We therefore could not calculate a consistent measure of compositional change using a metric such as Bray-Curtis distance. We instead constructed a more approximate measure of compositional change due to consumers. For each species or functional group reported, we calculated its proportional abundance in the consumer removal treatment (p_r), and its proportional abundance in the control treatment (p_c). We then calculated the absolute difference between these proportions for each species, i.e. $\Delta p = |p_r - p_c|$. For example, if ulvoid algae comprised 10% of aggregate prey abundance with consumers present and 40% of aggregate prey abundance with consumers absent, the absolute difference in relative abundance between treatments is $|0.1 - 0.4| = 0.3$. We used the largest Δp for the experiment as an indicator of how much compositional change occurred. We will refer to this quantity as *maximum change in relative abundance*. This quantity will be greatest when one species is completely dominant in one treatment but is absent from the other treatment, i.e. $p_c = 1$, $p_r = 0$. This metric therefore quantifies whether large changes occur in the relative abundance of common species. Species that are rare in both treatments will have low values of the metric, even if their abundances are measured with large sampling error.

METHODS – STATISTICS

We used the log response ratio described above as the response variable in a mixed model analysis. Log response ratios are a commonly used measure of effect size in compilations of ecological data since they summarize the effect of manipulations without requiring a measure of variance (Adams *et al.* 1997). Residual variation in a meta-analysis is composed of both within-experiment and between-experiment variation, and the separate contribution of each can be estimated under certain conditions (Hedges *et al.* 1999). We cannot separately estimate these contributions with our data, because standard errors were not available for treatment means in all studies. However, we did perform a weighted analysis using the sample size of each treatment to construct weights as in Adams *et al.* (1997). The

results of the weighted analysis did not differ from the unweighted analysis, and we present the unweighted analysis because we do not think that a large increase in sample size results in a large increase in precision in these experiments. Because the residual variation in our analysis did not visually deviate from normality we assume a normal approximation is adequate for significance tests.

We constructed a statistical model for the strength of consumer effects as follows. We constructed a mixed model with fixed effects for log prey richness, response variable type, prey type, community subset, consumer taxonomic richness, latitude, and experiment length. Prey richness was log transformed because the relationship with effect size appeared linear on this scale. We included a random intercept for habitat type, which allowed effect size to vary by habitat, and we also included a random slope that allowed the effect of prey richness to vary by habitat type. We modelled habitat type as a random effect because this variable had a moderate number of levels (six) and we were interested primarily in whether there was variation among habitats in general, as opposed to the difference between particular habitats. We included another random intercept for 'site' which controlled for potential non-independence of consumer effects at the same study site in different prey communities (e.g. high vs. low intertidal). There were few instances of multiple prey communities from the same site (six), but this term accounted for a moderate amount of variation.

All analyses were performed in R 2.8.1, using the nlme and lme4 packages (Bates 2007; Pinheiro *et al.* 2008, R Core Development Team 2008). We tested the significance of

fixed effects using the F statistic reported by lme and denominator degrees of freedom approximated as the trace of the 'hat' matrix that projects observed values onto fitted values (Hodges & Sargent 2001; Spiegelhalter *et al.* 2002).

RESULTS

The 49 studies that met our criteria represent a range of habitats, taxa, and sessile community diversity, from a broad geographical area including temperate and tropical locations in both hemispheres and on five continents (Fig. 1, Table 1). We found a significant relationship between prey community richness and the effect of consumers on the aggregate prey community (Table 1). The ratio of aggregate prey abundance in consumer removal vs. control treatments was on average ~ 12.5 at the lower limit of prey diversity (two species), and ~ 2 at the upper limit of 37 species (Fig. 2a). We also found that effect size was predicted by response variable type, with responses measured as biomass showing a greater effect size than those measured as cover or density (Table 1, Fig. 2b). None of the other potential predictors showed a significant relationship with effect size (Table 1).

Prey richness varied with habitat type such that subtidal and coral reef communities were more diverse on average (Fig. 1a), but the variance in consumer effect size explained by habitat type was approximately zero (Table 1). This indicates that the effect of prey diversity was not confounded with an effect of habitat type. In addition, there were no detectable differences among habitats in the slope of the relationship between effect size and prey diversity

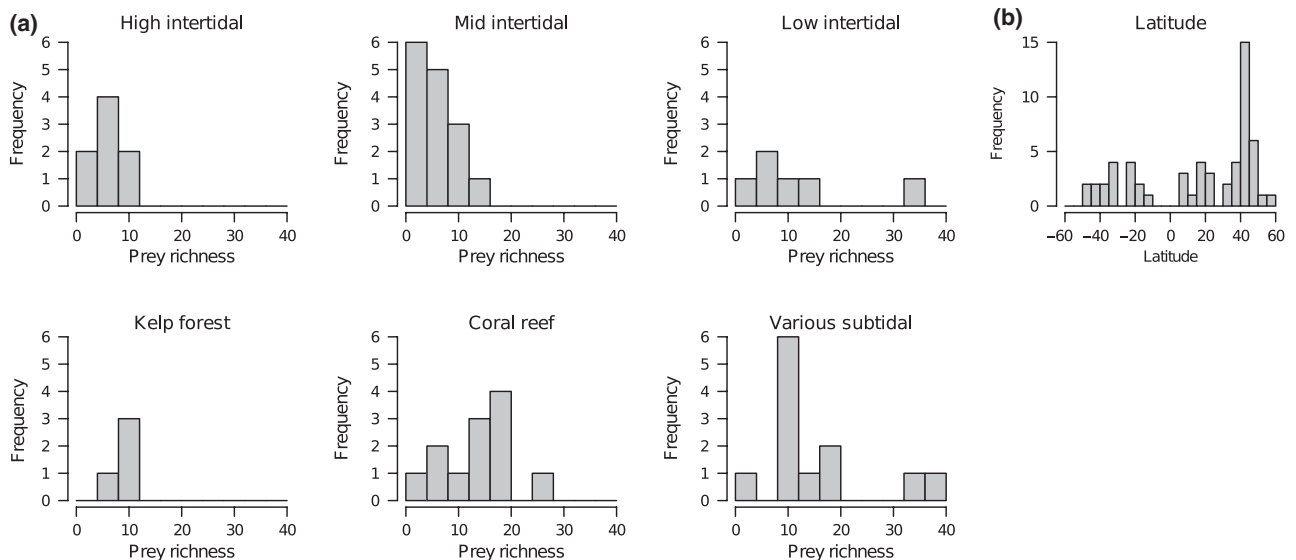


Figure 1 Characteristics of studies used in the analysis. (a) Representation of habitat types and prey richness among studies in the analysis. (b) Distribution of studies by latitude.

Table 1 Results of mixed model meta-analysis. Log ratio of aggregate prey abundance is analyzed as a function of prey richness and other variables

Fixed effect	Num. df	Den. df	F-value	p-value
Log prey richness	1	44.5	8.0	0.007
Response type	2	44.5	4.4	0.019
Community subset	1	44.5	1.5	0.22
Prey type	2	44.5	0.61	0.55
Consumer tax. richness	1	44.5	0.63	0.43
Consumer feeding niche	2	44.5	1.2	0.30
Latitude	1	44.5	0.005	0.95
Length	1	44.5	0.30	0.59
Random effect	Variance			
Intercept by site	0.45			
Intercept by habitat	~0			
Slope by habitat	~0			
Residual variance within sites	0.20			

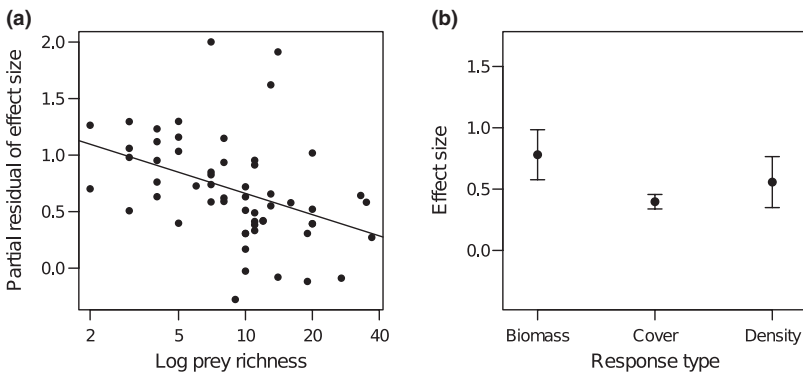


Figure 2 Significant predictors of consumer effect size. (a) Effect size vs. log prey richness. Effect size is plotted as partial residuals to account for the variation explained by other predictors. (b) Effect size vs. response type, raw data plotted.

(Table 1). Finally, in spite of small sample sizes a negative relationship between prey richness and effect size can be detected within two of the three habitat types with more than 10 samples (coral reef: slope = -0.3 , $P < 0.001$, $n = 12$; various subtidal: slope = -0.3 , $n = 12$, $P < 0.001$; mid-intertidal: slope = 0.07 , $P = 0.58$, $n = 14$).

We looked at the subset of the data in which percent cover was the response variable to better understand the relationship between prey richness and effect size, because the largest number of studies reported this response (40/57). These data indicate that percent cover of the prey community tends to be positively related to prey richness in general, but the relationship is stronger when consumers are present (Fig. 3). This suggests that the larger effect sizes observed in less diverse prey communities result primarily from lower prey abundance in the presence of consumers.

We used our metric for the maximum change in relative abundance of a species or functional group due to consumer removal to ask whether richness of the prey community or consumer effect size was related to the amount of compositional change in the prey community. Maximum

change in relative abundance was highly variable, with a median of 0.27 (Fig. 4). This metric was unrelated to prey richness or consumer effect size, suggesting that the amount of compositional change was typically substantial but not strongly related to our primary variables.

DISCUSSION

Our analysis has shown that sessile marine communities with greater species richness tend to show smaller effects of consumers on aggregate prey abundance. This pattern appears to be driven by a substantial drop in prey abundance in the presence of consumers, in low diversity systems (Fig. 3). This result is consistent with a causal role for prey diversity, which would likely arise from the tradeoffs among prey species that allow consumers to mediate coexistence in these systems (Paine 1966; Lubchenco 1978; Hay 1981). The pattern suggests that top-down control of aggregate prey abundance may be stronger in species-poor than species-rich prey communities, consistent with theory and some small-scale manipulations. However, our results are based on

Figure 3 Effect of consumers on the richness-cover relationship. Percent cover of the aggregate prey community vs. log prey richness when consumers are removed (a) or present (b). Lines are linear regression fits, the dotted line in (a) indicates a non-significant trend. For (a) $R^2 = 0.039$, d.f. = 37, $P = 0.229$; for (b) $R^2 = 0.20$, d.f. = 37, $P = 0.004$.

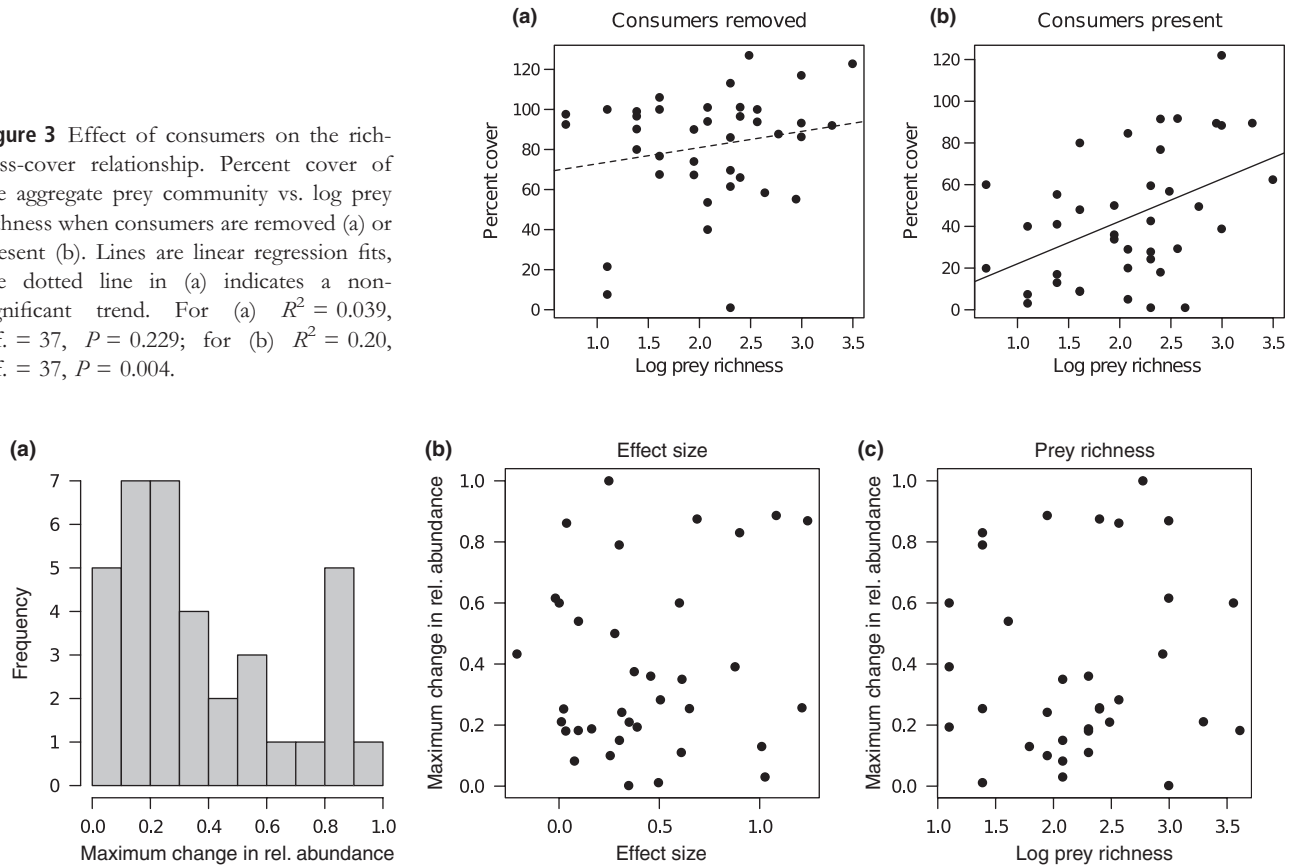


Figure 4 Compositional change due to consumers. Distribution of maximum change in relative abundance (a), and relationship of this metric to effect size (b) and prey richness (c).

variation in prey diversity that presumably covaries with other factors, so we cannot establish the cause of this pattern with certainty. To address the different ways this pattern could arise we now consider some alternate hypotheses that would produce an apparent relationship with prey diversity.

First, it is possible that more diverse prey communities show a smaller log response ratio because consumers happen to consume less in these systems overall, regardless of prey diversity. Separating some measure of intrinsic consumer strength from the effect of the diversity of its prey community would be difficult, but our data on compositional change (Fig. 4) imply that predation has a large impact on the composition of the prey community over the full range of prey diversity, and thus the pattern is likely not the result of consumer pressure being weak or absent in high prey diversity communities. A second, related possibility is that gross taxonomic composition of the prey community (e.g. corals, kelps, ascidians) drives variation in consumer impact, while diversity covaries with taxonomic composition but plays no causal role. We have tried to control for this possibility by including habitat and prey type as predictors in our analysis. Neither of these variables significantly pre-

dicted consumer effect size, implying that the differences between habitat types in prey richness do not drive the pattern we see. Nevertheless, taxonomic differences not captured by these categories could still be important. A final possibility is that productivity drives both prey diversity and the ability to sustain prey abundance in the face of predation. This is a plausible hypothesis that we cannot address with our dataset.

If prey diversity does drive the pattern we document, the effect of diversity could derive from a number of specific mechanisms. These are difficult to distinguish in a compilation of many studies, but we favour a mechanism based on the large differences in consumer resistance and competitive ability among sessile marine species. The large shifts in composition on average (Fig. 4) indicate differential susceptibility to consumers, and a tradeoff between competitive ability and consumer resistance could contribute to both the maintenance of diversity and the effect of diversity on consumer effect size in these communities. We can illustrate how this mechanism might work using two of the studies in our dataset as examples. In a study investigating the effects of herbivorous limpets on mid-intertidal algae, the algal

community was composed of a small number (four) of fast-growing consumer-susceptible species, and the aggregate effect of the limpets was to reduce algal abundance fivefold (van Tamelen 1987). However in a different mid-intertidal community with more algal species (10) that varied greatly in consumer susceptibility, the aggregate effect of limpets was to reduce algal abundance by < 20% (Sousa 1984). If the range of prey traits tends to increase with prey diversity (e.g. Striebel *et al.* 2009) then the difference between these two communities may be indicative of the effects of prey diversity in general.

A different hypothesized mechanism by which prey diversity could lessen consumer effects is the 'dilution effect' by which diverse prey communities reduce the efficiency of specialist consumers (Duffy *et al.* 2007), but we consider this unlikely for benthic marine communities where the dominant consumers are typically generalists (Paine 1980). It is also possible that in diverse prey communities consumer-resistant species provide associational refuges for consumer-susceptible species, but we have no information on the role of this mechanism across the studies we analysed. Regardless of the mechanism underlying an effect of prey diversity, the relationship we have described emerged in spite of the wide range of habitats and prey and consumer taxa present in these studies, all of which were field experiments. The implication is that the causal processes underlying this relationship are robust. These results support a similar meta-analysis of field and laboratory experiments of periphyton communities (Hillebrand & Cardinale 2004), and suggest that prey diversity could be related to consumer effects across a broad range of aquatic ecosystems.

Scaling up the results of diversity manipulations has proven difficult, as the number of manipulable species is often small and the spatial and temporal scales of experiments often preclude the effects of the very environmental heterogeneity that maintains species diversity. The meta-analytic approach we have used is one way to quantify the consequences of species diversity while allowing for other processes to operate unmanipulated. It further suggests that in addition to concerns over the effects of diversity loss on ecosystem functioning, different processes dominate the structuring of communities that are naturally diverse vs. those that are depauperate (Strong 1992). Other comparative work supports this contention (Frank *et al.* 2007). Future work in this vein will be benefitted by more thorough reporting of the composition and variability of communities in which experiments are performed, perhaps in online appendices. In addition, the strength of experimental and meta-analytic approaches could be combined by synthesizing experimental manipulations of diversity from a range of systems with observational data from similar systems, to test whether similar patterns emerge and how they differ across systems.

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SUPPORTING INFORMATION

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

Table S1 Spreadsheet of the data used in the analysis.

Appendix S1 List of studies used in the analysis.

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