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REPORT

Grazer diversity effects on ecosystem functioning in seagrass beds

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Abstract

High plant species richness can enhance primary production, animal diversity, and invasion resistance. Yet theory predicts that plant and herbivore diversity, which often covary in nature, should have countervailing effects on ecosystem properties. Supporting this, we show in a seagrass system that increasing grazer diversity reduced both algal biomass and total community diversity, and facilitated dominance of a grazer-resistant invertebrate. In parallel with previous plant results, however, grazer diversity enhanced secondary production, a critical determinant of fish yield. Although sampling explained some diversity effects, only the most diverse grazer assemblage maximized multiple ecosystem properties simultaneously, producing a distinct ecosystem state. Importantly, ecosystem responses at high grazer diversity often differed in magnitude and sign from those predicted from summed impacts of individual species. Thus, complex interactions, often opposing plant diversity effects, arose as emergent consequences of changing consumer diversity, advising caution in extrapolating conclusions from plant diversity experiments to food webs.

Keywords

Biodiversity, ecosystem functioning, grazing, marine, seagrass, secondary productivity.

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INTRODUCTION

Accelerating loss and homogenization of biodiversity worldwide have stimulated vigorous research to evaluate how changing diversity influences functional properties of ecosystems. It has long been appreciated that plant species composition influences ecosystem properties. But a growing body of theory and empirical data indicates that several ecosystem properties can also be enhanced by plant species richness through the mechanisms of complementary resource use, and more complete sampling of species functional traits, in more diverse assemblages (reviewed by Loreau *et al.* 2001). Empirical demonstrations of such plant diversity effects, primarily from ungrazed grasslands, have been cited in support of practical rationales for conserving biodiversity (Chapin *et al.* 2000; Lawler *et al.* 2002). Compared with the rich literature on plant diversity effects on ecosystem functioning, however, the potential consequences of declining animal diversity are poorly known, both because of the added complexity of theory for multi-trophic level systems (Holt & Loreau 2002) and because of sparse empirical evidence (Raffaelli *et al.* 2002; Schmid *et al.* 2002). Yet understanding the impacts of consumer diversity on ecosystem functioning is critically important because animals often face more severe extinction threats than plants (Chapin *et al.* 2000; Jackson *et al.* 2001), and because animals have strong direct and indirect impacts on ecosystem processes in many systems (Naiman 1988; Jones *et al.* 1994; Jackson *et al.* 2001). Indeed, consumer impacts on ecosystem processes were comparable with, or greater than, those of changing plant diversity in the very few studies where both factors were examined (Mulder *et al.* 1999; Naeem *et al.* 2000; Paine 2002). Thus, there is general recognition that incorporating consumers represents a frontier in understanding linkages between biodiversity and ecosystem function (Duffy 2002; Naeem 2002; Raffaelli *et al.* 2002).

Theory predicts that increasing herbivore diversity should reduce plant community biomass as the most efficient grazers come to dominate a system, leading to ‘overgrazing’ (Holt & Loreau 2002), which can also depress plant diversity and facilitate invasion of grazing-resistant species (Leibold *et al.* 1997). Thus, in a system with two trophic levels, changing diversities at plant and herbivore levels are expected to influence ecosystem processes in opposite directions, such that herbivores may counteract ecosystem responses predicted from plant processes alone. In laboratory experiments, the predicted decline in producer biomass with increasing consumer diversity was indeed observed when a single algal species supported the food web (Naeem & Li 1998), but not with multiple algae because of compensatory growth of resistant species under heavy grazing (Norberg 2000). Countervailing effects of autotroph and heterotroph diversity are also supported by experiments with aquatic microbes (Naeem *et al.* 2000) and herbivorous insects (Mulder *et al.* 1999); in both of these studies, addition of heterotrophs erased the positive relationship between diversity and production found in autotroph-only treatments. Whether consumer diversity *per se* influences ecosystem properties in more natural, open systems (Leibold *et al.* 1997) remains untested.

Here we report results of a mesocosm experiment that tested effects of grazer diversity on community and ecosystem properties using beds of eelgrass (*Zostera marina*) as a model system. Eelgrass is the northern hemisphere's most widespread and abundant marine macrophyte and the base of an economically important ecosystem (Hemminga & Duarte 2000). In addition to eelgrass itself, the major functional groups of benthic primary producers in eelgrass beds include macroalgae and microalgae, which grow both as epiphytes on eelgrass blades and directly on the sediment surface. Invertebrate grazers, primarily small crustaceans and gastropods, play a pivotal organizing role in temperate-zone seagrass ecosystems worldwide, facilitating seagrass dominance by consuming their competitively superior epiphytic algae (Jernakoff *et al.* 1996). Whereas seagrasses provide the major physical structure in these beds, the fast-growing, edible algae supply most of the primary production that supports higher trophic levels, including commercially exploited species (Klumpp *et al.* 1989). If unchecked by grazers, however, epiphytic algae can overgrow and suppress seagrasses, dramatically altering ecosystem structure and functioning. As grazer species differ considerably in their qualitative and quantitative impacts on the plant assemblage (Duffy & Hay 2000; Duffy & Harvilicz 2001; Duffy *et al.* 2001), grazer diversity may be predicted to have important consequences for eelgrass ecosystem structure and functioning. Our experimental results confirm that grazer species composition, richness, and interactions have pervasive impacts on eelgrass-bed ecosystem properties.

METHODS

Experimental design

We manipulated grazer species composition and diversity in an array of 45 outdoor tanks, 0.6 m diameter × 0.6 m deep, supplied with flowing water from the adjacent York River estuary (Virginia, USA). The water supply was filtered with 0.15-mm mesh to minimize grazer invasion, but allowed passage of microscopic propagules of algae and sessile invertebrates, allowing their recruitment into the mesocosms. We established nine grazer treatments ($n = 5$ mesocosms each), including each of six grazer species stocked alone, three species (random combinations), all six species together, and a grazer-free control. The six grazer species all are common in local eelgrass beds, and include the gastropod *Bittium varium*; amphipods *Cymadusa compta*, *Dulichiella appendiculata* and *Gammarus mucronatus*; and isopods *Erichsonella attenuata* and *Idotea baltica*. Given inherent logistical constraints and trade-offs in interpretive power of alternative experimental designs for detecting biodiversity effects (Allison 1999), we opted to include all six grazer species in monoculture. Such a design allows unambiguous tests of overyielding (Huston 1997; Loreau 1998), and partitioning of diversity effects into complementarity and sampling components (Loreau & Hector 2001). As a trade-off, we could only include three levels of species richness (1,3,6). Thus, we focused on the basic question of whether grazer diversity effects exist in this system, rather than on the form of such relationships, which are likely to differ considerably with context in any case (Cardinale *et al.* 2000). In August 2001, we planted 75 defaunated eelgrass shoots in clean sand, and added 120 grazers, in each mesocosm. Three- and six-species treatments received 40 and 20 individuals, respectively, of appropriate species in a replacement series design.

The experimental duration was 6 weeks (∼2–3 grazer generations), long enough for grazer relative abundances to adjust to natural levels and for all treatments to reach carrying capacity (Duffy & Harvilicz 2001), thus negating potential artefacts of initial differences in conspecific density (Huston *et al.* 2000). After 6 weeks, all organisms ≥0.5-mm were harvested, identified, and ash-free dry mass (AFDM) of each taxon was measured. AFDM of each grazer species present was estimated from body-size distributions (following Edgar 1990) in a sorted subsample (usually 1/8) from each mesocosm. Total grazer AFDM, pooled across all species present, was measured directly in the remainder of each sample by combustion. Surficial sediment was sampled with a 45 mm-diameter core, dried, acidified, and sediment organic carbon was measured using standard methods.

Statistical analysis

Because preponderance of single-species treatments and exclusion of eight contaminated mesocosms (see Results) resulted in an unbalanced design, we tested grazer diversity effects on a given response variable by resampling the data matrix with replacement 10 000 times and comparing observed statistics to the distribution of resampled values. For each response variable we tested two statistics: the difference between largest and smallest one-species

Table 1 Effects of grazer diversity on ecosystem properties. Composition tests variance among individual species in monocultures; richness tests the average change in response across levels of grazer species richness; and species interaction tests deviation of the response in the six-species treatment from that predicted by summing estimated impacts of individual species present

	P-value			
	Composition	Richness	Species interaction	$D_{\max}$
Grazer biomass	0.017	0.008	0.002	0.060
Algal biomass	0.081	0.017	0.179	−0.045
Eelgrass change in biomass	0.014	0.139	0.016	–
Botryllus biomass	0.962	0.005	0.027	0.816
Benthic diversity	0.087	0.035	0.055	−0.087
Dominance (whole)	0.007	0.032	0.657	−0.489
Dominance (fouling)	0.007	0.013	0.240	–
Sediment organic C	0.242	0.032	0.008	−0.008

P-values are from resampling tests (see text). Tests of composition and species interaction effects are two-tailed; richness tests are one-tailed, reflecting *a priori* expectations, except for sediment organic C (two-tailed). $D_{\max}$ cannot meaningfully be calculated for eelgrass mass change or dominance (fouling) as effects of different treatments differed in sign.

treatments (i.e. effect of species composition), and slope of the regression on number of stocked grazer species, excluding grazer-free controls (i.e. effect of species richness). Richness tests were one-tailed when they tested *a priori* predictions (Table 1). As an additional, conservative estimate of diversity effects on each variable, we calculated $D_{\max}$, the overyielding criterion, which measures the difference between the observed total response (yield) in mixture and the maximal monoculture response, as a proportion of the maximal monoculture response (Loreau 1998).

We tested effects of grazer species interactions on ecosystem responses as deviations from additive expectations based on per-capita grazer effects measured in monoculture (Norberg 2000). Per capita effect of each grazer on an ecosystem property was estimated as the regression coefficient on its log(10) abundance in a multiple regression including only grazer-free and single-species treatments. The regression equation was then used to predict responses in mixed-grazer mesocosms based on observed final abundances of each grazer species therein. Deviations of observed from predicted responses in the six-species treatment were assessed by resampling.

RESULTS

We excluded eight of 45 mesocosms from analysis because of contamination because final ash-free dry biomass of invading unstocked grazer species exceeded 500 mg. Despite such invasions, treatments maintained a gradient in grazer diversity: the Shannon–Wiener index, based on grazer biomass at the end of the experiment, averaged (±1 SE) 0.57 ± 0.08, 1.12 ± 0.10, and 1.35 ± 0.09 for one, three, and six-species treatments, respectively ($P < 0.0001$, resampling test).

Ecosystem properties at both consumer and prey levels responded strongly to grazer biodiversity. Paralleling previous terrestrial results at the plant level, diversity significantly enhanced (secondary) production at the grazer level. Populations of all but one grazer species grew at comparable or faster rates in mixture than in monoculture (Fig. 1). A regression of estimated biomass production per stocked individual in mixture vs. in monoculture had a slope of 2.2 (Fig. 1a), suggesting enhanced average production of individual grazer species at high diversity. This slope was not significantly different than 1.0, although sample size (6) and, thus, power of the test was low. However, total grazer biomass, which was measured directly, was significantly enhanced at high diversity ($P = 0.008$, Fig. 2a), averaging 56% higher than in the average monoculture. The positive, albeit small, value of $D_{\max}$ also supports overyielding of grazer biomass at high diversity (Table 1).

High grazer secondary production reflected more complete use of the algal resource in multi-species assemblages. Intense consumption at high grazer diversity essentially eliminated algae, reducing algal biomass ($P = 0.017$) by 87% compared with the average of single-species treatments and by 96% relative to grazer-free controls (Fig. 2b). In contrast, change in eelgrass biomass was unaffected by grazer diversity ($P = 0.139$), but strongly affected by grazer species composition ($P = 0.014$, Fig. 2c). Overall diversity of the eelgrass community was also significantly reduced at high grazer species richness ($P = 0.035$, Fig. 2e); the number of taxa recruiting naturally to six-grazer mesocosms was 14% lower than in the average single-grazer treatment, and 38% lower than in grazer-free controls, as diverse grazers suppressed establishment of edible algae, which dominated ungrazed mesocosms.

In contrast to the negative effect of grazers on algal establishment and total community diversity, grazer species richness strongly facilitated dominance by the tunicate

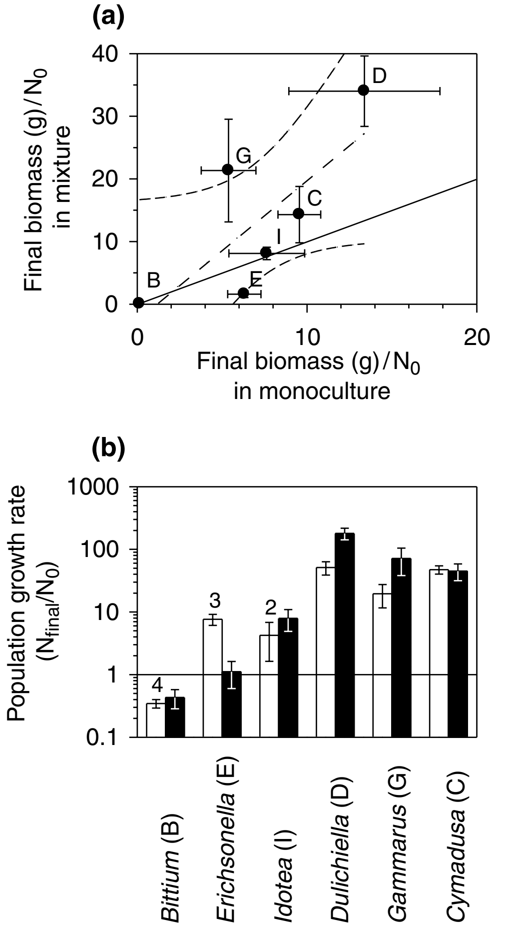

Figure 1 Grazer population growth and production in monocultures and mixture. (a) Final biomass production (±SE) of each grazer species in the six-species mixture vs. in monoculture. Production is normalized to the number of individuals initially stocked, thus incorporating both somatic and population growth. Diagonal solid line represents the null hypothesis of equal production per stocked individual in monoculture and mixture; dashed line represents the empirical regression with 95% CI. Biomass is expressed as ash-free dry mass. Letters correspond to genus names (panel b). (b) Population growth rates in monoculture (open bars) and mixture (shaded bars). N_0 and N_{final} are, respectively, initial and final numbers of individuals per mesocosm. Zero population growth is indicated by the horizontal line. $n = 5$ except where indicated above bar.

Botryllus schlosseri ($P = 0.003$), a sessile invertebrate that is resistant to several consumers (e.g. Teo & Ryland 1994). *B. schlosseri* reached nearly 3× higher biomass in the six-grazer treatment, where it was second in abundance only to eelgrass, than in the average monoculture (Fig. 2d), resulting in a strongly positive value of the overyielding criterion $D_{\max}$ (Table 1). In summary, increasing grazer diversity directionally altered eelgrass ecosystem composition, suppressing algae and shifting ecosystem biomass dominance from edible autotrophs towards resistant heterotrophs such as tunicates and sponges ($P = 0.032$, Fig. 3a). Indeed, excluding eelgrass, which serves primarily as habitat for these grazers, the remaining (fouling) assemblage shifted from 76% algae in the absence of grazers to 84% sessile invertebrates at high grazer diversity (Fig. 3b), a significant ($P = 0.013$) effect of grazer richness.

In addition to their direct effects on the eelgrass community, grazers indirectly changed organic carbon accumulation in underlying sediments (Fig. 2f), a fundamental controller of biogeochemical processes, nutrient remineralization, and benthic food availability in marine ecosystems, as in soils. Whereas grazing reduced sediment carbon overall compared with grazer-free controls, increasing grazer diversity enhanced sediment carbon accumulation above the average of single-species treatments ($P = 0.032$). This sediment C was apparently stored, in part, in benthic microalgal biomass as sediment chl *a* showed a similar but non-significant increase with grazer diversity (not shown), probably reflecting greater light penetration to sediments under heavy grazing.

Grazer diversity effects on ecosystem properties were clearly related in part to grazing intensity, which was highest in the multi-species treatments (Fig. 4). Nevertheless, grazing intensity alone explained a relatively small proportion of the variance in ecosystem responses, and both *Botryllus* and sediment carbon were greater at highest diversity than expected from grazing intensity alone (i.e. residuals in the six-species treatment were positive, Fig. 4), suggesting that indirect interactions also influenced these responses. Benthic diversity was unimodally related to grazing intensity (Fig. 4), presumably reflecting the common phenomenon of maximal diversity under intermediate disturbance (in this case, grazing).

DISCUSSION

Experimental studies in grasslands (reviewed in Tilman *et al.* 2002), aquatic algal microcosms (Naeem *et al.* 2000), salt marshes (Zedler *et al.* 2001), and freshwater wetlands (Engelhardt & Ritchie 2001) have documented higher primary production in high-diversity plant assemblages. More diverse sessile invertebrate assemblages similarly show more complete resource (space) use (Stachowicz *et al.* 1999). Our results provide the first experimental evidence of a parallel phenomenon at the level of mobile consumers, that is, enhanced secondary production and efficiency of resource use in more diverse grazer assemblages (see Naeem *et al.* 2000 for a similar phenomenon in decomposers). These findings from organisms as disparate as terrestrial plants, sessile invertebrates, marine herbivores, and bacteria suggest that enhancement of resource use and

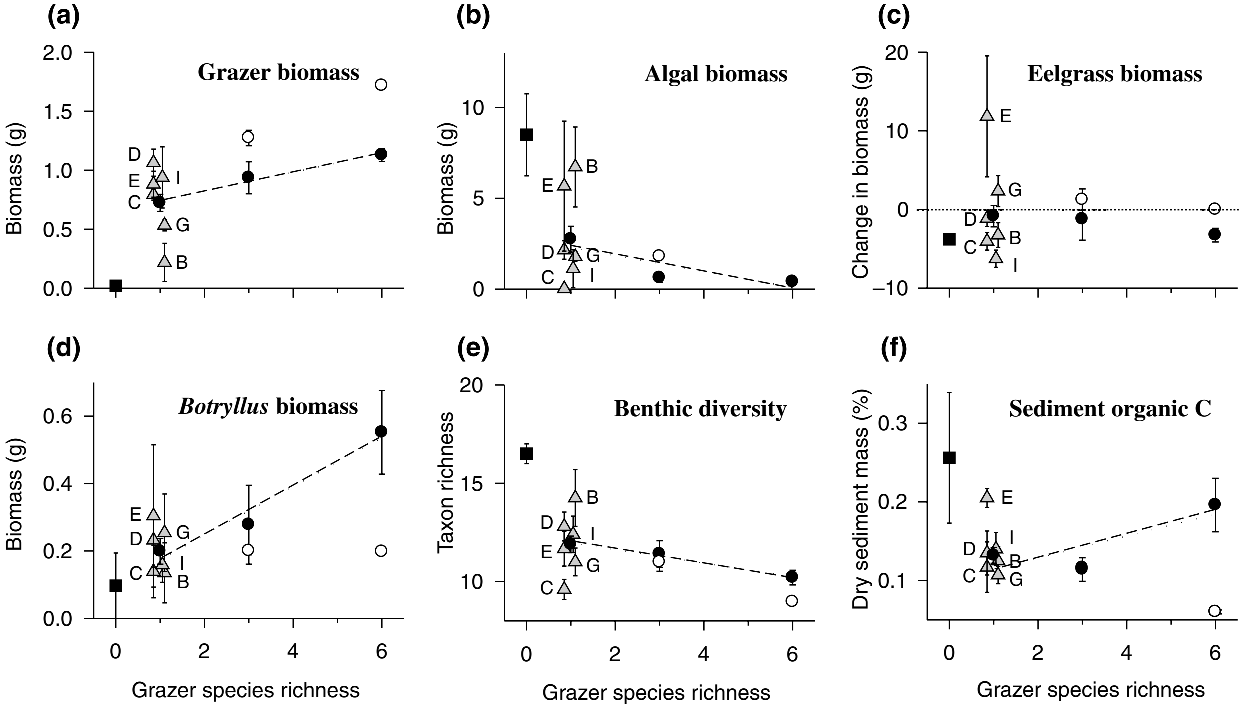

Figure 2 Effects of grazer diversity on ecosystem properties. Single-species treatments (triangles, offset for clarity) are identified by first letter of genus name. Squares represent grazer-free controls. Dashed lines show significant responses to grazer species richness (filled circles, see Methods for analysis). Unfilled circles show expected responses in multi-species treatments based on summing individual grazer effects (see Methods). Biomass is expressed as ash-free dry mass. Sample sizes as in Fig. 1.

production at high diversity is a robust ecological trend with considerable generality across taxa and ecosystems. Enhanced secondary production at high grazer diversity is also of potential practical importance. Small crustaceans such as the grazers we studied dominate diets of shallow-water fishes, and crustacean production is the best single predictor of fish production in vegetated marine ecosystems (Edgar & Shaw 1995; Taylor 1998). Thus, our results suggest that high biodiversity at this intermediate trophic level may enhance trophic transfer up the food chain, and potentially fishery yields.

Our finding that grazer diversity influences several ecosystem properties may appear to contradict a previous experiment in this system, which used only three of the grazer species and found no effect of grazer richness on any response variable (Duffy *et al.* 2001). It seems clear, however, that the richness effects we found (Fig. 2) are driven largely by the highest diversity treatment, with six species. The contrast between these two studies underscores the point that diversity effects may only become apparent when examining a relatively wide range in species richness. They also present an interesting contrast with the commonly suggested saturation of ecosystem functional properties at low levels of diversity (Schwartz *et al.* 2000). In this system, loss of a few species from current high levels of biodiversity may significantly influence ecosystem properties, a point with implications for conservation.

Mechanistically, enhanced secondary production at high grazer diversity could be mediated either by increased efficiency of grazing (more complete resource utilization), by stimulating increased primary production, or by some combination of these two mechanisms. The first possibility is consistent with documented differences among these grazers in the propensity to consume macroalgae, microalgae, and detritus (Duffy & Hay 2000; Duffy & Harvilicz 2001; Duffy *et al.* 2001), and in microhabitat use. For example, the clinging isopod *Erichsonella* rarely ventured away from eelgrass blades in our experiment, whereas the highly mobile amphipod *Gammarus* was frequently observed on the sediment surface, probably grazing on benthic microalgae and detritus there. The second possible mechanism, enhancement of primary production by diverse grazer assemblages, is consistent with the compensatory responses to grazing documented in other marine algae (Carpenter 1986) as well as in grasslands (McNaughton 1985). Enhancement by grazers of specific primary production, together with detritus feeding by some species, might also explain how secondary production could be maximal at high grazer diversity despite low standing biomass of algae.

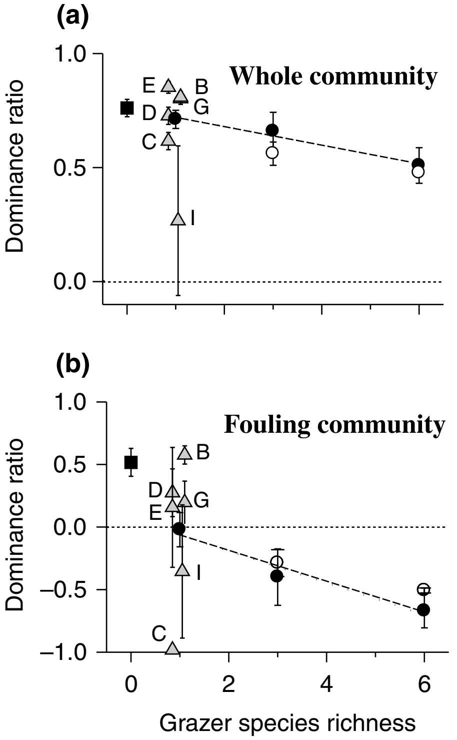

Figure 3 Effects of grazer diversity on relative dominance of autotrophs vs. invertebrate heterotrophs. Dominance ratio = (biomass of plants – biomass of invertebrates)/[biomass of (plants + invertebrates)]. Calculations in panel b exclude eelgrass and grazers. Biomass is expressed as ash-free dry mass. Symbols as in Fig. 2.

The negative effects of increasing grazer diversity on algal biomass and total community diversity in our experiment are contrary to previously documented effects of increasing plant diversity. In field studies, higher plant diversity was associated with higher plant biomass (Terrados *et al.* 1998) and higher diversity of associated animals (Parker *et al.* 2001) in seagrass beds, as in terrestrial grasslands (Siemann *et al.* 1998; Tilman *et al.* 2002). Thus, our results support theoretical predictions (Holt & Loreau 2002) that changing diversity at adjacent trophic levels has countervailing impacts on ecosystem properties. We also found that increasing grazer diversity produced a marked shift in prey species composition, from algal to sessile invertebrate dominance. This shift between resistant and edible taxa with changing grazing pressure has parallels in coral reefs (Hughes 1994), lake plankton (Leibold *et al.* 1997), and terrestrial vegetation (Naiman 1988), and suggests that well-known ecosystem phase shifts in these systems may be mediated partially by declining consumer diversity.

Within trophic levels, biodiversity can affect ecosystem processes via complementarity (including facilitation), whereby multi-species assemblages use a greater fraction of available resources, and/or by sampling, i.e. higher probability that diverse assemblages contain a species of strong effect. Both mechanisms are important in experimental plant assemblages (Loreau & Hector 2001; Loreau *et al.* 2001; Tilman *et al.* 2002). Analogous processes can explain diversity effects we observed at the grazer level. Enhancement of grazer biomass production and of *Botryllus*

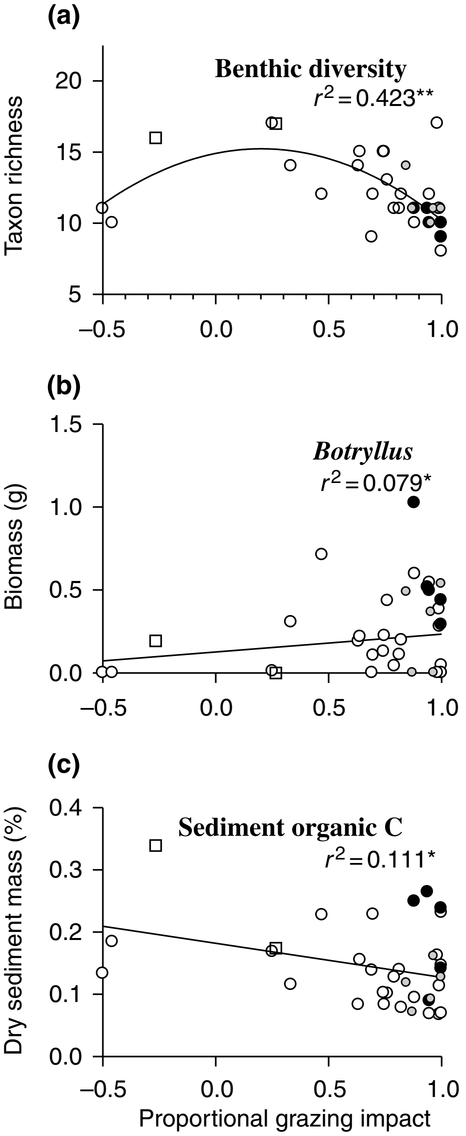

Figure 4 The role of grazing intensity in ecosystem responses. Grazing impact is expressed as proportional reduction in algal biomass relative to the mean biomass in grazer-free controls (squares, $n = 2$; note that zero grazing impact is defined as the mean of the two grazer-free replicates). Grazing impact is maximal in the three-species (grey circles) and six-species treatments (black circles), compared with single grazer species (white circles). Biomass is expressed as ash-free dry mass. $^*P < 0.05$, $^{**}P < 0.01$.

dominance at high grazer richness (Fig. 2) evidently involve complementarity, as indicated by positive values of the conservative (Loreau 1998) overyielding criterion, $D_{\max}$ (Table 1). For other ecosystem properties, responses at high grazer diversity did not exceed the most extreme monoculture response (Fig. 2), indicating that grazer richness effects resulted partly from sampling. Although the ecological relevance of the sampling effect has been questioned (Huston 1997; Wardle 1997; Huston *et al.* 2000), we consider it an important biodiversity effect for three reasons. First, in our system sampling simulates realistic compositional variance as most monocultures and mixtures approximate field assemblages observed at certain sites or seasons. Second, sampling and complementarity can jointly influence ecosystem function (Loreau & Hector 2001), an interaction obscured by the stringent overyielding criterion $D_{\max}$. Specifically, grazer biomass production exceeded monoculture expectations for three of six species and was below expectation for only one (Fig. 1a). Summing these production differentials across grazer species, and using Loreau & Hector's (2001) equation, 74% of the excess grazer production at high diversity was attributable to complementarity, whereas 26% was because of sampling.

The third and most general argument for sampling as an important biodiversity effect is that, even where sampling can explain individual ecosystem responses, only more diverse assemblages maximized multiple ecosystem responses simultaneously. This is because different grazers maximized different properties. For example, *Dulichiella*, *Cymadusa* and *Erichsonella* most strongly influenced grazer biomass, grazing impact, and sediment organic carbon, respectively, yet the six-species mixture achieved similarly extreme values for each of these response variables (Fig. 2) and thus resulted in an ecosystem state noticeably different than in any of the grazer monocultures. We suggest the term *multivariate dominance effect* for this phenomenon, in which diverse assemblages produce extreme values of multiple ecosystem properties simultaneously. To our knowledge, it has not been recognized before, presumably because much previous research has focused narrowly on the single response variable of plant biomass production. Yet it is likely to be a common diversity effect in the more general case where multiple ecosystem responses are of interest. A similar point was made by Petchey & Gaston (2002), who showed that as more variables were incorporated into their multivariate index of functional diversity, species were recognized as increasingly unique, and the relationship between species richness and (multivariate) functional diversity became more linear.

In multi-level food webs, emergent effects of biodiversity can also arise from interactions among trophic levels (e.g. Naeem & Li 1998; Downing & Leibold 2002). Such interactions often involve complex, indirect impacts (Menge 1995; Naeem *et al.* 2000), which can be detected as deviations from expected additive effects of consumer species present (Norberg 2000). These species-combination effects significantly influenced several ecosystem properties in our experiment (Fig. 2, Table 1), suggesting pervasive complex interactions even in this relatively simple system. The most dramatic of these involved *Botryllus* biomass and sediment organic carbon. For both of these variables, responses at high grazer diversity differed not only in magnitude, but also in sign from those predicted from single-species responses (Fig. 2). A likely explanation for these deviations, and the lower than predicted grazer biomass in mixture (Fig. 2a), is interference competition among grazers, and perhaps intra-guild predation. Similarly, the absence of a consistent grazer diversity effect on eelgrass biomass presumably reflects the shift from competitive suppression of eelgrass by dense algae, to facilitation by epiphyte grazing, to suppression by direct grazing of eelgrass, as grazer diversity increased.

In summary, as grazer diversity and impact increased, the eelgrass fouling community shifted from high biomass, high diversity, and dominance by edible algae to low biomass, low diversity, and dominance by a resistant invertebrate. These grazer-mediated changes are opposite in direction to those associated with increasing plant diversity in seagrass beds (Terrados *et al.* 1998; Parker *et al.* 2001) and grasslands (Siemann *et al.* 1998; Tilman *et al.* 2002), suggesting that effects of covarying plant and herbivore diversity on ecosystem functioning may counteract one another, on average, as diversity is lost in nature. Despite the near elimination of algae at high grazer diversity in our experiment, however, grazer overyielding analogous to that demonstrated in diverse plant assemblages resulted in higher secondary production of the small crustaceans that sustain many marine fish populations. This multifaceted shift in structure and function of the eelgrass ecosystem depended directly on a diverse grazer assemblage, via a multivariate dominance effect, as no single grazer species could produce all of the component changes in the system. The trophic processes involved are common in a variety of ecosystems, emphasizing that successfully predicting ecosystem-level consequences of eroding biodiversity, particularly in aquatic systems with strong top-down forcing (Cyr & Pace 1993; Shurin *et al.* 2002), will require close attention to food-web interactions.

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