

Community dominance by a canopy species controls the relationship between macroalgal production and species richness

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Abstract

By field manipulations of nutrients, propagules, and canopy cover in a shallow rocky subtidal, we show that dominance by a leathery macrophyte (*Fucus vesiculosus*) controls net production and the propagation of nutrient effects on understory algal species richness. On substrates with propagules, canopy cover prevented a significant loss of diversity from nutrient enrichment demonstrated outside canopy cover. On sterile substrates, negative canopy effects on diversity were counteracted by nutrient enrichment. Experimental manipulations produced a significant hump-shaped relationship between species richness and log net production, with low richness at low or high biomass production and highest richness at intermediate biomass production. By strong control of net primary production, canopy cover changed the algal understory community to an alternative production state and thereby generated a switch in the relationship between net primary production and species richness from negative outside canopy cover to positive inside. This demonstrates that species contributing to biological structure and habitat diversity can determine the responses of a coastal ecosystem to resource loading.

In a world where large-scale species trends are dominated by species erosion, increasing evidence from diverse ecosystems shows that species richness has significant effects on central ecological processes (Chapin et al. 2000). Important ecosystem properties such as primary production and nitrogen storage can increase with both species richness and functional-group diversity of plants and algae (Loreau et al. 2001; Kinzig et al. 2002; Bruno et al. 2005; van Ruijven and Berendse 2005). Consumer-mediated trophic interactions that control many ecosystems also seem highly dependent on richness, both of prey and consumer levels (Duffy et al. 2003; Hillebrand and Cardinale 2004). Such effects of species diversity on ecosystem function can be a simple linear relation between species richness and trait diversity (Loreau et al. 2001). However, higher diversity can also cause nonadditive changes in community processes, by increasing the probability of interspecific interactions such as facilitation (Cardinale et al. 2002) and intraguild predation (Finke and Denno 2004), or by including highly productive and dominant species that control the assembly (Chapin et al. 1997).

Species that produce canopies dominate many ecosystems because of their often massive, persistent, and extensive structures (Jones et al. 1997). Canopy-forming species can control ecosystem processes both by being

competitively superior and dominating primary production (Paine 2002), and by increasing habitat complexity and modifying the environment for associated organisms (Dayton 1975; Bruno et al. 2003). Thus, in many ecosystems a few dominant species may fundamentally alter ecosystem properties, which should generate highly skewed effects of biodiversity loss on ecosystem functioning (Solan et al. 2004). Habitats generated by canopy-forming species are often threatened by pollution, development, or overexploitation (Bruno et al. 2003), making the need to understand interactions between canopy-mediated processes, biodiversity loss, and habitat change a major challenge for conservation.

Here we explore the influence of a canopy-forming seaweed and resource availability on a macroalgal understory by field manipulations of canopy presence, nutrients, and recruitment history on a subtidal rocky shore in the southern Baltic Sea. Canopy-mediated processes are an important part of subtidal community dynamics, since subtidal communities are commonly patchy with large variations in the abundance of canopy-forming species. Nutrients often determine marine community production (Menge 2000) and nutrient loading is a common cause of habitat change in coastal ecosystems (Cloern 2001). On rocky shores, nutrient effects on macroalgal production depend on the presence of microscopic resting stages (overwintering propagules, Worm et al. 2001). We therefore included recruitment history in the design by exposing plots consisting of both a sterile artificial substrate and a bare natural stone with propagules (no macroscopic vegetation) to a nutrient enrichment gradient. Half the number of plots from each level of nutrient treatment were placed under seaweed canopy cover from adult subtidal *Fucus vesiculosus* L., the dominant leathery macrophyte in the Baltic Sea. A parallel experiment at the field site including artificial shadings and one level of nutrient enrichment revealed that canopy cover prevented increases in understory net biomass accumula-

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Table 1. MANOVA results of *Fucus* canopy and nutrient effects on net biomass production and species richness of understory macroalgae on substrates with different recruitment histories (presence of propagules or not).

Effect	df	Net biomass production		Species richness	
		<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
(a) Sterile substrates					
Canopy cover	1	82.25	<0.001	11.58	0.002
Nutrient enrichment	1	0.14	0.714	0.09	0.760
Canopy cover × nutrient enrichment	1	2.71	0.111	4.84	0.036
Error	28				
(b) Substrates with propagules					
Canopy cover	1	12.97	<0.001	0.42	0.52
Nutrient enrichment	1	0.01	0.923	5.33	0.029
Canopy cover × nutrient enrichment	1	3.17	0.086	5.26	0.029
Error	28				

tion from nutrient enrichment by limiting light for production (Eriksson et al. 2006). In this study we expand on previous work by focusing on nutrient effects on species richness and utilize a nutrient gradient to create a wide gradient of net biomass production. By this we are able to demonstrate that species richness and net production are closely related in the experimental system, and that canopy effects on biomass production also control the propagation of nutrient effects on species richness.

Materials and methods

The experiment was run from March to August 2004 at Maasholm, southern Baltic Sea, Germany (54°41'N, 10°0'E) at about 0.7–0.9 m depth below mean water level on a nontidal shallow sandy bottom scattered with stones. The patchy macroalgal community consists of one dominating canopy-forming fucoid, *Fucus vesiculosus* (hereafter *Fucus*), that covers ca 80% of stone surfaces, along with crust-forming species and a number of fast-growing ephemerals (for detailed species list see Worm et al. 2001). Net primary productivity in this macroalgal community can be up to 5,000 g m⁻² yr⁻¹ C, which indicates a high background productivity that is comparable to maximum values on coral reefs (Worm et al. 2002). During this study, ambient summer nutrient conditions fluctuated from 1.34 ± 0.30 to 2.02 ± 0.17 μmol L⁻¹ dissolved inorganic nitrogen, and from 0.42 ± 0.08 to 1.31 ± 0.15 μmol L⁻¹ phosphate, in June and August respectively (mean ± SE).

Each experimental plot consisted of one sterile artificial substrate and one natural stone with overwintering propagules. Artificial substrates were 10 cm × 20 cm bricks, whereas natural substrates were flat granite stones (top area about 15 cm × 20 cm) without macroscopic vegetation (starting biomass = 0) collected from 0–1 m depth at the start of the experiment. Half of the plots were placed under the shade of canopy cover from *Fucus* plants and the other half outside canopy cover but within 1–2 m of *Fucus* plants, in an alternating design separating each plot with at least 3 m (total number of plots = 32). Plots from each canopy cover treatment were randomly assigned to a gradient of nutrient enrichment including a duplicated

control of ambient conditions (0 [× 2], 10, 20, 40, 80, 160, and 320 g of slow-release NPK fertilizer pellets; Plantacote Depot 6 M, Urania Agrochem, Hamburg, Germany) following the method described in Worm et al. (2000). The pellets were sewn into net bags that were changed every 6 to 7 weeks. Background nutrient concentrations fluctuate highly during the year, but method development in the study area shows that nutrient treatments generate statistically significant increases in mean nutrient concentrations with 0% (no enrichment), 8% (low, 10–20 g), 38% (medium, 40–80 g), and 150% (high, 160–320 g) when measured continuously over a full growing season (Worm et al. 2000).

We estimated the cover of all macroalgal species on the natural stones monthly, using a 10 cm × 15 cm plexiglas sheet with 50 random dots. In August we brought both artificial substrates and natural stones to the lab, estimated cover as above, and carefully scraped off all the vegetation within the 10 cm × 15 cm area. Dry weight of all algae was determined after drying at 80°C for 48 h. Species richness (number of species, *S*) was extracted from August cover and biomass data. Factorial multivariate analysis of variance (MANOVA) was used to test for significant effects of canopy cover (exposed to canopy cover or not) and nutrients (incorporated as a continuous variable) on net biomass production and species richness, for each substrate type separately. Finally, we explored the relationship between net biomass production and species diversity (*S*) in the two canopy cover treatments.

Results and discussion

Canopy cover controlled net primary production of the understory: Macroalgal biomass was about 10-fold higher outside canopy cover than beneath canopy cover, both on sterile and natural substrates (Table 1; Fig. 1). The presence of propagules on natural substrates more than doubled the biomass accumulation compared to sterile substrates. Still, canopy cover dominated the experimental effects since biomass on stones with propagules under canopy cover was lower than biomass on artificial substrates outside canopy cover. There was a trend for a positive effect of nutrient enrichment on biomass

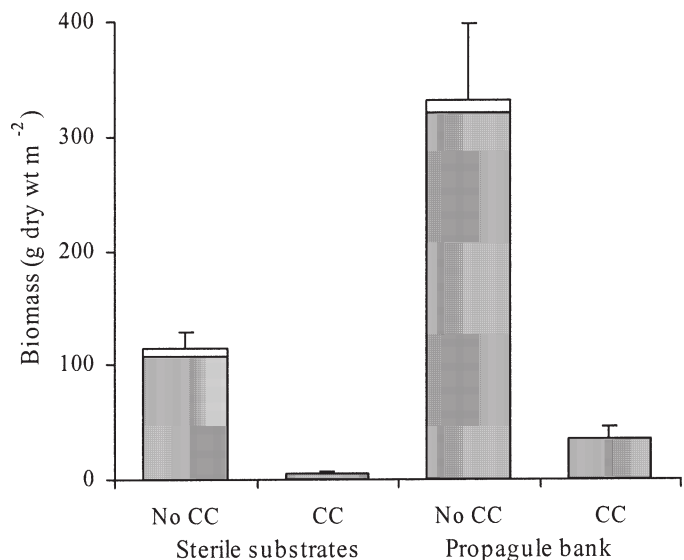


Fig. 1. Net biomass accumulation of understory macroalgae outside canopy cover (No CC) and under canopy cover of *Fucus vesiculosus* (CC), on substrates that were either sterile or preseeded with propagules at the start of the experiment. The gray shows the contribution of juvenile *F. vesiculosus* to biomass. Error bars show standard errors.

accumulation on stones with propagules, but only outside canopy cover (Table 1). Juvenile *Fucus* dominated macroalgal biomass on the experimental substrates completely (93.5% and 96.8% of total dry weight on sterile and propagule substrates, respectively) (Fig. 1). Thus, one dominant species (*Fucus*) controlled net primary production in the community, both by dominating biomass contribution via strong recruitment and juvenile growth, and by limiting net biomass accumulation of the understory via canopy-mediated processes.

Canopy control of biomass limited the spatial extent of *Fucus* in the understory strongly, resulting in a several-times-higher cover of *Fucus* juveniles outside canopy cover at the end of the experiment, both on natural (significant time \times canopy cover interaction, repeated-measures ANOVA, $F_5 = 15.1$, $p < 0.001$) and sterile substrates (one-way ANOVA, $F_1 = 49.7$, $p < 0.001$) (Fig. 2a). Since *Fucus* dominated understory biomass, the continuous increase in cover on the substrates with highest biomass production (substrates with propagules outside canopy cover) indicates that the algal community still accumulated biomass at the end of the experiment. Maximum biomass recorded on an experimental substrate ($0.79 \text{ kg dry wt m}^{-2}$) was five times less than on comparable natural stones with adult *Fucus* vegetation outside the experiment ($4.1 \pm 1.2 \text{ kg dry wt m}^{-2}$, mean \pm SE). By restricting *Fucus* spatial dominance, canopy cover promoted the spatial extension of mainly the red algal crust *Hildenbrandia rubra*, both on natural (significant time \times canopy cover interaction, repeated-measures ANOVA excluding the March sampling with no registered crusts, $F_4 = 16.8$, $p < 0.001$) and sterile substrates (one-way ANOVA, $F_1 = 43.0$, $p < 0.001$) (Fig. 2b). The significant canopy effects on net production and domi-

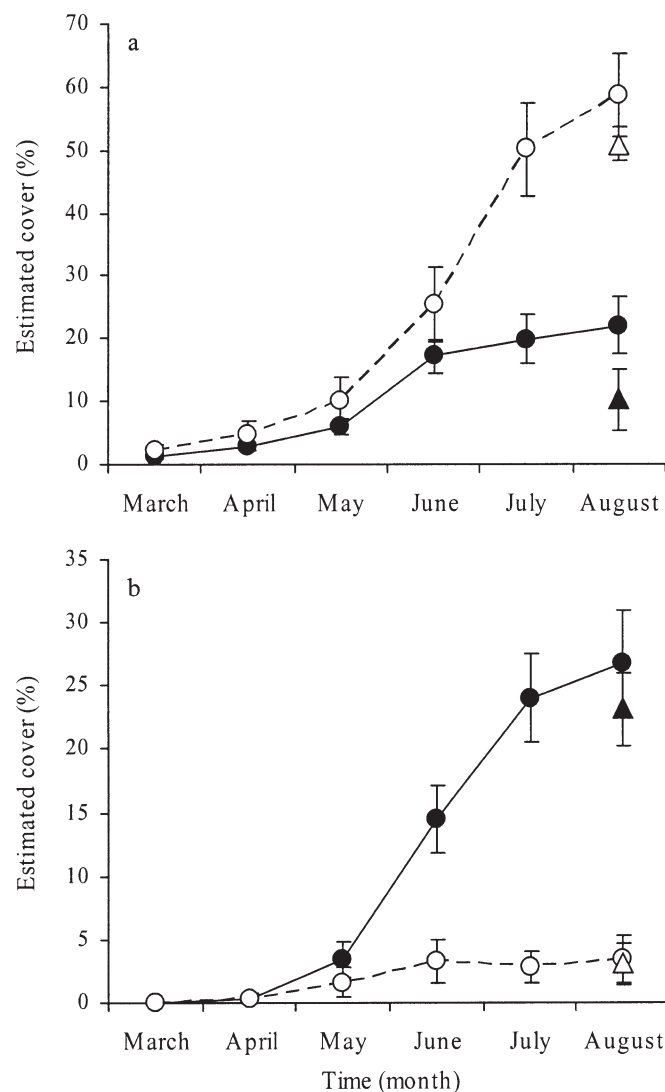


Fig. 2. Spatial cover of (a) juvenile *Fucus vesiculosus* and (b) the red algal crust *Hildenbrandia rubra*, outside canopy cover (open symbols) and under canopy cover of *F. vesiculosus* (filled symbols), on substrates with propagules present at the start of the experiment (circles) and on sterile substrates (triangles). Error bars show standard errors.

nating species distributions largely confirm experimental results from Eriksson et al. (2006).

Canopy cover can decrease net primary production by changing potential productivity, mortality rates, or rates of recruitment (Dayton 1975; Bertness et al. 1999). In the parallel experiment, comparable and dependent experimental effects from canopy cover and artificial shadings strongly suggest that canopy cover controls net production mainly by limiting light and thereby potential productivity in the study system (Eriksson et al. 2006). However, strong grazer control of community processes has also been demonstrated in the field area (Worm et al. 2002) and both low potential productivity and grazing reportedly favor algal crusts (Steneck and Dethier 1994). By increasing spatial structure, canopy macrophytes increase habitat diversity, which can attract grazers by providing shelter

and protection (Duffy and Hay 1991) and thereby indirectly decrease net production of understory algae by increased grazing. Accordingly, macroalgal biomass correlates strongly with grazer abundance and richness in the field area when including the canopy macrophytes in the samplings (A. Rubach unpubl. data). However, during the experiment, grazer abundances were consistently lower under canopies compared to outside canopies, restricting conclusions about differences in grazing intensity on understory algae.

In the present study, canopy cover also strongly controlled the propagation of nutrient effects on species richness (S) of the macroalgal understory, demonstrated by a significant interaction between canopy cover and nutrients both on sterile and natural substrates (Table 1). However, the interaction was clearly different between substrate types (Fig. 3). On natural substrates, canopy effects on species richness increased with increasing nutrient availability; nutrient enrichment reduced species richness outside canopy cover, whereas the presence of canopy cover prevented this loss of diversity (Fig. 3a). On sterile substrates, canopy effects decreased with increasing nutrient availability; canopy cover decreased species richness at ambient nutrients but had no influence in enriched conditions (Fig. 3b). On natural substrates where the presence of propagules generated a higher background net production compared with sterile substrates, *Fucus* spatial dominance increased outside canopy cover to exclude most other species at high nutrient enrichment. Canopy control of *Fucus* spatial dominance at high nutrient enrichment increased species richness by promoting both the inclusion of algal crusts and erect species (especially *Polysiphonia* spp.). Still, canopy presence excluded some ephemeral algae that were common outside canopy cover (such as *Pyliella littoralis* and *Ceramium strictum*). On sterile substrates only algal crusts developed under the canopies at ambient nutrient conditions, whereas nutrient enrichment increased species richness mainly by promoting the inclusion of juvenile *Fucus*. Thus, at the highest experimentally generated potential productivity (both high resource availability and presence of propagules), canopy-forming *Fucus* favored understory species richness, whereas at the lowest potential productivity (no enrichment and sterile substrates), canopy cover had a negative effect on species richness. Canopy control of nutrient effects on species diversity therefore seemed dependent on the background production potential generated by propagule presence or not. This suggests that detrimental effects of resource loading on biodiversity depend strongly on interactions between functional group composition and background productivity potential of the resident community.

Accordingly, net production and species richness were significantly related in the experiment, but the direction of this relationship ultimately depended on the presence of canopy cover or not (Figs. 4, 5). Species richness peaked at intermediate net production between the log-transformed means of biomass from the different canopy cover treatments, generating a hump-shaped relationship between species richness and log net production (Fig. 4). A multiple

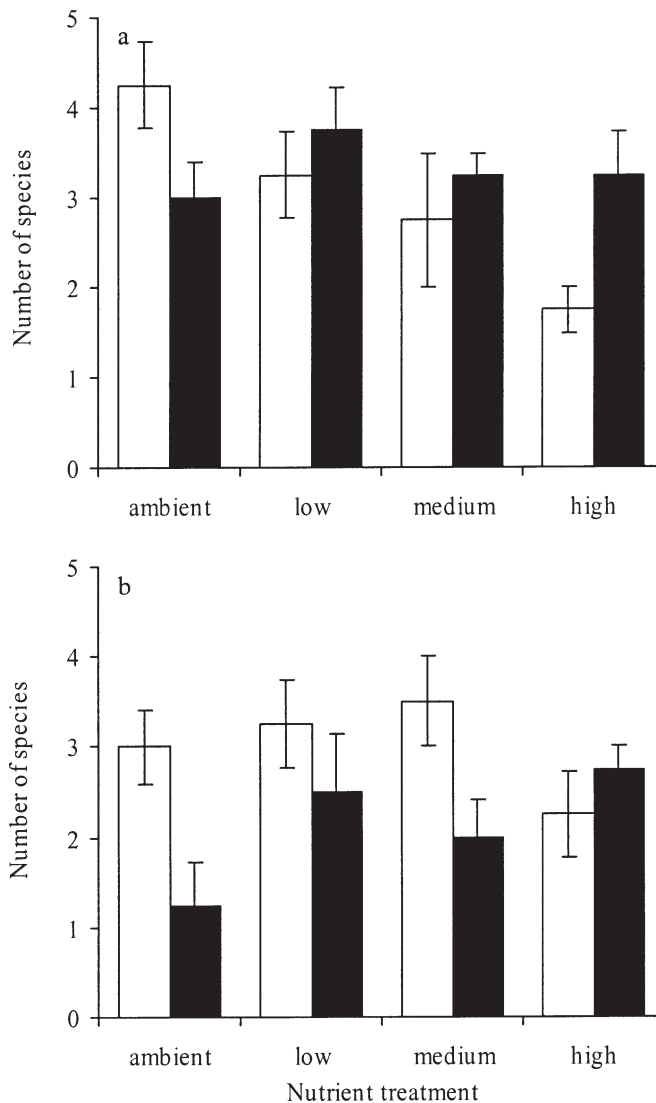


Fig. 3. Species richness of understory macroalgae exposed to different nutrient loads (ambient = 0, low = 10–20, medium = 40–80, and high = 160–320 g of added fertilizer pellets) outside canopy cover (white bars) and under canopy cover of *Fucus vesiculosus* (black bars). (a) Substrates with propagules at the start of the experiment and (b) sterile sampling substrates. Error bars show standard errors.

regression of species richness from log productivity generated a positive linear and a negative quadratic term, indicating that the relationship was best described by concave-down function ($R^2 = 0.394$, $p < 0.001$). On substrates outside canopy cover, there was a significant negative linear correlation between species richness and log net biomass production ($n = 32$, $r = -0.628$, $p < 0.001$; Pearson product moment correlation) (Fig. 5a). On substrates exposed to canopy cover, species richness and log net biomass production were positively correlated ($n = 32$, $r = 0.631$, $p < 0.001$) (Fig. 5b). The hump-shaped productivity–diversity relation strongly suggests that we can relate canopy effects on diversity to the effects on net productivity (Huston 1994). Thus, canopy control of net

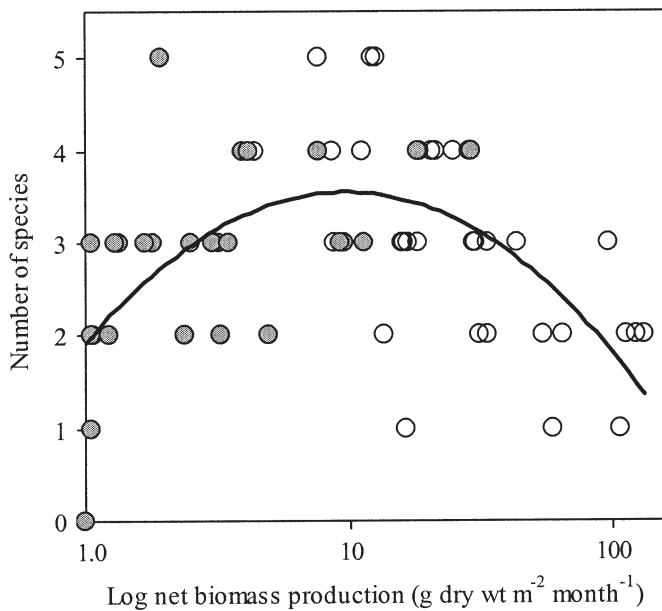


Fig. 4. Hump-shaped relationship between log net biomass production and species richness for understory macroalgae on plots outside canopy cover (open symbols) and under canopy cover of *Fucus vesiculosus* (gray symbols).

production generated a switch in the relationship between net primary production and species richness, from negative outside canopy cover to positive inside, by changing mean biomass from the right to the left side of the production range corresponding to the peak in species richness.

Considerable evidence suggests that effects on diversity by processes changing the net productivity, such as grazing (Worm et al. 2002) or disturbances (Huston 1994), depend on the potential productivity of the ecosystem. Wright and Jones (2004) proposed a conceptual model that predicts effects of organisms as physical ecosystem engineers on patch-scale species richness depending on primary productivity in the ecosystem and whether the engineer decreases or increases production of the engineered habitat. Similarly, the present results suggest that we can predict effects of functionally important species for local diversity processes from effects on net production in relation to background productivity, and thereby better understand consequences of biodiversity loss of dominant species for ecosystem properties.

Our study demonstrates a hierarchical bidirectionality between biodiversity and resource availability. A dominant macrophyte (*Fucus*) determined understory net primary production by modifying the local habitat. In the understory, net primary production was dependent on biomass accumulation of juvenile *Fucus*, and canopy presence and nutrient availability controlled species richness. Thus, one species contribution to habitat diversity dominated community production while understory species richness was a consequence of local habitat conditions, including nutrients. This suggests that functional group composition is a fundamental aspect of ecosystem function and shows that species contributing to biological structure and habitat diversity can control ecosystem responses to

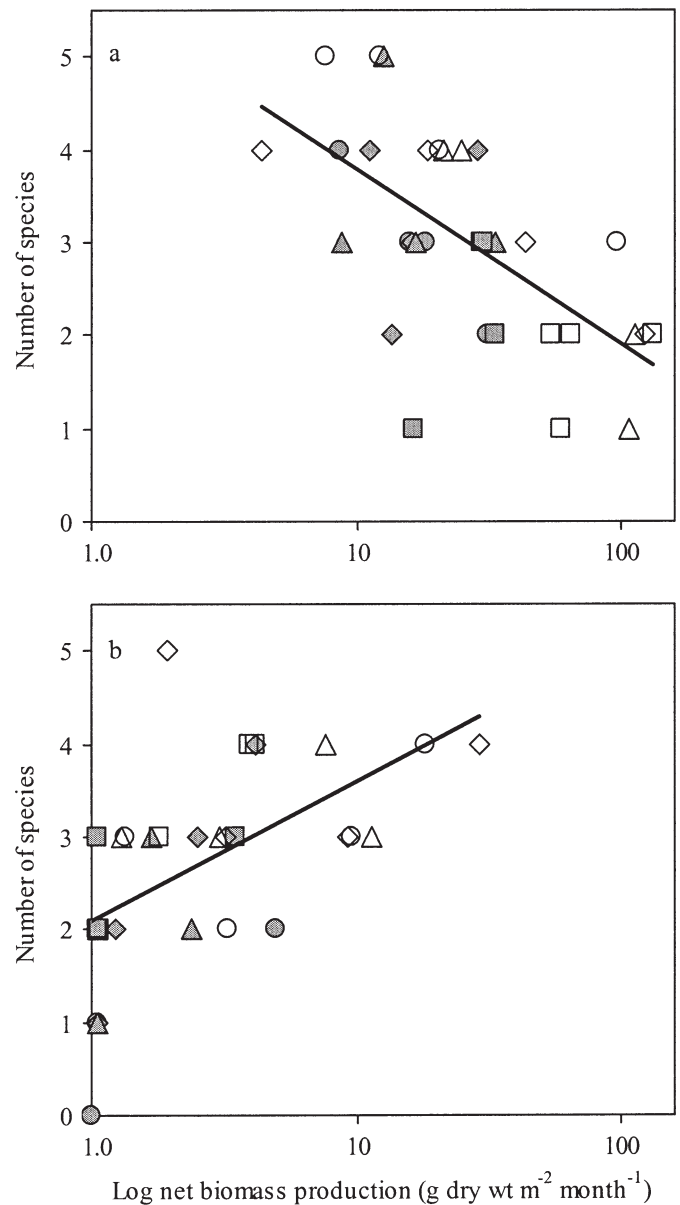


Fig. 5. Linear relations between log net biomass production and species richness for understory macroalgae: (a) outside canopy cover and (b) under canopy cover from *Fucus vesiculosus*. Circles = ambient nutrient conditions, diamonds = low (10–20), triangles = medium (40–80), and squares = high nutrient enrichment (160–320 g of added fertilizer pellets). Open symbols show substrates with propagules present at the start of the experiment and gray show sterile substrates.

resource loading in coastal ecosystems. The control of both community production and species richness by one single species also provides strong support for recent evidence suggesting that effects of changing biodiversity in natural ecosystems depend strongly on attributes of the resident species in the community (Wardle and Zackrisson 2005). This has immediate consequences for marine conservation, by suggesting that: (1) effects of invading species will depend strongly on the species already present in the community, where species identities are central in de-

termining susceptibility of an ecosystem to invasion (Fargione and Tilman 2005), and (2) consequences of habitat change and biodiversity loss will depend largely on the species that go extinct, emphasizing that cause and order of species loss determine effects on ecosystem function (Solan et al. 2004).

References

- BERTNESS, M. D., G. H. LEONARD, J. M. LEVINE, P. R. SCHMIDT, AND A. O. INGRAHAM. 1999. Testing the relative contribution of positive and negative interactions in rocky intertidal communities. *Ecology* **80**: 2711–2726.
- BRUNO, J. F., K. E. BOYER, J. E. DUFFY, S. C. LEE, AND J. S. KERTESZ. 2005. Effects of macroalgal species identity and richness on primary production in benthic marine communities. *Ecol. Lett.* **8**: 1165–1174.
- , J. J. STACHOWICZ, AND M. D. BERTNESS. 2003. Inclusion of facilitation into ecological theory. *Trends Ecol. Evol.* **18**: 119–125.
- CARDINALE, B. J., M. A. PALMER, AND S. L. COLLINS. 2002. Species diversity enhances ecosystem functioning through interspecific facilitation. *Nature* **415**: 426–429.
- CHAPIN, F. S., B. H. WALKER, R. J. HOBBS, D. U. HOOPER, J. H. LAWTON, O. E. SALA, AND D. TILMAN. 1997. Biotic control over the functioning of ecosystems. *Science* **277**: 500–504.
- , AND OTHERS. 2000. Consequences of changing biodiversity. *Nature* **405**: 234–242.
- CLOERN, J. E. 2001. Our evolving conceptual model of the coastal eutrophication problem. *Mar. Ecol. Prog. Ser.* **210**: 223–253.
- DAYTON, P. K. 1975. Experimental evaluation of ecological dominance in a rocky intertidal community. *Ecol. Monogr.* **45**: 137–159.
- DUFFY, J. E., AND M. E. HAY. 1991. Food and shelter as determinants of food choice by an herbivorous marine amphipod. *Ecology* **72**: 1286–1298.
- , J. P. RICHARDSON, AND E. A. CANUEL. 2003. Grazer diversity effects on ecosystem functioning in seagrass beds. *Ecol. Lett.* **6**: 637–645.
- ERIKSSON, B. K., A. RUBACH, AND H. HILLEBRAND. 2006. Biotic habitat complexity controls species diversity and nutrient effects on net biomass production. *Ecology* **87**: 246–254.
- FARGIONE, J. E., AND D. TILMAN. 2005. Diversity decreases invasion via both sampling and complementarity effects. *Ecol. Lett.* **8**: 604–611.
- FINKE, D. L., AND R. F. DENNO. 2004. Predator diversity dampens trophic cascades. *Nature* **429**: 407–410.
- HILLEBRAND, H., AND B. J. CARDINALE. 2004. Consumer effects decline with prey diversity. *Ecol. Lett.* **7**: 192–201.
- HUSTON, M. A. 1994. *Biological diversity*. Cambridge Univ. Press.
- JONES, C. G., J. H. LAWTON, AND M. SHACHAK. 1997. Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* **78**: 1946–1957.
- KINZIG, A. P., S. W. PACALA, AND D. TILMAN. 2002. The functional consequences of biodiversity. Empirical progress and theoretical expectations. Princeton Univ. Press.
- LOREAU, M., AND OTHERS. 2001. Ecology—biodiversity and ecosystem functioning: Current knowledge and future challenges. *Science* **294**: 804–808.
- MENGE, B. A. 2000. Top-down and bottom-up community regulation in marine rocky intertidal habitats. *J. Exp. Mar. Biol. Ecol.* **250**: 257–289.
- PAINE, R. T. 2002. Trophic control of production in a rocky intertidal community. *Science* **296**: 736–739.
- SOLAN, M., B. J. CARDINALE, A. L. DOWNING, K. A. M. ENGELHARDT, J. L. RUESINK, AND D. S. SRIVASTAVA. 2004. Extinction and ecosystem function in the marine benthos. *Science* **306**: 1177–1180.
- STENECK, R. S., AND M. N. DETHIER. 1994. A functional group approach to the structure of algal-dominated communities. *Oikos* **69**: 476–498.
- VAN RUIJVEN, J., AND F. BERENDSE. 2005. Diversity–productivity relationships: Initial effects, long-term patterns, and underlying mechanisms. *Proc. Natl. Acad. Sci. USA* **102**: 695–700.
- WARDLE, D. A., AND O. ZACKRISSON. 2005. Effects of species and functional group loss on island ecosystem properties. *Nature* **435**: 806–810.
- WORM, B., H. K. LOTZE, H. HILLEBRAND, AND U. SOMMER. 2002. Consumer versus resource control of species diversity and ecosystem functioning. *Nature* **417**: 848–851.
- WORM, B., H. K. LOTZE, AND U. SOMMER. 2001. Algal propagule banks modify competition, consumer and resource control on Baltic rocky shores. *Oecologia* **128**: 281–293.
- WORM, B., T. B. H. REUSCH, AND H. K. LOTZE. 2000. In situ nutrient enrichment: Methods for marine benthic ecology. *Int. Rev. Hydrobiol.* **85**: 359–375.
- WRIGHT, J. P., AND C. G. JONES. 2004. Predicting effects of ecosystem engineers on patch-scale species richness from primary productivity. *Ecology* **85**: 2071–2081.

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