

Consumer versus resource control of producer diversity depends on ecosystem type and producer community structure

Helmut Hillebrand^{††}, Daniel S. Gruner[§], Elizabeth T. Borer[¶], Matthew E. S. Bracken^{§||}, Elsa E. Cleland^{††}, James J. Elser^{††}, W. Stanley Harpole^{§§}, Jacqueline T. Ngai^{¶¶}, Eric W. Seabloom[¶], Jonathan B. Shurin^{¶¶}, and Jennifer E. Smith^{††}

[†]Institute for Botany, University of Cologne, Gyrhofstrasse 15, D-50931 Cologne, Germany; [§]Bodega Marine Laboratory, University of California at Davis, P.O. Box 247, 2099 Westside Road, Bodega Bay, CA 94923-0247; [¶]Department of Zoology, Cordley Hall 3029, Oregon State University, Corvallis, OR 97331-2914; ^{||}Marine Science Center, Northeastern University, 430 Nahant Road, Nahant, MA 01908; ^{††}National Center for Ecological Analysis and Synthesis, University of California, 735 State Street, Suite 300, Santa Barbara, CA 93103; ^{§§}School of Life Sciences, Arizona State University, Tempe, AZ 85287-4501; ^{§§}Department of Ecology and Evolutionary Biology, University of California, 321 Steinhaus Hall, Irvine, CA 92697; and ^{¶¶}Department of Zoology, University of British Columbia, 6270 University Boulevard, Vancouver, BC, Canada V6T 1Z4

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Consumer and resource control of diversity in plant communities have long been treated as alternative hypotheses. However, experimental and theoretical evidence suggests that herbivores and nutrient resources interactively regulate the number and relative abundance of coexisting plant species. Experiments have yielded divergent and often contradictory responses within and among ecosystems, and no effort has to date reconciled this empirical variation within a general framework. Using data from 274 experiments from marine, freshwater, and terrestrial ecosystems, we present a cross-system analysis of producer diversity responses to local manipulations of resource supply and/or herbivory. Effects of herbivory and fertilization on producer richness differed substantially between systems: (i) herbivores reduced species richness in freshwater but tended to increase richness in terrestrial systems; (ii) fertilization increased richness in freshwater systems but reduced richness on land. Fertilization consistently reduced evenness, whereas herbivores increased evenness only in marine and terrestrial ecosystems. Producer community evenness and ecosystem productivity mediated fertilization and herbivore effects on diversity across ecosystems. Herbivores increased producer richness in more productive habitats and in producer assemblages with low evenness. These same assemblages also showed the strongest reduction in richness with fertilization, whereas fertilization increased (and herbivory decreased) richness in producer assemblages with high evenness. Our study indicates that system productivity and producer evenness determine the direction and magnitude of top-down and bottom-up control of diversity and may reconcile divergent empirical results within and among ecosystems.

fertilization | herbivory | evenness | species richness | metaanalysis

Human activities have altered nutrient availability and the numbers and kinds of species in virtually all habitats on earth (1–3). These changes, in turn, strongly affect the diversity of primary producer communities. Local species richness is determined in part by the supply of new species via speciation and dispersal (4). The fate of these colonists, and therefore the diversity of a community, depends on differential species responses to intrinsic local-scale processes. Two local factors are often especially important: the ability to exploit or tolerate spatial variability in the supply of abiotic resources (bottom-up processes) and the ability to withstand consumption by herbivores (top-down processes) (5). These two forms of local control affect rates of extinction and colonization (and thus species richness) as well as the relative abundance, or evenness, of species within the community.

The response of producer diversity to alterations of resource and consumer abundance has been inconsistent within and

among producer communities and ecosystem types. Resource enrichment and herbivore manipulations can have positive or negative effects on producer diversity (6–8); no consensus has been reached as to what determines the direction or magnitude of these effects, although ecosystem productivity is thought to strongly influence community responses (9). Resource enrichment in unproductive environments may enhance diversity by allowing rare species to use new resources (10, 11) or persist in larger local populations that are less susceptible to stochastic extinction (12). In productive environments, however, resource enrichment may depress diversity by favoring competitively dominant species and thereby reducing evenness (13, 14). Likewise, the effects of consumers on plant diversity can also be positive or negative, depending on the balance between increased mortality and weakened competitive interactions due to herbivory (9, 15, 16). Consumers may promote stable coexistence if competitively dominant species suffer increased mortality (e.g., keystone predation) (17, 18), or may decrease richness when they are unselective or select rare species (19). Thus, the effects of consumers on coexistence depend on their diet specificity, their biomass removal efficiency, and the dominance structure of the prey assemblage (15).

Here, we present the results of a metaanalysis testing the generality of fertilization and herbivore effects on producer diversity across marine, freshwater, and terrestrial ecosystems. We expected systematic differences in the regulation of diversity by consumers and resources, because the importance of herbivory and the response of producers to resource supply vary among ecosystems. Herbivores in aquatic ecosystems remove a 3-fold greater fraction of primary production than those on land, and aquatic producers typically have shorter generation times and higher nutrient-uptake rates (20, 21). Moreover, other constraints on herbivory, such as body size ratios of herbivores to their prey (22) and producer food quality (20, 23), differ substantially between aquatic and terrestrial systems.

Interactions among herbivores, producers, and abiotic resources are central to understanding differences in trophic structure and composition between aquatic and terrestrial sys-

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Abbreviations: GLM, general linear model; MA, metaanalysis.

[†]To whom correspondence should be addressed. E-mail: helmut.hillebrand@uni-koeln.de.

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Table 1. Results of bivariate MA and GLM testing for significant impact of environmental variables on effect sizes of herbivory and fertilization and their interactive effect on richness and evenness of the producer community

Factor	Effects on species richness						Effects on evenness					
	Herbivory		Fertilization		Interaction		Herbivory		Fertilization		Interaction	
	MA	GLM	MA	GLM	MA	GLM	MA	GLM	MA	GLM	MA	GLM
System†	T > F**	T > M > F**	F > T***	/	NS	/	T > F***	/	NS	F = M > T+	NS	/
Productivity (rel. units)	0.062*	0.043+	-0.038*	/	NS	0.081+	NS	/	NS	0.086**	NS	/
Herbivore effect biomass	0.080**	/	—	—	NS	/	NS	/	—	—	NS	-0.081*
Fertilization effect biomass	—	—	NS	/	-0.119**	-0.217*	—	—	NS	/	NS	0.182***
Pielou's evenness (J)	-0.471**	-0.445**	0.267**	0.334**	0.414*	0.435*	—	—	—	—	—	—
Species richness (ln S)	—	—	—	—	—	—	-0.061*	-0.148***	NS	/	-0.144*	/
Experiment duration (ln d)	0.028**	-0.126***	-0.059**	-0.051***	NS	/	NS	/	NS	/	NS	/
Experiment size (ln m ²)	NS	/	-0.036**	/	NS	/	NS	/	-0.034*	/	0.036*	0.027*
Latitude,° N or S	NS	/	NS	/	/	/	-0.004*	/	NS	/	NS	/
F ratio (d.f.)	—	7.46 (5;45)	—	16.68 (2;63)	—	3.53 (3;22)	—	11.92 (1;92)	—	2.30 (3;81)	—	9.23 (3;22)
P	—	<0.0001	—	0.0024	—	0.0316	—	0.0008	—	0.0838	—	0.0004
R ²	—	0.453	—	0.346	—	0.325	—	0.115	—	NS	—	0.557

For each response variable, the significant parameter estimates (NS, not significant; /, not included in the final model, —, not applicable) and their significance levels (***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$; +, $P < 0.1$; NS, $P > 0.1$) are given as well as overall model statistics (F ratio with degrees of freedom, significance level, and R²). rel., relative; ln, natural log.

†Significant differences between terrestrial (T), freshwater (F), and marine (M) ecosystems are shown.

experimental duration and more negative fertilization effects in terrestrial relative to aquatic experiments (Fig. 1a).

The combined interaction effect size of herbivory and fertilization on producer species richness was positive when producer evenness was high (Table 1 and Fig. 2g); however, this positive interaction between herbivory and fertilization was restricted to communities showing weak to moderate biomass responses to fertilization (Fig. 2f; please note that this regression was non-significant when the two extreme points were omitted).

Effect sizes on evenness were only weakly affected by environmental variables relative to the strong environmental mediation of fertilization and herbivory effects on producer richness. Fertilization effects on evenness were consistent across all ecosystems, resulting in a nonsignificant final GLM (Table 1). Herbivores enhanced producer evenness mainly in communities with low species richness, but had near-neutral effects on evenness in speciose communities (Table 1 and Fig. 2h). As experiment size (i.e., the size of a single experimental unit) increased, herbivory and fertilization together tended to increase producer evenness (Table 1), suggesting that positive herbivore effects outweighed negative fertilization effects, especially in larger experiments (Fig. 2i).

Discussion

Few generalities have been previously identified regarding the role of consumers and resource availability in controlling producer diversity. In fact, negative and positive effects of both consumers and resources are commonly reported. Our synthesis provides a general framework for reconciling these divergent outcomes across ecosystems into a conceptual model (Fig. 3). This model is based on three primary results of our analysis. First, consumers and fertilization produced differing effects on producer richness and evenness, two distinct aspects of community diversity. Second, fertilization and herbivores affected producer evenness consistently across ecosystems, whereas effects on richness differed among marine, freshwater, and terrestrial

systems. Third, effects of fertilization and herbivores on producer richness were significantly related to producer community evenness and ecosystem productivity. Herbivores increase and fertilization decreases producer community evenness with different consequences for the intrinsic control of species richness (Fig. 3). By moving the community toward greater evenness, herbivores increase coexistence where productivity and dominance are high. Fertilization drives the community toward lower evenness, thereby reducing richness in communities already dominated by few species (Fig. 3).

Our results indicate that fertilization increased competitive dominance within producer assemblages across all ecosystem types but had different effects on richness in different ecosystems. In terrestrial ecosystems, fertilization reduced both species richness and evenness, consistent with studies showing increased dominance and competitive exclusion with high nutrient deposition (13, 32). This increased dominance by a few species is attributable in part to increased intensity of size-asymmetric competition for light because of increased average producer height (8). In aquatic habitats, fertilization also reduced evenness but enhanced species richness, which may be due in part to the low ability of producer species to monopolize light use in well mixed plankton communities (33–35). Alternatively, larger algal species in periphyton communities, often favored by fertilization, can provide habitat structure for additional life forms such as epiphytes (7).

Herbivory enhanced producer evenness across ecosystems but promoted richness only in terrestrial, but not aquatic, ecosystems. This ecosystem difference may arise from a number of general differences in plant–herbivore interactions between terrestrial and aquatic systems (21). Aquatic systems are characterized by larger body-size ratios between herbivores and producers, which might result in lower selectivity of the herbivore for prey species or prey parts (21). Second, it has been suggested that terrestrial producers have higher investment in structural defenses (36), and structurally defended producer

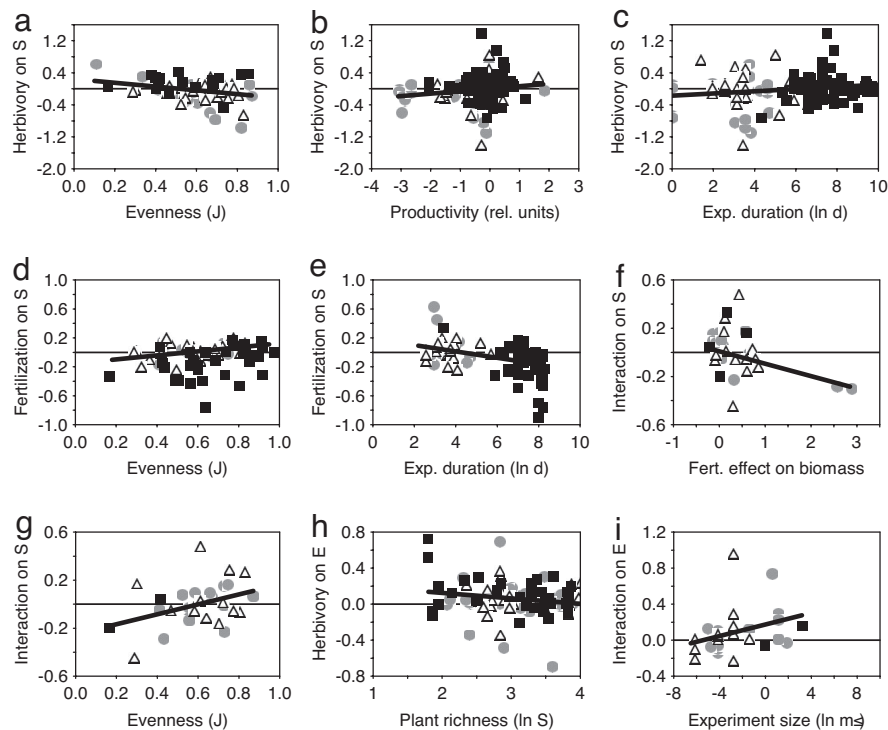


Fig. 2. Effect sizes of herbivory (*a–c* and *h*) and fertilization (*d* and *e*) and their interaction (*f*, *g*, and *i*) on producer species richness (*a–g*) and producer community evenness (*h* and *i*). Effect sizes are significantly related to producer community evenness (*a*, *d*, and *g*), ecosystem productivity (*b*), experiment duration (*c* and *e*), fertilization effects on producer biomass (*f*), producer community richness (*h*), and experiment size (*i*). Symbols represent freshwater (gray circles), marine (triangles), and terrestrial (black squares) systems. Horizontal lines indicate neutral effects, and thick lines indicate significant regressions from bivariate metaanalysis (see Table 1 for statistical results). rel., relative; Exp., Experiment; Fert., Fertilization; In, natural log.

species can provide associational resistance to neighboring plants (37). Both aspects may lead to differences in the spatial heterogeneity of consumption and competition between ecosystems. All of these aspects may lead to stronger consumer-mediated coexistence of producer species in terrestrial systems (Fig. 3), but our database does not provide the means to disentangle these hypotheses.

Beyond the ecosystem differences, we found that fertilization and herbivory effects on richness were strongly associated with producer community evenness. Positive herbivore effects on plant richness were confined to productive plant communities and those with low evenness. The response to fertilization became more positive when producer abundances were relatively evenly distributed. The association between consumer effects and productivity agrees well with earlier studies with more limited data sets (27, 28). We extend these previous syntheses by demonstrating how the effects of consumers on producer richness change along a gradient of resource availability rather than simply comparing fertilized versus unfertilized plots. The strong and opposite associations of herbivore and fertilization effects with producer community evenness reconciles the disparate results from isolated experiments through a common mechanism (Fig. 3). Herbivores, on average, increase evenness, but they enhance producer species richness only if evenness is low (16, 17). These results suggest that herbivores tend to disproportionately reduce the abundance of the most abundant taxa and increase richness only when preferred species are most dominant. In producer communities with numerous codominant species, consumer presence tends to cause extinctions and decrease species richness (15, 16). By contrast, fertilization, on average, decreases evenness (Fig. 3). In producer communities with low evenness, fertilization enhances the dominance of already successful competitors (Fig. 3) and accelerates local

extinction of rare species (38). In communities where dominance is low and many species are equally rare, fertilization enhances the persistence of rare species, presumably by increasing population sizes (6). Consequently, the evenness of the producer community also determines the interactive outcome of the combined manipulation of herbivory and fertilization, because positive statistical interactions were restricted to producer communities with high evenness.

Our metaanalysis involved an unprecedented number of experiments (274 in total) addressing producer diversity response to herbivory and/or fertilization. Nevertheless, some systems were underrepresented where few studies have been conducted. Although at least 80 studies were used to calculate each average effect size across systems, the system-specific database was narrower, especially for factorial terrestrial studies ($n = 5$). Given the moderate covariance between explanatory variables (see *Methods*), we used two separate analyses. The bivariate MA made use of the full data set but neglected the covariation among contextual explanatory variable. The GLM allowed a multivariate analysis reflecting the covariation between factors but required that all relevant variables were reported for a study. Therefore, the GLM comprised a reduced data set and prevented the test of nonlinear responses or higher-order interaction terms. Despite these caveats, the consistency between the MA and GLM analyses strengthen our confidence in the validity of the observed patterns.

Conclusions

Herbivores increase and fertilization decreases producer evenness across ecosystems, but these factors have contrasting effects on producer richness in aquatic and terrestrial ecosystems. The evenness and productivity of the producer community mediates the effects of consumer presence and resource supply on pro-

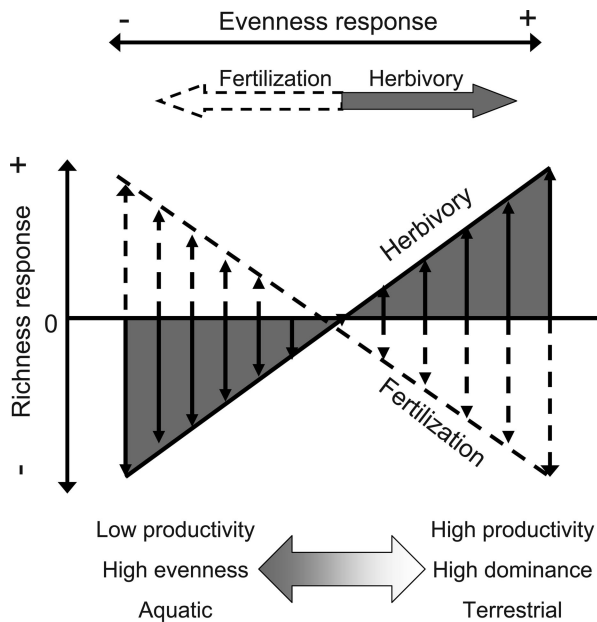


Fig. 3. Conceptual diagram of local control of producer diversity. The effects of herbivores and fertilization on producer richness differ across gradients of ecosystem productivity and producer community structure and between ecosystem types. Herbivore effects are denoted by solid arrows and lines, fertilization effects by broken lines. The effects of herbivores and fertilization on producer community evenness are consistent across gradients and systems.

ducer richness. In total, these results lead to a general framework for predicting when local manipulations should enhance or decrease plant species richness. Our cross-system quantification of herbivory and fertilization effects and their interactions is a major step toward a general understanding of local control of producer diversity with vital consequences for conservation and management of species diversity in natural systems. The effects of human perturbations of global biogeochemical cycles and food web structure on local-scale diversity will depend on consumer pressure, resource availability, and producer community structure. The response of producer diversity to enhanced global nutrient availability will depend on the stable persistence of consumer populations, whereas human pressure on consumer species will affect producer diversity differently in nutrient-poor compared with nutrient-rich environments.

Methods

This analysis was compiled from the ELSIE database (EcoLogical Synthesis of Interactive Experiments, see metadata on <http://knb.ecoinformatics.org/index.jsp>). Studies were selected by examining the abstracts of all publications returned from searches on ISI Web of Science by using the search strings [herbivor* or graz* or consum*] and [resourc* or nutrient* or fertili*] and [divers* or species richness or evenness]. We also included data from studies cited in published syntheses (27, 28). A list of studies can be found in [SI Table 2](#).

We used species richness and evenness to characterize two independent aspects of diversity (the number of distinct traits and their abundance distribution within the community) (39, 40). Richness included both species density and species richness measures, whereas evenness comprised different indices, such as Pielou's, Simpson's, or Hill's indices (39). We used the log response ratio as our effect size metric, which is one of the most commonly used effect metrics in ecological metaanalysis (31, 41). Unlike Hedge's *d*, the log response ratio does not require a measure of sample variability. Moreover, the analysis of treat-

ment responses relative to that of the control is more meaningful than the use of standard deviations to standardize differences between means when comparing between systems. Finally, the relative treatment responses could be compared irrespective of the measure of evenness used.

We used two different approaches to calculate effect sizes for factorial and nonfactorial studies. For factorial experiments, we calculated a main herbivore (H_M), a main fertilization (F_M), and an interaction effect (INT) as

$$H_M = \ln\left(\frac{H1F0 + H1F1}{H0F0 + H0F1}\right)$$

$$F_M = \ln\left(\frac{H0F1 + H1F1}{H0F0 + H1F0}\right)$$

$$INT = \ln\left(\frac{H0F0 + H1F1}{H1F0 + H0F1}\right)$$

where we used the average diversity at grazer presence ($H1$) and absence ($H0$) and ambient ($F0$) and fertilized ($F1$) treatment combination ("factorial metaanalysis").

Nonfactorial herbivore (H_{NF}) and fertilization (F_{NF}) effects were calculated as

$$H_{NF} = \ln\left(\frac{H1}{H0}\right)$$

$$F_{NF} = \ln\left(\frac{F1}{F0}\right)$$

By this approach, factorial main effects were directly comparable with effects in nonfactorial experiments, so that without any interaction, a given change in diversity resulted in the same effect size in the factorial and nonfactorial calculation. The factorial interaction effect size denotes whether diversity is higher (positive values) or lower (negative values) than expected from the main effects based on an additive model. Positive interactions can be based on the enhancement of factors favoring diversity or by the mitigation of diversity-reducing effects.

In addition to data on the responses of producer diversity to herbivory and/or fertilization, we recorded information on the environmental context and experimental design for each study. A complete list of the variables and calculations can be found in [SI Text](#). We combined the different aspects of background resource availability (N, P, light, and, for terrestrial studies, water) into one integrative productivity measure (for calculation, see also [SI Text](#) and [SI Table 3](#)),

As studies reported different numbers of the covariates, statistical tests differed in their degrees of freedom. We used unweighted MA of the log response ratios to calculate average effect sizes for all data and for each of the three study systems. Bootstrapped 95% confidence intervals were used to test whether effect sizes were significantly different from zero. A fixed-model analysis of heterogeneity (41) was used to test for significant differences of average effect sizes among terrestrial, freshwater, and marine ecosystems as well as between factorial and nonfactorial studies. We performed continuous meta-analyses (41) to test how effect sizes on diversity varied with (i) the experimental conditions (size and duration of experiments and latitude of experimental sites), (ii) the ecosystem productivity, (iii) the strength of herbivore or fertilization effects on biomass, and (iv) producer community evenness or richness. We used evenness as explanatory variable for effect sizes on richness and vice versa. For these metaanalyses, we report the slope of the regression and the bootstrapped significance value (999 randomizations).

We observed moderate covariance between the explanatory variables (see *SI Text* and *SI Table 4*). To select the optimal model for predicting variation in responses and to account for covariance among the explanatory variables (42), we used the Akaike information criteria (AIC) to select the most parsimonious general linear model (GLM). We report the statistics of the final selected model and estimates of the slopes for the variables included (Table 1).

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