

REVIEW AND  
SYNTHESISA cross-system synthesis of consumer and nutrient  
resource control on producer biomass

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**Abstract**

Nutrient availability and herbivory control the biomass of primary producer communities to varying degrees across ecosystems. Ecological theory, individual experiments in many different systems, and system-specific quantitative reviews have suggested that (i) bottom-up control is pervasive but top-down control is more influential in aquatic habitats relative to terrestrial systems and (ii) bottom-up and top-down forces are interdependent, with statistical interactions that synergize or dampen relative influences on producer biomass. We used simple dynamic models to review ecological mechanisms that generate independent vs. interactive responses of community-level biomass. We calibrated these mechanistic predictions with the metrics of factorial meta-analysis and tested their prevalence across freshwater, marine and terrestrial ecosystems with a comprehensive meta-analysis of 191 factorial manipulations of herbivores and nutrients. Our analysis showed that producer community biomass increased with fertilization across all systems, although increases were greatest in freshwater habitats. Herbivore removal generally increased producer biomass in both freshwater and marine systems, but effects were inconsistent on land. With the exception of marine temperate rocky reef systems that showed positive synergism of nutrient enrichment and herbivore removal, experimental studies showed limited support for statistical interactions between nutrient and herbivory treatments on producer biomass. Top-down control of herbivores, compensatory behaviour of multiple herbivore guilds, spatial and temporal heterogeneity of interactions, and herbivore-mediated nutrient recycling may lower the probability of consistent interactive effects on producer biomass. Continuing studies should expand the temporal and spatial scales of experiments, particularly in understudied terrestrial systems; broaden factorial designs to manipulate independently multiple producer resources (e.g. nitrogen, phosphorus, light), multiple herbivore taxa or guilds (e.g. vertebrates and invertebrates) and multiple trophic levels; and – in addition to measuring producer biomass – assess the responses of species diversity, community composition and nutrient status.

**Keywords**

Consumer–resource theory, factorial meta-analysis, fertilization, freshwater, herbivore exclusion, marine and terrestrial ecosystems, plant community, primary production, top-down and bottom-up control.

## INTRODUCTION

Pervasive anthropogenic changes to global nutrient cycles and consumer regimes challenge the ability of ecologists to predict the responses of primary production, food web structure, and ecosystem function to these perturbations. Nitrogen, phosphorus and other material elements (e.g. iron in the open ocean) limit primary productivity across a panoply of global ecosystems (Elser *et al.* 2007). However, the global input rates to nitrogen and phosphorus pools have more than doubled since pre-industrial times (Jefferies & Maron 1997; Vitousek *et al.* 1997; Falkowski *et al.* 2000), causing widespread aquatic eutrophication (Carpenter *et al.* 1998) and potential loss of terrestrial plant diversity as multiple resource limitations relax (Suding *et al.* 2005; Harpole & Tilman 2007). Similarly, human-caused changes in the intensity of top-down heterotrophic consumption, for example through release of top predators by trophic skew (Duffy 2003; Petchey *et al.* 2004; Worm *et al.* 2006), broad-scale introduction and pastoral management of grazers and browsers (Welch & Scott 1995), or the local reduction or extirpation of native herbivores (Hughes 1994), can change the standing biomass and species composition of primary producers on broad scales.

A longstanding issue in ecology concerns the relative importance of these resource ('bottom-up') vs. consumer ('top-down') controls of community and trophic level biomass within and across ecosystem types (Camerano 1880; Elton 1927; Lindeman 1942; Hairston *et al.* 1960; Murdoch 1966; Sih *et al.* 1985; Hunter & Price 1992; Power 1992; Hairston & Hairston 1993; Polis & Strong 1996; Polis 1999; Borer *et al.* 2006; Frank *et al.* 2007). Once a dichotomous controversy over which single process best accounted for patterns of primary production, contemporary research highlights the interdependence of resources and consumer impacts on food webs and ecosystems. For example, models and data predict that productivity influences the length of food chains, the intensity of consumer control and the rates of consumer-mediated feedbacks and recycling of limiting nutrients to the production base (Fretwell 1977; Oksanen *et al.* 1981; Power 1992; Abrams 1993; Wootton & Power 1993; Vanni *et al.* 1997; Kaunzinger & Morin 1998; Mikola & Setälä 1998; Persson *et al.* 2001; Flecker *et al.* 2002; Shurin & Seabloom 2005; Arim *et al.* 2007; Fox 2007). With the common recognition that both resources and consumers have important roles in most individual systems, research now concentrates on quantifying the relative and interactive strengths of resource and consumer control, and on predicting how these forces determine producer standing biomass, productivity and species diversity within and across ecosystems (Borer *et al.* 2006; Burkepile & Hay 2006; Hillebrand *et al.* 2007).

Ecologists have proposed that the relative strengths of consumer and resource control on standing producer

biomass should differ among major habitat types, particularly in water vs. on land (Strong 1992; Hairston & Hairston 1993; Polis & Strong 1996; Chase 2000; Shurin *et al.* 2006). Meta-analyses of predator removal experiments identified systematic differences in the magnitude of top-down control of producer biomass, with the strongest trophic cascades in lake plankton and marine benthos and weakest effects from terrestrial experiments (Shurin *et al.* 2002; Borer *et al.* 2005). The critical link in understanding this variation may be the trophic interaction between herbivores and producers, which in turn depends on resources (Polis & Strong 1996; Shurin *et al.* 2002). Cross system comparisons demonstrated that aquatic systems typically support higher abundance and biomass of heterotrophs, with threefold higher herbivory rates relative to terrestrial systems (Cyr & Pace 1993; Cyr *et al.* 1997; Cebrian & Lartigue 2004; Shurin *et al.* 2006). Systematic variation in consumer control has been attributed to numerous mechanisms that may depend wholly or in part on resource availability, such as variation in producer population turnover rates; consumer-producer body size ratios; herbivore selectivity and efficiency; plant resistance, tolerance and compensatory growth to herbivory; and stoichiometric mismatches among producer content and herbivore nutritional needs (Power 1992; Chase 2000; Elser *et al.* 2000; Shurin *et al.* 2002; Borer *et al.* 2005; Shurin *et al.* 2006; Hall *et al.* 2007b).

Previous studies provide widespread support for positive effects of experimental fertilization (Downing *et al.* 1999; Elser *et al.* 2007) and herbivore removal or exclusion (Huntly 1991; Bigger & Marvier 1998; Chase *et al.* 2000a; Coupe & Cahill 2003; Maron & Crone 2006) on producer community biomass across ecosystems. However, both models and case studies offer conflicting predictions and evidence as to whether these bottom-up and top-down factors should independently or interactively control plant biomass (Leibold 1989; Osenberg & Mittelbach 1996; Chase *et al.* 2000a; Persson *et al.* 2001; Hillebrand 2002). The potential for interactive outcomes is determined by a host of biological mechanisms (e.g. are herbivore populations static or dynamic; does autotroph palatability change with fertilization?). In an effort to formally define expectations from various biological mechanisms, we use a simple Lotka-Volterra food chain model (*see* Box 1) to generate predictions of the relative and interactive importance of resource and consumer controls. These models are based on a suite of three-level food chain models exploring the dynamics of basal resources ( $R$ ), one or more producers (autotrophs,  $A$ ) and an herbivore ( $H$ ; De Angelis 1975; Oksanen *et al.* 1981; Leibold 1989; Sarnelle 1992; Schmitz 1992; Grover 1995; Leibold 1996; Chase *et al.* 2000a,b). We review mechanistic scenarios where simple additivity among main effects of nutrient enrichment and herbivore removal should be expected, and then explore scenarios that predict emergent

## Box 1

To understand the expected signs and magnitudes of the fertilization effect, herbivore effect and their interaction across the wide range of systems covered in this meta-analysis, we have created a simplified series of models to predict the qualitative effects on autotroph standing biomass associated with different ecological processes. We use as our foundation a three-level model describing interactive dynamics of resources, autotrophs and herbivores (De Angelis 1992; Chase *et al.* 2000a), which assumes a constant resource supply rate, a type I functional response of autotrophs taking up resources, and a type I functional response of herbivores consuming autotrophs. It is well known that three-level food chains incorporating type II functional responses are extremely unstable, displaying limit-cycle or chaotic behaviour across much of their parameter space, even when the chains are persistent (i.e. all three species maintain population densities bounded away from zero indefinitely [Abrams & Roth 1994]). How generally other ecological factors such as spatial or behavioural heterogeneity can stabilize these dynamics, leading to stable equilibria, is an open question. For our purposes, the important point is that we cannot easily reach simple qualitative conclusions about the change in average (or equilibrium) biomass at different levels for such models. However, it is still reasonable to suppose that the results from type II functional responses will be intermediate between the case of a type I model (where the ability of consumers to take up resources never saturates) and a model with a fixed loss rate from consumers (where the ability of consumers to take up resources remains constant at all resource densities).

Emulating the notation of Chase *et al.* (2000a), we define  $R$  as the size of the resource pool and  $A$  and  $H$  as the densities of autotrophs and herbivores, respectively. The resource supply rate is  $S$ ;  $c_R$ ,  $c_A$  and  $c_H$  are loss rates of  $R$ ,  $A$  and  $H$  other than consumption by the next level;  $a_{RA}$  and  $a_{AH}$  are attack rates and  $b_{RA}$  and  $b_{AH}$  are conversion efficiencies for autotrophs taking up resources (subscript RA) and herbivores consuming autotrophs (subscript AH). The model then becomes

$$\frac{dR}{dt} = S - c_R R - a_{RA} R A$$

$$\frac{dA}{dt} = a_{RA} b_{RA} - c_A A - a_{AH} A H$$

$$\frac{dH}{dt} = a_{AH} b_{AH} A H - c_H H$$

Depending on the situation, we sometimes fix the density of herbivores; in general we refer to the density of herbivores (equilibrium or fixed) as  $\hat{H}$ .

The equilibrium density of autotrophs is therefore (other equilibria are demonstrated in Appendix S3):

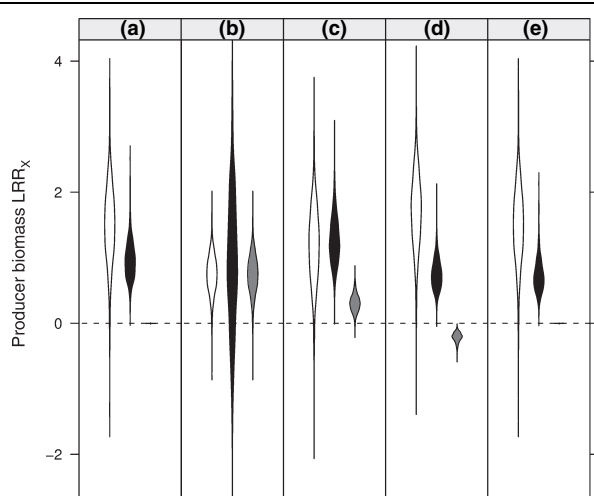
$$A^* = \frac{S b_{RA}}{c_A + a_{AH} \hat{H}} - \frac{c_R}{a_{RA}}$$

In general, we can understand competing formulations by considering the expected effects on the autotroph growth rate (proportional to  $S b_{RA}$ ) and loss rate ( $L_A = c_A + a_{AH} \hat{H}$ ). Unless the system is very leaky (i.e. the ratio of  $c_R$ , abiotic resource loss rate, to  $a_{RA}$ , autotroph resource uptake rate, is large), the autotroph equilibrium density will be proportional to resource supply rate  $S$  divided by autotroph loss rate  $L_A$ . Fertilization will have little effect when resource augmentation is ineffective – for instance, when autotrophs are limited by resources other than the one supplied. Herbivore removal will have little effect when the attack rate  $a_{AH}$  is low or the autotroph loss rate  $c_A$  is high. We define  $\Delta F = \ln(S_{\text{treatment}}/S_{\text{ambient}})$  as the log of the proportional increase in resource supply rate and  $\Delta H = \ln(c_A/L_A)$  as the proportional decrease in autotroph loss rate caused by herbivore removal; the directions of these effects match those in the main text.

As a baseline case, suppose that (i) the autotroph assemblage remains unchanged under both fertilization and herbivore exclusion and (ii) herbivore pressure remains constant under fertilization treatments (and the resulting increase in autotroph biomass) – for example, because herbivores are limited by other resources, by predators, or by the inability to track resources on experimental scales (Englund 1997). In this case (Box Fig. 1a, ‘baseline additivity’), the effect of adding fertilizer with or without herbivores present is  $\Delta F$  ( $LRR_F = +2\Delta F$ ) and the effect of excluding herbivores with or without fertilizer is  $\Delta H$  ( $LRR_H = +2\Delta H$ ). The combined effect of fertilization and herbivore exclusion is additive (i.e. the interaction term  $LRR_I = 0$ ).

When herbivores can respond to autotroph density via a type I functional response, we get the well-known result that increases in resource supply accumulate as herbivore biomass, leaving autotroph density  $A^*$  unchanged (Box Fig. 1b, ‘dynamic herbivores’). In this case, fertilization only increases autotroph biomass (by a log ratio of  $\Delta F$ ) in the absence of herbivores. When herbivores are excluded, autotrophs increase from their fixed herbivore-present equilibrium [ $c_H/(a_{AH} b_{AH})$ ] to the herbivore-free biomass ( $b_{RA} S/c_A$ ), a larger increase in the presence of fertilization.

## Box 1 (Continued)



**Box Figure 1** Qualitative model expectations for fertilization (white filled), herbivore removal (black) and interaction (grey) log response ratios ( $LRR_x$ ) under dynamical scenarios: (a) baseline additivity or static herbivory, (b) dynamic herbivores (saturating herbivores not shown because of sensitivity to parameters), (c) tolerance, (d) induced resistance, (e) consumer-mediated recycling. Each parameter value (presented in Appendix S3 Table 1) was first assigned a coefficient of variation = 0.2 and iterated 1000 times to generate randomized distributions for each parameter. Plotted here are violin density plots for models a–e, where the width and height of each represent the central tendency and range, respectively, of 1000 random draws from these parameter sets for each model.

Thus in systems where dynamic herbivores can escape predator control and incorporate increased productivity into their own tissues and populations (De Angelis 1992),  $LRR_F$  will be half as large as in the baseline case,  $LRR_H$  will be larger and  $LRR_I$  will be positive.

More realistic, saturating herbivore functional responses, or cases where herbivores are partly limited by top-down control, will lead to results intermediate between the

previous two cases (De Angelis 1992; Abrams & Roth 1994). If ambient resource supply rates and hence herbivore-free  $A$  are low, then the herbivore functional response will be close to linear and the results will approximate the dynamic-herbivore case; if ambient resource supply rates and hence  $A$  are high, herbivores will be saturated and unresponsive to fertilization and the results will be closer to the baseline case.

Changes in resource supply are also expected to change autotroph (and herbivore) traits via plasticity, within-species selection or species compositional shifts. As a guild, the autotrophs can thus become either more or less susceptible to herbivory with fertilization (Leibold 1989; Grover 1995; Leibold *et al.* 1997; Augustine & McNaughton 1998; Hall *et al.* 2006; Wise & Abrahamson 2007) and we can model the effects of these functional changes by making  $a_{AH}$  (and  $\Delta H$ ) an increasing or decreasing function of  $S$ , respectively. Assuming that herbivore density is static, shifts toward edibility will lead to *super-additive* effects (Box Fig. 1c, ‘tolerance’) and shifts toward inedibility will lead to *sub-additive* effects (Box Fig. 1d, ‘induced resistance’) of fertilization and herbivore exclusion on autotroph biomass.

Finally, herbivores can directly alter nutrient dynamics, contributing to increased recycling rates through waste production or sloppy feeding (Chapin *et al.* 1986; de Mazancourt *et al.* 1998). If nutrient availability increases with both supply rate ( $S$ ) and herbivore density ( $\hat{H}$ ),  $LRR_F$  decreases relative to our baseline and is an increasing function of  $\hat{H}$ . Because of the reduced loss of nutrients from consumption by herbivores,  $LRR_H$  also decreases relative to the baseline. However, on the log scale the increase in nutrient availability in the presence of herbivores acts independently of fertilizer addition (provided herbivore densities are static), resulting in an expected interaction effect ranging from zero to mildly positive (panel e).

super-additive (synergistic) or sub-additive (dampening) interactive effects.

This dynamical framework forms the scaffolding for direct interpretation of our factorial meta-analysis of log response ratios of producer community biomass to consumer and nutrient manipulations (Gurevitch *et al.* 2000; Hawkes & Sullivan 2001). Quantitative meta-analyses comparing herbivore and nutrient resource controls on producers have been published for aquatic periphyton (Hillebrand 2002), seagrasses (Hughes *et al.* 2004) and marine systems in general (Burkepile & Hay 2006). However, we lack a quantitative comparative synthesis across diverse ecosystem types to address the broad

predictions that: (i) bottom-up control is pervasive but top-down control is more influential in aquatic habitats relative to terrestrial systems and (ii) bottom-up and top-down forces are interdependent and typically show non-additive interactions that synergize or dampen relative influences on producer biomass. In the most comprehensive meta-analysis to date, we combined 191 factorial manipulations of herbivores and nutrients from freshwater ( $n = 116$ ), marine ( $n = 60$ ) and terrestrial ( $n = 15$ ) ecosystems in a quantitative assessment of the relative and interactive effects of fertilization and herbivory on the standing biomass of producers. Across ecosystems and habitats, we show that emergent interactive effects of

nutrient resource and consumer controls on community biomass are weak and rare. By comparing these results with our model predictions, we identify candidate mechanisms responsible for the observed patterns. We end with a research agenda for further exploration into mechanisms that dampen or amplify the relative and interactive strength of resource and consumer controls of producer communities.

## METHODS

### Data extraction

Studies analysed in this contribution are a subset from the ELSIE database (ecological synthesis of interactive experiments), created within a workshop hosted by the National Center for ecological analysis and synthesis (metadata available at [knb.ecoinformatics.org/](http://knb.ecoinformatics.org/)). Studies were selected by examining the abstracts of all publications returned from searches on ISI Web of Science (1965–2006) using the following search strings: [herbivor\* or graz\* or consum\*] and [resourc\* or nutrient\* or fertili\*]; ['top-down' and 'bottom-up' and ecolog\*]. We also included data from studies reported in other syntheses (Proulx & Mazumder 1998; Hillebrand 2002; Shurin *et al.* 2002; Borer *et al.* 2005; Hillebrand 2005; Burkepille & Hay 2006; Elser *et al.* 2007; Hillebrand *et al.* 2007) and searched both the literature cited in those papers and all subsequent citations of those analyses. Citations for the 83 included papers (containing 191 independent experiments) are listed in the Appendix S1.

Studies were included only if they (i) directly manipulated nutrient resource availability through fertilization of nitrogen (N), phosphorus (P), or both; (ii) manipulated herbivorous animal assemblages through mechanical exclusion, enclosure (such as in mesocosms), or chemical or manual removal; (iii) crossed these treatments in a full factorial design; and (iv) reported mean community-level biomass responses of producers to these factorial manipulations. Population-level studies and single species responses of producers were only considered if they were (i) drawn from a mono-dominant community (as judged by the original authors), or (ii) mean community-level biomass response(s) could be calculated from single species responses within a study. In several cases where all criteria were met but published data presentation was incomplete, we requested original data from authors. Although multiple levels of a factor (e.g. multiple nutrient levels) were extremely rare in the dataset, as standard practice we used the highest resource additions and most comprehensive herbivore removals that retained the full factorial design. Previous analyses expanding greatly on the present dataset showed that fertilization effect sizes across systems were independent of rates or quantities of applied nutrients (Elser *et al.*

2007). Those analyses did not demonstrate the rates are unimportant; instead, they showed that most investigators added nutrients in excess and successfully removed nutrient limitation in their experiments.

We defined a study as a temporally and spatially distinct sample with appropriate, consistent controls. Multiple studies could be reported from within one publication if the same experimental treatments were performed in multiple locations with differing physical and/or biological conditions. When multiple measures were reported over time from the same experiment, we used the last temporal sample in order to avoid phases of transient dynamics. Exceptions were made if some unusual disturbance affected some or all of the treatments or replicates. In these cases, we used the most robust values by deferring to the working knowledge and intuition of the original authors.

At the most basic level, studies were classified into three broadly recognized system categories: freshwater, marine and terrestrial. We divided these classes further into habitats defined primarily by physical habitat structure or strata (e.g. aquatic studies focused on benthic or pelagic producers) and the dominant producers in that medium or substrate (e.g. terrestrial habitats were grouped as herbaceous 'grasslands' or woody 'forests'). Examples such as salt marshes or wetlands were more difficult to classify. Operationally, studies addressing periphyton or macrophytes, submerged or floating, were defined as aquatic (marine or freshwater); whereas studies on above-water, rooted plants were assigned to terrestrial systems (e.g. *Spartina*, Gough & Grace 1998). The resulting eight habitat categories were defined as follows: lake pelagic, lake benthic, stream benthic (freshwater); coastal soft bottom, coastal rocky temperate reef, coral reef and oceanic (marine); grassland and forest (terrestrial). Other classification schemes are plausible, and other categories are possible within our scheme but were not included because appropriate empirical studies were lacking (e.g. stream pelagic). We could find only one oceanic pelagic study that met our criteria (Sommer 2000); this study was used in broad comparisons but dropped from habitat-level analyses.

Data were extracted from tables or digitized figures using the GrabIt! XP add-in for Microsoft Excel (Datatrend Software Inc., Raleigh, NC, USA). The preferred producer community metric was standing dry biomass per unit area, although we also accepted the following proxy variables that have been shown to be highly correlated with standing biomass (Buck *et al.* 2000): chlorophyll, ash-free dry mass, wet biomass, fixed carbon, biovolume, percent cover or net (total, aboveground, belowground) primary production per area. These inclusive criteria incorporated more studies into the database and allowed broad comparisons across systems. Where multiple acceptable biomass measures were reported, we entered all measures and calculated mean standardized

response ratios for each study. While productivity is often decoupled from standing stock biomass, particularly in systems with high turnover, twelve studies in our dataset reported both measurements and showed strong positive correlations (LRR<sub>H</sub>:  $r = 0.682$ ,  $P = 0.0146$ ; LRR<sub>F</sub>:  $r = 0.859$ ,  $P = 0.0003$ ; LRR<sub>I</sub>:  $r = 0.622$ ,  $P = 0.031$ ; d.f. = 10 for all). Counts of individuals within a community were excluded because organisms can vary in body size by orders of magnitude between systems, and because body size usually relates inversely to abundance (Cohen *et al.* 1993; Cyr *et al.* 1997). Because multiple studies were often reported from a single publication, and from a smaller pool of principal investigators, we assigned categorical variables indicating publication units and the identities of principal investigators. The robustness of our results was checked with diagnostics, for instance by comparison of log ratios computed from different biomass metrics within the same studies or after pooling studies by publication or laboratory source (Englund *et al.* 1999).

### Calculation of effect sizes

We used the log response ratio as the effect size metric (generally:  $\ln[\text{treatment}/\text{control}]$ ). The log response ratio (LRR) is one of the most commonly used effect metrics in ecological meta-analysis (Hedges *et al.* 1999; Lajeunesse & Forbes 2003). The analysis of treatment responses relative to that of the control is more meaningful than standardized absolute differences between means when comparing between systems. Unlike Hedge's  $d$ , the log response ratio does not require a measure of sample variability and does not weight individual studies by their variance, which would favour small-scale well-replicated studies over large-scale, presumably more realistic studies. Moreover, the distributions of log ratios typically conform to a normal distribution, making them suitable for a wide range of parametric statistical tests (Hedges *et al.* 1999). Finally, the log response ratio simplifies the interpretation of statistical interactions as in the cases of multiple predator interactions (Wootton 1994) and trait-mediated interactions (Okuyama & Bolker 2007). Calculating effects on the log response scale allows interpretation of positive and negative statistical interactions in terms of specific ecological interactions (Box 1).

We used factorial meta-analysis to calculate LRR effect sizes (Gurevitch *et al.* 2000; Hawkes & Sullivan 2001; Borer *et al.* 2006). To ease interpretation and facilitate direct comparison between the magnitudes of nutrient and herbivore main factors, we constructed the log ratios such that main effects were expected to be *positive*. That is, we assigned the controls as unfertilized (F0) and with herbivores present (H1); the fertilization and herbivore absence treatments were expected on average to increase producer biomass. For all factorial experiments included herein, we

calculated the main fertilization (LRR<sub>F</sub>), main herbivore (LRR<sub>H</sub>) and the interaction effect size (LRR<sub>I</sub>) as:

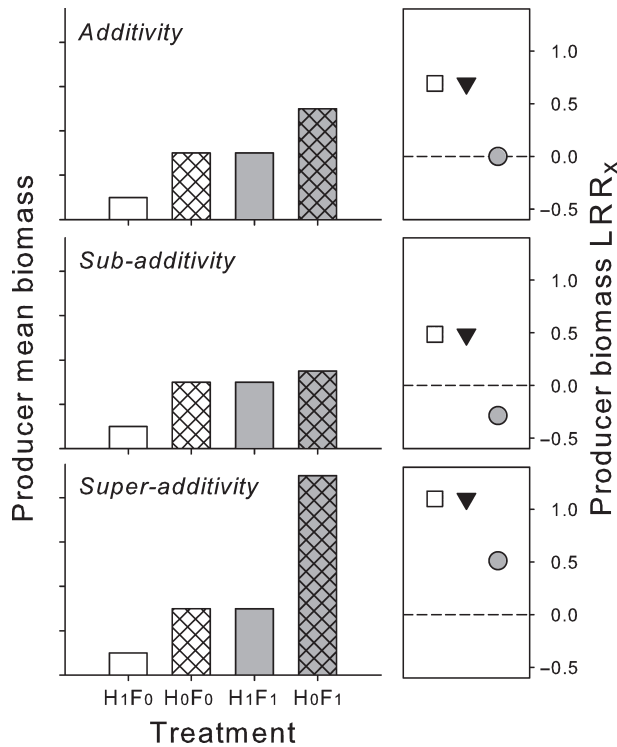
$$\text{LRR}_F = (\ln \bar{Y}_{\text{H0F1}} + \ln \bar{Y}_{\text{H1F1}}) - (\ln \bar{Y}_{\text{H0F0}} + \ln \bar{Y}_{\text{H1F0}}) \quad (1a)$$

$$\text{LRR}_H = (\ln \bar{Y}_{\text{H0F1}} + \ln \bar{Y}_{\text{H0F0}}) - (\ln \bar{Y}_{\text{H1F1}} + \ln \bar{Y}_{\text{H1F0}}) \quad (1b)$$

$$\text{LRR}_I = (\ln \bar{Y}_{\text{H1F0}} + \ln \bar{Y}_{\text{H0F1}}) - (\ln \bar{Y}_{\text{H1F1}} + \ln \bar{Y}_{\text{H0F0}}) \quad (1c)$$

We used the average biomass of grazed unfertilized ( $\bar{Y}_{\text{H1F0}}$ ), grazed fertilized ( $\bar{Y}_{\text{H1F1}}$ ), ungrazed unfertilized ( $\bar{Y}_{\text{H0F0}}$ ) and ungrazed fertilized ( $\bar{Y}_{\text{H0F1}}$ ) treatment combinations to calculate these log response ratios. Nonparametric 95% confidence intervals (CI) were calculated by bootstrap sampling from effect size pools with 999 iterations (Rosenberg *et al.* 2000). Non-overlapping CI were used as conservative tests for statistically significant differences in effect sizes among groups or a significant deviation of an effect size from zero.

A baseline case for interpreting the LRR effect sizes can be simplified as follows (Box Fig. 1a). Suppose fertilization and herbivore exclusion each affect the population growth rate of autotrophs such that at the end of the experiment the mean final biomass levels for the single-factor treatments are  $\Delta F \bar{Y}_{\text{H1F0}}$  and  $\Delta H \bar{Y}_{\text{H1F0}}$ , respectively, again where  $\bar{Y}_{\text{H1F0}}$  is the biomass of the grazed, unfertilized control. Further assume that the effects of fertilization ( $\Delta F$ ) and herbivore exclusion ( $\Delta H$ ) are independent, namely that one treatment does not alter the linear growth rate effect of the other. Under the combined treatment (i.e. fertilized and ungrazed), the resultant biomass of autotrophs will be  $\Delta F \Delta H \bar{Y}_{\text{H1F0}}$ , the product of the two independent effects and the control biomass. These treatments have multiplicative effects relative to the control biomass, as realized in an exponential growth model or from the equilibrium of a simple dynamic model. Because log-transformations are implicit to LRR, eqns 1a–c reduce to simple sums of  $\ln(\Delta F)$ ,  $\ln(\Delta H)$  and  $\ln(\bar{Y}_{\text{H1F0}})$ . Given that both factors have a positive effect on autotroph growth rate (i.e. both  $\Delta F$  and  $\Delta H$  exceed unity), each of the main effect ratios, LRR<sub>F</sub> and LRR<sub>H</sub>, will be positive. With independence of fertilizer and herbivore exclusion effects, however, the interaction effect (LRR<sub>I</sub>) will reduce to zero, and we define this as simple 'additivity' of effects. If the interaction effect is positive (or negative), we conclude that the joint effects of fertilization and herbivore exclusion are greater than (or less than) the product of the two main effects [defined as 'super-additivity' (or 'sub-additivity')] and thus the main effects are not independent. Notably, results from studies finding untransformed additive effects of treatments (fertilization:  $\Delta F + \bar{Y}_{\text{H1F0}}$ ;



**Figure 1** Potential main and interactive effects of fertilization and herbivore absence/removal on plant community biomass. The first column shows hypothetical mean community biomass in factorial fertilization (grey bars) and herbivore removal/exclusion (hatched bars) treatments; the second column shows the calculated patterns expected for log response ratios ( $LRR_x$ ) for the fertilization (open square) and herbivore exclusion (black triangle) main effects and their interaction (grey circle). The top row shows hypothetical additivity of the main factors; second row, sub-additive or dampening interaction; and third row, super-additive or synergistic interactive effects.  $LRR_x$  were calculated using empirical means and eqns 1a–c in the main text.

herbivore removal:  $\Delta H + \bar{Y}_{H1F0}$ ; fertilization and herbivore removal:  $\Delta F + \Delta H + \bar{Y}_{H1F0}$  would be defined as sub-additive here. Figure 1 translates, by hypothetical example, empirical means from the factorial treatment combinations into emergent additive, sub-additive and super-additive log response ratios, and the box provides empirical predictions for commonly reported relationships between fertilization and herbivore activity.

### Statistical analysis

A fixed-model analysis of heterogeneity (Rosenberg *et al.* 2000) using the  $Q$  statistic tested the null hypothesis that replicate effect sizes within groups represent a single effect size. A significant  $Q$  test suggests the presence of additional variation not explained by grouping variables (e.g.  $LRR_F$  by ecosystem type). A nonsignificant test suggests that effect

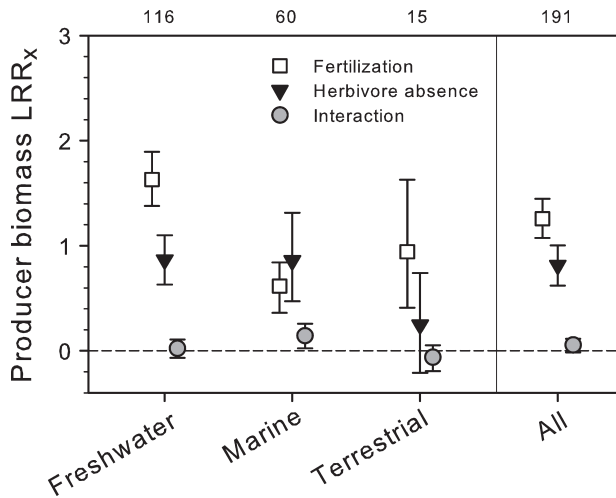
sizes across experiments are homogenous within a group, not the pooled average of opposing effects from a multimodal distribution (Hedges *et al.* 1999). We used this test to explore heterogeneity in effect sizes within ecosystems and habitat types, and within categorical methodological groups such as venue (lab, field experiment), consumer manipulation type (exclosure, enclosure, removal), consumer type (vertebrate, invertebrate, both) and predominant community producer type (phytoplankton, periphyton, macroalgae, herbaceous, woody).

In addition to the above categorical variables, we examined continuous variables representing experiment size (area of replication units), study duration, latitude and background ecosystem availability or total dry content of nitrogen and phosphorus. Most continuous variables, particularly for background nutrient measurements, lacked data for subsets of studies, making it problematic to use multiple regression and model selection with the multivariate dataset. Therefore, we explored relationships of these variables with LRR in separate regression analyses. We used the *R* statistical package for these analyses (<http://www.r-project.org/>).

### RESULTS

Our meta-analysis included 191 factorial manipulations of nutrient addition and consumer removal across freshwater, marine and terrestrial ecosystems. Across all systems, fertilization increased the standing biomass of producers 3.5-fold relative to controls (mean  $LRR_F = 1.26$ ; Fig. 2). This effect was highest in freshwater ( $LRR_F = 1.63$ ), intermediate in terrestrial studies ( $LRR_F = 0.94$ ) and lowest in marine experiments ( $LRR_F = 0.62$ ). The net effect of removing herbivores also was positive across all studies ( $LRR_H = 0.82$ ), with roughly equivalent effect sizes within freshwater and marine systems ( $LRR_H = 0.87 \approx 0.86$ , respectively) but with a variable and nonsignificant mean effect across 15 terrestrial studies ( $LRR_H = 0.25$ , 95% CI =  $-0.22$  to  $0.74$ ). The overall statistical interaction of fertilization and herbivore exclusion did not differ from simple additivity ( $LRR_I = 0.05$ ). We found similarly small interaction effect sizes in freshwater ( $LRR_I = 0.02$ ) and terrestrial ( $LRR_I = -0.06$ ) systems. However, the  $LRR_I$  from marine systems was significantly positive (i.e. greater than expected from additivity) showing a modest synergistic response to fertilization with herbivore removal ( $LRR_I = 0.14$ , CI =  $0.02$  to  $0.26$ ).

Broken down within habitat classifications,  $LRR_F$  was uniformly, significantly positive, although the strongest responses were observed in freshwater habitats (Fig. 3). Similarly, removal or exclusion of herbivores produced significantly positive  $LRR_H$  in all habitats except grasslands, where the effect was negative although still overlapping zero



**Figure 2** Natural log response ratio (LRR = ‘effect size’) of fertilization (white squares), herbivore absence (black triangles) and their interaction (grey squares) on producer biomass across freshwater, marine, terrestrial and all systems combined ( $n = 191$ ). Sample sizes for each category are given across the top panel. An LRR is statistically significant when the boot-strapped 95% confidence intervals do not overlap the dashed line of zero effect, and is statistically distinct from other LRR when 95% CI do not overlap. A significant interaction (LRR<sub>I</sub>) indicates super-additive (positive) or sub-additive (negative) effects of herbivore absence and nutrient addition.

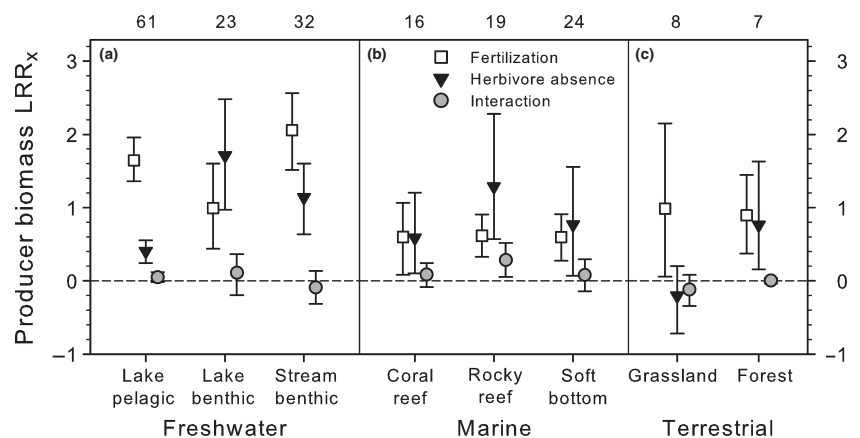
(LRR<sub>H</sub> = -0.203, CI = -0.72 to 0.20). The strength of herbivore control on producer biomass often rivalled the strength of resource control, most notably in all marine habitats, in lake benthos and in forests. The LRR<sub>F</sub> was significantly stronger than LRR<sub>H</sub> only in the pelagic zone of lakes, which represented the greatest replication of any habitat and apparently drove the pattern observed for freshwater systems (Fig. 2). Interaction effect sizes and CI bounded zero in all habitats except temperate rocky reefs, where the effect was significantly positive (LRR<sub>I</sub> = 0.28,

CI = 0.053 to 0.52). Again, the pattern within this habitat apparently drove the positive pattern observed in marine systems as a whole (Fig. 2).

Analyses of heterogeneity demonstrated significant variation between experiments in both LRR<sub>F</sub> and LRR<sub>H</sub> overall, but showed negligible variation in LRR<sub>I</sub> (Table 1). When partitioned among ecosystems and habitats, terrestrial systems showed negligible heterogeneity for all LRR, with the exception of LRR<sub>F</sub> in grassland habitats ( $Q = 18.41$ , d.f. = 7,  $P = 0.01$ ). All freshwater habitat divisions and coastal soft bottom communities in marine systems showed heterogeneity in LRR<sub>F</sub>, but responses in temperate rocky reefs ( $Q = 7.98$ , d.f. = 18,  $P = 0.98$ ) and coral reefs ( $Q = 6.76$ , d.f. = 15,  $P = 0.96$ ) were homogenous. Aquatic subsystems – except lake pelagic habitats ( $Q = 22.26$ , d.f. = 60,  $P > 0.99$ ) – retained significant heterogeneity in LRR<sub>H</sub>. Notably, no system- or habitat-level group showed significant unexplained heterogeneity in LRR<sub>I</sub>.

We also considered the mitigating or potentially confounding influence of various categorical and continuous covariates on factorial effect sizes. These complete results are presented in the online Appendix S2, but we highlight the key findings here. Across different dominant plant community types, fertilization and herbivore exclusion increased community biomass and there were no interactive effects, although relative response strengths varied within and among producer community types (Fig. S1a). Most studies ( $n = 159$ ) manipulated invertebrate herbivores, although 32 studies manipulated vertebrates (including 9/15 terrestrial studies), either alone or in combination with invertebrates (Fig. S1b). The average LRR<sub>H</sub> for invertebrates was significantly positive, but studies including vertebrate herbivores showed highly variable effects that overlapped with those from invertebrates alone. Fertilization effect sizes were somewhat stronger in removal experiments (relative to enclosure and exclosure studies, Fig. S1c) and in lab studies (relative to field studies, Fig. 1Sd).

**Figure 3** LRR<sub>X</sub> of fertilization (white squares), herbivore absence (black triangles) and their interaction (grey squares) on producer biomass across habitat types within freshwater (a), marine (b) and terrestrial (c) systems. Sample sizes for each habitat are given across the top panel (see Methods text for habitat definitions). An LRR is statistically significant when the boot-strapped 95% confidence intervals do not overlap the dashed line of zero effect, and is statistically distinct from other LRR when 95% CI do not overlap.





**Table 1**  $Q$  heterogeneity statistics for log response ratios of fertilization (LRR<sub>F</sub>), herbivore absence (LRR<sub>H</sub>) and the interaction effects (LRR<sub>I</sub>)

	d.f.	LRR <sub>F</sub>	LRR <sub>H</sub>	LRR <sub>I</sub>
Total	190	<b>343.72***</b>	<b>367.01***</b>	42.83
Freshwater	115	<b>225.58***</b>	<b>197.26***</b>	28.09
Lake pelagic	60	<b>89.95**</b>	22.26	4.52
Lake benthic	22	<b>49.11**</b>	<b>79.2***</b>	10.72
Stream benthic	31	<b>71.43***</b>	<b>63.79***</b>	12.21
Marine	59	53.57	<b>150.75***</b>	13.09
Coastal soft bottom	23	<b>38.35*</b>	<b>46.2**</b>	3.77
Coastal rocky reef	18	7.98	<b>62.62***</b>	5.28
Coral reef	15	6.76	<b>36.52**</b>	3.47
Terrestrial	14	22.29	13.79	0.88
Grassland	7	<b>18.41*</b>	3.35	0.8
Forest	6	3.86	6.94	0.018

$Q$  statistics, using fixed models of heterogeneity analysis (Hedges *et al.* 1999), are given for the total data set, and after partitioning among systems and habitats. Significant  $Q$  scores are indicated with bold font and asterisks ( $0.05 > P > 0.01^*$ ;  $0.01 > P > 0.001^{**}$ ;  $P < 0.001^{***}$ ).

The LRR were invariant as a function of latitude (absolute value), with the lone exception that LRR<sub>H</sub> showed stronger effects with increasing latitude within freshwater systems (Fig. S2a). Moreover, there were no linear correlations of LRR effect sizes with the area of experimental plots, within or across systems (Fig. S2b). However, the overall fertilization effect across all studies declined significantly with log-transformed experimental duration in days (Fig. S2c). This modest effect can be explained by the differing characteristic time scales used to capture producer dynamics within different systems and habitats. Typical terrestrial studies ran for multiple years (mean  $\pm$  SE duration in days,  $993.8 \pm 255.7$ ), freshwater studies averaged  $< 1$  month ( $27.7 \pm 6.6$ ) and marine studies were intermediate in duration ( $81.1 \pm 17.5$ ; 1-way ANOVA:  $F_{2,187} = 83.245$ ,  $P < 0.0001$ ). The one exception was that LRR<sub>I</sub> showed a modest trend from net positive to net negative with increasing duration in marine studies (Fig. S2c), yet study durations across habitat types in marine systems were not significantly different (Rocky reef:  $133.1 \pm 51.4$ ; Coral:  $67.8 \pm 15.4$ ; Soft bottom:  $52.2 \pm 8.8$ ; 1-way ANOVA:  $F_{2,56} = 0.205$ ,  $P = 0.815$ ).

The LRR showed no relationship with ambient total or available nitrogen (data availability restricted analyses to marine and freshwater systems, Fig. S3a). However, LRR<sub>I</sub> was weakly, negatively related to standardized phosphorus availability within aquatic systems overall, and in freshwater and marine systems individually (Fig. S3b).

## DISCUSSION

The evidence from 191 studies, as expected, shows clear statistical significance of both nutrient resources and herbivorous consumers in freshwater, marine and terrestrial systems and broad subhabitats within. Although herbivore effects within terrestrial herbaceous systems were variable and nonsignificant (Fig. 3; albeit hindered by small sample size,  $n = 8$ ), fertilization and herbivore effect sizes were comparable and overlapping within most habitat types. Overall, fertilization caused larger changes in producer biomass than herbivory (Fig. 2), but this difference was driven predominantly by the large number of freshwater studies, which were in turn dominated by lake phytoplankton studies (Fig. 3a). The near equivalence and marked independence of fertilization and herbivore effect sizes (as demonstrated by interaction effects that were predominantly indistinguishable from zero), qualitatively support our baseline additivity scenario (Box Fig. 1a) as the modal case. These data provide additional justification to retire the antediluvian notion that *either* top-down *or* bottom-up forces predominantly control plant biomass within major ecosystem types.

The statistical additivity and comparable strength of resource and herbivore effects provide qualified support for resource-control models, such as donor-control (De Angelis 1975), food-limitation (Schmitz 1992) and induced defenses (Vos *et al.* 2004). This class of models predicts fertilization effect sizes will be larger, more important than, and independent of modest herbivore effects (Chase *et al.* 2000a). Another qualitatively similar possibility is that consumers recycle mineral nutrients in waste products proportional to the losses incurred from herbivory, resulting in negligible net interactive effects on producer community biomass (Box Fig. 1e; de Mazancourt *et al.* 1998; Glibert 1998; Elser & Urabe 1999). Support for these scenarios comes from our analysis of lake pelagic studies: there were no significant interaction terms and fertilization effects were fourfold greater than, and non-overlapping with, herbivore effects (Fig. 3; LRR<sub>F</sub> = 1.64, 95% CI = 1.36 to 1.95; LRR<sub>H</sub> = 0.40, CI = 0.24 to 0.55; LRR<sub>I</sub> = 0.05, CI = -0.02 to 0.12). Previous analyses using a much larger fertilization dataset (including most studies contained herein) showed that fertilization effect sizes across systems were independent of rates or quantities of applied nutrients (Elser *et al.* 2007). Therefore, the great majority of studies successfully alleviated nutrient limitation, and system-specific tendencies in fertilization methods do not explain system differences in effect sizes. Similarly, herbivore manipulations across systems endeavoured to completely remove or exclude targeted consumer guilds and the limitations they impose on producer communities. In both cases, however, other limiting factors may have played

enhanced roles; we outline several important mechanisms below.

Numerous mechanisms are consistent with the pattern of additivity that characterizes our baseline model (Box Fig. 1a) and the simple nutrient recycling model (Box Fig. 1e). Herbivore population or behavioural responses to high resource patches may be limited in turn by top-down control of higher-order consumers (Oksanen *et al.* 1981), or intraguild processes, such as territoriality (Seabloom & Reichman 2001). Producer communities can compensate for herbivory at the individual, population and community levels (Trumble *et al.* 1993; Hawkes & Sullivan 2001; Seabloom 2007), and consumer communities may compensate for the removal of targeted guilds in experiments, for instance if invertebrates invade cages built to exclude larger vertebrate consumers (Ritchie 2000). These processes are less likely in laboratory or mesocosm experiments than in less tightly constrained field experiments. Although we observed stronger positive main effects in lab experiments, we observed no difference in the magnitude or direction of the interaction term (Appendix S2). However, neither our simple Lotka–Volterra characterization, nor the design of existing factorial herbivore and nutrient manipulations, can distinguish these possibilities that could explain the mechanistic additivity of resource and consumer controls.

Several notable exceptions in our analysis from the overall pattern of additivity may shed light on the mechanisms and parameter sets that can create nonlinear interactions of consumers and nutrients. Studies from coastal marine ecosystems (Fig. 2), and in particular, temperate rocky reef substrates (Fig. 3) yielded an emergent super-additive statistical interaction. Empirical examples consistent with this finding can be drawn from individual studies in other systems (e.g. Sarnelle 1992; Rosemond *et al.* 2000), but super-additivity was not the dominant pattern observed in this meta-analysis. Our results from temperate rocky reefs corroborate independent analyses by Burkpile & Hay (2006), who used datasets partially overlapping with ours and Hedges *d* as their metric of effect size. Dynamical scenarios suggest that functional or numerical responses of herbivores to greater abundance or quality of producers (Box Fig. 1b), or resource-mediated shifts in composition to tolerant and rapidly growing species (Box Fig. 1c) can generate this community response. Functionally important marine macrograzers can impose persistent pressure on algal communities because their algal resource populations turnover more rapidly than the macrograzers (Vance 1979). These herbivores may preferentially consume nutrient-rich producers, either in response to community shifts to more palatable species or increased quality of the same species (Boyer *et al.* 2004). Marine producers lack many carbon-rich structural compounds (e.g. lignins) that strengthen cell walls, increase resistance to herbivores, and

reduce digestibility in terrestrial systems (Polis & Strong 1996). As a result, at least in temperate systems, herbivore removal and nutrient enrichment often favour fast-growing weedy species that rapidly accumulate biomass (e.g. *Ulva*, Nielsen 2003; Valiela *et al.* 2004). While our analyses illuminate patterns across and within systems, more detailed analyses within communities are needed to fully explore these dynamics.

Another class of models predicts a sub-additive interaction in food webs comprising heterogeneity within prey trophic levels (Box Fig. 1d; Leibold 1989; Grover 1995; Leibold 1996; Hall *et al.* 2006). With increasing nutrient resource availability, producers may respond to grazing pressure through shifts in chemistry or composition to less edible, more resistant forms. This phenomenon has been reported most frequently in planktonic communities: zooplanktonic grazers can induce shifts in colony or individual size of plankters at the population level, or can precipitate species turnover and changes in community structure (Leibold 1996; Leibold *et al.* 1997; Long *et al.* 2007). Resistance also can arise through demographic transitions of producer communities to invulnerable life stages (Darcy-Hall & Hall 2008); for example in terrestrial systems, trees are invulnerable to most vertebrate and invertebrate grazers and browsers. However, while individual cases again can be identified in support of this scenario (e.g. Peterson *et al.* 1993; Liess & Hillebrand 2006), in the aggregate we fail to find conclusive, general support for sub-additive interactive effects on producer community biomass, indicating that overall, these responses are uncommon. Intriguing evidence from aquatic studies suggest that sub-additive effects may be more important in systems already severely eutrophied (Fig. S3; marine and freshwater  $LRR_I$  negatively related to ambient available phosphorus), or when experimental manipulations are pressed for a time period sufficient to observe plasticity in producer responses (Fig. S2b; marine  $LRR_I$  weakly, negatively related to study duration).

One plausible explanation for an interaction effect size near zero is that divergent positive and negative outcomes simply cancel, and the average effect subsumes processes from a distribution of effects with multiple peaks. However, our results from analyses of heterogeneity convincingly reject this explanation for  $LRR_I$  (Table 1). Statistically significant between-experiment variation, as measured by the  $Q$  statistic, rejects the null hypothesis that all effect sizes within a group represent a single homogenous effect size (Hedges *et al.* 1999). We report significant  $Q$ -values within systems and categorical indicator variables for  $LRR_H$  and  $LRR_F$  main factors – certainly illustrative of responses to the diversity of taxa, biotic venues, experimental methods, and other covariates included in our analysis. However, the uniformly small and nonsignificant  $Q$ -values for  $LRR_I$

provide no evidence for statistical averaging of negative and positive interactive effects.

The possibility for interactive outcomes may hinge critically on the time scales used in experiments. Typically, analyses of population or community limitation (*sensu* Osenberg & Mittelbach 1996) are assessed for short durations, whereas analyses of control or regulation necessarily require multiple generations to allow dynamics and feedback loops among species. In simple model aquatic systems, enriched consumer–resource systems can oscillate unpredictably over time scales that permit population dynamics (i.e. ‘paradox of enrichment’, Rosenzweig 1971; Diehl 2007). In terrestrial systems, herbivore selectivity of palatable plants can create different community outcomes in the long term (5+ years) relative to the short term (1–2 years) because plant community responses are time-lagged (Howe *et al.* 2006; Olofsson *et al.* 2007). If biomass removal is moderate or transitory, grazers can facilitate shifts to assemblages dominated by tolerant species better able to rapidly compensate for herbivory (Augustine & McNaughton 1998). Experiments with large vertebrate herbivores have demonstrated grazer-mediated shifts in plant communities away from woody cover to herbaceous cover (Altesor *et al.* 2006; Pringle *et al.* 2007). In a meta-analysis of individual plant population responses to herbivory and fertilization, Hawkes & Sullivan (2001) showed that opposing interactive responses depend on terrestrial plant growth form: basal meristem dicots compensated for herbivory more under high nutrient regimes (consistent with tolerance, Box Fig. 1c), whereas growth of dicot herbs and woody plants improved following herbivory in unfertilized treatments (consistent with induced resistance, Box Fig. 1d). Sustained numerical responses of herbivores may thus shift community composition in trajectories dependent on resources available to plants, but without appreciable changes in total community biomass (Olf & Ritchie 1998; Chase *et al.* 2000a; Hillebrand *et al.* 2007). Although we showed only weak dependence of LRR on study duration (Appendix S2), a greater range of durations across systems is clearly needed to provide additional power to test these hypotheses.

The size of an experimental arena can affect the spatial and temporal heterogeneity of responses, and thus may have profound effects on top–down and bottom–up dynamics. Increased heterogeneity decreases the efficiency of consumers in controlling plant community biomass (Hunter & Price 1992; Poff & Nelson-Baker 1997), although the heterogeneity imposed by herbivores on vegetation depends on the spatial scaling of the interaction (Adler *et al.* 2001; Flecker & Taylor 2004). Moreover, reduction in the spatial scale of an experiment increases the importance of edge dynamics and neighbourhood effects (Kawata *et al.* 2001; Palmer *et al.* 2003). Despite these clear-cut expectations, our analysis showed remark-

ably consistent effect sizes of herbivore removal and fertilization across a range of experimental scales, both across and within ecosystem types (Fig. S2b).

### Prospects and future directions

Quantitative syntheses are critically important for organizing current knowledge to identify consistent trends, testing and proposing hypotheses and identifying knowledge gaps and research needs for particular organisms, systems and mechanisms. In this analysis, we demonstrated the generality of several patterns: (i) herbivores and nutrient resources control producer community biomass to similar degrees across freshwater, marine and terrestrial systems and (ii) interactive outcomes, in the currency of producer community biomass, are generally weak and rare. We close with recommendations for areas of research that can fill in gaps identified in this analysis.

Many ecologists have called for expansion of the temporal and spatial scales of experiments and additional replication of community-wide experiments in understudied systems. Our literature search reaffirms the oft-repeated conclusion (Polis *et al.* 2000; Shurin *et al.* 2002; Borer *et al.* 2006) that community-level studies of trophic dynamics from terrestrial ecosystems lag behind the literature accumulating from aquatic systems. Rather than echoing a general call for more studies, we urge focused implementation, particularly in terrestrial systems, of standardized, replicated field experiments across a spatial network of sites that can serve as standardized tests of trends revealed through meta-analysis. Moreover, enhanced experimental designs particularly relevant to understanding resource and consumer control call for independent, factorial manipulations of (i) multiple herbivore taxa and guilds (e.g. vertebrates and invertebrates), (ii) multiple trophic levels and (iii) multiple producer resources (e.g. nitrogen, phosphorus, light). Researchers should not limit investigations to producer community biomass, but should also (iv) explore responses of tissue nutrient content, species diversity, community composition and biological invasions to better understand the ecological mechanisms that result in additive biomass responses.

Small and large herbivorous consumers can have different impacts on producer communities by virtue of the temporal and spatial scales by which they select resources. For example, along a 10-fold gradient of primary productivity in herbaceous systems, large bodied grazers increased plant diversity at high productivity and decreased diversity at low productivity (Bakker *et al.* 2006; also see Hillebrand *et al.* 2007). Smaller-bodied consumers typically reduced diversity because their finer-grained feeding selectivity could eliminate rare species (Bakker *et al.* 2006). Invertebrate or small vertebrate consumers can penetrate vertebrate exclosures,

whereas larger-bodied herbivores can invade plots treated chemically to remove invertebrates. Compensation by these non-target herbivores may dampen or negate the effects of removal of targeted consumer groups (Pace *et al.* 1998; Bakker *et al.* 2004; Pringle *et al.* 2007). To better understand the generality of these interactions, more experiments are needed that manipulate the relative abundance and species and functional composition of herbivore communities in concert with manipulations of resource levels (Leibold & Wilbur 1992; Silliman & Ziemann 2001; Bakker *et al.* 2006). Clearly, additional insight but attendant complexity will come from experimental designs that incorporate multi-trophic food webs (Leibold 1996).

In addition to the expansion of design and scope of studies in various habitats, we need continued improvement of our theoretical understanding of nutrient–herbivore interactions in food webs. Much of our ecological intuition about nutrient–herbivore interactions, such as that reviewed in Box 1, arises from conventional Lotka–Volterra theory where adding nutrients affects herbivores primarily by increasing overall producer productivity (a ‘food quantity’ effect). However, it is widely recognized that food quality also has major effects on herbivore performance in a wide variety of ecosystems (White 1993; Huxel 1999), that nutrients and light affect the quality of plant production by both direct and indirect means (Sturner *et al.* 1998; Hall *et al.* 2007a) and that consumer-driven nutrient recycling provides an explicit mechanism by which herbivores can directly alter the quality of their resource base (Elser & Urabe 1999). The elaboration of stoichiometrically explicit food web models (e.g. Andersen *et al.* 2004) offers promise in better understanding why grazer and nutrient manipulations may or may not produce non-additive effects in different systems.

Concomitant with the development of more explicit expectations from stoichiometric models, experimental studies are needed that independently manipulate multiple resources with herbivore treatments – bulk treatments of both N and P (and often complete Osmocote™ applications) were used in most studies included in this meta-analysis. However, a respectable fraction of studies, primarily in freshwater habitats, used multiple independent nutrient manipulations crossed with herbivore treatments (e.g. Winterbourn 1990; McCormick & Stevenson 1991; Fox & Morrow 1992; Rosemond *et al.* 1993; Karjalainen *et al.* 1998; Vrede *et al.* 1999; Hartley & Mitchell 2005; Liess & Hillebrand 2006; McIntyre *et al.* 2006; Sawatzky *et al.* 2006). A critical mass of these experiments will facilitate general evaluations of the predictions from stoichiometric models. Construction and evaluation of stoichiometric predictions will also require a tailored understanding of the scenarios operating under field conditions (e.g. what resources are most limiting? Are the consumers limited by

food quality or food quantity? Are the producers regulated by intense grazing or low nutrient supply?).

Finally, understanding the commonalities and differences in trophic structure between ecosystems requires more than measuring species or community biomass. The debate concerning top–down and bottom–up control has focused on the increase or decrease of standing biomass at different trophic levels. However, both herbivore presence and resource addition have strong and interdependent effects on the species richness and evenness of producer assemblages (Hillebrand *et al.* 2007). Shifts in community structure will affect the propagation of bottom–up and top–down transfer of biomass in food webs and can mediate the strength of trophic cascades (Thébault & Loreau 2003, 2005; Schmitz 2006). The efficiency of plant resource use and biomass production can depend on the number of species present (Cardinale *et al.* 2006) and the dominance or evenness in the plant assemblage (Hillebrand *et al.* 2007). On the other hand, consumption of plant biomass is enhanced by increased herbivore diversity (Cardinale *et al.* 2006), whereas plant diversity can have both positive and negative effects on the rates of herbivory (Hillebrand & Cardinale 2004; Gamfeldt *et al.* 2005). Thus, incorporation of the structure of plant and herbivore assemblages into the discussion of resource and consumer control will enhance our understanding of how these factors independently and interactively constrain ecosystem properties and processes.

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## SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

**Appendix S1** List of publications used for data extraction.

**Appendix S2** Consideration of categorical and continuous covariates.

**Appendix S3** Equilibria for resource–autotroph–herbivore models.

**Figure S1** LRR<sub>X</sub> of fertilization (white squares), herbivore absence (black triangles) and their interaction (grey squares) on autotrophs as a function of: (a) dominant producer community type (phytoplankton, periphyton, macroalgae, herbaceous, woody); (b) consumer type (invertebrates, vertebrates, or both); (b) experimental method (enclosures, exclosures, or chemical/mechanical removal); and (c) experimental venue (field or lab).

**Figure S2** Producer log response ratio (LRR) effect sizes for fertilization (LRR<sub>F</sub>), herbivore absence (LRR<sub>H</sub>) and their interaction (LRR<sub>I</sub>) as a function of (a) latitude (absolute value), (b) area of herbivore manipulation replicates (m<sup>2</sup>, ln-transformed), (c) study duration in days (ln-transformed).

**Figure S3** Producer log response ratio (LRR) effect sizes for fertilization (LRR<sub>F</sub>), herbivore absence (LRR<sub>H</sub>) and their interaction (LRR<sub>I</sub>) as a function of (a) available N and (b) available P. Nutrient variables were standardized within systems by dividing by systems means.

**Table S1** Parameter definitions and relative units (per standard area) for resource–autotroph–herbivore models (see Box 1).

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