

Enrichment scale determines herbivore control of primary producers

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Abstract Anthropogenic nutrient enrichment stimulates primary production and threatens natural communities worldwide. Herbivores may counteract deleterious effects of enrichment by increasing their consumption of primary producers. However, field tests of herbivore control are often done by adding nutrients at small (e.g., sub-meter) scales, while enrichment in real systems often occurs at much larger scales (e.g., kilometers). Therefore, experimental results may be driven by processes that are not relevant at larger scales. Using a mathematical model, we show that herbivores can control primary producer biomass in experiments by concentrating their foraging in small enriched plots; however, at larger, realistic scales, the same mechanism may not lead to herbivore control of primary producers. Instead, other demographic mechanisms are required, but these are not examined in most field studies (and may not operate in many systems). This mismatch between experiments and natural processes suggests that many ecosystems may be less resilient to degradation via enrichment than previously believed.

Keywords Top-down versus bottom-up · Eutrophication · Consumer–resource dynamics · Experimental bias · Ideal free distribution · Ecological resilience

Introduction

Ecologists have long sought to understand how communities are structured and how (or if) consumers [“top-down” effects (Hairston et al. 1960; Oksanen et al. 1981; Sih et al. 1985)] and resources [“bottom-up” effects (Ehrlich and Birch 1967; Osenberg and Mittelbach 1996)] control this process. This academic debate has pressing, real-world implications, because land and fertilizer use by humans increasingly alter the dynamics of nutrients that limit primary production in both terrestrial and aquatic systems (Elser et al. 2007; Nixon 2009; Vitousek et al. 1997). In aquatic systems, nutrient-stimulated primary production can lead to toxic algal blooms, hypoxia and fish kills (Britburg et al. 2009). In marine systems, added nutrients can stimulate the growth of algae (Lapointe 1997; Lapointe et al. 2004, 1992), which can elicit a suite of negative ecological effects, including declines of corals (McCook et al. 2001; Rasher and Hay 2010; Smith et al. 2006), seagrasses (Burkholder et al. 2007), and kelp (Connell et al. 2008). Indeed, effects of algae on marine systems and associated losses in biodiversity and ecosystem services (e.g., fisheries, storm surge protection) are critical conservation concerns (Bellwood et al. 2004; Fabricius 2005; Hughes et al. 2010; Vitousek et al. 1997).

Field experiments that simultaneously manipulate consumer density (via exclusion designs) and nutrient availability have been used to evaluate the role of consumers in controlling primary producers in the face of eutrophication (Burkepile and Hay 2006; Gruner et al. 2008). Results from

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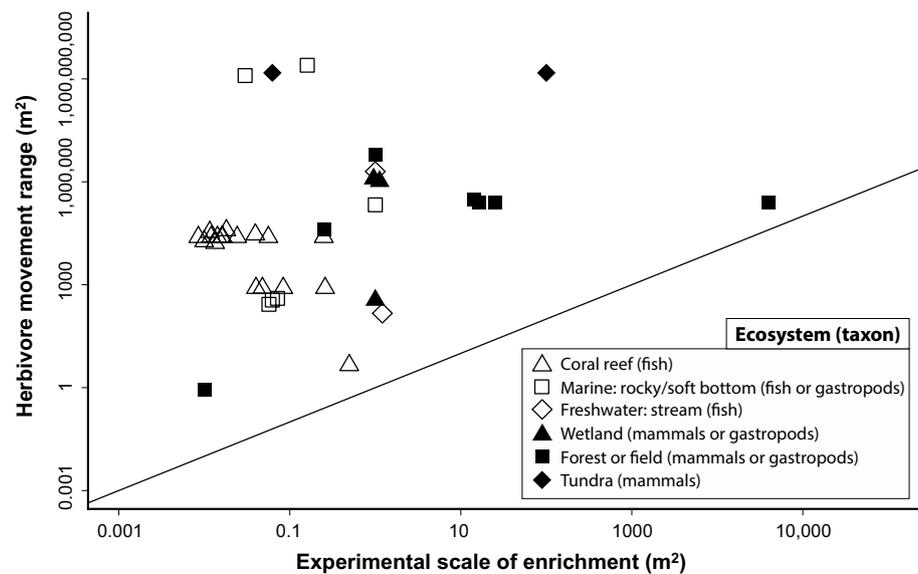
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Fig. 1 Herbivore movement range compared to experimental scale of enrichment in previous top-down versus bottom-up field experiments (nutrient addition fully crossed with herbivore exclusion) across systems and taxa (see Online Resource 1 for literature survey methods). The line indicates the 1:1 relationship, and overlapping points were jittered to show all points. The observed ratio of experimental scale to herbivore movement range was minuscule, with a median of 5.2×10^{-6}



these studies suggest that herbivores partially or fully compensate for the deleterious effects of enrichment on algal biomass and thus may facilitate the persistence or recovery of valuable marine ecosystems (Burkepile and Hay 2006). However, in nature, enrichment often occurs at spatial scales that are many orders of magnitude larger than the scale at which field manipulations are conducted. For example, coastal eutrophication due to nutrient enrichment has been documented across $\sim 30 \text{ km}^2$ off the northeast coast of Italy (Penna et al. 2004), $\sim 31 \text{ km}^2$ of inner Kaneohe Bay, Hawai‘i, USA (Smith et al. 1981), $>100 \text{ km}^2$ of both the Chesapeake Bay and Pamlico Sound, USA (Paerl et al. 2006), and $\gg 100 \text{ km}^2$ in the Great Barrier Reef, Australia (Bell et al. 2014). Yet, experiments are most often conducted at scales smaller than 1 m^2 (Burkepile and Hay 2006; Gruner et al. 2008). This mismatch in scale is well known (Burkepile and Hay 2006), although the effect of this possible bias has not been explicitly addressed. Thus, we are left uncertain how the results of small-scale field experiments might inform management of real ecosystems. Large-scale field manipulations would help, but they are rare and often unfeasible for both ethical and logistical reasons. Fortunately, consumer–resource theory frees us from these constraints and allows us to explore how well consumers can reduce effects of enrichment on primary producers and how these effects depend on spatial scale.

Traditional models of closed plant–herbivore systems posit that enrichment increases herbivore population growth, and, consequently, herbivore density. Increased density of herbivores then drives the abundance of primary producers back to the pre-enrichment state (Mittelbach et al. 1988; Oksanen et al. 1981; Rosenzweig 1971). Support for this mechanism has been provided by field experiments in closed systems with rapid consumer turnover [e.g.,

zooplankton in lakes (Carpenter and Kitchell 1988; Leibold 1989)]. However, in many other cases, experiments are conducted in open systems, with small plots accessible to herbivores that move over much larger spatial scales (Fig. 1). In these cases, herbivores can migrate in from surrounding areas, decoupling local resource dynamics from herbivore dynamics that operate at the regional scale. Furthermore, a true numerical demographic response by herbivores to enrichment would be unlikely or unimportant in many experiments, because: (1) the generation time of the focal herbivore often exceeds the duration of the experiment (Online Resource 1, Fig. A1); or (2) the offspring produced by local herbivores are dispersed over very large scales, as in many coastal marine systems (Hixon et al. 2002). Thus, the conditions of many field experiments preclude the application of consumer–resource theory developed for closed systems. In contrast, patch- or habitat-selection models may be more appropriate in these contexts.

Herbivores that are free to move between enriched and unenriched habitats may exhibit an “ideal free” distribution (Fretwell and Lucas 1970), in which herbivores have equal fitnesses in different habitats but their densities across the landscape are heterogeneous, reflecting underlying variation in resource production (Nicotri 1980; Oksanen et al. 1995; Power 1984; Sutherland 1983). In such scenarios, patch selection by herbivores (i.e., between enriched and unenriched patches) could drive responses of primary producers in top-down versus bottom-up field experiments, and the magnitude of these responses could depend on the spatial scale of the studies.

We used a mathematical model to evaluate whether the spatial scale of nutrient addition (from small experimental scales to larger, more natural scales) affects the ability of herbivores to control primary producers in the face of

enrichment. We solved our model analytically and found that across parameters space, increasing the scale of enrichment weakens herbivore control of primary producers. Our findings reveal a bias in previous short-term field experiments and suggest that many systems may be more vulnerable to ecologically harmful effects of nutrient enrichment than previously believed.

Model formulation and analysis

We used a mathematical model that simulates typical top-down versus bottom-up field experiments that consist of four treatments: caged plots that exclude herbivores versus open plots that permit herbivore access, crossed with ambient versus elevated nutrients. We designated $P_{i,j}$ as the density of the primary producer in the i th nutrient treatment (unenriched = U or enriched = E) and the j th herbivore treatment [indicating the presence (+), or absence (–) of herbivores]. To examine how increasing the size of experimental plots influences enrichment effects, we made the following assumptions:

1. The sessile primary producer grew logistically, with its intrinsic growth rate (r) and carrying capacity (K) greater in enriched versus unenriched habitat (i.e., $r_E > r_U$ and $K_E > K_U$).
2. Experimental plots were independent with respect to herbivore or nutrient treatments, i.e., plots were sufficiently separated to prevent the sharing of individual herbivores or nutrients.
3. Herbivores exhibited an ideal free distribution (Fretwell and Lucas 1970) over uncaged habitat within an area S_T , within which a single experimental plot was located. In effect, S_T represents the movement range of the herbivore. Thus, when a plot was uncaged and enriched, herbivore densities could differ between the enriched plot area, S_E , and the area of the surrounding, unenriched habitat, $S_{E,out}$ (Nicotri 1980; Oksanen et al. 1995; Power 1984; Sutherland 1983).
4. Herbivore density is sufficiently high that when herbivores redistribute themselves following enrichment, some herbivores remain in the unenriched areas surrounding the enrichment plot. As a result, and given assumptions 2 and 3, the equilibrium densities of primary producers in an enriched plot and the unenriched surrounding habitat within an area S_T will be equivalent in the presence of herbivores: i.e., $P_{E,+}^* = P_{E,+out}^*$, where “out” denotes unenriched habitat outside the enriched plot. We later relax this assumption.
5. Total herbivore abundance (N_T) was fixed within an area S_T (i.e., there was no reproduction, mortality, immigration or emigration). In other words, the timescale of the model

relative to herbivore generation time matched the short experimental duration that is characteristic of past studies (Online Resource 1, Fig. A1). Thus, for an unenriched open plot, herbivore density is $H_U = H_T = N_T/S_T$ (and homogeneous throughout S_T). In contrast, enriched, open plots create a locally heterogeneous landscape and thus the total herbivore abundance, N_T , must be partitioned between the enriched plot and the unenriched habitat that surrounds the plot: i.e., $N_T = S_E H_E + S_{E,out} H_{E,out} = S_E H_E + (S_T - S_E) H_{E,out}$, where H_E and $H_{E,out}$ are the herbivore densities in the enriched plot and the surrounding unenriched habitat, respectively (and both are >0 due to assumption 4).

6. Herbivores had a type I functional response, i.e., feeding rate increased linearly with the density of food (Holling 1966). The per capita consumption rate (α) was equal for herbivores feeding in enriched and unenriched habitat. (In Online Resource 2, we show that a type II functional response yields the same qualitative results, albeit more complex to solve.)

Given these assumptions, in the absence of herbivores (i.e., in caged plots), the equilibrium density of primary producers is set by their carrying capacity:

$$P_{U,-}^* = K_U, \text{ and} \tag{1}$$

$$P_{E,-}^* = K_E. \tag{2}$$

In the presence of herbivores, the dynamics of primary producers is set by the balance between logistic growth and herbivore consumption. For unenriched plots accessible to herbivores,

$$\frac{dP_{U,+}}{dt} = r_U P_{U,+} \left(1 - \frac{P_{U,+}}{K_U} \right) - \alpha H_U P_{U,+}, \tag{3}$$

and at equilibrium,

$$P_{U,+}^* = K_U \left(1 - \frac{\alpha H_U}{r_U} \right). \tag{4}$$

For enriched plots accessible to herbivores, we have to consider the dynamics of the enriched plot, as well as the adjacent unenriched habitat, because herbivores can distribute themselves between the two habitats. Thus, we have:

$$\frac{dP_{E,+}}{dt} = r_E P_{E,+} \left(1 - \frac{P_{E,+}}{K_E} \right) - \alpha H_E P_{E,+} \text{ and} \tag{5}$$

$$\frac{dP_{E,+out}}{dt} = r_U P_{E,+out} \left(1 - \frac{P_{E,+out}}{K_U} \right) - \alpha H_{E,out} P_{E,+out}. \tag{6}$$

Next, we set Eqs. 5 and 6 equal to 0 and solve for $P_{E,+}^*$ and $P_{E,+out}^*$, but based on assumptions of ideal free distribution (i.e., assumption 4: $P_{E,+}^* = P_{E,+out}^*$), we can

set these solutions equal to one another, and after a few more steps (involving substitutions for $H_{E,\text{out}}$ and H_E), we get the final solution:

$$P_{E,+}^* = \frac{K_E K_U [S_E r_E + (S_T - S_E) r_U - \alpha N_T]}{S_E r_E K_U + (S_T - S_E) r_U K_E}. \quad (7)$$

From this analytical solution, we see that the equilibrium density of primary producers ($P_{E,+}^*$) in uncaged, enriched plots always increases with the spatial scale of enrichment (S_E):

$$\frac{\partial P_{E,+}^*}{\partial S_E} = \frac{S_T K_E K_U r_E r_U (K_E - K_U)}{[S_E r_E K_U + (S_T - S_E) r_U K_E]^2} > 0. \quad (8)$$

This result (Eq. 8) was obtained assuming plots were independent (i.e., herbivores could not travel between plots: see assumption 2 above). If we relax this assumption (e.g., assume that all plots occur within the herbivore's foraging range), the qualitative result still holds (i.e., $\frac{\partial P_{E,+}^*}{\partial S_E} > 0$).

To quantify the scale dependence of the effect on primary producer biomass, we used results from our model (Eqs. 5–7), analyzed over a range of spatial scales and parameter values, to calculate the effectiveness of herbivores in controlling the enrichment effect on primary producers:

$$\text{Relative effectiveness of herbivores} = 1 - \left[\frac{(P_{E,+}^* - P_{U,+}^*)}{(P_{E,-}^* - P_{U,-}^*)} \right]. \quad (9)$$

This metric describes how well herbivores control the response of primary producers to added nutrients (numerator in second term) relative to the response of primary producers to nutrients in the absence of herbivores (denominator in second term). We then varied experimental plot size (S_E) to determine its effect on the equilibrium density of primary producers (Eqs. 1, 2, 4, 7) and the relative effectiveness of herbivores (Eq. 9).

When the scale of nutrient addition is small relative to the movement range of the herbivore (a ubiquitous characteristic of field experiments; Fig. 1), the density of primary producers in the enriched plots is low (Fig. 2a, b), and herbivore control of primary producers (Eq. 9) is very high (Fig. 2d, e). This is because herbivores move into the enriched plots from surrounding areas in response to localized increases in primary production. Thus, although production increases in the enriched plots, the increased density of the herbivores (via immigration) completely prevents an increase in the density of primary producers (when plots are very small). In contrast, primary producers increase in density (or biomass) in response to enrichment in the absence of herbivores.

However, as the scale of enrichment increases, herbivore density cannot respond to the same degree because of

the limited foraging area over which migration occurs. As a result, the density of primary producers increases with experimental scale (Fig. 2a–c) and herbivore control decreases (Fig. 2d–f). At very large scales (i.e., as the scale of the experiment approaches the scale of the herbivore's foraging range), the density of primary producers increases to its maximum (Fig. 2a–c), and herbivore control is reduced to its minimum (Fig. 2d–f). This large scale better matches real-world enrichment scenarios (Fig. 1; Bell et al. 2014; Paerl et al. 2006; Penna et al. 2004; Smith et al. 1981).

Although herbivore control of primary producers (Eq. 8) is qualitatively consistent across parameter space, the strength of that control depends upon parameters that govern the dynamics of the system (Fig. 2). In particular, herbivore control of primary producers is greater when enrichment causes a smaller increase in r or a greater increase in K of the primary producer, or there is a greater density (H_T) or individual feeding rate (α) of the herbivore. The effect of increasing K_E is perhaps counterintuitive, but it arises because increased K_E causes the numerator in Eq. 5 to increase less rapidly than the denominator; i.e., enrichment increases primary producer density more in the absence than in the presence of herbivores.

We derived the above results based on assumption 4. However, when herbivory is very weak relative to the effect of enrichment on primary producers, the immigration response of herbivores may be insufficient to keep the density of primary producers equal inside and outside of the enriched plot. This happens when all of the herbivores aggregate inside the enriched plot and none remain in the surrounding habitat. Thus, we can substitute $H_E = \frac{N_T}{S_E}$ into Eq. 5, resolve for the equilibrium and obtain:

$$P_{E,+}^* = K_E \left(1 - \frac{\alpha N_T}{r_E S_E} \right). \quad (10)$$

Under this condition, $\frac{\partial P_{E,+}^*}{\partial S_E} > 0$: i.e., the previous qualitative result (Eq. 8) still holds. Indeed, this relaxation of assumption 4 only reinforces our main finding: enrichment effects increase (and herbivore effects decline) with increasing plot size.

Discussion

Here, we provide the first explicit demonstration that the mismatch between the scales of experimental enrichment studies and the scale of herbivore movement (Fig. 1) can create the (potentially false) perception that herbivores can prevent increased biomass of primary producers: i.e., given the small size of experimental plots, herbivores can aggregate in response to increased food production. However, at larger enrichment scales, which are more indicative of real-world enrichment scenarios (but not

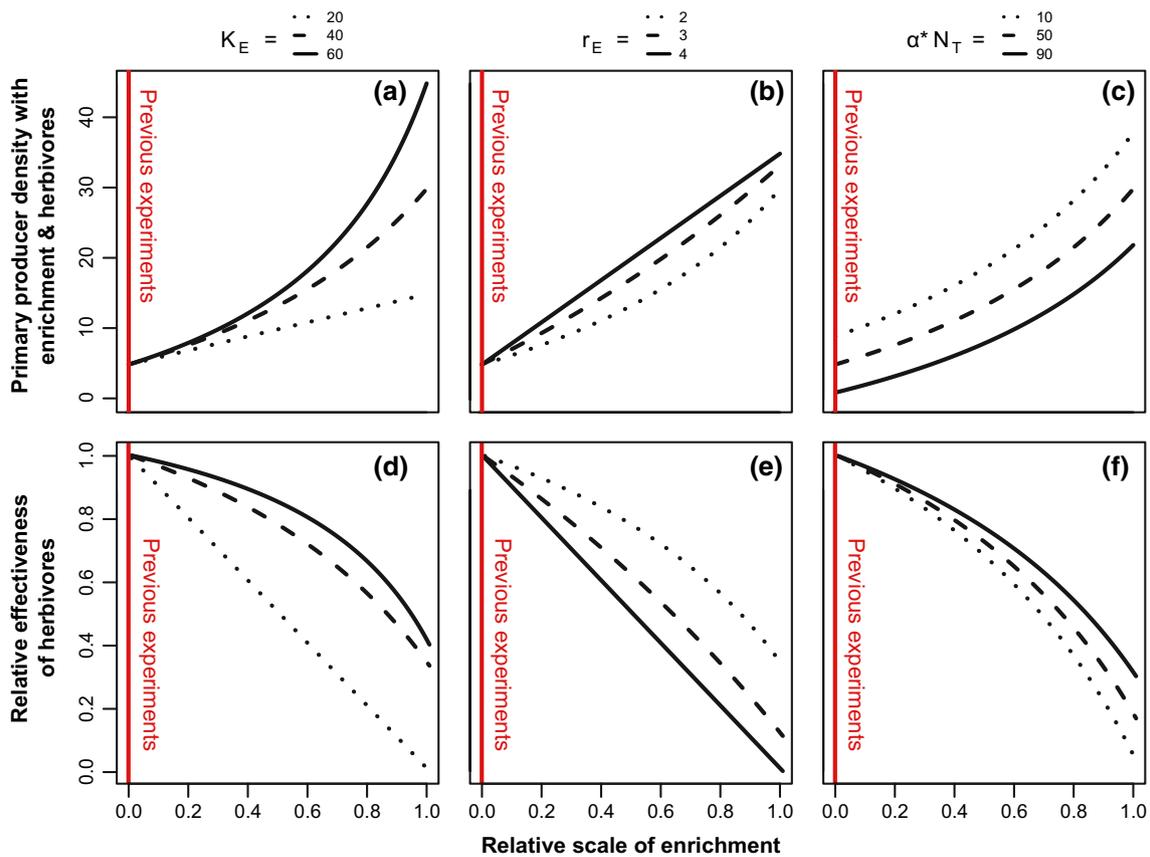


Fig. 2 The equilibrium density of primary producers in enriched plots with herbivores ($P_{E,+}$; from Eq. 7; **a–c**) and the relative effectiveness of herbivores in preventing increased density of primary producers in response to enrichment (Eq. 9; **d–f**), as a function of the scale of enrichment relative to the movement range of the herbivore. **a–c** y-intercepts of curves reflect the densities of primary producers in unenriched plots with herbivores ($P_{U,+}$ from Eq. 4). Curves were generated by changing the effect of enrichment on carrying capacity (K ;

a, d) or intrinsic growth rate (r ; **b, e**) or altering the herbivore population feeding rate (**c, f**). Otherwise, default parameter values were: $K_U = 10$, $K_E = 40$, $r_U = 1$, $r_E = 2$, $\alpha \times N_T = 50$. Vertical lines indicate the median scale of enrichment (scaled to herbivores movement range) from field experiments (i.e., 5.2×10^{-6} ; Online Resource 1). For **d–f**, a response of 1 indicates that herbivores completely prevent an increase in primary producers following enrichment. The code used to generate this figure is available in Online Resource 3

field experiments; Fig. 1), herbivores are less able to control primary producers because the potential immigration response is reduced. This mechanism is similar to that proposed by Englund (1997), in which prey migration into/out of cages could mask effects of predators when experiments were conducted in small plots. As cage size increased, the importance of movement decreased, and the within-plot manipulation (predator presence/absence) became relatively more important in driving observed effects. Our system differed somewhat from Englund’s (1997), however, because the consumer (herbivore) was mobile, but the resource (prey) was sessile. Our quantitative results also echo the conceptual arguments of Van de Koppel et al. (2005) in their general discussion of scale mismatch in consumer–resource interactions. Collectively, these studies indicate that when key players or processes operate at scales that exceed the grain of observation (e.g., plot size; Fig. 1), results can change

significantly (Fig. 2), simply because observational scales fail to match the natural contexts that they are meant to represent (see Levin 1992).

This mismatch may have important practical implications. For example, top-down versus bottom-up field experiments in marine systems suggest that mobile herbivores can mitigate, or even prevent, increases in algal biomass following enrichment (Burkepile and Hay 2006). As a result, coral reef managers may conclude that herbivores alone (if they are not over-exploited) can protect marine systems and their associated services from harmful effects of nutrient enrichment (Bellwood et al. 2004; Burkholder et al. 2007; Hughes et al. 2010). However, our results indicate that observed herbivore control of algal biomass in marine systems could be an artifact of the small spatial scale of field experiments relative to the large movement range of dominant herbivores (Figs. 1, 2).

These experimental biases can be reduced by improving the match between the experimental enrichment and movement patterns of herbivores. For example, systems in which herbivores move over smaller scales (e.g., small-bodied invertebrates) could be studied with less bias. Similarly, increasing the scale of experiments also could reduce the bias [e.g., as in whole lake or watershed experiments (Carpenter and Kitchell 1988; Schindler et al. 2008)], but this remains impractical in many systems, or can be difficult or impossible to replicate. Furthermore, alternative experimental approaches also could reduce bias: e.g., inclusion (rather than exclusion) cages (e.g., Ghedini et al. 2015; Silliman and Bertness 2002) can impose realistic consumer densities and eliminate the influx of consumers from the surrounding landscape into small enriched plots. This approach, however, remains impractical for many systems (e.g., those with large-bodied herbivores) and other potential problems may arise by confining herbivores (e.g., Quinn and Keough 1993).

Spatial scale is just one dimension of the potential problem. Similar challenges, as we have articulated, also exist with respect to the timescale of experiments, which often are much shorter than the timescale of population dynamics (Online Resource 1, Fig. A1). This temporal mismatch probably acts in the opposite direction than the spatial scale mismatch. For example, we would expect herbivore control to increase as their demographic rates change and drive changes in density; i.e., short-term experiments (which preclude demographic responses) likely underestimate potential control of primary producers by herbivores. Thus, the short timescale and small spatial scale of experiments could compensate for one another. Because field exclusion studies typically do not allow for population dynamics of herbivores (e.g., Online Resource 1, Fig. A1), we did not incorporate these population responses into our model. The extent to which the inference provided by our short timescale model will provide realistic insights about natural systems will depend on the potential for responses in the density of herbivores to enrichment. In natural systems, these considerations include:

1. Dispersal of herbivore offspring: if offspring are dispersed widely [as they are in many marine systems (Hixon et al. 2002)] then the local benefits of enrichment will be less likely to translate into local increases in herbivore density.
2. Trophic complexity: the numerical response of herbivores to increased primary production depends on the structure of the upper trophic levels: e.g., in a three-level food chain, increased production results in no change in herbivore density, but instead, an increase in their predator (Oksanen et al. 1981).

3. Interference among herbivores: higher herbivore interference (e.g., due to competition or territoriality) can cause herbivore populations to grow less at higher herbivore densities (Gresens 1995), restricting the numerical response to enrichment over timescales that extend well beyond herbivore generation times. However, interference may similarly limit the immigration and recruitment response to enriched patches over experimental timescales.
4. Feedbacks on consumer behavior and recruitment: herbivory can induce plant defenses (Agrawal 1998) and select for unpalatable or defended plant species (Augustine and McNaughton 1998). Shifts toward less edible plants will reduce herbivory rates as herbivore density increases, and thus limit further increases in herbivore density. Furthermore, nutrients may exacerbate these effects. For example, recent work in coral reefs show that primary producers (i.e., benthic algae) can reach a size at which they become unpalatable to most herbivores (Bellwood et al. 2012; Nyström et al. 2012) and can even reduce herbivore recruitment by producing negative settlement cues and degrading settlement habitat (Dixson et al. 2014; Paddock et al. 2009).

Our study highlights the need for future work to examine numerical responses, both via migration and via population dynamics, in a context that matches data to the scale of interest. Indeed, our results suggest that in many systems herbivores may be less capable of controlling primary producer biomass in natural settings [i.e., when enrichment occurs over square kilometers to hundreds of square kilometers (Bell et al. 2014; Paerl et al. 2006; Penna et al. 2004; Smith et al. 1981)] than would be expected based upon small-scale experiments [with enrichment manipulated at the \leq squared meter scale (Burkepile and Hay 2006; Gruner et al. 2008)]. Our model may further provide a mechanism to explain observed, long-term phase shifts from coral to algae in enriched coral reefs with intact herbivore communities (Hatcher and Larkum 1983; Ledlie et al. 2007; Walker and Ormond 1982), when such responses are not expected based upon experimental studies (e.g., Burkepile and Hay 2006). Consequently, anthropogenic nutrient enrichment, which continues to increase globally (Nixon 2009; Vitousek et al. 1997), could pose a greater threat to natural ecosystems, particularly coastal marine systems, than we previously believed.

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Author contribution statement M. A. G. and C. W. O. conceptualized the study; M. A. G., C. W. O. and J. J. developed the model; M. A. G. drafted the manuscript, and all authors revised the text.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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Title: Enrichment scale determines herbivore control of primary producers

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Online Resource 1: Literature survey methods, Fig. A1, and references for Fig. 1 and A1

Literature survey methods

We surveyed the literature for field experiments that fully crossed herbivore exclusions (using physical barriers; e.g., cages) with nutrient additions. Most of the experiments we surveyed came from the database compiled by and used in Gruner et al. (2008), which covered studies from 1965-2006. We used ISI web of knowledge and search strings including [herbivor* or graz* or consum*] and [resourc* or nutrient* or fertili*]; [top-down and bottom-up and ecolog*] to find additional experiments from 2007-2013. We recorded the experimental plot size used in each experiment, experimental duration, and the focal herbivore being excluded. When the focal herbivore was not reported, we assigned a known dominant herbivore from other studies of the same system. We then searched the literature for empirical estimates of individual movement range and age to sexual maturity for the focal herbivores, or, when this information was not

available, that of a close relative (i.e., congener or confamilial). We used the subset of studies (n=38) for which we could find information on both the movement range and age to maturation of the herbivore to create Fig. 1 & S1 (references used to create these figures are included below). We report herbivore movement range in surface area (m²). When movement range was reported in linear distance, we calculated the surface area of a circle (m²) with a radius equal to the linear distance, except for studies in freshwater streams, for which we calculated surface area from the measured herbivore movement distance along the stream multiplied by the stream width.

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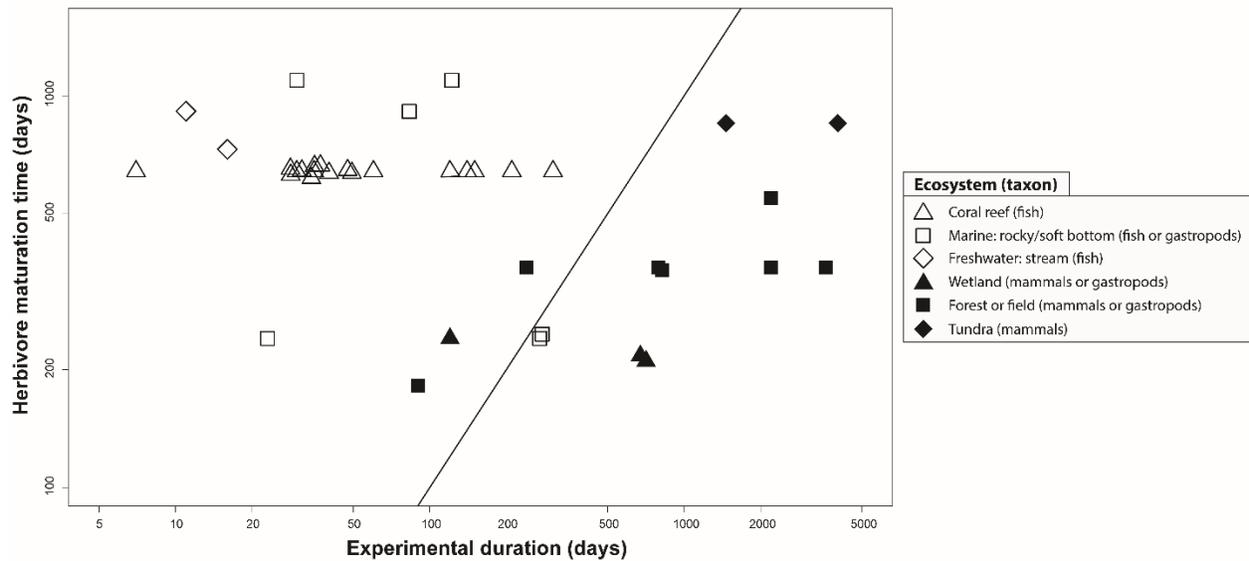


Figure A1: Herbivore age to sexual maturity compared to experimental duration in previous top-down versus bottom-up field experiments (nutrient addition fully crossed with herbivore

exclusion) across systems and taxa. The line indicates the 1:1 relationship, and overlapping points were jittered to show all points. In over 70% (27/38) of the studies, herbivore maturation time exceeded experimental duration, and the ratio of experimental duration to herbivore maturation time ranged from 0.010 to 9.9, with a median of 0.14.

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Online Resource 2: Incorporating a Type II functional response

In the main text, we evaluated the effects of herbivores on the density of primary producers in the presence of nutrient enrichment. To do so, we assumed herbivores had a Type I functional response. Here, we relax that assumption and show that if herbivores exhibit a Type II functional response, our qualitative results are unaffected: i.e., the equilibrium density of primary producers in enriched plots ($P_{E,+}^*$) increases with an increase in the size of the enriched plot (S_E): i.e., $\frac{\partial P_{E,+}^*}{\partial S_E} > 0$. This is the same result that we obtained in the main text, but with a Type I functional response (Eq. 8).

Under a Type II functional response, Equations 5 and 6 change to

$$\frac{dP_{E,+}}{dt} = r_E P_{E,+} \left(1 - \frac{P_{E,+}}{K_E}\right) - \frac{\alpha}{1 + \alpha h P_{E,+}} H_{E,+} P_{E,+} \text{ and} \quad (\text{A1})$$

$$\frac{dP_{E,+,\text{out}}}{dt} = r_U P_{E,+,\text{out}} \left(1 - \frac{P_{E,+,\text{out}}}{K_U}\right) - \frac{\alpha}{1 + \alpha h P_{E,+,\text{out}}} H_{E,+,\text{out}} P_{E,+,\text{out}}, \quad (\text{A2})$$

respectively, where h is the handling time associated with the consumption of the primary producer (all other parameters remain the same as in the main text). By assuming an ideal free distribution and non-dynamic herbivore populations, we obtain:

$$r_E S_E \left(1 - \frac{P^*}{K_E}\right) (1 + \alpha h P^*) + r_U S_U \left(1 - \frac{P^*}{K_U}\right) (1 + \alpha h P^*) - \alpha N_T = 0, \quad (\text{A3})$$

where $P^* = P_{E,+}^* = P_{E,+,\text{out}}^*$ and $S_U = S_T - S_E$. Eq. A3 has the solutions:

$P^* =$

$$\frac{-\alpha h (r_E S_E + r_U S_U) + \left(\frac{r_E S_E}{K_E} + \frac{r_U S_U}{K_U}\right) \pm \sqrt{(\alpha h r_E S_E + \alpha h r_U S_U - \frac{r_E S_E}{K_E} - \frac{r_U S_U}{K_U})^2 + 4[\alpha h \left(\frac{r_E S_E}{K_E} + \frac{r_U S_U}{K_U}\right)](r_E S_E + r_U S_U - \alpha N_T)}}{-2\alpha h \left(\frac{r_E S_E}{K_E} + \frac{r_U S_U}{K_U}\right)}.$$

For convenience, we reorganize the square root part to get:

$$P^* = \frac{-\alpha h(r_E S_E + r_U S_U) + \left(\frac{r_E S_E + r_U S_U}{K_E} + \frac{r_U S_U}{K_U}\right) \pm \sqrt{\left(\alpha h r_E S_E + \alpha h r_U S_U + \frac{r_E S_E + r_U S_U}{K_E} + \frac{r_U S_U}{K_U}\right)^2 - 4\alpha h \frac{r_E S_E}{K_E} \alpha N_T - 4\alpha h \frac{r_U S_U}{K_U} \alpha N_T}}{-2\alpha h \left(\frac{r_E S_E + r_U S_U}{K_E} + \frac{r_U S_U}{K_U}\right)}. \quad (\text{A4})$$

For persistence of both the herbivore and primary producer, the growth rate of the primary producer (in the enriched patch and its surrounding habitat) at low density must exceed the consumption by the herbivores: i.e., $r_E S_E + r_U S_U > \alpha N_T$. As a result, it can be shown that the sum of the terms under the square-root > 0 . Thus, the solutions in A4 are real (and not complex).

Next, we examine how the equilibrium density of primary producers changes with plot size. Thus, we implicitly find the derivative of Eq. A3, and obtain:

$$\frac{\partial P^*}{\partial S_E} = \frac{(-\alpha h P^* - 1) \left[\left(\frac{r_U}{K_U} - \frac{r_E}{K_E} \right) P^* + (r_E - r_U) \right]}{\alpha h (r_E S_E + r_U S_U) - \left(\frac{r_E S_E + r_U S_U}{K_E} + \frac{r_U S_U}{K_U} \right) (2\alpha h P^* + 1)}. \quad (\text{A5})$$

Note that this solution is a function of P^* . By inserting Eq. A4 into Eq. A5, it can be shown that the denominator of Eq. A5 is not equal to 0.

Next, we would like to show that $\frac{\partial P_{E,+}^*}{\partial S_E} > 0$. However, given the complexity of $P_{E,+}^*$ for a Type II functional response, it is difficult to prove that $\frac{\partial P_{E,+}^*}{\partial S_E} > 0$. Instead, below we take the opposite approach and prove that all of the conditions required to obtain $\frac{\partial P_{E,+}^*}{\partial S_E} \leq 0$ cannot occur.

Thus, we indirectly prove that $\frac{\partial P_{E,+}^*}{\partial S_E} > 0$.

To start, recall that $r_E > r_U$, $K_E > K_U$, and that $P^* > 0$. Note also, that Eq. A5 has the general form $\frac{\partial P^*}{\partial S_E} = \frac{AB}{C}$. Because A is always < 0 , we can specify 3 ways to achieve $\frac{\partial P^*}{\partial S_E} \leq 0$: 1) $B=0$; 2) $B >$ and $C > 0$, and 3) $B < 0$ and $C < 0$. We impose these three conditions, solve for P^* subject to these conditions, and later demonstrate that P^* cannot take on those values.

1) $B=0$: If $\left(\frac{r_U}{K_U} - \frac{r_E}{K_E}\right) P^* + (r_E - r_U) = 0$, then:

$$P^* = \frac{r_E - r_U}{\frac{r_E}{K_E} - \frac{r_U}{K_U}}$$

(A6)

2) B>0 and C>0: If $\left(\frac{r_U}{K_U} - \frac{r_E}{K_E}\right)P^* + (r_E - r_U) > 0$ and $\alpha h(r_E S_E + r_U S_U) - \left(\frac{r_E S_E}{K_E} + \frac{r_U S_U}{K_U}\right)(2\alpha h P^* + 1) > 0$, then:

2i) when $\frac{r_E}{K_E} - \frac{r_U}{K_U} \leq 0$, B is always >0, so from C>0, we get: $P^* < \frac{1}{2} \left(\frac{r_E S_E + r_U S_U}{\frac{r_E S_E}{K_E} + \frac{r_U S_U}{K_U}} - \frac{1}{\alpha h} \right)$, or

2ii) when $\frac{r_E}{K_E} - \frac{r_U}{K_U} > 0$, we get:

$$P^* < \min \left(\frac{r_E - r_U}{\frac{r_E}{K_E} - \frac{r_U}{K_U}}, \frac{1}{2} \left(\frac{r_E S_E + r_U S_U}{\frac{r_E S_E}{K_E} + \frac{r_U S_U}{K_U}} - \frac{1}{\alpha h} \right) \right) = \frac{1}{2} \left(\frac{r_E S_E + r_U S_U}{\frac{r_E S_E}{K_E} + \frac{r_U S_U}{K_U}} - \frac{1}{\alpha h} \right). \quad (\text{A7})$$

3) B<0 and C<0: If $\left(\frac{r_U}{K_U} - \frac{r_E}{K_E}\right)P^* + (r_E - r_U) < 0$ and $\alpha h(r_E S_E + r_U S_U) - \left(\frac{r_E S_E}{K_E} + \frac{r_U S_U}{K_U}\right)(2\alpha h P^* + 1) < 0$, then from B<0, we get that:

$\left(\frac{r_E S_E}{K_E} + \frac{r_U S_U}{K_U}\right)(2\alpha h P^* + 1) < 0$, then from B<0, we get that:

3i) if $\frac{r_E}{K_E} - \frac{r_U}{K_U} > 0$, then $P^* > \frac{r_E - r_U}{\frac{r_E}{K_E} - \frac{r_U}{K_U}}$;

3ii) if $\frac{r_E}{K_E} - \frac{r_U}{K_U} < 0$, then $P^* < \frac{r_E - r_U}{\frac{r_E}{K_E} - \frac{r_U}{K_U}} < 0$, which cannot be true; and

3iii) if $\frac{r_E}{K_E} - \frac{r_U}{K_U} = 0$, then B<0 cannot be satisfied;

and from C<0, we get $P^* > \frac{1}{2} \left(\frac{r_E S_E + r_U S_U}{\frac{r_E S_E}{K_E} + \frac{r_U S_U}{K_U}} - \frac{1}{\alpha h} \right)$.

Because there is only one possible inequality from $B < 0$ (3i-3iii) that can be true (inequality 3i),

we combine this inequality with that from $C < 0$ to yield the third possible condition for $\frac{\partial P^*}{\partial S_E} \leq 0$

as:

$$P^* > \max\left(\frac{r_E - r_U}{K_E - K_U}, \frac{1}{2}\left(\frac{r_E S_E + r_U S_U}{K_E + K_U} - \frac{1}{\alpha h}\right)\right) = \frac{r_E - r_U}{K_E - K_U} \text{ with } \frac{r_E}{K_E} - \frac{r_U}{K_U} > 0. \quad (\text{A8})$$

Equations A6, A7, and A8 define three possible conditions on P^* , and at least one must be satisfied to obtain $\frac{\partial P^*}{\partial S_E} \leq 0$. We next ask if these conditions on P^* are possible, and below, we

show that they are not. Therefore, we prove that $\frac{\partial P^*}{\partial S_E} > 0$. To do this, we use Eq. A4 to define the

range of possible values of P^* . There are two solutions to Eq. A4. Let's start with one of those solutions:

$$P_1^* = \frac{-ah(r_E S_E + r_U S_U) + \left(\frac{r_E S_E + r_U S_U}{K_E + K_U}\right) + \sqrt{(ahr_E S_E +ahr_U S_U + \frac{r_E S_E + r_U S_U}{K_E + K_U})^2 - 4ah\frac{r_E S_E}{K_E}\alpha N_T - 4ah\frac{r_U S_U}{K_U}\alpha N_T}}{-2ah\left(\frac{r_E S_E + r_U S_U}{K_E + K_U}\right)}. \quad (\text{A9})$$

Because $-4ah\frac{r_E S_E}{K_E}\alpha N_T - 4ah\frac{r_U S_U}{K_U}\alpha N_T < 0$, we can re-express Eq A9 as:

$$P_1^* > \frac{ah(r_E S_E + r_U S_U) - \left(\frac{r_E S_E + r_U S_U}{K_E + K_U}\right) - \sqrt{(ahr_E S_E +ahr_U S_U + \frac{r_E S_E + r_U S_U}{K_E + K_U})^2}}{2ah\left(\frac{r_E S_E + r_U S_U}{K_E + K_U}\right)} = -\frac{1}{ah}. \quad (\text{A10})$$

Alternatively, because $r_E S_E + r_U S_U > \alpha N_T$, we can also re-express Eq. A9 as:

$$P_1^* < \frac{ah(r_E S_E + r_U S_U) - \left(\frac{r_E S_E + r_U S_U}{K_E + K_U}\right) - \sqrt{(ahr_E S_E +ahr_U S_U - \frac{r_E S_E + r_U S_U}{K_E + K_U})^2}}{2ah\left(\frac{r_E S_E + r_U S_U}{K_E + K_U}\right)}. \quad (\text{A11})$$

If $ahr_E S_E +ahr_U S_U - \frac{r_E S_E}{K_E} - \frac{r_U S_U}{K_U} \geq 0$, then:

$$P_1^* < 0. \quad (\text{A12})$$

On the other hand, if $ahr_E S_E +ahr_U S_U - \frac{r_E S_E}{K_E} - \frac{r_U S_U}{K_U} < 0$, then:

$$P_1^* < \frac{ah(r_E S_E + r_U S_U) - \left(\frac{r_E S_E}{K_E} + \frac{r_U S_U}{K_U}\right)}{ah \left(\frac{r_E S_E}{K_E} + \frac{r_U S_U}{K_U}\right)} < 0. \quad (\text{A13})$$

Equations A10-A13 define the range of P_1^* , and this range is $-\frac{1}{ah} < P_1^* < 0$. Thus, the solution to P_1^* is not possible (because P^* cannot be less than zero).

Next, we turn to the second solution:

$$P_2^* = \frac{-ah(r_E S_E + r_U S_U) + \left(\frac{r_E S_E}{K_E} + \frac{r_U S_U}{K_U}\right) - \sqrt{(\alpha hr_E S_E + \alpha hr_U S_U + \frac{r_E S_E}{K_E} + \frac{r_U S_U}{K_U})^2 - 4\alpha h \frac{r_E S_E}{K_E} \alpha N_T - 4\alpha h \frac{r_U S_U}{K_U} \alpha N_T}}{-2\alpha h \left(\frac{r_E S_E}{K_E} + \frac{r_U S_U}{K_U}\right)}. \quad (\text{A14})$$

Because $-4\alpha h \frac{r_E S_E}{K_E} \alpha N_T - 4\alpha h \frac{r_U S_U}{K_U} \alpha N_T < 0$, we can re-express Eq. A14 as:

$$P_2^* < \frac{-ah(r_E S_E + r_U S_U) + \left(\frac{r_E S_E}{K_E} + \frac{r_U S_U}{K_U}\right) - \sqrt{(\alpha hr_E S_E + \alpha hr_U S_U + \frac{r_E S_E}{K_E} + \frac{r_U S_U}{K_U})^2}}{-2\alpha h \left(\frac{r_E S_E}{K_E} + \frac{r_U S_U}{K_U}\right)} = \frac{r_E S_E + r_U S_U}{\frac{r_E S_E}{K_E} + \frac{r_U S_U}{K_U}}. \quad (\text{A15})$$

Alternatively, because $r_E S_E + r_U S_U > \alpha N_T$ we can re-express Eq. A14 as:

$$P_2^* > \frac{-ah(r_E S_E + r_U S_U) + \left(\frac{r_E S_E}{K_E} + \frac{r_U S_U}{K_U}\right) - \sqrt{(\alpha hr_E S_E + \alpha hr_U S_U - \frac{r_E S_E}{K_E} - \frac{r_U S_U}{K_U})^2}}{-2\alpha h \left(\frac{r_E S_E}{K_E} + \frac{r_U S_U}{K_U}\right)}. \quad (\text{A16})$$

If $\alpha hr_E S_E + \alpha hr_U S_U - \frac{r_E S_E}{K_E} - \frac{r_U S_U}{K_U} \geq 0$, Eq. A16 becomes

$$P_2^* > \frac{r_E S_E + r_U S_U}{\frac{r_E S_E}{K_E} + \frac{r_U S_U}{K_U}} - \frac{1}{ah}. \quad (\text{A17})$$

Alternatively, if $\alpha hr_E S_E + \alpha hr_U S_U - \frac{r_E S_E}{K_E} - \frac{r_U S_U}{K_U} < 0$, Eq. A16 becomes

$$P_2^* > 0. \quad (\text{A18})$$

By combining condition A15 and either A17 or A18, we get:

$$\max\left(\frac{r_E S_E + r_U S_U}{\frac{r_E S_E}{K_E} + \frac{r_U S_U}{K_U}} - \frac{1}{ah}, 0\right) < P_2^* < \frac{r_E S_E + r_U S_U}{\frac{r_E S_E}{K_E} + \frac{r_U S_U}{K_U}}. \quad (\text{A19})$$

Finally, we will look at the three conditions, of which one must be met for $\frac{\partial P^*}{\partial S_E} \leq 0$, and

we will show that each condition cannot be satisfied, beginning with condition 1). Under Eq. A6:

i) if $\frac{r_E}{K_E} - \frac{r_U}{K_U} > 0$, then from Eq. A19, we get $P^* < \frac{r_E S_E + r_U S_U}{\frac{r_E S_E}{K_E} + \frac{r_U S_U}{K_U}} < \frac{r_E - r_U}{\frac{r_E}{K_E} - \frac{r_U}{K_U}}$, which

violates condition 1);

ii) if $\frac{r_E}{K_E} - \frac{r_U}{K_U} < 0$, then $P^* < 0$, which cannot be true; and

iii) if $\frac{r_E}{K_E} - \frac{r_U}{K_U} = 0$, then condition 1) becomes $r_E - r_U = 0$, which also cannot be true.

Next, we show that condition 2) cannot be satisfied. Under Eq. A7,

i) if $\frac{r_E S_E + r_U S_U}{\frac{r_E S_E}{K_E} + \frac{r_U S_U}{K_U}} - \frac{1}{\alpha h} > 0$, then from Eq. A19, we get $P^* > \frac{r_E S_E + r_U S_U}{\frac{r_E S_E}{K_E} + \frac{r_U S_U}{K_U}} - \frac{1}{\alpha h} >$

$\frac{1}{2} \left(\frac{r_E S_E + r_U S_U}{\frac{r_E S_E}{K_E} + \frac{r_U S_U}{K_U}} - \frac{1}{\alpha h} \right)$, which violates condition 2); and

ii) if $\frac{r_E S_E + r_U S_U}{\frac{r_E S_E}{K_E} + \frac{r_U S_U}{K_U}} - \frac{1}{\alpha h} \leq 0$, then $P^* < 0$, which cannot be true.

Finally, we show that condition 3) cannot be satisfied:

Because $\frac{r_E}{K_E} - \frac{r_U}{K_U} > 0$, from Eq. A19, we get $P^* < \frac{r_E S_E + r_U S_U}{\frac{r_E S_E}{K_E} + \frac{r_U S_U}{K_U}} < \frac{r_E - r_U}{\frac{r_E}{K_E} - \frac{r_U}{K_U}}$, which violates Eq. A8.

In summary, none of the complete set of three possible conditions required for $\frac{\partial P^*}{\partial S_E}$ to be less than or equal to zero can be satisfied. We have therefore shown that $\frac{\partial P^*}{\partial S_E} > 0$. Thus, herbivores with a Type II functional response should respond in a qualitatively similar way to a change in experimental scale as herbivores with a Type I functional response, as we discuss in the main text.

Online Resource 3: R code used to calculate model output

The following code is in the program R 3.1.1 (R Core Team 2013). This code uses the same notation of equations in main article, except here $aa = \alpha * N_T$, q is a multiplier that defines the scales of K_E or r_E , bb defines the scale of the x-axis, ETI is the function of P_E (Equation 7) under a type I functional response and $HerbTI1-3$ are the relative effectiveness of herbivores (Equation 9).

```
### Graph for primary producer density in response to enrichment and herbivores with changes
of  $K_E$ 

ST=100

KU=10

ru=1

re=2

aa<-50

q<-seq(2,6,2)

bb<-seq(0,1,0.01)

b<-0.5

KE<-q*KU

ETI<-function(SE,KE) { KE*KU*(SE*re+(ST-SE)*ru-aa)/(SE*re*KU+(ST-SE)*ru*KE) }

par(mar=c(4.5,4.8,1.5,0.8))

plot(bb, ETI(ST*bb, KE[1]), type='l', lty=3,lwd=2,xlab="", ylab=paste('Relative increase in
primary producer density(%)'), ylim=c(0,45))

for(i in 2:length(q))
```

```

{
  points(bb, ETI(ST*bb,KE[i]), type='l',lwd=2,lty=(4-i))
}

abline(v=0.00005,col='red',lwd=1)

### Graph for primary producer density in response to enrichment and herbivores with change of
rE
ST=100
KU=10
KE=40
ru=1
aa<-50
q<-seq(2,4,1)
bb<-seq(0,1,0.01)
re<-q*ru
ETI<-function(SE,re) { KE*KU*(SE*re+(ST-SE)*ru-aa)/(SE*re*KU+(ST-SE)*ru*KE)}
par(mar=c(4.5,4.8,1.5,0.8))
plot(bb, ETI(ST*bb,re[1]), type='l',lwd=2,lty=3,xlab='Relative scale of
eutrophication',ylab='',ylim=c(0,45))

for(i in 2:length(q))
{
  points(bb, ETI(ST*bb,re[i]), type='l',lwd=2,lty=(4-i))
}

```

```

}
abline(v=0.00005,col='red',lwd=1)

### Graph for primary producer density in response to enrichment and herbivores with change of
 $\alpha \cdot N_T$ 
ST=100
KU=10
ru=1
KE=40
re=2
aa<-seq(10,90,40)
bb<-seq(0,1,0.01)
ETI<-function(SE,aa) { KE*KU*(SE*re+(ST-SE)*ru-aa)/(SE*re*KU+(ST-SE)*ru*KE) }
par(mar=c(4.5,4.8,1.5,0.8))
plot(bb, ETI(ST*bb,aa[1]), lty=3,type='l',lwd=2,xlab="",ylab="",ylim=c(0,45))

for(i in 2:length(aa))
{
  points(bb, ETI(ST*bb,aa[i]), type='l',lwd=2,lty=(4-i))
}
abline(v=0.00005,col='red',lwd=1)

```

```
### Relative effectiveness of herbivores with change of KE/KU
```

```
ST=100
```

```
KU=10
```

```
KE=c(KU*2, KU*4, KU*6)
```

```
ru=1
```

```
re=2
```

```
aa<-50
```

```
SE<-seq(1,ST,0.05)
```

```
HerbTI<- array(data = NA, dim = c(length(KE), length(SE)))
```

```
plotTI<- array(data = NA, dim = c(length(KE), length(SE)))
```

```
for(i in 1:length(KE))
```

```
{
```

```
for(j in 1:length(SE))
```

```
{
```

```
HerbTI [i, j]<-1-(KE[i]*KU*(SE[j]*re+(ST-SE[j])*ru-aa)/(SE[j]*re*KU+(ST-  
SE[j])*ru*KE[i])-KU*(1-aa/ru/ST))/(KE[i]-KU)
```

```
plotTI [i, j]<-SE[j]/ST
```

```
}
```

```
}
```

```
par(mar=c(3,4.8,3,0.8))
```

```

plot(plotTI[1,],
HerbTI[1,],type='l',main=expression(paste('K'[E],'/K'[ST],'=')),lty=3,lwd=2,ylim=c(0,1),xlab='',y
lab=paste('Relative effectiveness of herbivores'))
points(plotTI[2,], HerbTI[2,],type='l',lty=2,lwd=2)
points(plotTI[3,], HerbTI[3,],type='l',lty=1,lwd=2)
abline(v=0.00005,col='red',lwd=1)
par(xpd=T)
legend(0.73,1.3,c(2,4,6),lty=c(3,2,1),lwd=c(2,2,2),cex=0.7,bty='n')
par(xpd=F)

```

Graph of relative effectiveness of herbivores with change of re/ru

```
ST=100
```

```
KU=10
```

```
KE=40
```

```
ru=1
```

```
re=c(4,3,2)
```

```
aa<-50
```

```
SE<-seq(1,ST,0.05)
```

```
HerbTI1<- array(data = NA, dim = c(length(re), length(SE)))
```

```
plotTI1<- array(data = NA, dim = c(length(re), length(SE)))
```

```
for(i in 1:length(re))
```

```
{
```

```

for(j in 1:length(SE))
{
  HerbTI1[i, j]<-1-(KE*KU*(SE[j]*re[i]+(ST-SE[j])*ru-aa)/(SE[j]*re[i]*KU+(ST-
SE[j])*ru*KE)-KU*(1-aa/ru/ST))/(KE-KU)
  plotTI1[i, j]<-SE[j]/ST
}
}

par(mar=c(3,4.8,3,0.8))

plot(plotTI1[1,],HerbTI1[1,],type='l',main=expression(paste('r'[E],'/r'[ST], '=')),lty=1,lwd=2,ylim
=c(0,1),xlab="",ylab=")

points(plotTI1[2,],HerbTI1[2,],type='l',lty=2,lwd=2)

points(plotTI1[3,],HerbTI1[3,],type='l',lty=3,lwd=2)

abline(v=0.00005,col='red',lwd=1)

par(xpd=T)

legend(0.73,1.3,c(2,3,4),lty=c(3,2,1),lwd=c(2,2,2),cex=0.7,bty='n')

par(xpd=F)

### Graph of relative effectiveness of herbivores with change of  $\alpha$  *NT

ST=100

KU=10

ru=1

KE=40

re=2

```

```

aa<-c(10,50,90)
SE<-seq(1,ST,0.05)

HerbTI3<- array(data = NA, dim = c(length(aa), length(SE)))
plotTI3<- array(data = NA, dim = c(length(aa), length(SE)))

for(i in 1:length(aa))
{
for(j in 1:length(SE))
{
HerbTI3[i, j]<-1-(KE*KU*(SE[j]*re+(ST-SE[j])*ru-aa[i])/(SE[j]*re*KU+(ST-SE[j])*ru*KE)-
KU*(1-aa[i]/ru/ST))/(KE-KU)
plotTI3[i, j]<-SE[j]/ST
}
}

par(mar=c(3,4.8,3,0.8))
plot(plotTI3[3,],HerbTI3[3,],type='l',lty=1,main=expression(paste('a*C'[T],'=')),lwd=2,ylab=",x1
ab=",ylim=c(0,1))
points(plotTI3[1,],HerbTI3[1,],type='l',lty=3,lwd=2)
points(plotTI3[2,],HerbTI3[2,],type='l',lty=2,lwd=2)
abline(v=0.00005,col='red',lwd=1)

par(xpd=T)
legend(0.73,1.3,c(10,50,90),lty=c(3,2,1),lwd=c(2,2,2),cex=0.7,bty='n')

```

```
par(xpd=F)
```

References

R Core Team (2013) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria