ASYMMETRY IN COMMUNITY REGULATION: EFFECTS OF PREDATORS AND PRODUCTIVITY

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Abstract. Eutrophication and predator additions and extinctions are occurring in ecosystems worldwide. Although theory predicts that both will strongly alter the distribution of biomass in whole communities, empirical evidence has not been consolidated to quantitatively determine whether these theoretical predictions are generally borne out in real ecosystems. Here we analyze data from two types of trophic cascade studies, predator removals in factorial combination with fertilization and observed productivity gradients, to assess the role of top-down and bottom-up forces in structuring multi-trophic communities and compare results from these analyses to those from an extensive database of trophic cascade studies. We find that herbivore biomass declines and plant biomass increases in the presence of predators, regardless of system productivity. In contrast, while plants are increased by fertilization, this effect does not significantly increase herbivores in either the presence or absence of predators. These patterns are consistent among marine, freshwater, and terrestrial ecosystems and are largely independent of study size and duration. Thus, top-down effects of predation are transferred through more trophic levels than are bottom-up effects of eutrophication, showing strong asymmetry in the direction of control of biomass distribution in communities.

Key words: bottom-up forces; eutrophication; extinction; factorial meta-analysis; top-down forces; trophic cascade.

INTRODUCTION

In an age of global eutrophication (Vitousek et al. 1997) and anthropogenic additions or dramatic reductions and even extinctions of predators (Fritts and Rodda 1998, Pauly et al. 1998, Alroy 2001, Ruzycki et al. 2003), successful ecosystem management requires knowledge about the responses of biological communities to simultaneous changes in nutrient concentrations and predator composition. Theory predicts that both the top-down effects of predation and the bottom-up effects of nutrient enrichment should strongly control the biomass of all trophic levels in a community (Fretwell 1977, Oksanen et al. 1981), with predators indirectly controlling plant biomass and nutrients indirectly controlling predator biomass.

Recent reviews of empirical work support these conclusions for the control of plant and herbivore biomass in communities (Power 1992, Polis 1999, Menge 2000, Polis et al. 2000) while recognizing the role that a variety of other factors, including omnivory, intraguild predation, and the spatial and temporal scale of species interactions, can play in mediating the effects of predators and nutrients. However, most empirical work in this area has examined the direct and indirect

influence of either nutrients or predators, but few studies have examined both effects concurrently, and even fewer have addressed these questions in communities with more than two trophic levels. Thus, studies have shown that nutrients affect plants that affect herbivores, or vice versa, or that predators affect herbivores, providing insight into the direction of trophic control for subsets (or different parts) of a community, but not for entire multi-trophic communities containing plants, herbivores, and predators. An important exception is a single-system meta-analysis of freshwater food webs (Brett and Goldman 1997) that found that fish predators indirectly increase phytoplankton biomass, whereas nutrient addition increases phytoplankton but does not significantly increase zooplankton biomass. This study has important implications about the relative strength of bottom-up and top-down controls on the biomass distribution in freshwater pelagic communities. However, it is unclear whether this pattern found in lakes is general across ecosystems or whether it is a freshwater-specific anomaly. A fundamental question remains: are there generalities among multi-trophic communities in the relative strengths of top-down and bottom-up forces?

While relatively few studies in any particular ecosystem type have independently manipulated both predators and fertilization and quantified both the plant and herbivore biomass response, sufficient studies with this design have now been performed in many different

systems to allow a synthetic exploration of these questions. Here we synthesize the evidence for the relative strength of predators and plant productivity in controlling the biomass distribution among trophic levels across multiple ecological systems. Directional control of community structure (bottom-up vs. top-down) can be assessed by measuring the relative strength of direct interactions but, perhaps more importantly, indirect interactions. So if herbivore biomass responds more strongly to system productivity than to predator biomass (or abundance), then communities are structured primarily by bottom-up forces, whereas a stronger response by plants to predators compared to system productivity would indicate greater top-down control. Insights into the relative impact and interactions between predators and productivity on community biomass distribution will promote more focused ecosystem management strategies in the face of predator additions and extinctions and eutrophication.

METHODS

We collected data from 121 published studies that provided concurrent measures of plant biomass (e.g., grams per square meter) and either herbivore biomass or density (e.g., number of individuals per square meter) in the presence and absence of predators (Predator Manipulation data set). Our search criteria included examination of past system-specific meta-analysis data sets of trophic cascades, searches on the Web of Science and other search engines for studies in which predators were manipulated and herbivore and plant biomass (or density) were measured, and citations within those papers. For simplicity, we use the term "plant" for all autotrophs (algae and vascular plants). We did not include studies reporting only plant response metrics such as leaf damage or number of galls, because there is no clear evidence that these measures translate into predictable long-term changes in primary producer biomass (Stiling and Moon 2005). As a consequence of this criterion, we were unable to include many otherwise suitable studies (e.g., Stiling and Moon 2005). However, we accepted percent plant cover as a surrogate measure of plant biomass in some marine and terrestrial studies. For studies presenting multiple dates, we used the final sampling date in our analysis. Although we included six studies (five marine benthic and one lake benthic) that were "natural experiments" in which predators were not directly manipulated, predator effect sizes were similar between natural and planned experiments. The 121 studies that fulfilled all of these criteria represent empirical work performed in nine ecological systems (agricultural, forest/shrubland, grassland, lake benthos, lake plankton, marine benthos, marine plankton, salt marsh, and stream) and include a broad range of species and methods (for details, see Borer et al. [2005]). Subsets of this data set have been examined to answer other questions about community structure and function (see Shurin et al. 2002, Borer et al. 2005, Halpern et al. 2005).

We examined the effects of predators and productivity on plant and herbivore biomass using two subsets of this larger data set that have not previously been analyzed: studies that manipulated both predators and fertilization (23 studies; Fertilization data set) and studies that manipulated predators and recorded independent measures of ecosystem productivity (29 studies; Productivity data set; see Appendix). The Fertilization data set was composed of studies from eight ecological systems (forest, 1; grassland, 6; lake benthos, 1; lake plankton, 8; marine benthos, 2; marine plankton, 2; salt marsh, 1; and stream, 2), and thus represents a diverse subsample of the Predator Manipulation data set. The Productivity data set was comprised of two types of studies: 20 were performed in lakes, where productivity was measured as micrograms of phosphorus per liter, and nine were in grasslands, where productivity was assessed by removing predators and herbivores and measuring plant biomass (in grams per square meter). Here, we focus on the Productivity ($n = 29$) and Fertilization ($n = 23$) data sets, but compare them to the Predator Manipulation data set ($n = 121$) to confirm that these are unbiased subsets of the more comprehensive data set.

We use meta-analysis to examine the relative effects of top-down and bottom-up factors in controlling plant and herbivore biomass. To determine the strength of top-down control, we examine the natural log of the ratio of herbivore and plant biomass with vs. without predators (e.g., herbivore log ratio = ln[herbivore biomass with predators/herbivore biomass without predators]). Thus, a negative value of this ratio indicates suppression by predators. Bottom-up control is quantified similarly, using the natural log of the ratio of fertilized vs. unfertilized treatments (positive values indicate biomass increases with fertilization). This type of meta-analysis is used to examine general patterns among empirical studies (Arnqvist and Wooster 1995, Gurevitch and Hedges 1999, Osenberg et al. 1999), is relatively insensitive to sample size (Englund et al. 1999), meets assumptions of parametric analyses (Hedges et al. 1999), and has direct biological interpretation as the proportional change in the response variable (Shurin et al. 2002). To examine both the main effects and interactions in the Fertilization data set, we employed factorial meta-analysis using the log ratio response (Gurevitch et al. 2000, Hawkes and Sullivan 2001). We calculated the effect sizes for each main effect and interaction as follows:

$$L_{\text{predator}} = [\ln(\overline{U}_{3F}) + \ln(\overline{U}_{3C})] - [\ln(\overline{U}_{2F}) + \ln(\overline{U}_{2C})]$$

$$L_{\text{fertilization}} = [\ln(\overline{U}_{3F}) + \ln(\overline{U}_{2F})] - [\ln(\overline{U}_{3C}) + \ln(\overline{U}_{2C})]$$

$$L_{\text{interaction}} = [\ln(\overline{U}_{2C}) + \ln(\overline{U}_{3F})] - [\ln(\overline{U}_{2F}) + \ln(\overline{U}_{3C})]$$

where, for each study, $\overline{U}$ represents either the mean value for the plant or herbivore biomass, predator treatments are either three-level food webs (predators present = 3) or two-level food webs (predators absent =

TABLE 1. Results of a factorial meta-analysis examining the relative direct and indirect effects of predator removal and fertilization on plants and herbivores for 23 studies in eight systems.

Factor	Mean	t	P
Plant response			
Predator	0.64	3.14	0.005
Fertilization	1.92	2.81	0.010
Predator × Fertilization	0.14	1.18	0.250
Herbivore response			
Predator	−1.30	−4.82	<0.001
Fertilization	0.22	0.39	0.700
Predator × Fertilization	−0.16	−1.11	0.298

Note: Means represent the mean effect sizes (see *Methods*); because treatment means are summed in the main effect calculation, mean values are twice as high as individual treatment means.

2), and communities are either fertilized (F) or unfertilized controls (C). Because this analysis sums the log biomass from two treatments, effect values (e.g., $L_{predator}$) are approximately twice that of the actual treatment log ratio responses (see Table 1). We present single treatment log ratio response values in figures (e.g., Fig. 1).

We examined the Fertilization data set for biological (e.g., predator size, plant generation time) and methodological (e.g., study duration, study area) factors explaining residual variance using multiple regression. The covariate values for each study in the Fertilization data set and methods for their collection are presented in Borer et al. (2005); covariates examined are listed in Table 2. We used regression to analyze the Productivity data sets. We conducted all analyses in SAS (version 9.1; SAS Institute, Cary, North Carolina, USA) using both weighted (by sample size) and unweighted log ratios (Hedges and Olkin 1985), and, because both approaches produced qualitatively the same results, we present the unweighted analyses here.

RESULTS

Fertilization directly increased plant biomass more than twofold in the presence and absence of predators. In contrast, although herbivore biomass increased with fertilization in 61% of the two-level studies and 65% of the three-level studies, overall, the indirect effect of fertilization did not significantly increase herbivore biomass (Fig. 1, Table 1). This result was qualitatively similar among systems (Table 3). Thus, across 23 empirical studies in eight ecosystem types (Fertilization data set; see *Methods*), fertilization increased plant biomass but did not indirectly alter herbivore biomass.

Herbivore biomass was reduced in the presence of predators in the Predator Manipulation data set ($n = 121$, see *Methods*), and this overall response did not differ from the mean response of the Fertilization subset ($n = 23$; ANOVA $P = 0.33$; Fig. 2) suggesting that the Fertilization data set is an unbiased subset of the larger

data set. The presence of predators increased plant biomass more strongly in the Predator Manipulation than in the Fertilization data set (ANOVA $P = 0.04$; Fig. 2), suggesting that the Fertilization data set may underestimate the strength of the indirect positive effect of predators on plant biomass (i.e., trophic cascades).

In the Predator Manipulation data set, the presence of predators reduced herbivore biomass (t test $P < 0.0001$) and indirectly increased plant biomass (t test $P < 0.0001$; Fig. 2). In the Fertilization data set, the absolute value of the direct effect of predators on herbivores (Fig. 2, Table 1) was comparable in magnitude to the direct effect of fertilization on plants (Fig. 1, Table 1). Herbivores were similarly reduced by predation in studies both with and without fertilization (Table 1, Fig. 2). Thus, the magnitude of the predator effect does not interact with fertilization. In concurrence with these results, in both terrestrial and lake systems in which measures of system productivity were available (Productivity data sets; see *Methods*), the effect of predators on both herbivores and plants was uncorrelated with productivity (Fig. 3).

Community responses to fertilization and predator manipulations were qualitatively similar among ecosystems. In the Fertilization data set ($n = 23$), the magnitude of the indirect effects of predators on plants (i.e., trophic cascades) was greatest in lake systems and in larger experiments relative to predator body size, as discussed previously (Shurin et al. 2002, Borer et al. 2005; Tables 2 and 3). Neither the effect of fertilization on plant and herbivore biomass nor the interaction between fertilization and predation was explained by
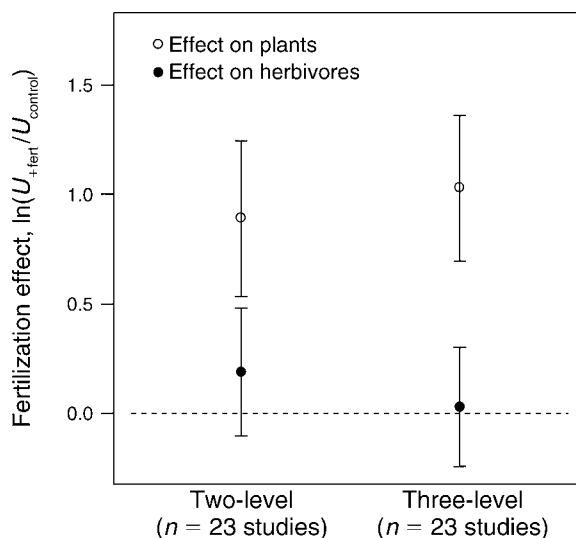

FIG. 1. Effect of fertilization (mean ± SE) on plants and herbivores in communities with predators (three-level) and without predators (two-level). Positive values indicate that biomass of plants and herbivores increases with fertilization. The y-axis units are the log ratio of biomass with (U_{+fert}) and without ($U_{control}$) fertilization (see *Methods*).

TABLE 2. Summary of multiple regressions examining biological and experimental covariates affecting the results of 23 experimental factorial manipulations of predators and nutrients; data are shown only for significant ($P < 0.05$) regressions based on backwards selection.

| | | | Predator effect | | | |
| | | | Plants | | Herbivores | |
Variable	Units†	Range‡	Slope	P	Slope	P
Area of experimental unit	m^2	−2.3 to 13.5			0.429	0.010
Duration of experiment	d	1.6 to 7.8			0.438	0.012
Experimental area/predator body mass	g/m^2	−5.3 to 11.9	0.107	0.002	0.435	0.005

Notes: The log response ratios (predator removal, fertilization, or the predator removal × fertilization interaction) were regressed on 14 explanatory factors. Only predator removal was significant: $r^2 = 0.39$ for effect on plants; $r^2 = 0.55$ for effect on herbivores. Because of low variability among studies, low explanatory power, or insufficient data, the following traits were not significant in any models: duration/plant generation, predator vertebrate, predator ectotherm, predator body mass, predator mobility, herbivore vertebrate, herbivore ectotherm, and plant generation time. There were insufficient data for herbivore body mass and herbivore body mass/area of experimental unit.

† Original units are given. The data were log_e-transformed for analysis.

‡ Log_e-transformed values.

any of the measured covariates (Table 2). The magnitude and direction of the direct top-down (predators on herbivores), direct bottom-up (fertilizer on plants), and indirect bottom-up (fertilizer on herbivores) effects did not vary by ecosystem (Table 3), and this result remains unchanged when we compare freshwater ($n = 11$), marine ($n = 5$), and terrestrial ($n = 7$) system means. Thus, the patterns we present here are robust to ecosystem, community composition, and methodology.

Discussion

Our results suggest that there is a general asymmetry in the rate at which perturbations to the top and bottom of food chains attenuate. Predators have strong top-down effects across entire food chains, while the bottom-up influence of eutrophication primarily affects plant productivity. Although direct top-down effects of predators on herbivores and bottom-up effects of nutrients on plants are strong, only the top-down forces were consistently transmitted beyond the adjacent trophic level. These results are consistent across marine, freshwater, and terrestrial systems and are largely independent of study size and duration. Thus, the results of this analysis have far-reaching implications: removal of predators will have more extensive multi-trophic implications for communities than will eutrophication, and the biomass of primary producers will be strongly influenced by both ecosystem eutrophication and predator additions or removals.

One important challenge, common to studies of concurrent consumer and nutrient manipulations (e.g., McQueen et al. 1989, Menge 2000, Hillebrand 2002), is that consumption and nutrient supply are very different processes, and experimental alterations of predator

TABLE 3. System means (with SE in parentheses) from 23 experimental factorial manipulations of predators and nutrients in eight systems.

| | | Predator effect | | | | Fertilization effect | | | |
| | | Fertilized | | Control | | Three-level | | Two-level | |
System	N	Plants	Herbivores	Plants	Herbivores	Plants	Herbivores	Plants	Herbivores
Forest	1	−0.22 (NA)	−0.15 (NA)	−0.15 (NA)	0.09 (NA)	2.34 (NA)	1.22 (NA)	3.28 (NA)	2.34 (NA)
Grassland	6	0.14 (0.21)	−0.68 (0.40)	0.15 (0.14)	−0.25 (0.35)	0.72 (0.23)	0.59 (0.48)	0.56 (0.22)	0.72 (0.23)
Lake benthos	1	0.33 (NA)	−0.47 (NA)	0.21 (NA)	−0.19 (NA)	−0.08 (NA)	0.34 (NA)	−0.20 (NA)	−0.08 (NA)
Lake plankton	8	1.02 (0.23)	−0.99 (0.27)	0.60 (0.15)	−1.01 (0.26)	1.06 (0.35)	0.41 (0.33)	0.63 (0.48)	1.06 (0.35)
Marine benthos	2	0.09 (0.23)	−0.69 (0.45)	0.27 (0.20)	−0.03 (0.03)	−0.11 (0.04)	−0.13 (0.08)	0.07 (0.07)	−0.11 (0.04)
Marine plankton	2	−0.11 (0.22)	−0.83 (0.13)	−0.20 (0.13)	−1.18 (0.21)	0.17 (0.17)	−0.23 (0.23)	0.08 (0.08)	0.17 (0.17)
Saltmarsh	1	0.01 (NA)	−0.70 (NA)	−0.15 (NA)	−1.17 (NA)	1.00 (NA)	1.27 (NA)	0.84 (NA)	1.00 (NA)
Stream benthos	2	−0.06 (0.52)	−0.18 (0.08)	0.12 (0.27)	−0.07 (0.11)	3.73 (3.58)	−2.30 (2.62)	3.91 (3.33)	3.73 (3.58)
P		0.092	0.908	0.171	0.282	0.276	0.131	0.182	0.313
Model r^2		0.51	0.15	0.45	0.39	0.39	0.48	0.44	0.38

Notes: NA indicates that standard errors are not available. Metric is the effect used in the log response ratio (either predator removal or fertilization). Treatment is the corresponding factorial treatment. Response is the trophic level of the response (either plants or herbivores). The last two rows are r^2 and P values testing for differences among systems. Note that the results do not differ qualitatively for models in which the two most well-represented systems (lake plankton and grasslands) are treated as separate binary variables (model df = 1) relative to the results shown here in which separate parameters are estimated for each system (model df = 4).
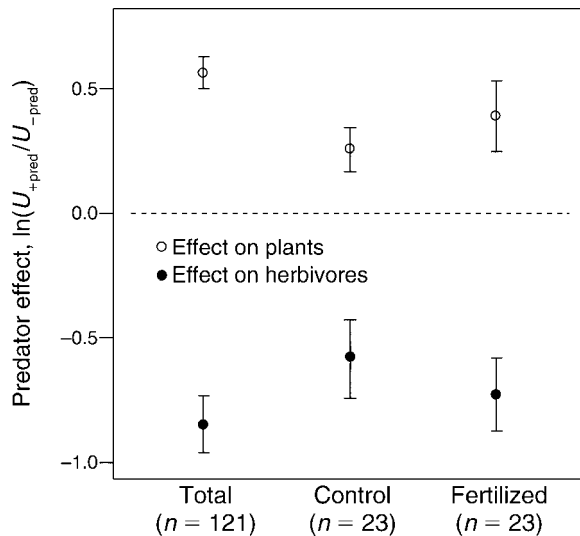
Fig. 2. Effect of predators (mean ± SE) on plants and herbivores across all Predator Manipulation studies (Total), and the Fertilization subset that simultaneously manipulated predator abundance and nutrient input (Control vs. Fertilized). Positive values indicate that biomass increases in the presence of predators compared to their absence. The y-axis units are the log ratio of biomass with (U_{+pred}) and without (U_{-pred}) predators (see Methods).

abundance and nutrient supply may not necessarily be equivalent treatments or produce similar direct effects. However, in the current study, the direct effects of predator and nutrient manipulations have similar effect magnitudes, although the direct effect of nutrient manipulation resulted in a somewhat larger response than did the manipulation of predators. These similar effect magnitudes imply that investigators obtained comparable direct effects from these very different experimental manipulations.

Importantly, the mean magnitude of the resulting top-down indirect effect (predator–plant) was three times that of the bottom-up indirect effect (nutrient–herbivore), despite the stronger direct effect of nutrients on plants. Our finding that bottom-up effects attenuate more rapidly than do top-down effects mirrors results in a similar meta-analysis examining the effect of predators and fertilization on freshwater plankton communities (Brett and Goldman 1997), but demonstrates that the pattern of greater top-down indirect effects is consistent among ecological systems and is not unique to the freshwater plankton. Thus, the current analysis highlights the generality of slower attenuation of top-down vs. bottom-up forces across ecosystems.

Such cross-system generalizations provide profound insight into the nature of biomass control in communities and quantitatively identify the critical link for
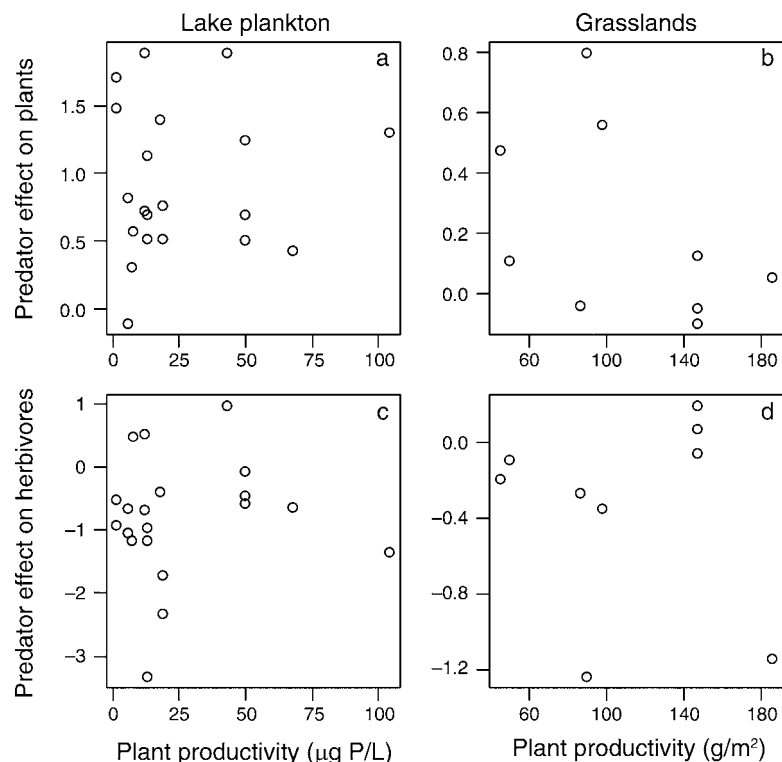

Fig. 3. Relationships between plant productivity in (a, c) lake plankton and (b, d) grassland ecosystems and the effect of predators on (a, b) plants and (c, d) herbivores under differing ecosystem productivity. Each point represents a single study. Correlations were as follows: (a) $r = 0.07$, $n = 20$, $P = 0.75$; (b) $r = -0.46$, $n = 9$, $P = 0.21$; (c) $r = 0.08$, $n = 20$, $P = 0.73$; (d) $r = -0.12$, $n = 9$, $P = 0.76$. Data presented in (a) and (b) also are analyzed in Borer et al. (2005).

determining how different forces are propagated through the community (i.e., across the plant–herbivore link). Similar analyses also have shown the importance of this herbivore–plant link for both influencing the strength of trophic cascades (Shurin et al. 2002) and the stability of plant biomass (Halpern et al. 2005). Our cross-system approach to these analyses suggests that results are consistent across a variety of species and types of species interactions. Importantly, our results indicate that despite differences among ecosystems in the strength of trophic cascades (Shurin et al. 2002), the top-down control of community structure is consistently transmitted further than bottom-up control. Past work in terrestrial (e.g., Hunter and Price 1992, Schmitz et al. 2004), freshwater (e.g., Power 1992, Carpenter and Kitchell 1993, Brett and Goldman 1996), and marine intertidal systems (e.g., Menge 2000) has shown how different species-specific and system-specific factors, such as plant edibility, recruitment dynamics, omnivory, system openness, competition for resources, and differences in the spatial and temporal scale of predator and prey population dynamics, may influence when and why top-down and bottom-up forces act to control biomass distribution. These various factors are indeed important for understanding system- and location-specific dynamics of top-down vs. bottom-up regulation, but overall we demonstrated that, across ecosystems, the effects of predation attenuate more slowly than the effects of productivity.

Simple trophic theory predicts that in a community with only plants and herbivores, herbivore biomass should increase with ecosystem productivity while plant biomass remains unchanged, while in a community that also includes predators, plant biomass should increase with productivity while herbivore biomass remains unchanged (Oksanen et al. 1981). In the current empirical test of these theoretical predictions, both predictions are upheld for three-level communities (plants, herbivores, and predators); increased productivity led to increased plant biomass and no change in herbivore biomass. In contrast, neither theoretical prediction was borne out in the two-level empirical communities. In addition, theory predicts that in three-level communities the effects of predators on lower trophic levels will increase with productivity (Oksanen et al. 1981). This prediction was not borne out in our analysis of empirical tests.

Why are herbivores in predator-free communities unable to take advantage of increased ecosystem productivity as is predicted by this simple community theory? Why do predator effects on herbivores and plants not vary along a gradient of productivity? Theoretical and empirical studies in which plants in two-level communities escape herbivory at high productivity invoke heterogeneity within trophic levels as an explanation (e.g., Chase et al. 2000). Clearly species interactions will play an important role in determining whether bottom-up or top-down effects act more

strongly in controlling local community dynamics (Leibold 1989, Hunter and Price 1992, Leibold et al. 1997, Menge 2000, Hart 2002, Chalcraft and Resetarits 2003). In particular, the relative composition of edible vs. defended plants has been implicated as a key source of variation in the strength of trophic cascades and the degree to which shifts in productivity are translated into herbivore biomass (Murdoch 1966, Leibold et al. 1997, Persson 1999, Polis 1999). For example, as system productivity increases, herbivore control of plants may decline because the plant community may become increasingly defended against herbivory (Leibold et al. 1997). Stoichiometry (e.g., C:N or N:P ratios) also has been implicated as an important factor regulating communities by controlling the efficiency of consumption in predator–prey and herbivore–plant interactions (Elser et al. 1996, 2000b, Brett and Muller-Navarra 1997, Polis 1999). Recent work on the stoichiometry of terrestrial arthropods has shown that predators tend to contain 15–25% more body nitrogen than herbivores whereas herbivores contain 10–20 times more nitrogen than the plants they consume (Elser et al. 2000a, Fagan et al. 2002, Denno and Fagan 2003), suggesting that resource stoichiometry may limit herbivores more than predators (Polis 1999). In addition, predator and herbivore physiological efficiency (e.g., endotherm vs. ectotherm) is very important for explaining the strength of top-down control (Borer et al. 2005). Refocusing research on nutritional quality and plant defense rather than on species identity per se in future studies may help further elucidate why the herbivore–plant link is more resistant to bottom-up perturbations.

We note that spatial and temporal scales of the studies included in the current analysis are unlikely to explain the weak herbivore response to fertilization. The studies incorporated into this analysis covered a broad range of durations (5 days to 6.5 years) and spatial extent (0.1 m^2 to 73 ha). In spite of this, we found only one case (direct effect of predators on herbivores) in which either of these factors provided any explanation of data variance. Thus, these factors do not alter our conclusions, nor do they provide insight into the lack of response of herbivores to fertilization, in particular.

Relatively few studies have simultaneously manipulated predators and nutrient concentrations, and even fewer have measured the effect on both plants and herbivores. Full factorial manipulations are necessary to quantitatively assess the direction of control for community biomass distribution. Although the relatively more pervasive influence of predation compared to system productivity has been found in individual empirical studies (e.g., Dawes-Gromadzki 2002, Boyer et al. 2003), our study quantifies this relationship and highlights the generality of this finding across ecosystems. In addition, our results demonstrate that the decoupling in community dynamics between herbivores and plants observed in marine systems (Menge 2000) is

general to freshwater, marine, and terrestrial communities.

Our analyses are not without their data limitations. Although studies performed in eight different ecosystems manipulated both predators and productivity and most studies included in our analysis quantified the response of multiple species at each trophic level, few studies included complete food webs. Within-ecosystem sample size also was small for all but grassland and lake ecosystems, making rigorous cross-ecosystem comparisons difficult. The relative dearth of such studies leads one to consider what we might find with increased analytical power. Because means provide unbiased estimators (Snedecor and Cochran 1989), we expect that the addition of more studies will not change our main result that top-down indirect effects are relatively stronger than bottom-up indirect effects. However, because statistical power increases with increasing sample size (Snedecor and Cochran 1989), with more studies, we may find that fertilization significantly increases the impact of predation on plant and herbivore biomass or that herbivores increase with fertilization in the absence of predators, if relatively weakly. Further factorial manipulations of nutrients and a multitude of predator types will deepen our understanding of the biological processes driving these patterns.

The literature on top-down vs. bottom-up community regulation is vast and varied. Consensus on the relative importance of each in controlling communities has not been reached, except to acknowledge that both forces may be important in structuring communities (Hunter and Price 1992, Leibold et al. 1997, Menge 2000, Moran and Scheidler 2002). The analysis presented here is the first to quantitatively synthesize studies from multiple systems that allow direct comparison of top-down and bottom-up forces (i.e., studies that measure plant and herbivore response to predators and nutrient manipulations in three-level food chains). This analysis shows that general rules exist. Both top-down and bottom-up forces have strong direct effects on adjacent trophic levels. Predator removal increases herbivore abundance and fertilization leads to increased plant biomass in most cases. Furthermore, in contrast to predictions from trophic theory, there are no significant interactions between the effects of predator removal and fertilization. However, these forces differ greatly in the degree to which they attenuate through a food chain. Top-down effects generally resonate beyond the herbivore level of food chains to create trophic cascades. In contrast, the bottom-up effects created by fertilization have less consistent indirect effects on herbivore abundance.

The asymmetry in the effects of top-down and bottom-up forces has striking implications for efforts to manage biological communities; shifts in predator abundance and composition will have profound effects at all trophic levels (e.g., Fritts and Rodda 1998, Alroy 2001), while eutrophication is more likely to cause increased plant productivity that is not controlled by herbivores. The inability of herbivores to fully compensate for increased plant productivity may explain the prevalence of such consequential impacts as anoxia-induced fish kills created by algal blooms in freshwater and marine ecosystems. Thus, we expect that both ecosystem eutrophication and predator additions or extinctions will trigger formidable effects at the base of food webs via both direct impacts on plant biomass that are not transmitted up the food-chain and indirect cascades instigated through alterations in predation pressure.

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APPENDIX

References to studies used to create the fertilization and productivity data sets (*Ecological Archives* E087-171-A1).