

## WHAT DETERMINES THE STRENGTH OF A TROPHIC CASCADE?

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**Abstract.** Trophic cascades have been documented in a diversity of ecological systems and can be important in determining biomass distribution within a community. To date, the literature on trophic cascades has focused on whether and in which systems cascades occur. Many biological (e.g., productivity : biomass ratios) and methodological (e.g., experiment size or duration) factors vary with the ecosystem in which data were collected, but ecosystem type, per se, does not provide mechanistic insights into factors controlling cascade strength. Here, we tested various hypotheses about why trophic cascades occur and what determines their magnitude using data from 114 studies that measured the indirect trophic effects of predators on plant community biomass in seven aquatic and terrestrial ecosystems. Using meta-analysis, we examined the relationship between the indirect effect of predator manipulation on plants and 18 biological and methodological factors quantified from these studies. We found, in contrast to predictions, that high system productivity and low species diversity do not consistently generate larger trophic cascades. A combination of herbivore and predator metabolic factors and predator taxonomy (vertebrate vs. invertebrate) explained 31% of the variation in cascade strength among all 114 studies. Within systems, 18% of the variation in cascade strength was explained with similar predator and herbivore characteristics. Within and across all systems, the strongest cascades occurred in association with invertebrate herbivores and endothermic vertebrate predators. These associations may result from a combination of true biological differences among species with different physiological requirements and bias among organisms studied in different systems. Thus, although cascade strength can be described by biological characteristics of predators and herbivores, future research on indirect trophic effects must further examine biological and methodological differences among studies and systems.

**Key words:** herbivore; indirect effect; meta-analysis; predator; productivity; trophic cascade.

### INTRODUCTION

Trophic cascades, indirect positive effects of predators on plant biomass, have been observed in many systems (Brett and Goldman 1996, Micheli 1999, Pinnegar et al. 2000, Schmitz et al. 2000, Halaj and Wise 2001). A current debate is whether cascades are stronger or more likely in some systems than in others (Pace et al. 1999, Polis 1999, Polis et al. 2000). The ecological literature abounds with predictions about the relative strength of predator effects on plants among ecosystems (e.g., Strong 1992, Polis and Strong 1996, Polis 1999, Oksanen and Oksanen 2000), but in spite of these cross-ecosystem predictions, studies synthesizing data have tended to focus on the evidence for trophic cascades in one or two ecosystem types.

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A recent meta-analysis using data from six ecological systems demonstrates that cascades are strongest in the marine benthos, intermediate in lakes and streams, and weakest in the marine plankton and grasslands (Shurin et al. 2002). This cross-system analysis, including 102 studies that report the biomass of plants in systems with and without predators, is the only study to date that has assessed the relative magnitude of cascading trophic effects among multiple ecological systems. Although it is valuable to know that cascade strength differs among systems, this information does not produce a mechanistic understanding of trophic cascades, and little is known about the true causes of variation in the magnitude of cascading effects within or among systems. Here we use existing data to examine hypotheses about *why* trophic cascades occur and whether the causes are consistent across ecosystems.

Hypotheses about why trophic cascades occur can be roughly categorized into five groups (e.g., Persson 1999, Polis et al. 2000). First, high *spatial heteroge-*

TABLE 1. Factors measured or estimated for each study and related to hypothesis categories about the causes of trophic cascades.

Hypotheses and factors	Data collected (value)
Spatial heterogeneity	
Predator caging	predator caged (0) or predator not in a cage (1)
Experiment (enclosure) size	reported (or estimated) area of study (m <sup>2</sup> )
Community regulation: within and among trophic levels	
Predator feeding specialization	specialist (0), generalist (1), or omnivore (2)
Predator richness (in study)	no. predator species reported in study
Herbivore richness (in study)	no. herbivore species in study
Plant richness (in study)	no. plant species reported in study
Resource availability and quality	
Plant (re)generation time <sup>†</sup>	estimated days to sexual or asexual production of new individuals (days)
System productivity	reported plant biomass production in absence of predators and herbivores (μ/L and g/m <sup>2</sup> )
Fertilization studies	studies manipulating nutrients <i>and</i> predators
Duration	
Study duration	study duration (days)
Study duration/plant generation time	derived via combination of two factors (days/day)
Efficiency	
Predator taxonomy	predator invertebrate (0) or vertebrate (1)
Predator size <sup>‡</sup>	estimated as species mean mass (g)
Predator mobility	predator sessile (0) or mobile (1)
Predator thermal regulation	predator ectotherm (0) or endotherm (1)
Predator metabolism (invertebrate, vertebrate ectotherm, vertebrate endotherm)	derived via combination of two factors with average mass-specific metabolic rates <sup>§</sup>
Herbivore taxonomy	herbivore invertebrate (0) or vertebrate (1)
Herbivore mobility	herbivore sessile (0) or mobile (1)
Herbivore thermal regulation	herbivore ectotherm (0) or endotherm (1)
Herbivore metabolism (invertebrate, vertebrate ectotherm, vertebrate endotherm)	derived via combination of two factors with average mass-specific metabolic rates <sup>§</sup>

<sup>†</sup> Categorical estimates by autotroph type: 1 for microalgae, 10 for calcareous algae or coralline turf, and 365 for macroalgae and annual vascular plants.

<sup>‡</sup> For comparability among studies, we used estimated means for each species even when actual data were available.

<sup>§</sup> Average values for mass-specific metabolic rates (normalized by the production : biomass ratio for consumers, therefore unitless) are calculated from Yodzis and Innes (1992) for invertebrate (0.1), vertebrate ectotherm (0.6), and vertebrate endotherm (3) categories.

neity should weaken cascades because refugia for herbivores will reduce the search efficiency of predators, thereby reducing the magnitude of the indirect effect of predators on plants (Polis et al. 2000). Second, *food webs that deviate from a linear food chain* include interactions within a guild (e.g., competition, intraguild predation) or among trophic levels (e.g., omnivory) and will show reduced cascade strength due to weaker and more diffuse interactions among trophic levels (Fagan 1997, Leibold et al. 1997, Agrawal 1998). Third, *high resource availability and quality* will promote cascades by increasing consumption rates by herbivores, thereby increasing the impacts of primary consumers on primary producers (Leibold 1989, Cebrian 1999, Polis 1999). Fourth, indirect effects of predators on plants will decrease if the plants have time to regenerate or be replaced by inedible species, so cascades should

decrease with increasing *study duration* (Polis and Winemiller 1996, Persson 1999, Polis 1999). Finally, high *predator or herbivore efficiency* (e.g., low metabolic costs, strong numerical or functional responses) will increase cascade strength via high consumer conversion efficiency (Strong 1992, Polis 1999). Although factors may fall into more than one category, this framework provides a starting point for understanding the characteristics of organisms and ecosystems associated with trophic cascades.

We examined the relationship between the strength of trophic cascades and the biological and methodological factors related to the five categories listed above (Table 1). Much of the discussion about the relative strength of trophic cascades among systems has focused on biological differences among systems (Strong 1992, Polis and Winemiller 1996, Shurin et al. 2002).

TABLE 2. Biological and methodological factors quantified by ecosystem type (means with 1 SD in parentheses) from 114 publications used in the current study to assess the most important and general factors associated with trophic cascades ( $n$  represents the number of studies included for each system).

Parameter	Units	Agriculture ( $n = 9$ )	Grassland ( $n = 14$ )
Predator taxonomy	binary	0.0 (0.0)	0.2 (0.4)
Predator thermal regulation	binary	0.0 (0.0)	0.1 (0.4)
Predator mobility	binary	1.0 (0.0)	1.0 (0.0)
Predator specialization	binary	0.6 (0.7)	1.1 (0.4)
Predator size <sup>†</sup>	ln(grams)	-4.1 (3.3)	1.2 (3.6)
Predator metabolism	none <sup>‡</sup>	0.1 (0.1)	0.6 (1.0)
Predator richness	count	3.4 (4.4)	1.4 (0.9)
Herbivore taxonomy	binary	0.0 (0.0)	0.1 (0.3)
Herbivore thermal regulation	binary	0.0 (0.0)	0.1 (0.3)
Herbivore mobility	binary	1.0 (0.0)	1.0 (0.0)
Herbivore metabolism	none <sup>‡</sup>	0.1 (0.0)	0.3 (0.8)
Herbivore richness	count	1.7 (0.7)	5.0 (8.1)
Plant generation time <sup>†</sup>	ln(days)	5.9 (0.0)	5.9 (0.0)
Plant richness	count	1.6 (1.3)	6.8 (6.4)
Predator caging	binary	0.2 (0.4)	0.1 (0.4)
Experiment size <sup>†</sup>	ln(meters <sup>2</sup> )	3.1 (1.8)	1.6 (4.6)
Study duration <sup>†</sup>	ln(days)	3.9 (0.8)	4.6 (1.1)
Study duration/plant generation time <sup>†</sup>	ln(days/day)	-2.0 (0.8)	-1.3 (1.1)

Notes: For parameter definitions and further descriptions of each factor under Units, see Table 1; for the complete data set, see the digital Supplement.

<sup>†</sup> Presented as ln(Factor).

<sup>‡</sup> Averages of mass-specific metabolic rates (normalized by the production : biomass ratio of consumers, and therefore unitless) for vertebrate endotherms, vertebrate ectotherms, and invertebrates from Yodzis and Innes (1992).

However, system-specific methods for studying trophic cascades may systematically bias our estimates of cascade strength by constraining factors such as spatial heterogeneity or study duration (e.g., whole system studies vs. small experimental plots). We first develop multiple regression models to determine the best descriptors of trophic cascades. We then examine the correlation (strength and direction) of each factor across the entire data set and compare this value with the correlation of each factor within ecological systems to establish which biological and methodological factors are general characteristics of cascades.

#### METHODS

We collected data from 114 published papers that included some measure of plant community biomass (e.g., grams per square meter) in the presence and absence of predators (see Supplement). These are the same studies examined in Shurin et al. (2002), with the inclusion of 12 additional recently published experiments. Here, we divided the terrestrial studies into two categories, agricultural biological control ("agriculture") and natural grassland/shrubland ("grassland"). We use the terms "plant" and "primary producer" interchangeably throughout to indicate autotrophs (vascular plants and algae). Following Shurin et al. (2002), we did not include studies reporting only plant response metrics such as leaf damage, because there is no clear evidence that these measures translate into long-term changes in primary producer biomass, the ecosystem response underlying the original trophic cascade concept (Hairston et al. 1960). We tabulated the biological and methodological information provided in each pub-

lication, with other generally available species information (e.g., species mean size). We list all quantifiable factors in Table 1.

We compared the effect of predators on plant biomass using meta-analysis, an analytical tool used to examine general patterns across studies (Arnqvist and Wooster 1995a, Gurevitch and Hedges 1999, Osenberg et al. 1999, Lajeunesse and Forbes 2003). The response variable in our meta-analysis was the log ratio of plant biomass with and without a predator ("cascade strength"). Thus, positive log ratio values represent a trophic cascade: an increase in plant biomass in the presence of a predator. In contrast to many response metrics, the log ratio does not vary with the level of replication or the magnitude of the average biomass in a study (Englund et al. 1999) and meets the assumptions of parametric analyses (Hedges et al. 1999). The log ratio is based on the important assumption that plant biomass has reached equilibrium. This assumption was supported by an assessment of available time series data from those studies reporting multiple sampling dates (as in Shurin et al. 2002). For all studies presenting multiple sampling dates, we used the final sampling date in our analyses.

We did not include the precision of each study's estimates in this analysis (i.e., variance weighting) for several reasons. First, weighting primarily affects estimates of dispersion and has little effect on estimates of mean response (Englund et al. 1999). Second, and more importantly, many studies did not report precision estimates (for example, unreplicated, whole-system studies), so an analysis of only those studies including variance estimates would bias the analysis toward

TABLE 2. Extended.

Lake benthos <i>n</i> = 12	Lake plankton <i>n</i> = 22	Marine benthos <i>n</i> = 8	Marine plankton <i>n</i> = 14	Stream <i>n</i> = 33
0.5 (0.5)	0.9 (0.3)	0.8 (0.3)	0.3 (0.5)	0.8 (0.4)
0.0 (0.0)	0.0 (0.0)	0.5 (0.5)	0.0 (0.0)	0.0 (0.0)
1.0 (0.0)	1.0 (0.0)	0.9 (0.2)	1.0 (0.0)	0.9 (0.3)
1.2 (0.4)	1.1 (0.2)	1.2 (0.4)	1.1 (0.4)	1.3 (0.5)
3.9 (1.3)	1.3 (1.1)	8.1 (2.0)	2.3 (1.5)	5.1 (1.8)
0.4 (0.3)	0.6 (0.1)	1.7 (1.4)	0.2 (0.2)	0.5 (0.2)
1.5 (0.8)	1.5 (1.1)	3.6 (3.8)	1.2 (0.4)	2.2 (4.4)
0.0 (0.1)	0.0 (0.0)	0.1 (0.2)	0.0 (0.0)	0.0 (0.1)
0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
1.0 (0.1)	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)	0.8 (0.4)
0.1 (0.1)	0.1 (0.0)	0.1 (0.1)	0.1 (0.0)	0.1 (0.1)
...	10.0 (0.0)	3.2 (5.4)	4.3 (2.0)	9.6 (6.6)
0.0 (0.0)	0.0 (0.0)	4.8 (1.5)	0.0 (0.0)	0.0 (0.0)
11.0 (0.0)	...	6.9 (3.4)	4.0 (1.0)	10.8 (9.4)
0.0 (0.0)	0.0 (0.0)	0.9 (0.4)	0.0 (0.0)	0.0 (0.0)
0.2 (2.2)	2.3 (2.3)	11.4 (7.6)	-0.4 (0.7)	0.6 (2.2)
4.6 (0.2)	4.0 (0.5)	7.7 (1.9)	3.3 (0.7)	3.5 (0.5)
4.6 (0.2)	4.0 (0.5)	2.7 (3.1)	3.2 (0.7)	3.5 (0.5)

small-scale, well-replicated experiments (Arnqvist and Wooster 1995a, Englund et al. 1999). Here, we have included a greater number of studies rather than limiting the analysis to studies with precision estimates, because increased sample sizes decrease the probability of Type I estimation errors in meta-analyses (Arnqvist and Wooster 1995b, Englund et al. 1999, Lajeunesse and Forbes 2003).

To assess the most important and general factors associated with the log ratio of the predator effect on

plant biomass in each study, we created multiple regression models (1) for the overall data set and (2) within the system from which the data were collected. The second analysis was performed by regressing over the residuals after removing the effect of the system. Thus, the overall data set analysis produces a model including factors that best describe the variance in the entire data set, while the within-system analysis quantifies factors best describing variance in cascade strength within each system. Because the data matrix

TABLE 3. Univariate regression models (of a possible 114 studies) of cascade strength vs. biological and methodological factors within and among systems.

Factor	<i>n</i>	Within system (residuals after removing system means)			Overall (models across all available data)		
		ss	<i>P</i>	$\beta$	ss	<i>P</i>	$\beta$
Predator taxonomy	114	0.186	0.47	0.085	<b>5.121</b>	< <b>0.01</b>	<b>0.446</b>
Predator thermal regulation	114	<b>1.705</b>	<b>0.03</b>	<b>0.548</b>	<b>6.307</b>	< <b>0.01</b>	<b>1.053</b>
Predator mobility	114	<b>1.610</b>	<b>0.03</b>	<b>0.613</b>	0.765	0.21	0.423
Predator specialization	114	0.237	0.41	-0.101	0.010	0.89	-0.020
Predator size†	112	0.011	0.86	0.003	<b>3.768</b>	< <b>0.01</b>	<b>0.052</b>
Predator metabolism	114	<b>2.979</b>	< <b>0.01</b>	<b>0.200</b>	<b>9.100</b>	< <b>0.01</b>	<b>0.350</b>
Predator richness	114	0.604	0.19	-0.025	0.164	0.56	-0.013
Herbivore taxonomy	114	<b>1.821</b>	<b>0.02</b>	<b>-0.974</b>	1.586	0.07	-0.909
Herbivore thermal regulation	114	0.755	0.14	-0.873	1.727	0.06	-1.320
Herbivore mobility	114	0.003	0.99	<0.001	0.003	0.94	0.018
Herbivore metabolism	114	1.063	0.08	-0.353	<b>1.888</b>	<b>0.05</b>	<b>-0.471</b>
Herbivore richness	98	0.079	0.64	0.005	0.644	0.27	0.014
Plant generation time†	112	0.235	0.41	0.018	0.262	0.47	-0.019
Plant richness	51	0.003	0.94	0.001	0.351	0.48	0.013
Predator caging	114	0.558	0.21	-0.237	0.703	0.23	0.266
Experiment size†	112	0.778	0.13	-0.020	1.054	0.14	0.023
Study duration†	112	0.382	0.30	-0.044	<b>2.381</b>	<b>0.03</b>	<b>0.110</b>
Study duration/plant generation time†	110	0.484	0.24	-0.027	1.651	0.07	0.050

Notes: Tables 1 and 2 define the values and units for each factor, *n* represents the number of studies used in the analysis of each factor, ss is the model sums of squares, the *P* value shows the significance of each univariate model, and  $\beta$  represents the predicted slope of the univariate regression model. Models in boldface are significant at *P* < 0.05, meeting our criterion for inclusion in the multivariate models.

† Model fit is for the natural log of the factor.

TABLE 4. Final multiple regression models for the overall data set (without regard to system) and the within-system data set (model using residuals after removing the effect of system type).

Factor	df	Type III ss	F	P
Overall model ( $n = 112$ , residual $df = 107$ , model $r^2 = 0.31$ )				
Predator taxonomy	2	4.109	5.86	<0.01
Predator thermal regulation	1	8.667	24.72	<0.001
Herbivore metabolism	1	6.545	18.67	<0.001
Within-system model ( $n = 112$ , residual $df = 106$ , model $r^2 = 0.18$ )				
Predator mobility	2	2.281	3.74	0.03
Predator metabolism	1	2.920	9.58	<0.01
Herbivore taxonomy	2	3.431	5.63	0.01

Note: For the models,  $n$  represents the number of studies included in the model.

had missing data, regression models that included all 18 factors would have included only 38 of the 114 original studies. For this reason, we used univariate regression to pre-screen variables for inclusion in the multiple regression models, including only factors significant in univariate tests ( $P < 0.05$ ) in the multiple regression models. We used backward selection to iteratively remove factors with the lowest Type III ss from the multiple regression models until the overall and within-system models contained only significant factors. Inferences based on statistical significance were derived only from multiple regression analyses.

We compared the Pearson correlation of each factor with the overall data set log ratios to the Pearson correlation of the same factor after removing the effect of ecosystem type (i.e., analysis of residuals after removing system means). Finally, we analyzed the subset of studies that simultaneously manipulated predators and nutrient availability to plants to determine relationships between productivity and cascade strength.

We analyzed studies with a mixture of categorical values (e.g., both vertebrate and invertebrate predators in a single study) as ordinal with the mixture treated as an intermediate category. For studies with several values for a continuous variable (e.g., different plant generation times), we analyzed the mean value of the variable for the study. These models were not substantially different from models that subsumed the mixture into one of the categories.

We used SAS release 8.2 (SAS Institute, Cary, North Carolina, USA) for all analyses.

## RESULTS

An assessment of mean values (Table 2) shows that some factors (e.g., predator size, plant generation time, experimental arena size, and study duration) were remarkably different among systems. Other variables, such as several of the herbivore characteristics, were similar among systems. The univariate model slopes showed that, with few exceptions, predator and her-

bivore characteristics had the same effect direction in the overall- and within-system models, whereas strictly methodological factors had the opposite slope directions in the two models (Table 3).

Predator taxonomy and thermal regulation and herbivore metabolism, explained 31% of the variation in cascade strength in the multiple regression model of the overall data set (Table 4). Invertebrate predators (e.g., spiders, jellyfish, insect predators) were associated with weak cascades, but, in contrast, invertebrate herbivores were associated with strong cascades (Fig. 1). A similar pattern emerged after removing the effect of system. Predator metabolism, herbivore taxonomy (Fig. 2), and predator mobility explained 18% of the within-system variance. Thus, predator and herbivore characteristics from the Efficiency category (Table 1) provided the best explanation of trophic cascade patterns both within systems and across the entire data set.

Both biological and methodological factors were significantly correlated with cascade strength ( $r < -0.2$  or  $r > 0.2$ ), but no factor was significantly correlated both in the overall data set and after removing the effect

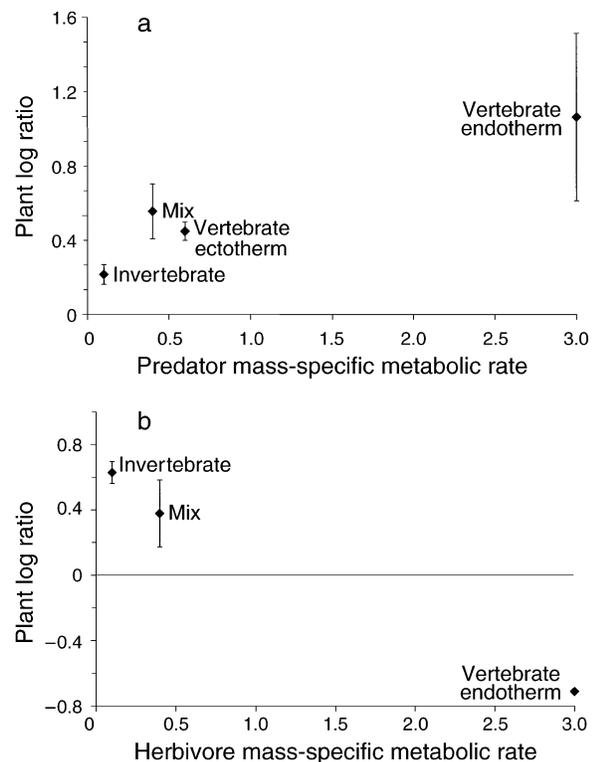
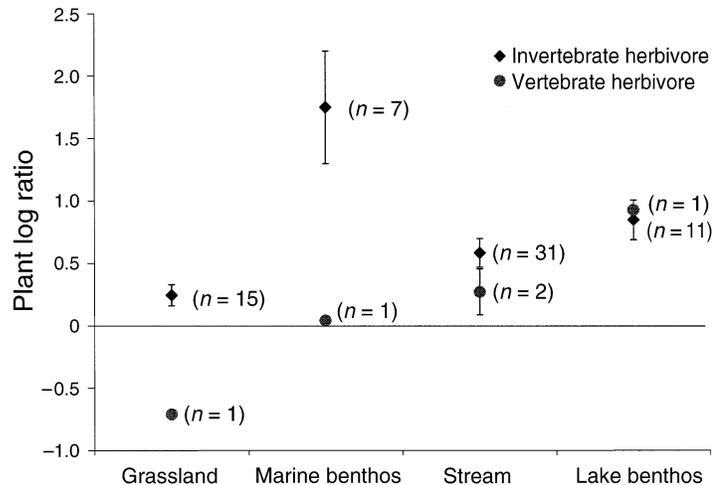


FIG. 1. Response of plant log ratio (cascade strength; mean  $\pm$  1 SE) to (a) predator and (b) herbivore mass-specific metabolic rate. (a) The overall cascade strength was strongest with ectothermic vertebrate predators, but (b) declined with increasing metabolic rate for herbivores. The univariate models for these factors are presented in Table 3. "Mix" represents studies with both invertebrates and vertebrate ectotherms.

FIG. 2. In three of the four systems examining vertebrate herbivores, vertebrates have a significantly lower mean cascade strength (mean  $\pm$  1 SE;  $P = 0.01$ ; Table 4). It is interesting to note that the vertebrates in both the stream and lake benthos studies were tadpoles, while the grassland vertebrate (rabbit) was the only endothermic herbivore in the data set. Our data set included no studies with vertebrate herbivores in the three missing systems (agriculture, lake plankton, and marine plankton).



of system (Fig. 3). Correlation coefficients of all 18 factors ranged from +0.4 to -0.4, and factors with significant univariate models also had significant correlations with trophic cascades (Fig. 3). Many factors showed little association with cascades at either scale, including predator and herbivore richness and herbivore mobility.

Factors with the same correlation direction both within systems and over the entire data set (e.g., herbivore metabolism and predator size; Fig. 3) were biological characteristics of predators and herbivores and generally fell into the Efficiency category of Table 1. As in the multiple regression model for the overall data set, cascade strength declined as herbivore metabolic rate increased from invertebrate to vertebrate ectotherm to vertebrate endotherm (Figs. 1b and 2).

In contrast, factors with opposite correlation signs within systems and across the entire data set (e.g., study duration; Fig. 3) were most often associated with system-specific methods and generally fell into the Heterogeneity and Duration categories of Table 1. Overall cascade strength had a significant positive correlation with only one discordant factor, study duration (Fig. 3), primarily because long studies in the marine benthos reported strong cascades (Fig. 4a). The correlation of study duration with cascade strength was no longer significant after removing the effect of plant generation time (Fig. 4b) or system (as in Shurin et al. 2002).

An examination of the subset of studies in which a measure of system fertility was either reported or manipulated in conjunction with predator manipulations suggests that productivity was a poor predictor of cascade strength. Twenty lake studies and nine terrestrial studies reported plant standing crop (e.g., grams per square meter) in the absence of predators and herbivores, but the correlation with cascade strength was not significant (Lake,  $r = 0.08$ ,  $P = 0.75$ ; Grassland,  $r = -0.46$ ,  $P = 0.21$ ). In addition, 16 studies conducted in five of the seven study systems simultaneously manipulated nutrients and predators, providing a second

test of the importance of system productivity. While the mean cascade strength was larger in treatments with elevated nutrients (no fertilization =  $0.37 \pm 0.12$  [means  $\pm$  1 SE], fertilization =  $0.57 \pm 0.18$ ), this effect was not significant (paired  $t$  test,  $P = 0.26$ ).

#### DISCUSSION

As predicted by the Efficiency Hypothesis, biological characteristics of predators and herbivores are good predictors of the magnitude of trophic cascades. Predator taxonomy and thermal regulation and herbivore mass-specific metabolic rates describe 31% of the var-

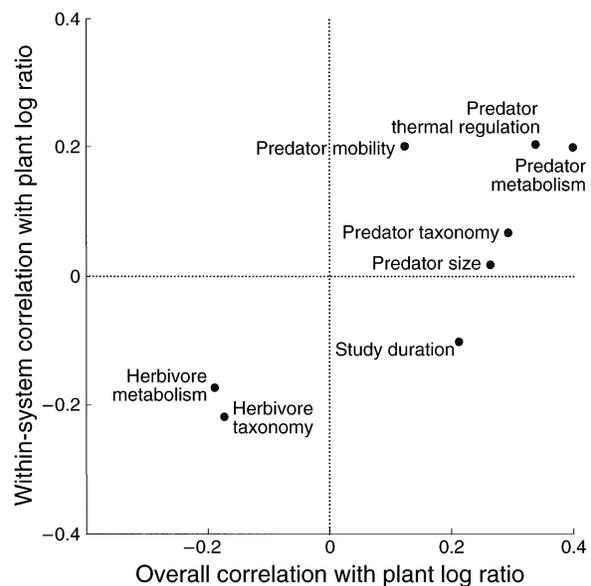


FIG. 3. Pearson correlation analysis of cascade strength with biological and methodological factors in the overall data set and within systems. Only factors significant in the univariate analyses are plotted (see Table 3). All plotted factors have significant correlations ( $P < 0.05$ ) with either the overall or the within-system data set. In all cases, a correlation of  $\geq |0.2|$  is significant. Table 1 explains factor names.

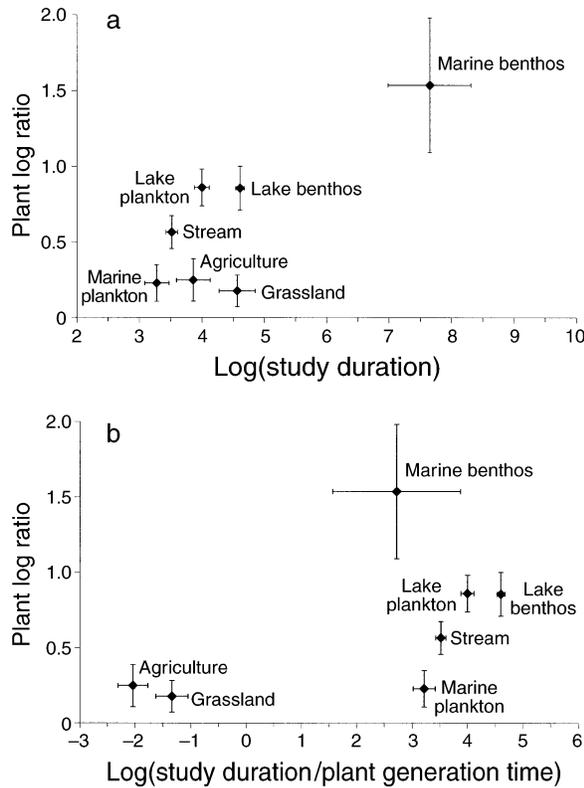


FIG. 4. Response of cascade strength (mean  $\pm$  1 SE) to study duration (a) before and (b) after accounting for plant regeneration times. (a) Overall, cascade strength increased with study duration (originally measured in days). However, study durations in the marine benthos, the system with the highest mean cascade strength, tend to be longer than in other systems. (b) After accounting for plant regeneration times in each study, the mean cascade strength was no longer associated with study duration. Both terrestrial systems are noticeably different from other system types. Univariate models are presented in Table 3.

iation in cascade strength among 114 studies conducted in seven ecosystems, and similar predator and herbivore characteristics describe nearly 20% of the variation within systems. Although these factors are apparently strictly biological, our data included only one study of an endothermic herbivore (rabbits) and five studies of endothermic predators. This type of methodological bias in study organisms, particularly toward invertebrate herbivores, has plagued all recent examinations of trophic cascades (Brett and Goldman 1996, Pinnegar et al. 2000, Schmitz et al. 2000, Halaj and Wise 2001). Across our entire data set, the predators associated with the strongest cascades were endothermic vertebrates (i.e., humans and otters), but this pattern was driven primarily by the association of this metabolic group with extremely strong cascades in marine benthic studies. In contrast, terrestrial endothermic predators (passerine birds and fox and cat predators) produced some of the weakest reported cascades (cascade strength = 0.06 and  $-0.71$ , respectively). Thus,

the importance of metabolic efficiency in describing cascade strength may not only be caused by biological characteristics of species, but may also indicate methodological biases in the types of organisms studied in each ecosystem. This issue clearly requires further testing within and among systems.

Our results suggest that invertebrate herbivores cause stronger trophic cascades than do vertebrate herbivores both within and among systems, a pattern found in a meta-analysis of herbivore effects on plants (Bigger and Marvier 1998). Several lines of evidence suggest that herbivores may be crucial determinants of cascade strength (Polis and Strong 1996, Persson 1999, Shurin et al. 2002). In particular, Polis and Strong (1996) argue that high grazing efficiency combined with high predation vulnerability provide a context of strong, recipient-controlled links that can lead to trophic cascades. A meta-analysis of studies quantifying risk-reward trade-offs in herbivores suggests that cascade strength could be predictable by the type of predation-avoidance behavior employed by herbivores (Schmitz et al. 2004). In addition, an earlier meta-analysis of the data presented here implicates herbivores as the prime mediators of cascade strength because many studies showed strong predator control of herbivores, but weak herbivore control of plants (Shurin et al. 2002). Empirical observations show, however, that herbivores can be very efficient in both aquatic (Elser and Goldman 1991, Sala and Graham 2002) and terrestrial systems (Crawley 1997, McNaughton 2001). Conversely, defenses by both plants (Huntly 1991) and herbivores (Murdoch 1966, Menge and Sutherland 1987, Abrams 1993) can reduce herbivore foraging efficiency, leading to weaker cascades (Strong 1992).

In contrast to the predictions of the Resource Availability Hypothesis, our results suggest that high system productivity per se does not generate substantially larger cascading effects. Although this result contradicts simple trophic theory (Oksanen et al. 1981), it corroborates the results of a meta-analysis of the role of eutrophication in marine pelagic trophic cascades (Micheli 1999). The lack of a distinct productivity effect may be caused by plants becoming increasingly defended against herbivory as system productivity increases (Leibold et al. 1997), reducing the strength of recipient-control in the system. System productivity, plant turnover rates (i.e., regeneration), and palatability to herbivores are intertwined factors that can affect biomass distribution within a food web (Cebrian 1999, Persson 1999, Polis 1999). Stoichiometry (e.g., the C:N and N:P ratios at each trophic level) has been implicated as a crucial factor affecting transfer efficiency between trophic levels (Elser et al. 1996, Brett and Muller-Navarra 1997, Polis 1999). Cyr and Pace (1993) reported that zooplankton consume a three-fold greater proportion of primary productivity in lakes than is consumed by terrestrial herbivores. Phytoplankton growth rates and nitrogen content are both substantially greater than

those of terrestrial plants (Cebrian 1999, Elser et al. 2000). Plant productivity, nutritional quality, and turnover rates of plants are quite different among systems, but are closely related to palatability and should determine the strength of top-down control (Carpenter et al. 1992, Cebrian 1999). Future studies of trophic cascades that specifically quantify plant palatability (e.g., C:N ratio of plants), stoichiometric similarity among plants, herbivores, and predators, and alterations of system productivity promise to be profitable.

The Community Regulation Hypothesis suggests that diversity within trophic levels may limit trophic cascades through compensatory dynamics within trophic levels (Holt and Polis 1997, Pace et al. 1999); however, species diversity at each of the three trophic levels in this study was not related to trophic cascade intensity. Two recent meta-analyses examining terrestrial trophic cascades found larger cascades in lower diversity communities (Schmitz et al. 2000, Halaj and Wise 2001). Most studies of trophic cascades examine species- rather than community-level cascades by manipulating, quantifying, and reporting only interactions in a small subset of the community (Polis 1999). There may therefore have been too little variability in the diversity of organisms manipulated in the studies included in the current survey to detect relationships between diversity and cascade strength.

Our ability to evaluate the importance of the Heterogeneity and Duration Hypotheses was limited by strong among-system methodological biases. Substantial bias toward small spatial and temporal scales in trophic cascade experiments has been identified here and in other recent meta-analyses (Brett and Goldman 1996, Schmitz et al. 2000, Halaj and Wise 2001). These biases can affect the generality of conclusions about cascade strength because methodological factors can alter biologically important elements of each system in predictable ways. For example, study duration can affect comparisons of cascade strength among systems owing to system-specific growth, recruitment, and turnover rates (Brown 1986, Huntly 1991, Menge 1997, Persson 1999). Spatial and temporal heterogeneity, constrained by arena size or study duration, can disrupt control by consumers over their resources (Warner and Chesson 1985, Hunter and Price 1992, Menge 1992).

Although we brought as many studies as possible to bear on the question of why trophic cascades occur, the studies were restricted to a few community types and organisms. Terrestrial studies, for example, were dominated by experiments with arthropods in agricultural systems and grasslands, a bias that has been noted previously (Persson 1999). This bias contrasts with the lake, marine, and stream systems, where studies with vertebrate predators outnumbered those with invertebrates by approximately 2:1. In addition, only marine benthic and grassland studies included endothermic predators, and only a single study examined an endothermic herbivore. Sedentary predators and herbivores

were common only in stream studies. Although vertebrate herbivores were examined in studies in four systems, these comprised only five of the 114 studies. Fewer than half the studies reported the total number of plant species studied, and only a small subset of these listed plant species names. Although we can draw a great deal of information about why trophic cascades occur from existing studies, many biological combinations remain to be examined.

A particularly troubling gap in the information on the indirect effects of predators on plants is the paucity of studies in terrestrial systems (Pace et al. 1999, Persson 1999, Polis 1999). Although we included 23 terrestrial studies, primarily from agriculture (nine studies) and natural grasslands (14 studies), this represents only 20% of the total data set. Hopefully, the relative abundance of aquatic compared to terrestrial studies available for this analysis will inspire terrestrial ecologists, in particular, to perform long-term studies at large spatial scales measuring predator (vertebrate and invertebrate) effects on plant biomass in a diversity of ecosystems.

Biological processes are clearly important in driving variation in the strength of top-down control. Metabolic and taxonomic groups of predators and herbivores explained more than 30% of the variability in trophic cascade strength across all 114 studies and nearly 20% of variation within each system, supporting resource conversion efficiency as the strongest factor driving variation in cascade strength. Invertebrate herbivores, in particular, consistently produced stronger cascades than did vertebrates, both within and among systems, while invertebrate predators produced the weakest cascades. In contrast, the interaction between system-specific methodology and biology clearly demands careful, thoughtful comparisons among systems. Longer studies produced stronger cascades across all systems, but this effect disappeared after accounting for plant regeneration times. In addition, while studies in the five aquatic systems usually included multiple plant generations, terrestrial studies in both natural and agricultural systems were shorter than a single plant generation.

This meta-analysis has shown that herbivore and predator efficiency influence trophic cascade strength, whereas species richness and system productivity were not associated with the strength of trophic cascades. In addition, we have identified strong methodological biases among ecological systems. Thus, further progress in understanding the unexplained variation in trophic cascade magnitude will require empirical studies manipulating multiple factors within systems and studies that employ comparable methods in diverse systems.

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#### SUPPLEMENT

Fully abstracted biological and methodological data (and associated literature citations) used in a cross-system meta-analysis of correlates of the strength of trophic cascades are available in ESA's Electronic Data Archive: *Ecological Archives* E086-028-S1.