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Trophic Cascades in Terrestrial Systems: A Review of the Effects of Carnivore Removals on Plants

Oswald J. Schmitz,[1,2,*] Peter A. Hambäck,[1] and Andrew P. Beckerman[1]

1. School of Forestry and Environmental Studies, Yale University, New Haven, Connecticut 06511;
2. Department of Ecology and Evolutionary Biology, Yale University, New Haven, Connecticut 06511

ABSTRACT: We present a quantitative synthesis of trophic cascades in terrestrial systems using data from 41 studies, reporting 60 independent tests. The studies covered a wide range of taxa in various terrestrial systems with varying degrees of species diversity. We quantified the average magnitude of direct effects of carnivores on herbivore prey and indirect effects of carnivores on plants. We examined how the effect magnitudes varied with type of carnivores in the study system, food web diversity, and experimental protocol. A meta-analysis of the data revealed that trophic cascades were common among the studies. Exceptions to this general trend did arise. In some cases, trophic cascades were expected not to occur, and they did not. In other cases, the direct effects of carnivores on herbivores were stronger than the indirect effects of carnivores on plants, indicating that top-down effects attenuated. Top-down effects usually attenuated whenever plants contained antiherbivore defenses or when herbivore species diversity was high. Conclusions about the strength of top-down effects of carnivores varied with the type of carnivore and with the plant-response variable measured. Vertebrate carnivores generally had stronger effects than invertebrate carnivores. Carnivores, in general, had stronger effects when the response was measured as plant damage rather than as plant biomass or plant reproductive output. We caution, therefore, that conclusions about the strength of top-down effects could be an artifact of the plant-response variable measured. We also found that mesocosm experiments generally had weaker effect magnitudes than open-plot field experiments or observational experiments. Trophic cascades in terrestrial systems, although not a universal phenomenon, are a consistent response throughout the published studies reviewed here. Our analysis thus suggests that they occur more frequently in terrestrial systems than currently believed. Moreover, the mechanisms and strengths of top-down effects of carnivores are equivalent to those found in other types of systems (e.g., aquatic environments).

* E-mail: oswald.schmitz@yale.edu.

A large body of ecological research has shown that carnivores can have strong direct effects on the structure and dynamics of herbivore prey communities via predator-prey interactions (Sih et al. 1985; Schoener 1993; Menge 1995, 1997). A key unresolved issue in terrestrial community ecology is whether those strong effects are frequently transmitted beyond the carnivores' prey base to plant species. The existence of such effects on plants, called "trophic cascades," is regarded as key evidence that top carnivores have a dominant indirect influence on the abundance of plant species.

We provide here a graphical and meta-analytic synthesis of data from studies on terrestrial food webs to evaluate quantitatively the general prevalence of trophic cascades in terrestrial systems. Our analysis is based on 60 independent tests of trophic cascades reported in 41 studies. According to current convention, a trophic cascade occurs when changes in carnivore abundance alter the distribution and abundance of plants on a community-wide basis (Polis 1999). Most of the studies we examined, however, measured interactions among the dominant species or subsets of full communities. Consequently, our review on trophic cascades, by default, is an evaluation of species cascades (sensu Polis 1999) rather than the classical community-level cascades (sensu Polis 1999).

Recent studies suggest that we should not expect trophic cascades to be common in terrestrial systems (Strong 1992; Polis and Strong 1996; Polis 1999). There are a number of reasons why trophic cascades might be an exception rather than the rule. First, terrestrial plants typically contain antiherbivore defenses that can weaken the effects of herbivores on plants relative to effects of carnivores on herbivores (Strong 1992; Polis and Strong 1996). Second, trophic cascades are thought to be restricted to communities with low species diversity where one species or a few species dominate the community (Strong 1992). Terrestrial food webs are often thought to be represented by many species. Species in such systems tend to be linked in a

highly interconnected network of interaction pathways. Trophic cascades should be less common in such systems because the effect of a single species will be differentiated among many pathways in the food web (Strong 1992). Finally, trophic cascades are not expected in some low-diversity systems because of the way herbivore populations are limited by plant-resource supply (Schmitz 1992). There are cases where carnivores may decrease herbivore population density, but herbivores compensate by increasing per capita plant consumption because of reductions in intraspecific competition for plant resources. The consequence is that there is no net change in plant consumption by the herbivore population as a whole (Schmitz 1992, 1993).

The objective of our synthesis is to gain insight into the kinds of terrestrial systems and ecological conditions in which we are likely to see trophic cascades. These were the questions motivating our synthesis: First, what is the magnitude of carnivore-indirect effects on plants mediated by herbivore density and behavior? It should be difficult to detect an effect of carnivore removals on plant abundance if carnivore effects on species in lower trophic levels are quite weak, as suggested by Strong (1992) and Polis and Strong (1996). Second, do effect magnitudes generally attenuate down the trophic chain; that is, is the indirect effect of carnivores on plants generally weaker than the direct effect of carnivores on herbivores? Third, does the type of predator have a bearing on the effects of removing carnivores from a food web? For instance, does the size of predators relative to prey matter? Fourth, does the length of the study affect the outcome of removing predators on plants? Fifth, do effect magnitudes vary with the species diversity in food webs? If food webs represented by many species are more likely to diffuse effects, carnivore removals should have a weaker effect on plants in high-diversity compared to low-diversity systems (Polis and Strong 1996). Sixth, do experimental methods alter effect magnitudes? For example, in syntheses of competition experiments (Gurevitch et al. 1992), it has been suggested that mesocosm experiments generally inflate initial species densities, thereby causing larger effect sizes than do natural field experiments.

Methods

Literature Search

We conducted a comprehensive search for studies satisfying three criteria for the detection of cascading effects. First, our goal was to examine trophic cascades under natural field conditions. We therefore excluded studies on biocontrol under greenhouse conditions or in agricultural plantations, which can be predisposed to show such top-down effects. Second, we required that the study involve experimental manipulations of densities of at least one carnivore feeding on an herbivore species in a mesocosm or field experiment or involve comparisons between sites with and without carnivores by way of an observational experiment. By our definition, a mesocosm experiment is conducted in enclosures where the experimenter determines the initial densities of carnivores and herbivores both in control and experimental treatments. A field experiment is basically a carnivore-removal or carnivore-introduction experiment. An observational experiment is one in which the observer compares herbivore- and plant-response variables in plots where carnivores are naturally present with those where carnivores are naturally absent. Our criteria for including an observational experiment was that the plant and herbivore species had to be the same in both carnivore-present and carnivore-exclusion treatments. Third, we required that at least one plant-response variable was measured during the course of the study. The plant variable could be damage, biomass, or reproductive output. The damage class included damage to leaves as well as to other tissues, such as seeds. The biomass class included final biomass as well as biomass growth. The reproductive-output class was preferentially seed output, but in some cases, we accepted ovule or fruit production. We excluded studies that provided incomplete information, such as those in which results were only reported for some group or subgroup within a designated experimental community.

We conducted several different searches to ensure that our data set was as inclusive as possible. We first conducted an electronic search for the following keywords: "cascading effect," "indirect effect," "predat∗ and herbivor∗," "top-down control," "top-down effect," and "trophic cascade." This search identified 16 articles. We also searched for the keywords: "bottom-up control" and "donor-control." This search did not yield any articles beyond the previous 16. To find studies that did not include these keywords, we searched for the following words: "yield," "parasit∗," "enem∗," "loss∗," and combinations of these words, but this produced no additional articles. To explore the large literature on the role of ants in protecting plants from herbivory, we searched for the following words: "ant-plant mutualism" and "ants and herbiv∗." This produced six additional articles that met our criteria. We augmented the electronic search for suitable articles by thoroughly examining issues of *The American Naturalist*, *Ecological Entomology*, *Ecological Monographs*, *Ecology*, *Oecologia*, and *Oikos* from the past 15 yr. The choice of these particular journals was based on where we found relevant articles in previous searches. This search produced another seven articles. Discussion with colleagues provided five more articles. Finally, we used the Science Citation Index to iden-

tify studies that cited the 34 articles identified with the previous search methods. This last search produced seven additional articles.

Data Extraction and Effect Size Estimation

We extracted mean values for the control (all trophic levels present) and carnivore-removal treatment groups, the associated standard deviations, and the sample sizes. This information was obtained directly from text or tables or estimated from graphs. Whenever data were presented graphically in the form of time series, we selected values from the end of the time series to decrease the chance that we were evaluating transient dynamics after the start of the experiment. In cases where only the standard error was reported, we calculated the standard deviation by multiplying the standard error by $\sqrt{n}$. In some studies, the means and error estimates were reported separately for different species or species groups within a trophic level with no aggregate estimates for the entire trophic level. We calculated mean and error estimates for the entire trophic level by using standard statistical pooling techniques, assuming independence among subgroups (see table 1). In a few cases, responses were measured on very different scales, such as folivore number per leaf and seed predator number per flower head, which precluded a calculation of total mean.

We estimated effect size by using the log ratio between control and experimental mean, that is, $\log(X_j^E/X_j^C)$, where X_j^E and X_j^C are the mean values of the experimental treatment and the control, respectively, for the jth study. The advantage of the log ratio estimator over other meta-analytic statistics (e.g., the standard d_{ip}, the difference between treatment and control means divided by a pooled SD; Gurevitch and Hedges 1993) is that it has greater biological meaning: log ratios of abundance correspond directly to proportional changes in species abundance per unit time, independent of the measured variation in abundance (Osenberg et al. 1997).

It has also been suggested that care should be taken to estimate effect size with due consideration for timescales. When measuring rate of population change, the log ratio estimate should be divided by time; when examining effects at steady state, dividing by time is unwarranted (Osenberg et al. 1997). Our review focused on steady state conditions, so we did not divide the estimate by time.

We first calculated the variance of the log response ratios for each comparison separately, as described by Hedges et al. (1999). We then conducted a mixed-model meta-analysis (Gurevitch and Hedges 1993) by using MetaWin (Rosenberg et al. 1997). We used a mixed-model analysis because we could not assume that there was one true effect size across all studies in a class. Confidence intervals (CI)

for the meta-analytic statistics were estimated by using bootstrapping, and *P* values were estimated through randomization. Before performing a meta-analysis on log response ratios, Hedges et al. (1999) recommend that both $\sqrt{n^C}X^C/s^C$ and $\sqrt{n^E}X^E/s^E$ are >3 for the majority of studies in the sample. We calculated $\sqrt{n^C}X^C/s^C$ and $\sqrt{n^E}X^E s^E$ for the studies in our sample and found that the lower of these two values was <3 in 16% of the cases and <2 in 7% of the cases, indicating that our data set largely meets this condition.

To evaluate whether the effects of top carnivores attenuate at lower trophic levels (second question), we plotted the magnitudes of the indirect effect of carnivores on plants for each study against the corresponding magnitudes of the direct effect of carnivores on herbivore densities. The rationale for this analysis is that if the data lie along a 45° reference line, representing equivalence of direct- and indirect-effect magnitudes, then the effect magnitudes do not attenuate. If the data cluster to the left of the reference line, then top-down effects are attenuating; if they cluster to the right of the line, then top-down effects are intensifying. We base our comparison on a 1 : 1 correspondence between direct- and indirect-interaction strengths of top carnivores on herbivores and on plants simply to ascertain whether there is some empirical basis for the claim that carnivore effects commonly attenuate in terrestrial food webs (Polis and Strong 1996).

Results

Overview of Carnivore-Removal Experiments

The diversity of study systems was large, covering lizard and bird removals in subtropical and temperate systems, ant-removal experiments in a host of environments worldwide, and other arthropod-removal experiments in temperate and boreal systems. There was a clear dominance of tests on the effect of ant removal (35 tests). Vertebrate carnivore removals were equal in number to arthropod carnivore removals (10–12 tests each; table 1). All studies involved only arthropod herbivores. Vertebrate herbivores, especially mammals, can have important effects on plant biomass (Huntly 1991; Olff and Ritchie 1998), and predation is an important mortality factor for many mammal herbivores (Boutin 1992; Oksanen and Oksanen 1992; Messier 1995; Sinclair and Arcese 1995). But the experimental evaluation of top-down effects in systems with mammalian herbivores is still largely lacking. In our opinion, the two studies we found that involved mammalian herbivores only provided correlative evidence for trophic cascades (McLaren and Peterson 1994) or had insufficient information to quantify effect magnitudes in the community being manipulated (Gutierrez et al. 1997).

Table 1: Description of study systems and log response ratios of the effect of top predator removal on herbivore density, plant damage, plant biomass, and plant reproductive output

Source	Carnivore	Herbivore Type[a]	Herbivore Div.[b]	Plant Type	Plant Div.[b]	Study Type[c]	Study Length[d]	Habitat type[e]	Log response ratio Herbivore density	Log response ratio Plant damage[f]	Log response ratio Plant biomass	Log response ratio Plant reproduction
Vertebrate top predators:												
Atlegrim 1989, figs. 1, 2	Birds	Leaf feeder	H	Shrub	L	E	2.5	Boreal	−.85 ± .29	1.14 ± .29	...	...
Atlegrim 1989, figs. 1, 2	Birds	Leaf feeder	H	Shrub	L	E	2.5	Boreal	−1.02 ± .34	.44 ± .19	...	...
Atlegrim 1989, figs. 1, 2	Birds	Leaf feeder	H	Shrub	L	E	2.5	Boreal	−1.04 ± .30	1.29 ± .21	...	...
Atlegrim 1989, figs. 1, 2	Birds	Leaf feeder	H	Shrub	L	E	2.5	Boreal	−.95 ± .24	.79 ± .18	...	...
Atlegrim 1989, figs. 1, 2	Birds	Leaf feeder	H	Shrub	L	E	2.5	Boreal	−1.62 ± .44	.70 ± .23	...	...
Bock et al. 1992, figs. 5, 6	Birds	Leaf feeder	H	Herb	H	E	36	Prairie	−.78 ± .09	.74 ± .10	.03 ± .04[g]	...
Chase 1998, figs. 5, 6	Lizard	Leaf feeder	M	Herb	H	E	2	Prairie	−1.27 ± .44	...	.68 ± .14	...
Dial and Roughgarden 1995, fig. 7	Lizard	Leaf feeder[h]	H	Tree	I	E	6	Trop	−.67 ± .13	.71 ± .18	...	...
Marquis and Whelan 1994, fig. 2	Birds	Leaf feeder	H	Tree	I	E	19	Temp	−.55 ± .12	.42 ± .19	.25 ± .06	...
Spiller and Schoener 1996, fig. 5	Lizard	Leaf feeder	H	Herb	L	E	42	Co trop	−.31 ± .07	.70 ± .34	...	...
Spiller and Schoener 1996, fig. 5	Lizard	Leaf feeder	H	Herb	L	E	36	Co trop	−.02 ± .05	1.25 ± .51	...	...
Ant top predators:												
Barton 1986, tables 4, 5	Ants	Leaf feeder	H	Tree	I	E	3	Subtrop	−.12 ± .12[g]	...	...	.87 ± .24
Barton 1986, tables 4, 5	Ants	Leaf feeder	H	Tree	I	E	3	Subtrop	−.06 ± .11[g]	...	...	.18 ± .18
Barton 1986, tables 4, 5	Ants	Leaf feeder	H	Tree	I	E	3	Subtrop	.05 ± .13[g]	...	...	.30 ± .21
Devall and Thien 1989, table 4	Ants	Community	H	Herb	I	E	NA	Co trop	...	...	...	1.19 ± .67
Devall and Thien 1989, table 4	Ants	Community	H	Herb	I	E	NA	Co trop	...	...	...	1.03 ± .49
Devall and Thien 1989, table 4	Ants	Community	H	Herb	I	E	NA	Co trop	...	...	...	.00 ± .61
Devall and Thien 1989, table 4	Ants	Community	H	Herb	I	E	NA	Co trop	...	...	...	1.68 ± .60
Devall and Thien 1989, table 4	Ants	Community	H	Herb	I	E	NA	Co trop	...	...	...	.69 ± .30
Devall and Thien 1989, table 4	Ants	Community	H	Herb	I	E	NA	Co trop	...	...	...	.34 ± .40
Devall and Thien 1989, table 4	Ants	Community	H	Herb	I	E	NA	Co trop	...	...	...	.29 ± .26
Floate and Whitham 1994, figs. 2b, 3f	Ants	Leaf feeder	L	Tree	I	E	.75	Temp	−2.69 ± 1.03[g]	.83 ± .25	...	...
Fonseca 1994, tables 1, 2	Ants	(Leaf feeder)	M	Tree	I	E	17	Trop	−1.47 ± .31	2.25 ± .73	...	...

Source	Predator	Guild	Size	Plant				Climate				
Gaume et al. 1997, text	Ants	(Leaf feeder)	M	Tree	I	O	...	Co trop	...	2.53 ± .59	...	...
Horvitz and Schemske 1984, table 2	Ants	Leaf feeder	L	Herb	I	E	2.3	Trop	...	...	...	.79 ± .14
Inouye and Taylor 1979, table 3	Ants	Seed feeder	H	Herb	I	E	GS	Mont	−.37 ± .29	.23 ± .12	...	.03 ± .08
Inouye and Taylor 1979, table 3	Ants	Seed feeder	H	Herb	I	E	GS	Mont	−1.07 ± .57	...	...	−.10 ± .16
Inouye and Taylor 1979, table 3	Ants	Seed feeder	H	Herb	I	E	GS	Mont	−.03 ± .09	.17 ± .01		.03 ± .05
Koptur 1984, table 2	Ants	Leaf feeder	M	Tree	I	E	9	Trop	...	1.14 ± .09	...	...
Laine and Niemelä 1980, fig. 5	Ants	Leaf feeder	L	Tree	L	O	...	Boreal	−.66 ± .33[i]	.76 ± .15[i]	...	...
Letourneau 1998, tables 2, 4	Ants	Community	H	Shrub	I	E	18	Trop	...	1.50 ± .79	.53 ± .16	.62 ± .23
Letourneau et al. 1993, table 4	Ants	Leaf feeder	M	Tree	I	O	...	Trop	−2.87 ± .85	.91 ± .37	...	...
Mackay 1991, fig. 2	Ants	Community	H	Tree	I	E	6	Arid sc	...	.25 ± .22	...	...
Messina 1981, table 4	Ants	Leaf feeder	L	Herb	I	O	...	Temp	−.01 ± .09	...	.21 ± .04	1.90 ± .33
Moog et al. 1998, text	Ants	Leaf feeder	M	Tree	I	E	...	Trop	...	2.08 ± .56	...	...
Oliveira 1997, table 4	Ants	Community	H	Shrub	I	E	5		...	...	...	.16 ± .53
Schemske 1980, table 3	Ants	Seed feeder	L	Herb	I	E	2	Trop	...	...	...	1.49 ± .32[g]
Stephenson 1982, table 2	Ants	(Leaf feeder)	M	Tree	I	E	3.5	Temp	...	...	.37 ± .09	.27 ± .14
Vasconcelos 1991, table 3	Ants	NA	M	Shrub	I	E	3	Trop	...	3.58 ± .32	...	3.81 ± 3.61
Vasconcelos and Casimiro 1997, table 3	Ants	(Leaf feeder)	L	Tree	I	O	...	Trop	...	.99 ± .32	...	...
Vasconcelos and Casimiro 1997, table 3	Ants	(Leaf feeder)	L	Tree	I	O	...	Trop	...	.60 ± .37	...	...
Vasconcelos and Casimiro 1997, table 3	Ants	(Leaf feeder)	L	Tree	I	O	...	Trop	...	2.37 ± .46	...	...
Whalen and Mackay 1988, table 6	Ants	Community	H	Tree	I	E	.5	Trop	−.91 ± .34	1.43 ± .60	...	...
Whalen and Mackay 1988, table 6	Ants	Community	H	Tree	I	E	.5	Trop	.40 ± .30	.07 ± .63	...	...
Whalen and Mackay 1988, table 6	Ants	Community	H	Tree	I	E	.5	Trop	−.10 ± .47	.23 ± .55	...	...
Warrington and Whittaker 1985, tables 2, 4	Ants	Leaf feeder	H	Tree	I	E	4	Temp	−1.09 ± .15	1.30 ± .16	...	...
Other top predators:												
Beckerman et al. 1997, table 1	Spider	Leaf feeder	L	Herb	H	M	2	Temp	−.08 ± .22	...	−.04 ± .21	...

Table 1: (*Continued*)

Reference	Carnivore[a]	Herbivore[a]	[b]	Plant		[c]	[d]	Habitat[e]				
Chase 1996, fig. 3*a*; personal correspondence	Spider	Leaf feeder	L	Herb	H	M	2.5	Mont	−.11 ± .37	...	.09 ± .12	...
Fraser and Grime 1998, figs. 2, 5, 6	Ladybird	Sapsucker	L	Herb	M	M	1.5	Temp	−.27 ± .17[g]	...	.09 ± .04[g]	...
Gilreath and Smith 1988, table 3	Insects	Sapsucker	L	Cacti	L	E	22	Prairie	...	...	2.89 ± 1.01	...
Gomez and Zamora 1994, text	Parasitoid	Seed feeder	L	Shrub	I	E	...		...	...	...	.71 ± .29
Hambäck et al. 2000, fig. 5; text	Ladybird	Community	M	Herb	L	O	...	Boreal	−1.10 ± .43	.27 ± .20	...	1.40 ± .53
Louda 1982, table 2, text	Spider	Community	H	Shrub	I	O	...	Arid sc	...	.39 ± .21	...	.16 ± .06
Moran and Hurd 1998, figs. 2, 3	Mantid	Community	H	Herb	H	E	3	Temp	−.37 ± .11	...	.28 ± .11	...
Moran et al. 1996, figs. 3, 4	Mantid	Community	H	Herb	H	E	2	Temp	−.21 ± .10	...	.46 ± .14	...
Polis and Hurd 1996, table 26.5	Spider	Leaf feeder	H	Shrub	I	E	2.5	Co trop	...	.99 ± .16	...	...
Schmitz 1993, fig. 6	Spider	Leaf feeder	L	Herb	H	M	.75	Temp	−.24 ± .17	...	.11 ± .46	...
Schmitz 1994, table 3; fig. 3	Spider	Leaf feeder	L	Herb	H	M	1	Temp	−1.14 ± .20	...	.02 ± .11[g]	...
Schmitz 1998, table 3; figs. 4, 5	Spider	Leaf feeder	M	Herb	H	M	2	Temp	−.06 ± .17[g]	...	.03 ± .19[g]	...
Schmitz et al. 1997, figs. 5, 6	Spider	Leaf feeder	L	Herb	H	M	1.5	Temp	−.34 ± .17	...	.56 ± .30[g]	...

Note: Mean $\pm \sqrt{v}$, where v is the variance of the log response ratio estimate in the individual study (Hedges et al. 1999).

[a] Studies in parentheses do not specify herbivore species. Type "community" includes cases when excluded herbivores are of several different types.

[b] Diversity per replicate: I = individuals, L = several individuals of 1 species, M = 2–4 species, H > 4 species; studies lacking information were set to medium.

[c] E = carnivore exclosure, M = mesocosm, O = observational study.

[d] Length of predator exclusion in months; GS = growing season; for observational studies this is not known.

[e] Habitat types: arid sc = arid scrubland, boreal, co trop = coastal tropical, mont = montane, prairie, subtrop = subtropical, temp = temperate deciduous, trop = tropical.

[f] The effect size on plant damage is viewed from the plant's perspective to conform with the sign structure of plant biomass and reproduction; that is, the log response ratio on plant damage has a positive sign whenever the presence of top carnivores decreased plant damage.

[g] Data in original article separated between species, families, or orders. To calculate total effect size, we pooled groups, assuming that densities were independent. Pooled densities were calculated by adding averages, whereas pooled plant damage was calculated as $1 - (1 - D_1)(1 - D_2)$, where D_i is the damage of type i. Pooled SD was calculated by adding variances of each group (Sokal and Rohlf 1998).

[h] Only Orthoptera and Blattaria.

[i] <20 m from ant mount = with ants; >20 m from ant mount = without ants.

The length of experimental manipulations ranged from 1 mo to 3.5 yr (table 1). In 81% of the studies, the duration of a single manipulation was a single-field season of 6 mo or less. Typically, studies involving vertebrate carnivores were longest in duration (mean = 14 mo) compared to studies involving ant removals (5 mo) or removals of spiders, ladybird beetles, and other arthropod carnivores (4 mo).

The spatial extent of all studies ranged from small to very small. The most common treatment was to exclude carnivores from individual trees or herbaceous plants, even though the trees sometimes were large. Plot sizes in mesocosm experiments ranged from .1 to .5 m^2. In the largest-scale field experiment (Spiller and Schoener 1996), plot sizes were still only 84 m^2.

Ecologic Insights from the Meta-Analysis

Do Carnivores Generally Have an Indirect Effect on Plants through Their Effects on Herbivore Density or Behavior? The majority (45/60) of studies individually reported significant effects of carnivore removal on some plant variable. In certain studies, trophic cascades were predicted not to occur, and they did not occur (e.g., Schmitz 1993; Chase 1996). The meta-analysis revealed that carnivore removals had a significant positive-direct effect on herbivore number ($\overline{L}^* = .49$, CI = .14), a significant positive-indirect effect on plant damage ($\overline{L}^* = .95$, CI = .23), and significant negative-indirect effects on plant biomass ($\overline{L}^* = -.22$, CI = .11) and plant-reproductive output ($\overline{L}^* = -.50$, CI = .17).

Do Effect Magnitudes Generally Attenuate Down the Trophic Chain? For those studies that measured both direct effects of carnivores on herbivores and indirect effects of carnivores on plants, the effect magnitude of carnivore removal on plant biomass was weaker than the effect magnitude of carnivores on herbivore density ($Q_b^* = 3.56$, $n = 13$, $P = .1$, P value based on randomization; fig. 1). The effect magnitude of carnivore removal on either plant damage or plant reproduction was not significantly different from the effect of carnivores on herbivore density (plant damage: $Q_b^* = .011$, $n = 21$, $P > .9$; plant reproduction: $Q_b^* = 1.47$, $n = 8$, $P > .35$, P values based on randomization; fig. 1). In all three cases, there was considerable significant variation between studies within groups (plant damage: $Q_{wi} = 180.7$, $P < .001$; plant biomass: $Q_{wi} = 68.9$, $P < .001$; plant reproduction: $Q_{wi} = 50.8$, $P < .001$). To examine this variation in more detail, we plotted the magnitude of the direct effect of carnivores on herbivores against the corresponding magnitudes of indirect effects on plants (fig. 2). This analysis reveals that the 95% confidence limits for plant damage and plant biomass (fig. 2, CI ≈ $1.96 \times \sqrt{v}$;
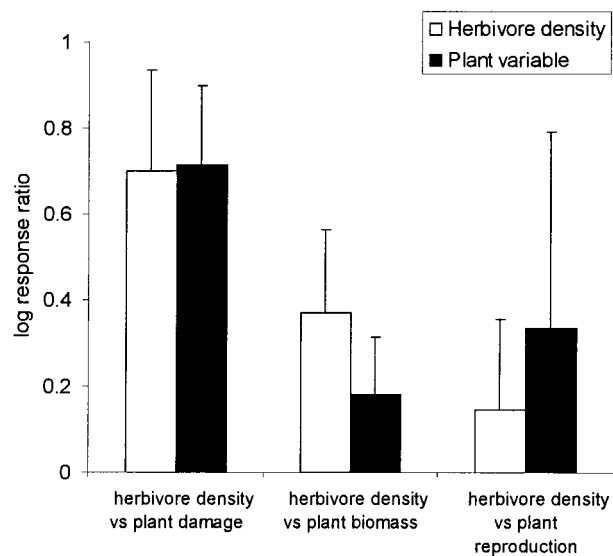

Figure 1: Comparison of mean effect magnitudes of carnivore removal on herbivore density and plant damage, biomass, or reproductive output in studies that measured both herbivore density and one plant variable (mean ± bootstrapped CI). Note that the sign on the effect magnitude of carnivore removal on herbivore density is reversed to ease comparison.

Hedges et al. 1999) in the majority of the studies encompass the 45° line. This indicates that there is no general attenuation nor intensification of top-down effects. However, there are significant deviations from the 45° trend line (fig. 2).

When considering plant damage (fig. 2), there are six cases that deviate significantly from the 45° line, of which four fall in the domain of attenuation (i.e., to the left of the 45° line). Two cases of attenuation (those closest to the line) come from Atlegrim (1989) and seem to represent spatial variation in the strength of top-down effects; that is, there does not seem to be an ascribable biologic mechanism. Another case of attenuation comes from Letourneau et al. (1993). Here, it appears to result from antiherbivore defenses: the focal plant species has pubescent leaves, a form of structural antiherbivore defense. The final case comes from Floate and Whitham (1994), but there is insufficient information provided to identify the mechanisms leading to attenuation. The two cases falling to the right of the 45° line, suggesting intensification of top carnivore effects, come from an ant-removal study by Whalen and Mackay (1988) and a lizard removal by Spiller and Schoener (1996). In both cases, the deviation seems to represent random variation in response.

Comparisons of effect magnitudes on herbivore density and plant biomass reveal four cases of attenuation (fig. 2B). The two cases on the extreme left (fig. 2B) come from studies by Schmitz (1994) and Chase (1998). Both studies
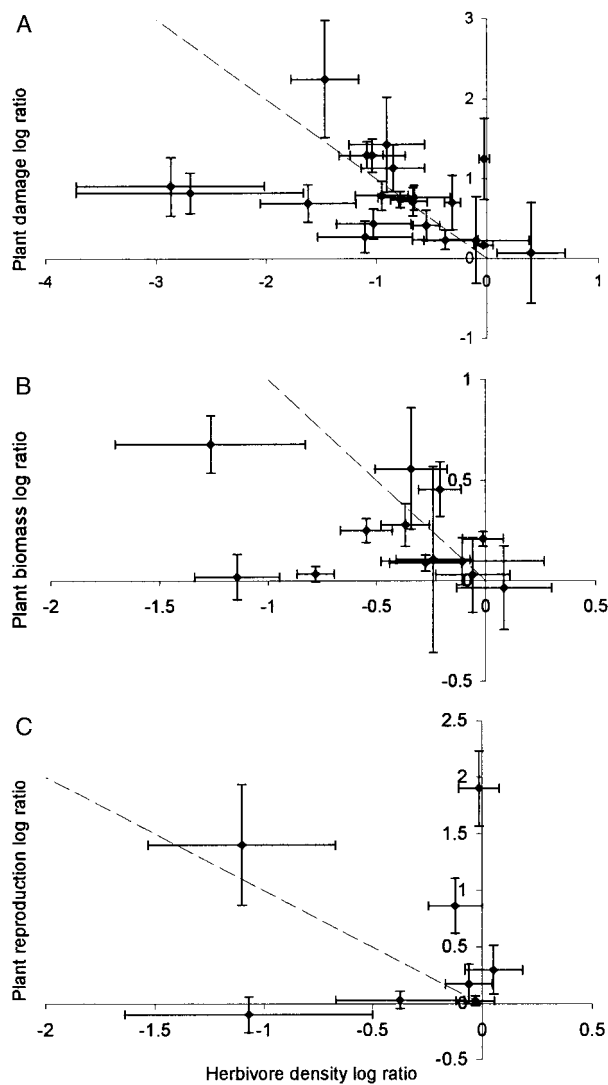
Figure 2: Relationship between the magnitude of direct effects of carnivore removal on herbivore density and indirect effect of carnivore removal on plants shown for individual studies (mean $\pm \sqrt{v}$). The hatched line represents perfect correspondence (45°) between direct and indirect effects.

involved grasshopper herbivores but differed in the type of carnivore (spiders vs. lizards). In the study by Schmitz (1994), the effect of top predators on plants was measured for the entire plant trophic level. In reality, there are two plant categories (defended and edible) that have strong but opposite responses to carnivore removals. Carnivore removals have indirect-negative effects on edible plants because herbivores preferentially feed on those plants, and carnivores have indirect-positive effects on defended plants because defended plants compete with edible plants (Schmitz 1994). Thus, carnivores have no net effects on

plants when responses are measured on the plant trophic level as a whole (Schmitz 1994). In Chase (1998), there is a similar antagonistic response of forbs and grasses to removal of carnivores, again because herbivores preferentially feed on one plant group. These studies illustrate that it is possible to conclude wrongly that top predators have no indirect effect on lower trophic levels in communities if one simply measures the aggregate response of all species within each lower trophic level, that is, examine community-level cascades rather than species cascades (see Polis 1999). The third study showing attenuation involves bird predation on insects feeding on oak trees (Marquis and Whelan 1994). In this case, the attenuation may arise because oak saplings tend to be defended by antiherbivore chemistry (tannins), thereby weakening the strength of herbivore effects. The final case of attenuation was observed in a study by Bock et al. (1992) for arid zone grassland, involving bird predation on grasshopper herbivores. This system is similar to those studied by Schmitz (1993) and Chase (1996), where attenuation is expected theoretically (Schmitz 1992, 1993).

Comparisons of effect magnitude of carnivores on herbivore density and seed production indicate a bimodal distribution, with most studies falling along one or the other axis (fig. 2C). The large deviations along each axis come from two studies examining the effects of ants on herbaceous plant seed production (Inouye and Taylor 1979; Messina 1981). Inouye and Taylor (1979) found that the indirect effect of ants on plant seeds attenuated relative to effects of ants on herbivorous insects. The ants scared away herbivorous insects, causing a dramatic reduction in herbivore density on particular host plants. But the density reduction did not result in dramatic changes in seed production by the host plant. Messina (1981) found that the direct effect of ants on the abundance of two leaf-chewing beetle species was weak, but indirect effects of ants on plant seed production were strong. One candidate explanation for this outcome is that the continuous harassment of beetles by ants altered beetle foraging behavior, leading to a behaviorally mediated cascade (e.g., Beckerman et al. 1997; Schmitz et al. 1997; Schmitz 1998).

In summary, in those cases in which we found attenuating top-down effects, the attenuation resulted either from some form of plant-antiherbivore defense in the focal plant species, from pooling categories of plants that individually had antagonistic responses to top-down effects, or from unexplainable spatial variation in the strength of top-down effects. In contrast, we found no evidence for these mechanisms in studies that were deemed not to deviate significantly from the 45° trend line. For example, studies that displayed no significant deviation were often focused on one plant species (hence, species cascades), and

those focal plants did not seem to contain antiherbivore defenses.

Do Effect Magnitudes of Removing Carnivores Depend on the Type of Carnivore? Because of the confounding effects of carnivore type and study type in reported papers, we did this comparison only on the effect of vertebrate versus invertebrate carnivores in experimental studies with high herbivore diversity. The mean effect of removing vertebrate versus invertebrate carnivores did not have a significantly different magnitude on either herbivore density (mean log response ratio and bootstrapped [CI]; $-.72$ [$-.98$, $-.49$] vs. $-.37$ [$-.67$, $-.14$]; $n = 11$, 14; $Q_b^* = 3.58$; $P < .1$), plant damage (mean log response ratio and bootstrapped [CI]; .77 [.95, .60] vs. .52 [.98, .22]; $n = 10$, 9; $Q_b^* = 1.00$; $P > .30$), or plant biomass (mean log response ratio and bootstrapped [CI]; .28 [.68, .03] vs. .43 [.54, .34]; $n = 3$, 5; $Q_b^* = 0.79$; $P > .4$).

Did the Length of the Study Affect the Outcome? There was no effect of study length on effect magnitudes. However, virtually all studies were done for one season only. Thus, there was limited recourse to examine the multiyear effects on interaction strengths.

Do Effect Magnitudes of Carnivore Removal on Plants Vary with Herbivore Diversity in Food Webs? Because of low sample size, this comparison was only done for experimental studies removing invertebrate carnivores. In the analysis, we compared the effect magnitudes of carnivore removal on plant variables between studies with more (high diversity) or less (low-medium diversity) than four herbivore species. The focus was on herbivore diversity because the studies typically examined effects on one or two plant categories and involved one or two predator species. The effect magnitude of carnivore removal on plant damage was significantly higher in low-diversity systems compared to high-diversity systems (mean log response ratio and bootstrapped [CI]; 1.83 [2.97, 1.04] vs. .59 [.98, .24]; $n = 5$, 9; $Q_b^* = 11.34$; $P < .05$). There was also a strong tendency that the effect magnitude of carnivore removal on plant reproduction was higher in low-diversity systems compared to high-diversity systems (mean log response ratio and bootstrapped [CI]; .72 [1.23, .38] vs. .32 [.55, .16]; $n = 5$, 9; $Q_b^* = 4.44$; $P < .1$). These results thus corroborate the suggestion that more complex food webs generally dampen the strength of trophic cascades (Polis and Strong 1996).

Do Effect Magnitudes of Carnivore Removal on Plants Vary with the Type of Study? This question turned out to be impossible to distinguish from the effects of species diversity and type of predator. We therefore only report the mean effect magnitude for carnivore removal on each plant variable in each type of study. The effect magnitude of carnivore removal on plant damage was significantly different from 0 in both experimental ($\overline{X} \pm$ CI, $.94 \pm .28$, $n = 24$) and observational ($\overline{X} \pm$ CI, $.99 \pm .41$, $n = 8$) studies. The effect magnitude of carnivore removal on plant biomass was significantly different from 0 in experimental studies ($\overline{X} \pm$ CI, $.37 \pm .18$, $n = 8$), but not in mesocosm studies ($\overline{X} \pm$ CI, $-.03 \pm .05$, $n = 7$). Finally, the effect magnitude of carnivore removal on plant-reproductive output was significantly different from 0 in experimental studies ($\overline{X} \pm$ CI, $.45 \pm .19$, $n = 27$).

Discussion

Our review indicates that trophic (species) cascades were detected quite frequently in terrestrial study systems (45 of 60 tests). The average magnitude of direct effects of top carnivores on herbivores and of indirect effects of top carnivores on plants, when measured as log response ratios, were equal to or stronger than those found in aquatic systems (Brett and Goldman 1996). Moreover, like aquatic systems (Menge 1997), the indirect effects of carnivores on these systems manifest themselves very rapidly (within a 6-mo study season in most cases).

In those cases where attenuation was significant, it was often because of biological conditions, as proposed by Strong (1992), that is, because of plant antiherbivore defenses. Our study also supported the prediction (Polis and Strong 1996) that trophic cascades are weaker in food webs with a higher species diversity in intermediate levels of the food web. However, we still do not know the basis for this outcome. For instance, it is not apparent whether the food webs representing many species that were included in our study were composed of parallel linear food chains or whether they were truly highly reticulate, an assumption required by Polis and Strong's (1996) prediction. We therefore reiterate a point made earlier by Paine (1980), Cohen et al. (1993), and Wootton (1997) that our understanding of trophic interactions (specifically, the relationship between species diversity and trophic control) could be greatly improved if future studies offer more details about the species composition, modes of interaction, and the degree of interconnectedness among the study species.

It is noteworthy, however, that conclusions about effect magnitudes of carnivores on plants varied with the response variable examined. Average effect magnitudes for plant damage were much higher than those for plant biomass and reproduction. Moreover, carnivore effects attenuated when plant responses were measured as plant biomass, but they did not attenuate when responses were measured as plant damage (fig. 1). Plant damage is a short-term response and is a direct reflection of herbivore den-

sity. Thus, the measure may not completely capture the effects of herbivory on plants because biomass growth and reproduction in a season may not be directly influenced by immediate tissue damage (e.g., scars, mines leaf damage). Moreover, plants can make compensatory adjustments in biomass production or reproductive output over the longer term in response to changes in community composition arising from trophic manipulations. These responses may be less dependent on herbivore density. So, the strength of effect of carnivores on plant damage, mediated through herbivore density, can be quite high relative to response variables that require longer periods of time before effects manifest themselves (see also Letourneau and Dyer 1998).

This point is illustrated by the studies of Marquis and Whelan (1994) and Bock et al. (1992), in which carnivore effects on both plant damage and plant biomass were measured. The data (table 1) indicate that top-down effects attenuate when the plant-response variable is biomass, but they remain as strong as carnivore effects on herbivores when effects on plants are measured as damage. These were the only studies that measured effects on both plant variables, so we cannot comment whether damage and biomass will consistently give different conclusions. However, it does indicate that we should be cautious about inferring community-level processes from short-term measures of impact (damage). At the very least, such measures should be calibrated to response variables that require longer periods to manifest themselves and that are more likely representative of food chain– or food web–level effects (e.g., growth in plant biomass).

An important message from a few of the studies is that simply measuring plant responses to carnivore removals may not provide a complete understanding of direct and indirect effects of carnivores in natural systems. Rather, it may be equally important to understand the pathways through which effects of carnivores pass down to plants. For instance, Letourneau (1998) showed that, even though ants caused decreased rates of leaf herbivory and increased rates of seed production, changes in leaf herbivory were not the mechanism causing an increased seed production. Instead, the positive-indirect effect of ants on plant-reproductive output was caused by the effects of ants on a stem-boring weevil and on a floral pathogen. In another example, Spiller and Schoener (1996) showed that lizard removals had no net effect on plants, even though lizards suppressed the abundances of arthropod herbivores, implying attenuating top-down effects. However, lizard removal resulted in a significant increase in the abundance of web spiders, whose abundance is normally reduced by intraguild lizard predation. Once lizards were removed, web spiders assumed the role of top carnivores in the community. Thus, intraguild responses of web spiders to

lizard removals weakened the overall downward effect of removing lizards.

These examples show that detecting or failing to detect trophic cascades in a study system does not, by itself, illuminate whether species abundance and dynamics in a study system are controlled by top carnivores. We strongly recommend that one also examine the mechanisms of trophic interactions to obtain a complete picture of trophic control. In most studies reviewed here, it was very difficult to obtain some general sense of the mechanisms of trophic control. Most often, the studies simply reported on the statistical presence/absence of an effect. Some studies, however, did provide mechanistic details, and we discovered that top carnivore effects may be transmitted downward to the plant trophic level by changes in herbivore behavior in addition to, or in place of, reductions in herbivore density caused by predation.

Knowing which mechanisms are mediating the top-down effects is important because it can affect the sign of the indirect effect of predators on plants. In the conventional view, trophic cascades are propagated by an overall reduction in the density of herbivores feeding on plants. In this case, top predators will have a net-positive-indirect effect on plants (Schoener 1993; Schmitz 1998). Alternatively, carnivores could have net-positive-indirect effects on some plants and net-negative-indirect effects on other plants if they cause herbivores to adjust their foraging behavior or switch habitats in response to predation risk (Schmitz 1998). Switching resource use by herbivores in response to risk means that it is not appropriate to examine all plants collectively as a single trophic level when evaluating top-down effects (see also Polis 1999). This is because the negative- and positive-indirect effects, summed over different resource categories, could cancel each other out. The overall impression would be that top consumers have no net effect on the plant trophic level when in reality they can have profound effects on plant species composition of communities.

Our review focused on the strength of top-down effects via trophic cascades in terrestrial systems based on data collected from the published literature. This literature has inherent biases because of the "file drawer" problem, in which ecologists choose not to report on studies that do not show an expected outcome. Trophic cascades in terrestrial systems, although not a universal phenomenon, are a consistent response throughout the published studies reviewed here. Trophic cascades are common in many types of environments, and they occur despite variation in carnivore type, food web diversity, and experimental protocol. Moreover, the patterns and strengths of top-down effects of carnivores are equivalent to those found in other types of systems (e.g., aquatic environments).

Thus, we feel that our conclusions from this review are robust.

The insights from this review are the basis on which to refine research addressing trophic control. There is a significant need for more detailed information on the relationship between species diversity in food webs and trophic interactions in these webs, as well as research addressing the behavioral, physiological, and morphological mechanisms mediating food web interactions. These details can provide insight into the local-, regional-, and macro-scale patterns of trophic interaction, perhaps making it possible to develop new, general principles of trophic interactions across small and large ecologic scales (Polis 1999). This was, after all, the original intended purpose of classical theory that has motivated the vast amount of research on trophic interactions in food webs (Hairston et al. 1960; Oksanen et al. 1981; Fretwell 1987).

Acknowledgments

Literature Cited

Atlegrim, O. 1989. Exclusion of birds from bilberry stands: impact on insect larval density and damage to bilberry. Oecologia (Berlin) 79:136–139.

Barton, A. M. 1986. Spatial variation in the effect of ants on an extrafloral nectary plant. Ecology 67:495–504.

Beckerman, A. P., M. Uriarte, and O. J. Schmitz. 1997. Experimental evidence for a behavior-mediated trophic cascade in a terrestrial food chain. Proceedings of the National Academy of Sciences of the USA 94: 10735–10738.

Bock, C. E., J. H. Bock, and M. C. Grant. 1992. Effects of bird predation on grasshopper densities in an Arizona grassland. Ecology 73:1706–1717.

Boutin, S. 1992. Predation and moose population dynamics: a critique. Journal of Wildlife Management 56: 116–127.

Brett, M. T., and C. R. Goldman. 1996. A meta-analysis of the freshwater trophic cascade. Proceedings of the National Academy of Sciences of the USA 93: 7723–7726.

Chase, J. 1996. Abiotic controls of trophic cascades in a simple grassland food chain. Oikos 77:495–506.

———. 1998. Central place forager effects on food chain dynamics and spatial pattern in Northern California meadows. Ecology 79:1236–1245.

Cohen, J. E., R. A. Beaver, S. H. Cousins, D. L. DeAngelis, L. Goldwasser, K. L. Heong, R. D. Holt, et al. 1993. Improving food webs. Ecology 72:252–258.

Devall, M. S., and L. B. Thien. 1989. Factors influencing the reproductive success of Ipomoea-pes-caprae (Convolvulaceae) around the Gulf of Mexico. American Journal of Botany 76:1821–1831.

Dial, R., and J. Roughgarden. 1995. Experimental removal of insectivores from rain forest canopy: direct and indirect effects. Ecology 76:1821–1834.

Floate, K. D., and T. G. Whitham. 1994. Aphid-ant interaction reduces chrysomelid herbivory in a cottonwood hybrid zone. Oecologia (Berlin) 97:215–221.

Fonseca, C. R. 1994. Herbivory and the long-lived leaves of an Amazonian ant-tree. Journal of Ecology 82: 833–842.

Fraser, L. H., and J. P. Grime. 1998. Top-down control and its effect on biomass and composition of three grasses at high and low soil fertility in outdoor mesocosms. Oecologia (Berlin) 113:239–246.

Fretwell, S. D. 1987. Food chain dynamics: the central theory of ecology? Oikos 50:291–301.

Gaume, L., D. McKey, and M.-C. Anstett. 1997. Benefits conferred by "timid" ants: active antiherbivore protection of the rainforest tree *Leonardoxa africana* by the minute ant *Petalomyrmex phylax*. Oecologia (Berlin) 112:209–216.

Gilreath, M. E., and J. W. Smith. 1988. Natural enemies of *Dactylopius confusus* (Homoptera: Dactylopiidae): exclusion and subsequent impact on *Opuntia* (Cactaceae). Environmental Entomology 17:730–738.

Gomez, J. M., and R. Zamora. 1994. Top-down effects in a tritrophic system: parasitoids enhance plant fitness. Ecology 75:1023–1030.

Gurevitch, J., and L. V. Hedges. 1993. Meta-analysis: combining the results of independent experiments. Pages 378–398 in S. M. Scheiner and J. Gurevitch, eds. Design and analysis of ecological experiments. Chapman & Hall, New York.

Gurevitch, J., L. L. Morrow, A. Wallace, and J. S. Walsh. 1992. A meta-analysis of competition in field experiments. American Naturalist 140:539–572.

Gutiérrez, J. R., P. L. Meserve, S. Herrera, L. C. Contreras, and F. M. Jaksic. 1997. Effects of small mammals and vertebrate predators on vegetation in the Chilean semiarid zone. Oecologia (Berlin) 109:398–406.

Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960.

Community structure, population control, and competition. American Naturalist 94:421–425.

Hambäck, P. A., J. Ågren, and L. Ericson. 2000. Associational resistance: insect damage to purple loosestrife reduced in thickets of sweet gale. Ecology (in press).

Hedges, L. V., J. Gurevitch, and P. Curtis. 1999. The meta-analysis of response ratios in experimental ecology. Ecology 80:1150-1156.

Horvitz, C. C., and D. W. Schemske. 1984. Effects of ants and an ant-tended herbivore on seed production of a neotropical herb. Ecology 65:1369–1378.

Huntly, N. J. 1991. Herbivores and the dynamics of communities and ecosystems. Annual Review of Ecology and Systematics 22:477–503.

Inouye, D. W., and O. R. Taylor. 1979. A temperate region plant-ant-seed predator system: consequences of extra floral nectar secretion by *Hellianthella quinquenervis*. Ecology 60:1–7.

Koptur, S. 1984. Experimental evidence for defense of *Inga* (Mimosioideae) saplings by ants. Ecology 65:1787–1793.

Laine, K. J., and P. Niemelä. 1980. The influence of ants on the survival of mountain birches during an *Oporinia autumnata* (Lep. Geometridae) outbreak. Oecologia (Berlin) 47:39–42.

Letourneau, D. 1998. Ants, stem borers, and fungal pathogens: experimental tests of fitness advantage in *Piper* ant-plants. Ecology 79:593–603.

Letourneau, D., and L. A. Dyer. 1998. Experimental test in lowland tropical forest shows top-down effects through for trophic levels. Ecology 79:1678–1687.

Letourneau, D. K., F. Arias, and M. Jebb. 1993. Coping with enemy-filled space: herbivores on *Endospermum* in Papua-New Guinea. Biotropica 25:95–99.

Louda, S. M. 1982. Inflorescence spiders: a cost/benefit analysis for the host plant, *Haplopappus venetus* Blake (Asteraceae). Oecologia (Berlin) 55:185–191.

Mackay, D. A. 1991. The effects of ants on herbivory and herbivore numbers on foliage of mallee eucalypt, *Eucalyptus incrassata* Labill. Australian Journal of Ecology 16:471–483.

Marquis, R. J., and C. J. Whelan. 1994. Insectivorous birds increase growth of white oak through consumption of leaf-chewing insects. Ecology 75:2007–2014.

McLaren B. E., and R. O. Peterson. 1994. Wolves, moose and tree rings on Isle Royale. Science (Washington, D.C.) 266:1555–1558.

Menge, B. A. 1995. Indirect effects in marine rocky intertidal interaction webs: patterns and importance. Ecological Monographs 65:21–74.

———. 1997. Detection of direct versus indirect effects: were experiments long enough? American Naturalist 149:801–823.

Messier, F. 1995. Trophic interactions in two northern wolf-ungulate systems. Wildlife Research 22:131–146.

Messina, F. J. 1981. Plant protection as a consequence of an ant-membracid mutualism: interactions on goldenrod (*Solidago* sp.). Ecology 62:1433–1440.

Moog, J., T. Drude, and U. Maschwitz. 1998. Protective function of the plant-ant *Cladomyrma maschwitzi* to its host, *Crypteronia griffithii*, and the dissolution of the mutualism (Hymenoptera: Formicidae). Sociobiology 31:105–112.

Moran, M. D., and L. E. Hurd. 1998. A trophic cascade in a diverse arthropod community caused by a generalist arthropod predator. Oecologia (Berlin) 113:126–132.

Moran, M. D., T. P. Rooney, and L. E. Hurd. 1996. Top-down cascade from a bitrophic predator in an old-field community. Ecology 77:2219–2227.

Oksanen, L., and T. Oksanen. 1992. Long-term microtine dynamics in north Fennoscandian tundra: the vole life-cycle and the lemming chaos. Ecography 15:226–236.

Oksanen, L., S. D. Fretwell, J. Arruda, and P. Niemelä. 1981. Exploitation ecosystems in gradients of primary productivity. American Naturalist 118:240–261.

Olff, H., and M. E. Ritchie. 1998. Effects of herbivores on grassland plant diversity. Trends in Ecology & Evolution 13:261–265.

Oliveira, P. S. 1997. The ecological function of extrafloral nectaries: herbivore deterrence by visiting ants and reproductive output in *Caryocar brasiliense* (Caryocaraceae). Functional Ecology 11:323–330.

Osenberg, C. W., O. Sarnelle, and S. D. Cooper. 1997. Effect size in ecological experiments: the application of biological models in meta-analysis. American Naturalist 150:798–812.

Paine, R. T. 1980. Food webs: linkage, interaction strength, and community infrastructure. Journal of Animal Ecology 49:667–685.

Polis, G. A. 1999. Why are parts of the world green? multiple factors control productivity and the distribution of biomass. Oikos 86:3–15.

Polis, G. A., and S. D. Hurd. 1996. Allochthonous input across habitats, subsidized consumers and apparent trophic cascades: examples from the ocean-land interface. Pages 275–285 *in* G. Polis and K. Winemiller, eds. Food webs: integration of patterns and dynamics. Chapman & Hall, New York.

Polis, G. A., and D. R. Strong. 1996. Food web complexity and community dynamics. American Naturalist 147:813–846.

Rosenberg, M. S., D. C. Adams, and J. Gurevitch. 1997. MetaWin: statistical software for meta-analysis with resampling tests. Version 1.0. Sinauer, Sunderland, Mass.

Schemske, D. W. 1980. The evolutionary significance of extrafloral nectar production by *Costus woodsonii* (Zin-

giberaceae): an experimental analysis of ant protection. Journal of Ecology 68:959–967.

Schmitz, O. J. 1992. Exploitation in model food webs with mechanistic consumer-resource dynamics. Theoretical Population Biology 41:161–183.

———. 1993. Trophic exploitation in grassland food webs: simple models and a field experiment. Oecologia (Berlin) 93:327–335.

———. 1994. Resource edibility and trophic exploitation in an old-field food web. Proceedings of the National Academy of Sciences of the USA 91:5364–5367.

———. 1998. Direct and indirect effects of predation and predation risk in old field interaction webs. American Naturalist 151:327–342.

Schmitz, O. J., A. P. Beckerman, and K. M. O'Brien. 1997. Behaviorally-mediated trophic cascades: the effects of predation risk on food web interactions. Ecology 78:1388–1399.

Schoener, T. W. 1993. On the relative importance of direct vs. indirect effects in ecological communities. Pages 365–411 *in* H. Kawanabe, J. E. Cohen, and K. Iwasaki, eds. Mutualism and community organization: behavioral, theoretical, and food-web approaches. Oxford University Press, Oxford.

Sih, A., P. Crowley, M. McPeek, J. Petranka, and K. Strohmeier. 1985. Predation, competition and prey communities: a review of field experiments. Annual Review of Ecology and Systematics 16:269–311.

Sinclair, A. R. E., and P. Arcese. 1995. Serengeti II: dynamics, management and conservation of an ecosystem. University of Chicago Press, Chicago.

Sokal, R. R., and F. J. Rohlf. 1998. Biometry. 3d ed. W. H. Freeman, New York.

Spiller, D. A., and T. W. Schoener. 1996. Food web dynamics on some small subtropical islands: effects of top and intermediate predators. Pages 365–411 *in* G. Polis and K. Winemiller, eds. Food webs: integration of patterns and dynamics. Chapman & Hall, New York.

Stephenson, A. G. 1982. The role of extrafloral nectaries of *Catalpa speciosa* in limiting herbivory and increasing fruit production. Ecology 63:663–669.

Strong, D. R. 1992. Are trophic cascades all wet? Differentiation and donor control in speciose ecosystems. Ecology 73:747–754.

Vasconcelos, H. L. 1991. Mutualism between *Maieta guianensis* Aubl., a myrmencophytic melastome, and one of its ant inhabitants: ant protection against insect herbivores. Oecologia (Berlin) 87:295–298.

Vasconcelos, H. L., and A. B. Casimiro. 1997. Influence of *Azteca alfari* ants on the exploitation of *Cecropia* trees by a leaf-cutting ant. Biotropica 29:84–92.

Warrington, S., and J. B. Whittaker. 1985. An experimental field study of different levels of insect herbivory induced by Formica rufa predation on sycamore (*Acer pseudoplatanus*). I. Lepidoptera larvae. Journal of Applied Ecology 22:775–785.

Whalen, M. A., and D. A. Mackay. 1988. Patterns of ant and herbivore activity on five understory Euphorbiaceaous saplings in submontane Papua New Guinea. Biotropica 20:294–300.

Wootton, J. T. 1997. Estimates and tests of per capita interaction strength: diet, abundance, and impact of intertidally foraging birds. Ecological Monographs 67:45–64.