

IDEA AND  
PERSPECTIVE

## Predation on mutualists can reduce the strength of trophic cascades

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**Abstract**

Ecologists have put forth several mechanisms to predict the strength of predator effects on producers (a trophic cascade). We suggest a novel mechanism – in systems in which mutualists of plants are present and important, predators can have indirect negative effects on producers through their consumption of mutualists. The strength of predator effects on producers will depend on their relative consumption of mutualists and antagonists, and on the relative importance of each to producer population dynamics. In a meta-analysis of experiments that examine the effects of predator reduction on the pollination and reproductive success of plants, we found that the indirect negative effects of predators on plants are quite strong. Most predator removal experiments measure the strength of predator effects on producers through the antagonist pathway; we suggest that a more complete understanding of the role of predators will be achieved by simultaneously considering the effects of predators on plant mutualists.

**Keywords** Food web, indirect effects, meta-analysis, pollination success, predator removal, trophic cascade.

*Ecology Letters* (2006) 9: 1173–1178

Ecologists have long recognized the importance of predators in structuring the composition and relative abundance of herbivore and plant trophic levels (e.g. Hairston *et al.* 1960). For example, through a pathway known as a trophic cascade, predators have indirect positive effects on plants by reducing herbivores (e.g. Paine 1980; Pace *et al.* 1999). To quantify the relative strength of a trophic cascade, ecologists typically employ predator removal (or addition) experiments and measure subsequent changes in producer abundance; over 100 such experiments have been conducted in a variety of different ecosystems (Shurin *et al.* 2002; Borer *et al.* 2005). These experiments have yielded variable results, ranging from quite strong to negligible effects of predators.

In order to quantify and describe the overall strengths of, and variation in, trophic cascades, several quantitative meta-analyses have been conducted (Schmitz *et al.* 2000; Borer *et al.* 2005; Brett & Goldman 1996; Shurin *et al.* 2006). In particular, the contrast between aquatic and terrestrial ecosystems has received significant attention, leading to an emerging generalization that trophic cascades tend to be stronger in aquatic ecosystems than in terrestrial ecosystems (Strong 1992; Polis & Strong 1996; Shurin *et al.* 2002, 2006; Borer *et al.* 2005). Several mechanisms have been proposed to explain why aquatic trophic cascades may be stronger

than terrestrial ones (reviewed in Chase 2000; Shurin *et al.* 2006), including that terrestrial ecosystems have: (i) producer species with more structural and chemical defences against herbivory (Polis & Strong 1996; Polis 1999); (ii) less size structure and predator gape limitation (Hairston & Hairston 1993); (iii) food webs that are more diverse and reticulate (i.e. more omnivory) (Strong 1992; Polis & Strong 1996); and (iv) greater stoichiometric constraints on herbivore growth (Elser *et al.* 2000; Shurin & Seabloom 2005). In addition, there are also several possible methodological differences between studies conducted in different types of ecosystems, including the number of species included in the studies, as well as the temporal and spatial scales at which studies are conducted (Chase 2000; but see Borer *et al.* 2005).

While these mechanisms all contribute to explaining variation in the strength of trophic cascades between aquatic and terrestrial ecosystems, there is still a considerable amount of variation in predator effects that is not explained by any of these mechanisms. In addition, the strengths of trophic cascades are also quite variable both within aquatic and terrestrial ecosystems. For example, while trophic cascades appear to be overall weaker in terrestrial ecosystems (Shurin *et al.* 2002), there are several notable cases of strong terrestrial trophic cascades (e.g. Schmitz *et al.* 2000).

Here, we suggest a novel mechanism that may help predict the strength of predator effects on producers. Specifically, we expect that predators will have overall weaker effects on producers that have direct mutualisms with other animals (e.g. producers that rely on pollinators), if predators also consume those mutualists. This is because the indirect positive effect afforded to producers by predators eating antagonists (herbivores) can be offset by an indirect negative effect on producers by predators eating mutualists.

In this article, we discuss the conditions in which producer reliance on mutualists may weaken the overall strength of trophic cascades. Specifically, when (i) producers have direct mutualisms with other animals; (ii) predators have strong direct or indirect effects on mutualists; and (iii) mutualisms have strong effects on producer fitness and population growth rate. We then quantitatively review experimental studies that have tested for predators effects on producers through their effects on mutualists, and demonstrate that these effect sizes can be as large as those found in typical trophic cascade experiments. Finally, we discuss how our hypothesis could be tested. Currently, most trophic cascade experiments do not consider appropriate time scales or measure appropriate response variables to elucidate the effects of predators on producers through their effects on both mutualists and antagonists.

Indirect negative effects of predators on producers through their effects on mutualists will occur only in systems in which producers have direct mutualisms. Such mutualisms are particularly apparent in terrestrial ecosystems. In terrestrial ecosystems, it is estimated that over 90% of flowering plant species utilize animal pollinators for reproduction (Buchmann & Nabhan 1996). Similarly, many plant species have seeds adapted for animal dispersal (Howe & Smallwood 1982). For these flowering plant species, it is possible for predators to have indirect negative effects through their consumption of mutualists, and indirect positive effects through their consumption of herbivores (Fig. 1). However, for non-flowering producers with no apparent direct mutualisms, such as algae in aquatic pelagic ecosystems, predators can only have indirect positive effects on producers (Fig. 1).

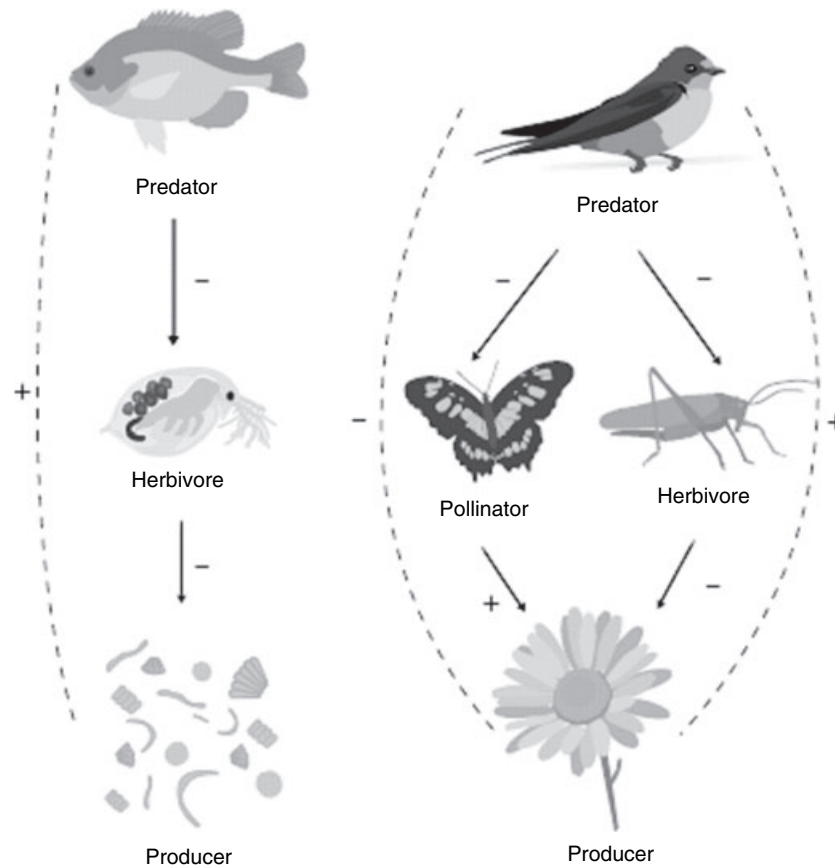
In order for predators to have strong indirect effects on producers through their effects on their mutualists, the producers must be highly reliant on mutualists for their fitness. In the case of plants and pollinators, plants fitness most depends on pollinator visitation when: (i) plants utilize animal pollinators instead of abiotic vectors (e.g. wind); (ii) plants cannot fertilize in the absence of pollinators (e.g. they have a self-incompatible breeding system); and (iii) plants cannot reproduce asexually (e.g. clonal growth) (Knight *et al.* 2005a). In addition, plant populations differ greatly in the degree to which they are seed limited (Turnbull *et al.* 2000), and so may show diverse responses to predator-driven

changes in the abundance of mutualistic pollinators and seed dispersers. Furthermore, the population dynamics of long-lived plant species is often more sensitive to changes in adult survivorship than in seed production and germination whereas the population dynamics of short-lived plant species is often highly sensitive to the production and fate of seeds (e.g. Bond 1994; Ashman *et al.* 2004). Thus, pollinators and seed dispersers are expected to have more dramatic effects on the abundance of short-lived plant species.

Predators vary in their specialization for different prey types; predators that primarily consume pollinators or seed dispersers should have primarily negative indirect effects on plants, whereas those that primarily consume herbivores should have overall positive indirect effects on plants. In addition, many species act simultaneously or sequentially as pollinators of flowers, dispersers of seeds, herbivores, and/or seed predators. For example, many Lepidoptera have larvae (caterpillars) consume the leaves of a plant, whereas the adults (butterflies and moths) pollinate that same plant (e.g. Thompson & Fernandez 2006). Similarly, many large herbivores consume plant leaves as antagonists and simultaneously disperse consumed seeds through their excretion (e.g. Vellend *et al.* 2006). Finally, several studies have recognized the importance of indirect interactions between mutualists and antagonists of plants (Hambäck 2001, Strauss & Irwin 2004), which will be further complicated by the presence of a predator. In all, predation on mutualists and antagonists can result in net positive, negative or neutral indirect effects of predators on producers.

There is mounting experimental support from terrestrial ecosystems that many different types of predators can reduce the abundance and/or alter the behaviour of pollinators, and thus have indirect negative effects on plant reproductive success (Table 1). In order to determine whether the magnitude of the indirect negative effects of predators on plants through pollinators is on the same scale as the indirect positive effect of predators on plants through herbivores found in previous meta-analyses (Shurin *et al.* 2002; Borer *et al.* 2005), we performed a quantitative meta-analysis (Gurevitch *et al.* 2001).

We used Web of Science to search the scientific literature for published papers on predator effects on plants through their effects on pollination using the key words 'predat\*' and 'pollinat\*'. We considered papers published after 2001, when the first paper on this topic was published (Dukas 2001). We selected papers in which predator presence was experimentally manipulated on flowering plants, and in which pollinator visitation rate and/or the reproductive success of those plants was quantified. We also included observational studies in which predators occurred in discrete categories of high and low densities. We considered two types of response variables: pollinator visitation rate [no. visits/



**Figure 1** (a) A trophic cascade in a pelagic aquatic ecosystem, which includes a predator (bluegill), herbivore (daphnia) and producer (algae). In this case, predators can only have indirect positive effects of producers. (b) A trophic cascade in a terrestrial ecosystem, which includes a predator (barn swallow), herbivore (grasshopper), pollinator (butterfly) and producer (flowering plant). In this case, predators can have indirect positive and negative effects on producers. Solid lines indicate direct effects whereas dotted lines indicate indirect effects.

flower (or inflorescence, plant)/time unit] and plant reproductive success (fruit set or number of seeds per fruit). In all, we had 10 data records on pollination success and 11 data records on reproductive success.

For each data record and response variable, we calculated the magnitude of predator effects (effect size) as the 'log response ratio' ( $\ln R$ ),

$$\ln R = \ln \left( \frac{\bar{X}^P}{\bar{X}^{NP}} \right),$$

where  $\bar{X}$  is the mean and P and NP denote predator and no predator (or reduced predator) treatments (Hedges *et al.* 1999) respectively. A negative effect size indicates that plants in the presence of predators experienced lower visitation rates from pollinators (or lower reproductive success) than plants in the absence of predators. We used a random effects model and calculated a weighted mean effect size and 95% bootstrap CI for each response variable using MetaWin 2.0 (Rosenberg *et al.* 1999).

We found that predators overall had large effects on both pollination and reproductive success of plants. Average effect sizes of predators were significantly negative for visitation rate of pollinators ( $-0.34$  mean effect size;  $-0.19$  to  $-0.45$ , 95% CI) and plant reproductive success ( $-0.22$  mean effect size;  $-0.13$  to  $-0.39$ , 95% CI). These effects correspond to a 40.5% decrease in visitation rate and a 25% decrease in reproductive success, and thus are likely to have biological significance. Moreover, the magnitude of these indirect negative effects of predators through the pollinator pathway was similar to, or even exceeded, the indirect positive effects of predators through the herbivore pathway found in previous meta-analyses (Schmitz *et al.* 2000; Shurin *et al.* 2002; Borer *et al.* 2005).

We are unaware of similar studies that have shown indirect negative effects of predators on plants through their consumption of seed dispersers. However, seed dispersers are taxonomically diverse, including mammals, birds, insects, reptiles and fish, all of which have natural predators

**Table 1** Results from natural and experimental studies examining the indirect negative effects of predators on pollination and reproductive success of plants

Reference	Predator type	Pollinator type	Plant species	Effect size	
				Pollinator visitation rate	Plant reproductive success
Dukas & Morse (2003, 2005)*	Crab spider	Bees	<i>Asclepias syriaca</i>	-0.06	0.0056
Suttle (2003)	Crab spider	Various insects	<i>Leucanthemum vulgare</i>	-0.41	-0.18
Muñoz & Arroyo (2004)	Lizard	Various insects	<i>Chuquiraga oppositifolia</i>	-0.19	-0.25
	Bird (flycatcher)	Various insects	<i>Chuquiraga oppositifolia</i>	-0.05	-0.08
Robertson & Maguire (2005)	Crab spider	Various insects	<i>Lepidium papilliferum</i>	-0.27	n/a
Dukas (2005)	Predatory wasp	Bumblebees	<i>Rubbeckia occidentalis</i>	-1.91	n/a
	Predatory wasp	Bumblebees	<i>Solidago</i> sp.	-1.78	n/a
	Predatory wasp	Bumblebees	<i>Aconitum columbianum</i>	-0.59	-0.22
Meehan <i>et al.</i> (2005)†	Bird (swallow)	Various insects	<i>Melilotus officinalis</i>	n/a	-0.66, -0.64, -0.61, -0.52
Knight <i>et al.</i> (2005b)	Dragonflies	Various insects	<i>Hypericum fasciculatum</i>	-0.72	-0.69
	Dragonflies	Various insects	<i>Sagittaria latifolia</i>	-0.70	-0.10

For each study, the identity of the predator, pollinator(s) and plant is shown. Effect sizes for pollinator visitation rate [pollinator visits per flower (or inflorescence, individual) per time unit] and plant reproductive success (fruit set or number of seeds per fruit) are calculated for each study using the log response ratio.

\*Pollinator visitation rate published in the 2003 manuscript, reproductive success published in the 2005 manuscript; these results were from different experiments.

†Four separate populations or years examined and the effect size for each is shown for reproductive success. We only considered data in two discrete categories: near predators (1–50 m) or far from predators (> 400 m).

which may regulate their abundance. Thus, while it remains to be quantified, we expect that predators have indirect negative effects on plants through their effects on their seed dispersers.

Our proposed mechanism for variation in the strengths of trophic cascade within and between ecosystems – due to variation in predation on, and the relative importance of, mutualisms – cannot be evaluated with current information for several reasons. First, the time scales over which predator indirect effects on plants will emerge may differ among antagonist and mutualist pathways. Antagonists, through their consumption, directly influence plant biomass, even if the system is not yet at equilibrium. Alternatively, mutualists influence seed production and dispersal, and thus predator effects on plant abundance through this pathway will likely only emerge after multiple plant generations. Because a majority of trophic cascade experiments occur over very short-time scales (but see Sinclair *et al.* 2000; Hambäck *et al.* 2004), they cannot readily discern the importance of the mutualistic pathway relative to the antagonistic pathway. Second, experiments in terrestrial ecosystems often use the percentage of herbivore damage to leaves as a response variable. This response variable is not influenced by mutualists. Third, many mutualists have large foraging ranges, and experimental cages which exclude predators may be too small to influence the populations and/or behaviour of these mutualists. Finally, many experimental cages which examine the relative impact of

predators on producers through herbivores exclude mutualists altogether.

We suggest two ways to more fully consider both the indirect positive and indirect negative effects of predators on producers through the antagonist and mutualist pathways respectively. First, long-term predator enclosure (or enclosure) experiments at large spatial scales will incorporate both pathways and allow sufficient time for both processes to occur. Second, the system can be decomposed to experimentally examine the effects of changes in the abundance of mutualists and antagonists due to the presence of predators on the population and community-level dynamics of the constituent plant species. One way to do this would be to use demographic matrix model projections of the plant populations under different conditions of mutualisms and antagonists (Knight 2004), and to explicitly include the effects of predation on both interactions.

While appropriate tests of our hypothesis have not been conducted, we can consider the types of systems where the mutualist pathway is expected to reduce the overall strength of the trophic cascade. For example, some of the best evidence for strong trophic cascades in terrestrial ecosystems comes from grasslands where the majority of plants (grasses) are wind pollinated, and other plants (e.g. goldenrods) rely considerably on clonal reproduction (reviewed in Schmitz *et al.* 2000). We expect in these systems that the strong observed trophic cascade will not likely be offset by predator effects on plant mutualists.

Alternatively, in other systems, such as some tropical rainforests, where plants may be more reliant on mutualists (Bond 1994), the strengths of trophic cascades may depend more on predator effects on mutualists.

In closing, we note that the majority of experimental studies examining the indirect effects of predators on plants have focused on the effects on herbivores or pollinators, considered separately, with far more attention given to the former interaction. However, in the complexity of natural ecosystems, a more complete understanding of the role of predators will require a more explicit simultaneous consideration of both the antagonists and mutualists that are embedded within the food web. This broader view will help us understand the variable role of predators within and among ecosystems.

## ACKNOWLEDGEMENTS

We are grateful to L. Beaton, N. Griffin, D. Gruner, E. Pressier, O. Schmitz, W. Ryberg, and two anonymous referees for their helpful comments, and the National Center for Ecological Analysis and Synthesis, the University of Florida Foundation, and Washington University in St Louis for financial support.

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Editor, Oswald Schmitz

Manuscript received 30 March 2006

First decision made 4 May 2006

Manuscript accepted 3 July 2006