to compile regional and global databases of empirical measurements of ecosystem condition to further validate the efficacy of our approach.

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Effects of Predator Hunting Mode on Grassland Ecosystem Function

Oswald J. Schmitz

The way predators control their prey populations is determined by the interplay between predator hunting mode and prey antipredator behavior. It is uncertain, however, how the effects of such interplay control ecosystem function. A 3-year experiment in grassland mesocosms revealed that actively hunting spiders reduced plant species diversity and enhanced aboveground net primary production and nitrogen mineralization rate, whereas sit-and-wait ambush spiders had opposite effects. These effects arise from the different responses to the two different predators by their grasshopper prey—the dominant herbivore species that controls plant species composition and accordingly ecosystem functioning. Predator hunting mode is thus a key functional trait that can help to explain variation in the nature of top-down control of ecosystems.

Species are most likely to have strong effects on ecosystems when they alter factors that regulate key ecosystem functions such as production, decomposition, and nitrogen mineralization (*1*). These effects can be direct, as when selectively feeding herbivores alter plant community composition and hence alter the quality and quantity of plant material entering the soil organic matter pool to be decomposed and mineralized (*1–6*); or indirect, as when predators alter the way in which herbivores affect plant community composition (*7–10*). The exact nature of a species' effect will, however, depend on traits that determine the way it

functions (*1*, *11*). Explaining such trait dependency is an important hurdle to overcome in developing predictive theories of species effects on ecosystem function (*1*). This endeavor is currently hampered by a limited understanding of what kinds of species' traits control functioning (*11–15*).

Here I report on a 3-year experiment quantifying the effect of one important functional trait of top predator species—their hunting mode—on the nature of indirect effects emerging at the ecosystem level (Fig. 1). Predators can propagate indirect effects down trophic chains in at least two ways (*16*). They can alter the numerical abundance of herbivore prey by capturing and consuming them. Alternatively, their mere presence in a system can trigger herbivore prey to modify foraging activity in a manner that reduces predation risk. A general rule, derived

from empirical synthesis, is that these different kinds of effect are related to predator hunting mode, irrespective of taxonomic identity (*17*). Sit-and-wait ambush predators cause largely behavioral responses in their prey because prey species respond strongly to persistent point-source cues of predator presence. Widely roaming, actively hunting predators may reduce prey density, but they produce highly variable predation risk cues and are thus unlikely to cause chronic behavioral responses in their prey. These hunting mode–dependent herbivore responses should lead to different cascading effects on the composition and abundance of plant species within ecosystems (*9*, *18*) that should further cascade to affect ecosystem function (*10*). Predator effects do indeed cascade to influence ecosystem functions, and they vary with predator species (*10*, *19–22*). But the basis for variation in predator species effects remains unresolved.

This study was carried out in a grassland ecosystem in northeastern Connecticut. The important plant species in this ecosystem (determined by their interaction strengths) may be effectively represented within three functional groups of plants: (i) the grass *Poa pratensis*, (ii) the competitively dominant herb *Solidago rugosa*, and (iii) a variety of other herb species, including *Trifolium repens*, *Potentilla simplex*, *Rudbekia hirta*, *Crysanthemum leucanthemum*, and *Daucus carota*. The important animal species are the generalist grasshopper herbivore *Melanopuls femurrubrum* and the spider predators *Pisaurina mira* and *Phidippus rimator* (*23*). *Pisaurina mira* is a sit-and-wait predator in the upper canopy of the meadow.

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Phidippus rimator actively hunts its prey throughout the entire meadow canopy. Under local conditions in this field, these spiders exist approximately in a 1:1 ratio of abundance (*23*).

The experiment was composed of 14 circular mescoms, 1.6 m in diameter and 1.5 m high, that were placed over naturally growing vegetation in the field (*24*). Each treatment (sit-and-wait predator and actively hunting predator) was randomly assigned to mesocosms in a matched-pairs design. I measured levels of seven key ecosystem properties and the three ecosystem functions aboveground net primary production (ANPP), organic matter decomposition rate (decomposition), and nitrogen mineralization rate (N mineralization), within each mesocosm when the experiment was initiated and after 3 years (*24*).

From initially indistinguishable conditions between treatments (table S1), I saw striking directional differences in ecosystem properties and functions between predator treatments (Fig. 2). Relative to initial conditions, actively hunting predators caused a reduction in plant species evenness and enhanced ANPP and N mineralization, whereas sit-and-wait predators had slight positive effects on plant species evenness but reduced ANPP and N mineralization.

These differences were the result of predator hunting mode–dependent effects on plant community composition [multivariate analysis of variance (MANOVA) Wilks' lambda test = 0.393, df = 3, 10, $P < 0.025$]. The biomass of the competitive dominant plant *S. rugosa* was 168% higher in treatments containing the actively hunting predator than in treatments containing the sit-and-wait predator (Fig. 3A). The biomass of other herbs was 47% lower in treatments containing actively hunting predators than in treatments containing sit-and-wait predators (Fig. 3A). There were no treatment effects (both $P > 0.40$) on grass biomass and total plant biomass (Fig. 3A). The shifting composition of *S. rugosa* and other herb species caused plant species evenness to be 14% lower in the actively hunting predator treatments than in the sit-and-wait predator treatments (Fig. 3B). The mechanism driving these differences in plant composition is a tradeoff choice that grasshoppers must make between feeding on grasses and seeking refuge in and feeding on the competitive dominant plant *S. rugosa* when facing predators (*18*). Grasshoppers tend not to exhibit chronic foraging shifts in response to widely roaming active hunters such as *P. rimator* that present weak and variable cues, whereas they do exhibit chronic foraging shifts when facing sit-and-wait *P. mira*, which provides persistent cues (*18*). These hunting mode–dependent grasshopper responses in turn determine the nature of the indirect control that spiders exert over the competitive dominant plant *S. rugosa* (Fig. 1).

By indirectly controlling plant community composition, predators altered an important regulating factor (*1*, *25*) that led to hunting mode–dependent differences in ecosystem functions (Fig. 4). ANPP was 163% higher in actively hunting predator treatments than in sit-and-wait predator treatments (Fig. 4A). Plant matter decomposition rate (Fig. 4B) was not different between treatments ($P > 0.40$). N mineralization in actively hunting predator treatments was 33% higher than in sit-and-wait predator treatments (Fig. 4C). To resolve how a lack of difference in plant organic matter decomposition may have translated into differences in N mineralization, I measured the C:N ratio (a measure of quality) of the plant litter subjected to decomposition in the two treatments (*24*). I found plant litter quality to be 14% higher in active predator treatments than in sit-and-wait predator treatments [C:N in
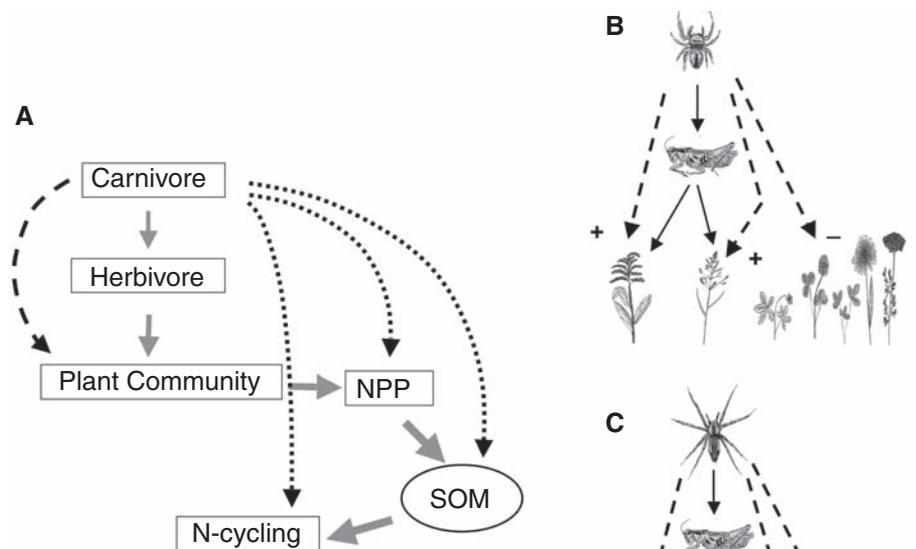
Fig. 1. Hypothesized predator indirect effects on plant community composition (dashed lines) and on ecosystem functions (dotted lines). (**A**) Predators can influence ecosystem function via the direct causal chain (depicted by solid arrows) running from predators through herbivores through plant community composition. Plant community composition in turn regulates NPP: the quality and quantity of plant matter entering the soil organic matter pool (*24*) to be decomposed and produce N mineralization. In the study ecosystem, predator indirect effects on plant community composition depended on how predators affect their grasshopper herbivore *M. femurrubrum* prey. (**B**) The actively hunting spider *P. rimator* causes density reductions of the grasshopper, which leads to indirect positive effects on grass and *S. rugosa* and an indirect negative effect on other herbs because the competitive dominant plant *S. rugosa* suppresses other herbs. (**C**) The sit-and-wait spider *P. mira* causes grasshopper foraging shifts from preferred nutritious grass to safer *S. rugosa*. This predator has indirect positive effects on grasses and other herbs and an indirect negative effect on *S. rugosa*. These hunting mode–dependent differences in plant composition are predicted to have different effects on ecosystem function.

Fig. 2. Net deviations from initial plant diversity and levels of ecosystem functions in different predator hunting mode treatments. Actively hunting predators suppress plant species evenness and enhance productivity and N mineralization, whereas sit-and-wait predators have opposite effects. Values are mean ± 1 SD. Determinations of significance for each treatment and variable are based on a one-way *t* test for difference from 0% change, $n = 7$ replicates. *$P = 0.05$.
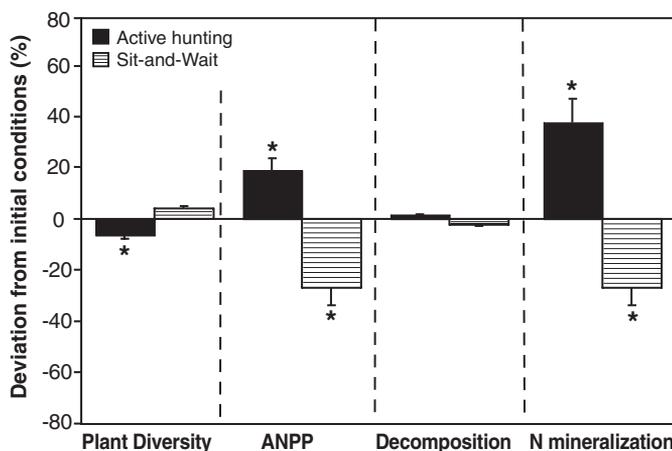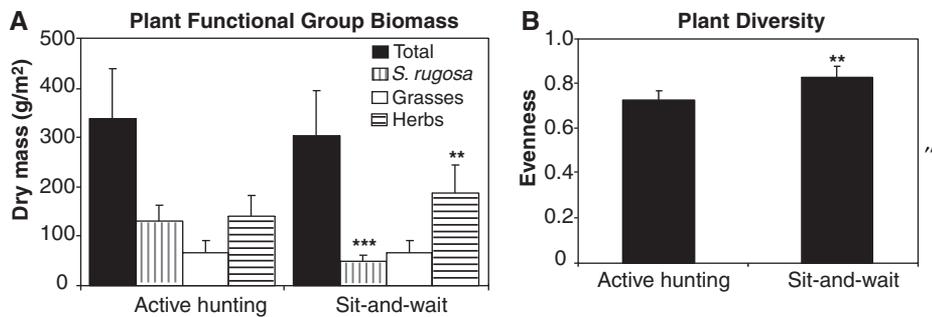
Fig. 3. Effects of manipulating predator hunting mode on the composition of the meadow plant community. (**A**) Actively hunting predator treatments had higher *S. rugosa* abundance and lower abundance of other herbs than did sit-and-wait predator treatments. There were no treatment effects on total plant biomass and grass biomass. (**B**) Changes in plant species functional group composition led to changes in plant species diversity, measured as evenness to account for *S. rugosa* dominance effects. Values are mean ± 1 SD. Determinations of the effect of treatment differences on the biomass of each plant functional group and on plant diversity are based on one-way paired *t* tests following MANOVA, $n = 7$ replicates. **$0.05 < P < 0.01$, ***$P \ll 0.01$.

active = 34.1 ± 1.7 (SEM) versus C:N in sit-and-wait = 38.9 ± 1.9 (SEM)], indicating that active predator treatments had significantly higher availability of N per unit of plant matter decomposed than did sit-and-wait treatments (one-tailed paired *t* test, $P < 0.05$, $n = 7$ replicates).

This experiment helps to explain why species in higher trophic levels sometimes enhance productivity, decomposition, and elemental cycling and at other times reduce the level of those functions (*26*). These differences are brought about by a simple causal chain: a predator hunting mode–dependent herbivore response leading to different indirect effects on plant community composition that in turn cascades to affect ecosystem functioning (Fig. 1).

The single-predator experimental treatments in this study are, however, an abstraction of natural system structure in two respects. First, it is not a highly reticulate system, so top-down effects propagate downward fairly linearly. Second, natural systems typically contain coexisting, multiple predator species. Thus, the nature and strength of top-down effects of predator species diversity on ecosystem function, especially when passing through a reticulate network, may be quite different than in single-predator treatments (*12, 27, 28*). Nevertheless, the current study represents an important precursor to a multiple-predator study in that it elucidates the mechanism and pathway by which an important predator functional trait can influence ecosystem function. Moreover, recent synthesis (*29*) suggests that the concept of predator hunting mode can be extended to explain variation in top-down effects that arise when different combinations of predator species coexist.

The recognition that predators may play important roles in ecosystems has prompted concern that the loss of top predators will lead to profound changes in the diversity and abundance of species in lower trophic levels of ecosystems, and ultimately in ecosystem functions (*1, 7, 12, 20, 25, 30*). The normal presumption

in ecosystem science, however, is that predator species cause qualitatively similar kinds of indirect effects on ecosystems (*1, 31*). This experiment instead shows that we must begin to consider the mechanisms by which predators hunt their prey in order to develop clearer understanding of predator effects on ecosystems and to develop effective ecosystem conservation efforts. An appealing feature of framing theory using hunting mode as a functional trait is that it may offer generalizable understanding about the source of contingency in prey responses to predators (*17, 29*). Moreover, hunting mode is a trait that is readily ascertained through natural history observation of predators in the field. The link between predator hunting mode and ecosystem function thus offers considerable promise for developing theory aimed at using predator functional traits as a key predictor of ecological dynamics.

Fig. 4. Effects of manipulating predator hunting mode on three key ecosystem functions. Actively hunting predators caused higher rates of ANPP (**A**) and N mineralization (**C**) than did sit-and-wait predators. Predator treatments had no effect on decomposition (**B**). Values are mean ± 1 SD. Determinations of treatment differences are based on one-way paired *t* tests, $n = 7$ replicates. *$P = 0.05$, **$0.05 < P < 0.01$.

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