

REPORT

## Top predator control of plant biodiversity and productivity in an old-field ecosystem

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### Abstract

Predators can have strong indirect effects on plants by altering the way herbivores impact plants. Yet, many current evaluations of plant species diversity and ecosystem function ignore the effects of predators and focus directly on the plant trophic level. This report presents results of a 3-year field experiment in a temperate old-field ecosystem that excluded either predators, or predators and herbivores and evaluated the consequence of those manipulations on plant species diversity (richness and evenness) and plant productivity. Sustained predator and predator and herbivore exclusion resulted in lower plant species evenness and higher plant biomass production than control field plots representing the intact natural ecosystem. Predators had this diversity-enhancing effect on plants by causing herbivores to suppress the abundance of a competitively dominant plant species that offered herbivores a refuge from predation risk.

### Keywords

Diversity and productivity, grasshoppers, indirect effects, old-field ecosystem, plant diversity, predators and ecosystem function, spiders, top-down control, trait-mediated effects, trophic cascade.

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### INTRODUCTION

Ecology abounds with detailed mechanistic insight into the nature of predator effects on ecosystems (Sih *et al.* 1985; Pimm 1991). Predators can have strong effects on the abundance and diversity of prey species (Schoener & Spiller 1996; Paine 1966; Crooks & Soule 1999) and the consequences of those effects frequently ramify beyond the predators' prey base to affect the abundances of plant trophic levels (Brett & Goldman 1996; Menge 1997; Pace *et al.* 1999; Schmitz *et al.* 2000; Shurin *et al.* 2002). Yet, most contemporary evaluations of the relationships between species diversity and ecosystem function like primary production focus almost exclusively within the plant trophic level, ignoring impacts of higher trophic levels (Loreau *et al.* 2001; Paine 2002). This stems, in part, from a long-standing view that terrestrial ecosystems are primarily driven by bottom-up processes where plant diversity and productivity, determined by climate and soil–plant interactions, govern the dynamics and abundances of species in higher trophic levels (Loreau *et al.* 2001). It is also a consequence of strikingly few reported cases (Gutierrez

*et al.* 1997; Fraser & Grime 1998; Paine 2002) that explicitly evaluate the effect of top predators on plant diversity.

Here I show that the top predators may be an important, overlooked determinant of plant diversity and productivity in a terrestrial system. The research builds on a long-term study that derived a mechanistic understanding of species interactions in a New England meadow ecosystem. This system was comprised of spider predators, leaf-chewing and sap feeding herbivores, and grass and herb plants.

The study combines three central concepts in ecology. It addresses how a top-down cascade involving a simple complement of dominant species organized in a fairly, linear food chain [a so-called species cascade (Polis 1999)] can lead to important changes in community-level pattern and process. It illustrates how this community-wide effect can be predicted by knowing how individual level-behaviour scales to community-level interactions and dynamics. Finally, it offers insight into the way top-down cascading effects in food webs can lead to changes in biodiversity and ecosystem functioning.

## MATERIALS AND METHODS

### Natural history and background

The research was completed in a meadow in north-eastern Connecticut, USA. Overall, this system contains 18 species of plants, although fewer coexist locally. Sampling, by clipping 50, 1 m<sup>2</sup> plots, sorting plants to species, drying at 60 °C and weighing revealed that the dominant (>90.6% biomass) species are the herbs *Solidago rugosa*, *S. graminifolia*, *Potentilla simplex*, *Daucus carota*, *Trifolium repens*, and the grass *Poa pratensis*. Other herb species include *S. altissima*, *S. canadensis*, *Asclepias syriaca*, *T. agrarium*, *Chrysanthemum leucanthemum*, *Aster novaeangliae*, *Fragaria canadensis*, *Erigeron canadensis*, *Hieracium aurantiacum*, *Rhynchospora hirta* and the grasses *Phleum pratense* and *Holcus* sp. Faunal sampling within 25, 1 m<sup>2</sup> areas using a combination of direct observation, standard sweep net surveys and an electric-powered backpack aspirator indicates that there are two temporally segregated herbivore insect feeding guilds (sap-feeders and leaf-chewers) present each year. The sap-feeding guild comprised mainly of the generalist spittle bug *Philaenus spumarius*, the *Solidago*-specialist plant bug *Lopidea media*, the planthoppers *Campylenchia latipes* and *Stichtocephala festina*, the generalist pentatomid *Acrosternum bilare*, the milkweed bug *Lygaeus kalmii* and a grass specialist plant bug *Leptopterna dolabrata* is present during early June to mid-July. The leaf-chewing guild, comprised of the specialist grasshopper *Chorthippus curtipennis* and the generalist grasshopper *Melanoplus femurrubrum* begins in early mid-July and persists to late September. The field contains several species of hunting spider predators including the nursery web spider *Pisaurina mira*, the jumping spider *Phidippus rimator*, the wolf spider *Rabidosa rabida* and the crab spider *Misumena vatia* which are dominant in the vegetation layer of the field during the summer period and are observed to consume both sap-feeding and leaf-chewing insects. Mammalian herbivores such as woodchucks *Marmota monax* do not reside in the field. Deer (*Odocoileus virginianus*) visit the field infrequently and selectively eat flower heads, leaving erect stems in the midst of flower patches. Such characteristic damage was not observed in our plots. Live-trapping revealed that meadow voles *Microtus pennsylvanicus* exist at exceeding low densities (c. 7 ha<sup>-1</sup>, equivalent to 0.0028 animals per experimental plot) and thus have little or no impact on the vegetation.

Field experimentation (Schmitz 1998; Uriarte & Schmitz 1998) revealed that the dominant players in this system are the hunting spider *P. mira*, the grasshopper herbivore *M. femurrubrum*, the grass *P. pratensis* and the competitive dominant herb *S. rugosa*. *Melanoplus femurrubrum* grasshoppers eat both *P. pratensis* and *S. rugosa*. But they prefer *P. pratensis* in the absence of predators and can inflict considerable damage to it (Beckerman *et al.* 1997; Schmitz *et al.* 1997; Schmitz & Suttle 2001). Mortality risk caused by predator

presence forces grasshoppers largely to forego feeding on grass and to seek refuge in and forage on leafy *S. rugosa*, thereby causing high damage levels to this species (Beckerman *et al.* 1997; Schmitz 1998). Thus, *P. mira* spiders exert strong top-down control by having a positive indirect effect on *P. pratensis* abundance and a negative indirect effect on *S. rugosa* abundance.

The emerging hypothesis is that *P. mira* should have a strong diversity-enhancing effect on plants by causing grasshoppers to undergo a habitat shift and thereby suppress the abundance of the competitively dominant *S. rugosa* (Fig. 1). This amounts to a multi-trophic level variant of the classic keystone predation hypothesis (Paine 1966; Leibold 1996) in which *P. mira* acts as an *indirect* keystone predator.

### Study design

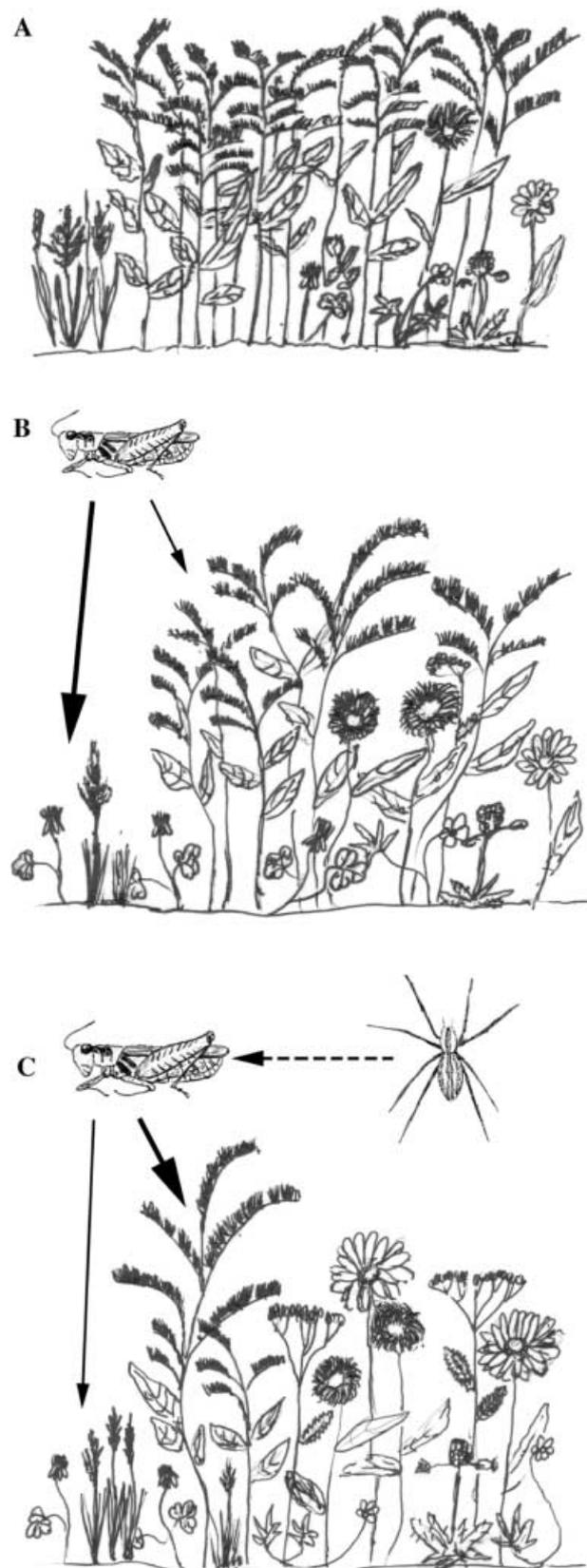
I tested this hypothesis with a multi-year (1999–2001) randomized block field experiment that manipulated the number of trophic levels in 2 m × 2 m field plots. I used a block design to randomize out the effects of a slope and soil moisture gradient in the field. I measured the effects of each manipulation on plant diversity and productivity. Thus, the pattern in plant diversity in this experiment emerges naturally from the trophic manipulations; it is not manipulated directly.

The experiment consisted of two treatments and a control randomly assigned to each of 10 blocks. The control was the natural field system containing plants, herbivores and predators: hereafter three trophic level treatment. I created a predator exclusion treatment (hereafter, two trophic level treatment containing herbivores and plants) by surrounding 2 m × 2 m plots with a 45-cm wide aluminium sheet–metal barrier, buried 5–10 cm in the ground. All arthropod predators within the exclusion plots were removed by hand at the beginning of the experiment. Semi-weekly inspections of plots were conducted to ensure the persistent absence of arthropod predators. Finally, a pesticide treatment was created to prevent damaging herbivory (hereafter, one-trophic level treatment containing only plants). Organic pyrethroid insecticide was applied to these treatment plots every 15 days using a backpack sprayer. Pesticide was diluted in water and the solution was applied at a concentration of 0.21 L m<sup>-2</sup> in each spraying period. This type of pesticide has no demonstrated adverse effects on plant growth (Root 1996).

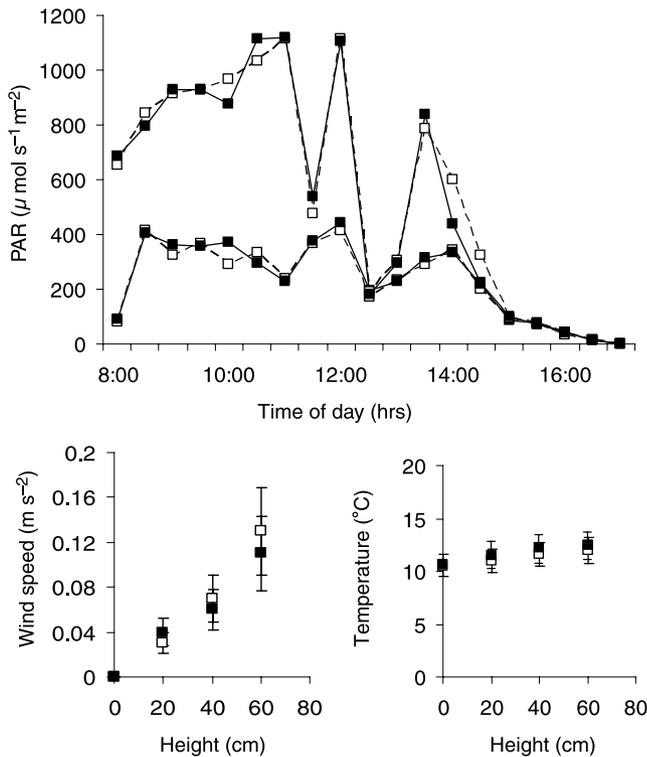
Sampling, using a standard 1.6 m × 1.6 m sampling quadrat, gridded at 0.2 m intervals, revealed that initial plant community structure (number of plant species and percentage of quadrat covered by a species) was statistically similar among treatment plots (all ANOVAS  $P > 0.25$ ). I also evaluated the potential for a systematic bias in microclimatic

conditions consequent to enclosing plots with sheet metal. Biophysical variables [photosynthetically active radiation (PAR), wind speed and ambient air temperature] important to plant growth (Drake *et al.* 1989) were measured in a representative enclosed and a paired open plot at four elevations above ground (0, 20, 40 and 60 cm). The PAR was measured using a LI-COR LI-250 light meter coupled to a LI-190SA quantum sensor (Li-Cor Inc., Lincoln, NE). Wind speed was measured using a Kestrel 1000 wind meter (Nielsen Kellerman Chester, PA) accurate to  $0.3 \text{ m s}^{-1}$ . Ambient air temperature was measured using a Cole-Parmer Digi-Sense 8523 thermistor thermometer (Cole-Parmer Instrument Co., Chicago, IL), coupled to an air probe accurate to  $0.1 \text{ }^\circ\text{C}$ . Measurements at each elevation were taken at five locations within each plot every  $\frac{1}{2}$  h between 08:00 and 17:00 hours. Measured values for each  $\frac{1}{2}$ -h period were averaged to obtain a representative plot value. Comparison of PAR and average daily wind speed and temperature revealed no systematic bias in microclimate between open and enclosed plots (Fig. 2) consistent with similar evaluations for other field enclosures (Drake *et al.* 1989).

Each year, individual plant species within plots were sampled non-destructively once per month throughout the growing season (May to September) using the  $1.6 \text{ m} \times 1.6 \text{ m}$  sampling quadrat. I quantified the number of plant species in a plot and percentage plot area covered by each plant species. I quantified plant species diversity using two indices: species richness and evenness. Species richness (S) is the standard measure in studies of diversity/productivity relationships (Tilman *et al.* 2001). Plant species richness does not account for changes in species abundances. Yet, I hypothesize that top predators in my system should indirectly alter the proportional representation of those plant species whose abundance would otherwise be suppressed by the dominating effect of *S. rugosa* (Fig. 1). Species



**Figure 1** The hypothesized mechanism for underlying changes in plant species diversity consequent to trophic manipulations in the study system. In the absence of grasshopper herbivores and spider predators (A), *Solidago rugosa* should dominate the field plots and suppress the abundance of other herb species. In the absence of spider predators (B), herbivores should preferentially forage on grasses (indicated by thick arrow) and consume herb species, including *S. rugosa*. Such herbivory should reduce the abundance and hence dominating effect of *S. rugosa*. Plant species diversity should increase, relative to (A), because plant species become more equitably represented in field plots, i.e. plant species evenness increases. In the presence of spiders (C), grasshoppers should largely forego feeding on grass and seek refuge from predation risk in *S. rugosa* (behavioural effect of spiders on grasshoppers denoted by dashed line), forage most heavily on this species (denoted by thick arrow) and thus suppress its abundance even more than in (B). This should lead to higher plant species evenness than in (B).



**Figure 2** Comparison of microclimatic conditions important to plant growth in an open plot (open squares) and a paired plot surrounded by aluminium sheet metal (solid squares) to evaluate the potential for a systematic bias due to a ‘sheet-metal effect’. The upper frame presents values of photosynthetically active radiation (PAR) at ½-h sampling intervals throughout the day at 0 cm (lower curves) and 60 cm (upper curves) above the ground (the trends for 20 and 40 cm are similar). Lower frames present daily mean ± 1 SE ( $n = 19$ ) wind speeds and ambient temperatures.

evenness is one measure that combines the two mechanistic factors – dominance and plant species abundance – that are important in this and other old-field systems (Wilsey & Potvin 2000). More generally, variation in plant diversity as a result of biotic interactions among plant species often results from evenness effects (Chapin *et al.* 2000; Stirling & Wilsey 2001). I quantified evenness using the standard Shannon index,  $J' = (-\sum p_i \log p_i) / \log S$ , where  $p_i$  is the abundance (percentage cover) of species  $i$  in a plot. Evenness values close to 0 indicate one or a few species dominate and many other species are rare; values close to 1 indicate that species are equally abundant.

As an index of productivity, I estimated dry plant biomass production ( $\text{g plot}^{-1} \text{d}^{-1}$ ) by calculating the differences in plant biomass between 31 May 2001 and 19 June 2001; and 19 June 2001 and 19 July 2001, and dividing each difference by the intervening number of days. These two periods represent independent growth condi-

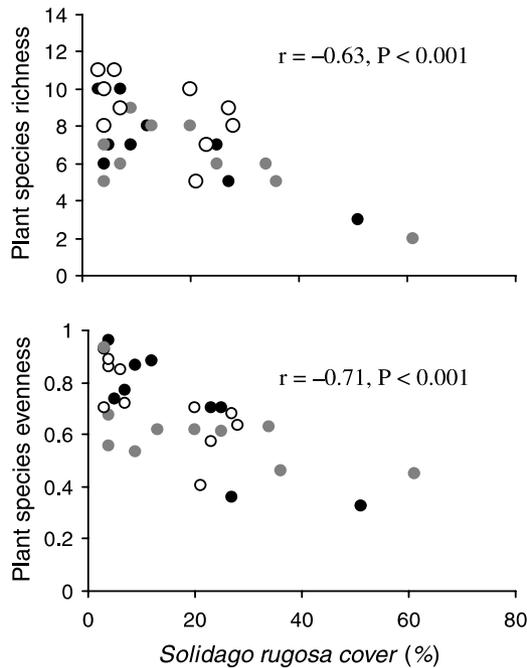
tions (wetter spring, drier summer) in the field and so enable an assessment of the consistency of the productivity response. I converted non-destructive sample estimates of percentage cover into estimates of dry biomass using regression equations. To do this, mean height of a species in a plot was measured concurrently with each sampling of plant species cover using a meter stick on five random plants of a species. Plant species biomass was then estimated using multiple regression equations describing prior calibrations of plant species dry mass in relation to species percentage cover and species height. Sampling non-experimental plots for plant species height and percentage cover and then clipping, drying at 60 °C and weighing each species provided data for these regressions. Such equations produced  $R^2$  values between 85 and 92% depending on the plant species.

Finally, I estimated the strength of the top-down effect of predators on plants as the log ratio  $[\ln(Np_+ / Np_-)]$  of total estimated July 2001 dry plant biomass in plots in the presence ( $Np_+$ ) and absence ( $Np_-$ ) of predators (Schmitz *et al.* 2000; Shurin *et al.* 2002).

**RESULTS**

In the absence of herbivores and predators, *S. rugosa* percentage cover was negatively related to plant species richness and evenness (Fig. 3). Because the strength of the correlations could be determined by two outlying values of *S. rugosa* percentage cover (51 and 61%), I reanalysed the data after removing those values. The correlation between species richness and *S. rugosa* cover and evenness and cover declined to  $-0.42$  ( $P < 0.03$ ) and  $-0.65$  ( $P < 0.02$ ), respectively. This suggests that species evenness is a comparatively more robust descriptor of the relationship between plant diversity and *S. rugosa* abundance.

Randomized block ANOVA on July 2001 data (chosen because it represents the height of the growing season and thus avoids the confounding effects of plant senescence beginning in August) revealed that there were significant, cumulative treatment effects on percentage *P. pratensis* cover ( $P < 0.05$ , d.f. = 2, 18) and percentage *S. rugosa* cover ( $P < 0.02$ , d.f. = 2, 18). Block effects were not significant ( $P > 0.15$ ). A Tukey test revealed that 3 years of predator exclusion resulted in significantly lower *P. pratensis* and *S. rugosa* cover relative to the one-trophic level, plant-only treatment (Fig. 4). Sustained predator presence (three trophic level treatment) resulted in increased *P. pratensis* cover and decreased *S. rugosa* cover relative to the predator exclusion treatment. This indirect positive effect of predators on *P. pratensis* and negative indirect effect on *S. rugosa* (Fig. 4) is consistent with previous studies in this system (Beckerman *et al.* 1997; Schmitz 1998), but observed at a 4× larger scale and over a 3× longer period.



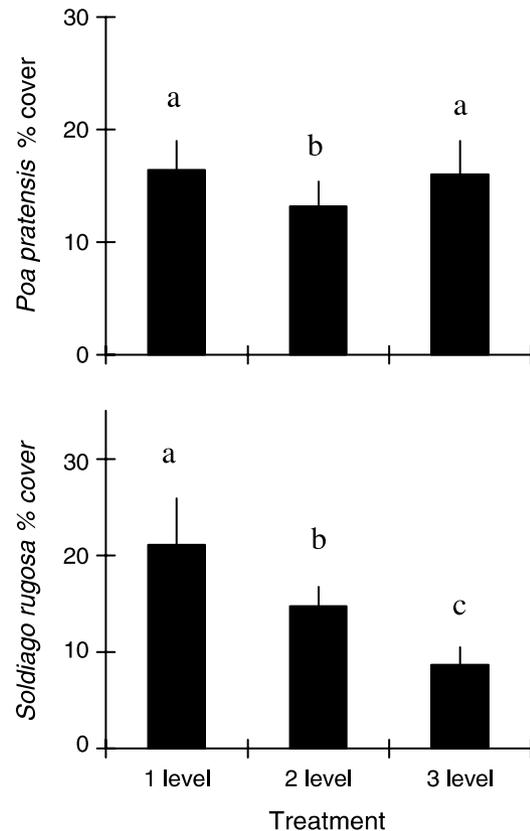
**Figure 3** Relationship between 2 m × 2 m plot area covered by *Solidago rugosa* and plant species richness and evenness within the plot, illustrating the dominating effect of *S. rugosa* on plant species diversity. Evenness values closer to 0 indicate one or a few species dominate and many other species are rare; values close to 1 indicate that species are equally abundant. Symbols: 1999 ○, 2000 ●, 2001 ●, plot values.

Manipulation of trophic structure caused significant shifts in plant species richness and evenness combined (randomized block MANOVA, Wilks Lambda 0.737, d.f. = 4, 36,  $P = 0.06$ ). A posteriori randomized block ANOVAS revealed that this significance was entirely due to treatment effects on plant species evenness ( $P < 0.02$ , d.f. = 2, 18): there was no significant treatment effect on plant species richness ( $P > 0.5$ , d.f. = 2, 18). A Tukey test supported the prediction that plant species evenness should be higher in three trophic level control plots than in either the two or one trophic level treatments (Fig. 5). By contrast, there were significant (ANOVAS, both  $P < 0.01$ , d.f. = 2, 18), decreases in estimated plant productivity with increasing number of trophic levels in early and mid-summer (Fig. 6).

The strength of predator effects on plants was estimated to be  $0.62 \pm 0.107$  (95% CI).

## DISCUSSION

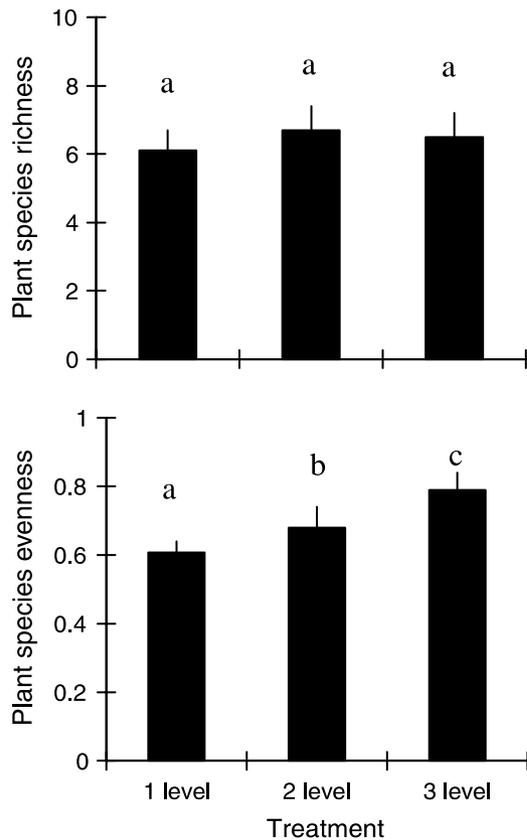
A substantial body of evidence demonstrates that top-down effects of predators are generally weaker in terrestrial systems than in aquatic systems, when the effects are measured as *total*



**Figure 4** Effect of sustained 3-year, trophic level manipulations on the plot area covered by *Poa pratensis* and *Solidago rugosa*, illustrating the positive and negative indirect effect of predators on *P. pratensis* and *S. rugosa*, respectively. Values shown are mean and 1 SE ( $n = 10$  replicate plots). Bars with different lower case letters indicate significant differences based on a Tukey test at  $P < 0.05$ . Treatments: 1 level = plants only; 2 level = plants and herbivores; 3 level = plants, herbivores and carnivores.

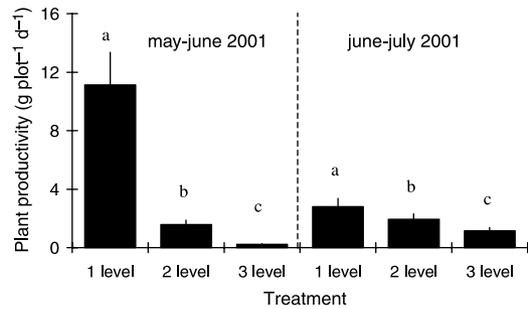
*plant trophic level biomass or abundance* (Strong 1992; Shurin *et al.* 2002). Indeed, this study is not an exception: the estimated effect magnitude of top predators on plants was slightly higher than observed in previous short-term cage experiments in my system, but fell within the range for field and cage experiments in other terrestrial systems (see Table 1 in Schmitz *et al.* 2000). It is also within the range of comparatively 'weak' values for terrestrial systems generally (Shurin *et al.* 2002). At face value then, this observation would support the current view that it is reasonable to downplay the importance of higher trophic levels in consideration of the relationships between terrestrial plant diversity and ecosystem function (Loreau *et al.* 2001).

However, examining plant responses using an aggregate measure of plant species abundance can give misleading insight into higher trophic level effects on community structure and the ensuing ecosystem function. Indeed,



**Figure 5** Effect of sustained 3-year, trophic level manipulations on plant species richness and evenness. Evenness values closer to 1 indicate that the plot covered by each plant species is comparatively equal relative to lower evenness values. Values shown are mean and 1 SE ( $n = 10$  replicate plots). Bars with different lower case letters indicate significant differences based on a Tukey test at  $P < 0.05$ . Treatments: 1 level = plants only; 2 level = plants and herbivores; 3 level = plants, herbivores, and carnivores.

interactions in my system did not conform to the classic notion (Strong 1992) that top-down effects in terrestrial systems should diffuse along myriad trophic pathways linking species over the entire food web. Despite the high species richness in all trophic levels in this system (see Natural history and background), top-down effects appeared to transmit linearly down a chain comprised of a dominant predator and herbivore species to the plant species, consistent with a growing body of new evidence in other terrestrial ecosystems (Moran *et al.* 1996; Post *et al.* 1999; Schoener & Spiller 1999; Terborgh *et al.* 2001). Furthermore, using previous mechanistic insight about the chain of interactions among the dominant species (Beckerman *et al.* 1997; Schmitz *et al.* 1997; Schmitz 1998) – viz. *P. mira* spiders causing grasshoppers to shift habitat use thereby suppressing the competitively dominant *S. rugosa*: an indirect keystone predation effect (Fig. 1) – I was able



**Figure 6** Effect of sustained 3-year, trophic level manipulations on plant dry mass production, measured during two sampling periods in 2001. Values shown are mean and 1 SE ( $n = 10$  replicate plots). Bars with different lower case letters indicate significant differences based on a Tukey test at  $P < 0.05$ . Treatments: 1 level = plants only; 2 level = plants and herbivores; 3 level = plants, herbivores and carnivores.

to predict reliably that removing higher trophic levels in the field experiment should lead to a reduction in plant species evenness (Fig. 5). This suggests that the effects of antipredator behaviour of herbivores, which is typically assumed to be short-term and thus attenuate on the time-scale of ecosystem dynamics, may indeed have cumulative longer-term impacts on community structure. This evidence, coupled with the observation that keystone predation effects may be frequent in many systems (Menge 1995; Leibold 1996), suggests that it might become untenable to argue that higher trophic levels ought to have little or no effect on plant species diversity simply because the strength of trophic cascades, based on aggregate measures of plant biomass, are weak (Loreau *et al.* 2001).

Most contemporary studies of the relationship between terrestrial plant diversity and ecosystem function such as productivity usually quantify diversity in terms of species richness (but see e.g. Wilsey & Potvin 2000; Wilsey & Polley 2002). The absence of change in species richness in my experiment would indicate that there is no direct effect of species diversity on ecosystem function. That conclusion would, however, again be an artefact of an inappropriate functional measure of a plant species attribute, in this case diversity, given the natural history and mechanism of species interactions in the field system. In the experimental system, most of the plant species sampled after 3 years existed in all plots at the onset of experimentation and there were no new, invading herb or grass species given the successional stage of the system. Thus, there was no a priori expectation that species richness should change and indeed none was detected. However, trophic manipulations caused the complexion (evenness) of the plant community to change and this translated into changes in productivity, measured as dry

biomass production (Fig. 6). This measure of productivity changed with trophic manipulation because in the absence of herbivory, *S. rugosa* grew very rapidly into tall stems. Herbivores, especially in the presence of predators, stunted the height of and thinned *S. rugosa* thereby suppressing the most productive plant species in this ecosystem and creating a more open and patchy environment. This allowed less productive herb species, which were otherwise intolerant of shady conditions caused by *S. rugosa*, to proliferate.

The interactive effect of predators on plant diversity and productivity has implications for studies that seek to understand which combinations of plant species or plant functional groups enhance ecosystem services like productivity by systematically manipulating a single (within trophic level) dimension of biodiversity. Natural systems contain at least two dimensions of biodiversity: species diversity within trophic levels and trophic level diversity within the ecosystem (Paine 2002). So, tightly controlled biodiversity experiments, which ignore higher trophic levels, remove a potentially important, interactive effect on indices of productivity (Fig. 4). Thus it will be difficult to resolve the current debate (reviewed in Loreau *et al.* 2001; Tilman *et al.* 2001) about true plant diversity-productivity relationships in nature without considering the diversifying effects of higher trophic levels on plants (see also Paine 2002). In this respect, a classic trophic cascade paradigm may be too restrictive for framing questions about trophic control of diversity and productivity. Hence, a perspective that considers mechanisms underlying 'biodiversity cascades' may provide deeper insight into diversity-productivity relationships in ecosystems (see also Dyer & Letourneau 2003).

This study raises important questions in attempts to conserve ecosystem function such as plant production by protecting biodiversity. The two-dimensional nature of diversity, and associated inverse relationship between trophic diversity and productivity, reported here and elsewhere (Paine 2002), illustrates a trade-off that has important ethical implications for the application of economic valuations to biodiversity conservation. Do we preserve trophic diversity on the one hand and allow for lowered levels of a valued ecosystem function (e.g. productivity); or do we preserve only one trophic level (and by default let higher levels go extinct) to maximize the valued ecosystem function? This trade-off is not easily reconciled and certainly is not considered in contemporary valuations of ecosystem services of biodiversity (Daily 1997). However, it is an issue that must be increasingly confronted as human-scale environmental impacts leading to top predator loss cause shifts in biodiversity of lower trophic levels in ecosystems (e.g. Crooks & Soule 1999; Berger *et al.* 2001; Terborgh *et al.* 2001).

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