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PREDATORS HAVE LARGE EFFECTS ON ECOSYSTEM PROPERTIES BY CHANGING PLANT DIVERSITY, NOT PLANT BIOMASS

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Abstract. Cascading effects of predators on total plant trophic-level biomass tend to be weaker in terrestrial than in aquatic systems. Accordingly, it is hypothesized that top predator effects on terrestrial plant diversity and on ecosystem function should likewise be weak or unimportant. This report presents a test of this hypothesis using data from a long-term field experiment. The five-year experiment manipulated the trophic structure of an old field ecosystem by excluding either predators or predators and herbivores relative to an unmanipulated, natural control. Long-term manipulations led to systematic treatment effects on community properties (plant trophic-level biomass, plant species biomass, plant species evenness) and on ecosystem properties (supply rate of solar radiation, N mineralization rate). The strengths of top predator effects on community properties were modest compared with nonterrestrial systems. But, predator-caused changes in plant community structure via alteration of plant dominance, and hence plant species evenness, strengthened effects on ecosystem properties. Counter to the hypothesis, weak trophic cascades do not necessarily lead to weak indirect effects of predators on ecosystem properties.

Key words: *ecosystem function; indirect keystone predation; interaction strength; nitrogen supply; plant diversity; plant dominance effects; predator indirect effects; trophic cascade.*

INTRODUCTION

Ecologists have become increasingly interested in studying the linkage between two important components of natural systems: pattern in the distribution and relative abundance of species, i.e., biodiversity, and the quantity and rate of biogeochemical cycling, resource supply, and plant production, i.e., ecosystem function (Johnson et al. 1996, Chapin et al. 1997, Loreau et al. 2001, Kinzig et al. 2002, Worm and Duffy 2003, Hooper et al. 2005). Insights about mechanisms underlying such linkages have been derived almost exclusively from experiments on species interactions within a single trophic-level, usually plants (Hooper et al. 2005). Yet trophic cascades may cause magnitudes of changes in plant composition and production that rival those observed in experimental manipulations of species diversity within the plant trophic-level (Duffy 2003). This implies that biodiversity–ecosystem function relationships should be examined in two orthogonal dimensions: horizontal diversity within trophic-levels

and vertical trophic-level diversity within ecosystems (Duffy 2002, Paine 2002, Dyer and Letourneau 2003, Schmitz 2003, Thébault and Loreau 2003, Ives et al. 2005).

An important, emerging challenge, then, is to understand how vertical trophic-level diversity and ensuing trophic interactions, which are community processes, cascade to influence the biotic composition of communities and, in turn, how effects on biotic composition further cascade to affect the biophysical properties of ecosystems that ultimately shape ecosystem processes (Chapin et al. 1997, Pastor and Cohen 1997, Thébault and Loreau 2003).

The idea that trophic cascades govern terrestrial community structure and ecosystem function has not been raised without controversy. Over the last 10 years, there has been lively debate (Strong 1992, Polis and Strong 1996, Pace et al. 1999, Persson 1999, Polis 1999, Polis et al. 2000, Shurin et al. 2002) that has led to the broad perception that trophic cascades are generally weaker in terrestrial systems than in aquatic systems. This has then led to the hypothesis that cascading effects should attenuate in terrestrial systems (Strong 1992, Polis and Strong 1996), and subsequently, to the hypothesis that cascading effects may have little

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influence on relationships between terrestrial plant diversity and ecosystem properties (Loreau et al. 2001, Thébault and Loreau 2003).

Here I present results of a long-term experiment in an old field ecosystem that evaluates these hypotheses. I show that much of the reasoning that argues for attenuating effects, which derives from the requirement that plant responses be measured in terms of total trophic-level biomass (Polis 1999, Polis et al. 2000), can give misleading insight into the nature and importance of higher trophic-level effects on ecosystems. Indeed, I detected cascading effects on ecosystem properties, such as elemental cycling and light supply. These effects resulted from cascading effects altering the community composition (species dominance and evenness) of the plant trophic-level rather than total trophic-level biomass, defined as a cryptic cascade (Tessier and Woodruff 2002). I show that higher trophic-levels can have important effects on plant diversity and ecosystem properties consistent with qualitative theoretical expectations (Pastor and Cohen 1997, Thébault and Loreau 2003). These results argue for rethinking the nature of terrestrial cascades and their link with ecosystem processes.

METHODS

Natural history

The study was conducted in a 1.5-ha old field at the Yale-Myers Research Forest in northeastern Connecticut, USA. The most abundant plant species were the perennial herb *Solidago rugosa* and grass *Poa pratensis*. Other herb species included *Chrysanthemum leucanthemum*, *Daucus carota*, *Fragaria canadensis*, *Hieracium aurantiacum*, *Potentilla simplex*, *Rudbeckia hirta*, *Solidago altissima*, *Solidago graminifolia*, and *Trifolium repens*. The field contained two main insect herbivore feeding guilds (Schmitz 2004). Sap feeders are present from early June to mid to late July; leaf chewers begin in early to mid July and persist until late September, when they and their plant resources succumb to frost. The insect herbivores face several species of hunting spider predators, which exist in the vegetation layer of the field during the entire summer period (Schmitz 2004).

Despite the complexity, plant species abundances in this system seem to be controlled primarily by indirect keystone predation involving a top spider predator, *Pisaurina mira*, whose risk effects have been repeatedly shown (reviewed in Schmitz 2004) to change the foraging preferences of the generalist grasshopper *Melanoplus femurrubrum* from a grass, *P. pratensis*, to a competitively dominant herb, *S. rugosa* (Schmitz 2004). In the absence of herbivore mediation, *S. rugosa* tends to suppress the abundance of other herb species (Schmitz 2004).

Experimental design

I conducted a multiyear (1998–2003), randomized, block field experiment that manipulated the number of

trophic-levels in 2×2 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.

The experiment comprised two treatments and a control randomly assigned to each of 10 blocks, each lasting the full duration of the experiment. The controls contained natural levels of plants, herbivores, and predators (three-level treatment). The two treatments involved systematic exclusion of trophic-levels. (1) Predators were excluded (two-level treatment containing herbivores and plants) by surrounding the treatment plots with a 45 cm wide, aluminum sheet metal barrier buried 5–10 cm in the ground and then maintaining a 30-cm mowed buffer strip around the perimeter of the enclosed plot. The barrier did not bias microclimatic conditions important to plant growth such as photosynthetically active radiation, wind speed, ambient air temperature, and precipitation (Schmitz 2003). All arthropod predators within the exclusion plots were removed by hand at the beginning of the experiment. Semiweekly inspections of plots ensured the persistent absence of arthropod predators. (2) Predators and herbivores were excluded (one-level treatment containing only plants) by applying organic pyrethroid insecticide (Ortho Tomato and Vegetable Killer, Chevron Chemical Company, Orlando, Florida, USA; 15 mL of insecticide in 4 L of water) with a backpack sprayer every 15 days. A 0.21 L/m^2 concentration of pesticide was applied in each period. The pesticide application amounts to a watering level two orders of magnitude lower than the mean rainfall received by all plots for the same period (Ovadia and Schmitz 2004) and so should not lead to a systematic watering bias on plant production in the pesticide treatment. The experiment was not designed to manipulate plant diversity directly; rather, the pattern in plant diversity in this experiment emerged from the trophic manipulations. Sampling, using a standard 1.6×1.6 m sampling quadrat, gridded at 0.2-m intervals, revealed that initial plant species richness and relative abundance was statistically similar among treatment plots (all ANOVAs $P > 0.25$).

Each year, individual plant species within plots were sampled nondestructively once per month throughout the growing season (May to September) using the 1.6×1.6 m sampling quadrat. I quantified the number of plant species in a plot and the percentage of plot area covered by each plant species.

In old fields, both the amount of photosynthetically active sunlight reaching the ground level and soil nitrogen supply seem to be the most important resources for plants (Tilman 1988, Cain et al. 1991, Uriarte 2000). So during summer 2003, I measured the long-term treatment effects on solar radiation input and on N mineralization rate concurrently with monthly plant sampling. I measured photosynthetically active solar radiation (PAR, micromoles per square meter per second) striking the ground by placing an LI-190SA

quantum sensor coupled to an LI-250 Light Meter (LI-COR, Lincoln, Nebraska, USA) on the ground surface in the center of each experimental plot in each block. I allowed the readings to stabilize for 10 seconds before recording a measurement. I used a buried-bag method (Hart et al. 1994) to estimate soil N mineralization rate (milligrams per gram per month). Within the center of each 2×2 m plot, one soil core (10 cm long and 5.08 cm in diameter) was removed using a metal corer, transferred to a 1.5 L gusseted polyethylene bag, and transported to the laboratory for processing. A companion core was taken within 20–30 cm of the first core, transferred to a bag, and then replaced into its hole to incubate. After 28 days, the field-incubated cores were removed and processed and fresh cores were taken, bagged, and replaced into their holes to incubate. Soil cores were extracted in 2 mol/L KCl using standard procedures (Hart et al. 1994). Extracted samples were refrigerated until analyzed for nitrate and ammonium content by colorimetric assays at the University of Georgia Soil, Water, and Plant Analysis Laboratory (Athens, Georgia, USA). I also measured, in the center of each plot, soil surface temperature using a Digi-Sense 8523 thermistor thermometer (Cole-Parmer Instrument, Chicago, Illinois, USA), coupled to a surface probe accurate to 0.1°C . I measured soil moisture (percentage water content) using a Dynamax ML2x Theta Probe (Dynamax, Houston, Texas, USA).

Data analysis

I estimated dry plant species biomass in each plot (grams per square meter) using regression equations to convert nondestructive sample estimates of percentage cover for each plant species into estimates of dry biomass (Schmitz 2003).

I estimated plant species diversity as species evenness because it combines plant dominance and plant species abundance, factors that have been found to be important determinants of diversity effects in old field systems (Wilsey et al. 2005). Evenness was calculated using the standard Shannon index, $J' = (-\sum p_i \log p_i) / \log S$, where p_i is the relative abundance of species in a plot. July and August evenness values were averaged for each plot.

I calculated the N mineralization rate using standard methodology (Hart et al. 1994), which converts wet mass concentrations of nitrate and ammonium in samples to dry mass concentrations. Net mineralization rate was expressed as the difference in the sum of dry mass nitrate and ammonium concentration between consecutive, monthly (28-day) sampling periods. For each plot, I averaged the values for the June–July and the July–August sampling periods.

I used randomized-block ANOVA to test for treatment effects on community variables (plant trophic-level biomass, plant species biomass, plant species evenness) and ecosystem variables (N mineralization rate, PAR, soil temperature, soil moisture). When ANOVA re-

vealed significant effects, I conducted Tukey's tests to identify which treatment means differed.

To compare the strengths of predator indirect effects directly with measures from previous studies (Shurin et al. 2002, Duffy 2003), I calculated effect magnitudes using the log ratio $[\ln(V_{P+}/V_{P-})]$ where V_{P+} and V_{P-} are community variables (dry trophic-level plant biomass, dry plant species biomass, or evenness) and ecosystem variables (N mineralization rate or PAR) in the presence (three-level treatment, P+) and absence (two-level treatment, P-) of the predator trophic-level. Interaction strengths were calculated using treatment values in each block as a matched pair. This yielded 10 replicated estimates to calculate the interaction strength mean and 95% confidence limit (Hedges et al. 1999).

RESULTS

Randomized-block ANOVA (all tests, $df = 2, 18$) revealed significant treatment effects on all community and ecosystem variables, except soil temperature and moisture (Fig. 1). Block effects were not significant (all $P > 0.15$).

Total plant biomass (Fig. 1a) was similar in the two-level and three-level treatment but both were significantly lower than the one-level treatment (Table 1). This pattern in total biomass was attributed largely to compensatory changes in the different plant species. Biomass of *P. pratensis* (Fig. 1b) was similar in the one-level and three-level treatments and was significantly higher (Table 1) than in the two-level treatment (Fig. 1b), indicative of a positive indirect effect of predators. *S. rugosa* abundance declined significantly (Table 1) with increasing number of trophic-levels (Fig. 1b), indicative of a negative indirect effect of the top predator. The collective abundance of other herb species (Fig. 1b) was similar in the one- and two-level treatment, but both were significantly lower than in the three-level treatment (Table 1), indicative of a positive indirect effect of predators. Plant species evenness (Fig. 1c) increased significantly (Table 1) with increasing numbers of trophic-levels. N mineralization rate (Fig. 1e) and PAR (Fig. 1f) likewise increased significantly (Table 1) with increasing number of trophic-levels.

The indirect effect of predators on total plant biomass was low (-0.002 ± 0.004 , all values mean and 95% CI) but it increased for individual plant groups. Effect magnitudes for *P. pratensis*, *S. rugosa* and other herbs were respectively: 0.25 ± 0.18 ; -0.48 ± 0.14 ; 0.22 ± 0.19 . The indirect effects of predators on ecosystem variables were stronger yet: N-mineralization rate, 0.82 ± 0.15 ; photosynthetically active radiation, 1.24 ± 0.19 . These interaction strengths were significantly higher than for community variables, based on non-overlapping confidence intervals

DISCUSSION

This study contributes toward a new research direction in community and ecosystem ecology (Duffy

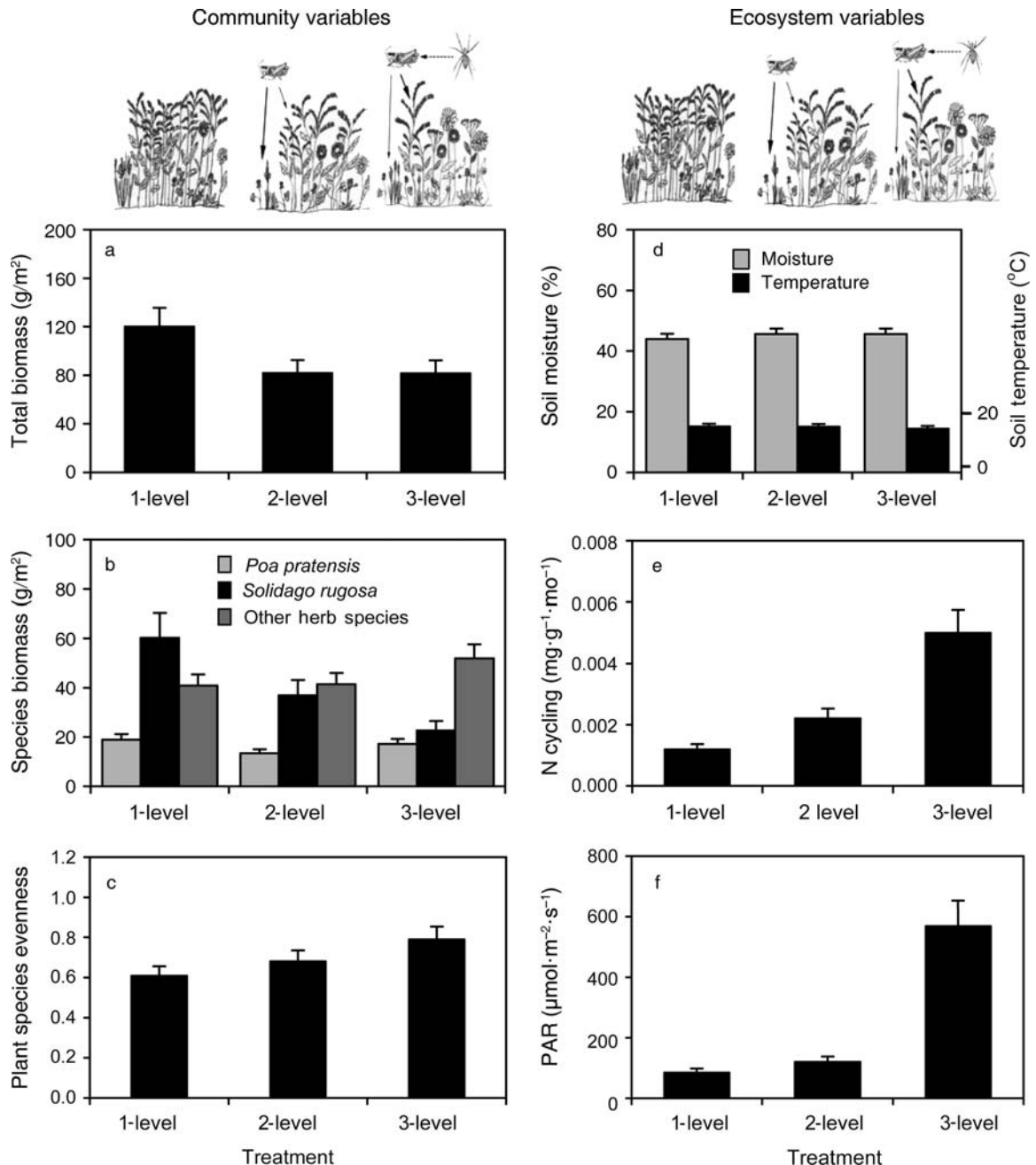


FIG. 1. Effect of sustained five-year trophic-level manipulations on community and ecosystem variables. Community variables include: (a) total plant biomass; (b) biomass of the grass *Poa pratensis*, the dominant herb *Solidago rugosa*, and other herb species collectively; and (c) plant species evenness. Ecosystem variables include: (d) soil moisture and temperature; (e) N mineralization rate; and (f) photosynthetically active radiation (PAR, in micromoles of quanta) reaching the soil surface. Values shown are mean \pm SE ($n = 10$ replicate plots). Treatments: 1-level, plants only; 2-level, plants and herbivores; 3-level, plants, herbivores, and carnivores.

2002, Paine 2002, Dyer and Letourneau 2003, Schmitz 2003, Thébault and Loreau 2003, Worm and Duffy 2003, Ives et al. 2005), one that actively considers the effects of higher trophic-levels on the link between plant diversity and ecosystem function. Recent calls to steer thinking in this direction (e.g., Duffy 2002, Thébault and Loreau 2003) recommend conceptualizing ecosystems as

chains of interacting carnivores and herbivores in which herbivores feed on a diverse array of plants. This framework assumes that the indirect effects of top-predators on ecosystems are mediated largely by density changes of consumers in intermediate trophic-levels.

Such a conceptualization of a trophic cascade, however, would not explain the outcome of the

manipulative experiments presented here, owing to negative effects propagated by trait-mediated indirect interactions. Previous research in this system demonstrated that species of spider predators that cause density reductions, largely of grasshoppers, only have *positive* indirect effects on all plant species (Schmitz and Suttle 2001). By contrast, the *negative* indirect effect of top predators on *S. rugosa* observed here (Fig. 1b) is consistent with observations that the dominant spider predator, *P. mira*, which has weak density effects on the grasshoppers, causes them to undergo habitat shift to decrease predation risk (Schmitz and Suttle 2001). Such habitat shift leads to *S. rugosa* suppression with a consequent rise in abundance of other herb species (Fig. 1b) and plant species evenness (Fig. 1c)—an indirect keystone effect. At the outset, then, the nature of the cascading effect observed in the system conforms more to idealizations of trophic cascades that consider individual-level, behavioral (foraging behavior) effects rather than merely density effects (e.g., Pastor and Cohen 1997, Schmitz et al. 2004).

At the community level, the experiment revealed an altogether weak cascade strength (cf. Shurin et al. 2002) when the effect was measured as total plant trophic-level biomass. This weak effect derived from much stronger, but interactive, indirect effects of predators on the different plant species. Predators had a positive indirect effect on *P. pratensis* and other herb species and a negative, indirect effect on *S. rugosa* (Fig. 1b). *S. rugosa* had the comparatively strong response because it was able to proliferate very rapidly, once top-down control was removed (Schmitz 2003). The magnitude of the changes in plant species biomass due to changes in plant diversity reported here matched the median value of changes in plant biomass derived from systematic manipulations of plant diversity in studies focused solely on the plant trophic-level (see Duffy 2003: Table 1). This reinforces the view that higher trophic-levels can have important control over plant diversity and biomass productivity relationships (Duffy 2003).

At the ecosystem level, changes in *S. rugosa* dominance (hence species evenness) can consistently explain changes in the supply rate of both N and solar radiation. In the absence of higher trophic-levels, *S. rugosa* grew into dense stands with low light penetration to the soil surface (Fig. 1b and f). Also, *Solidago* species are known to produce litter that is recalcitrant to decomposition, leading to low soil N supply (Uriarte 2000). Decreases in *S. rugosa* abundance should then lead to rising supply rates of nitrogen and solar radiation. Such decreases in abundance brought about by adding trophic-levels to the system did indeed result in a more open and patchy environment with higher N supply and solar radiation (Fig. 1e and f). This allowed other herb species, which may otherwise have been intolerant of shady conditions and low N supply caused by *S. rugosa*, to proliferate (Fig. 1b). Such herbs, however, are less dense and lower in stature (on the order of 20% lower; O. J. Schmitz,

TABLE 1. Results of field experiment evaluating the effect of trophic-level manipulations on community and ecosystem response variables.

Response variable	Tukey's test result†
Community level	
Total plant biomass	1 > (2, 3)
<i>Poa pratensis</i> biomass	(1, 3) > 2
<i>Solidago rugosa</i> biomass	1 > 2 > 3
Other herb species biomass	(1, 2) < 3
Plant species evenness	1 < 2 < 3
Ecosystem level	
Soil temperature	1 = 2 = 3
Soil moisture	1 = 2 = 3
N mineralization rate	1 < 2 < 3
Photosynthetically active radiation	1 < 2 < 3

† Significance of differences is based on ANOVAs ($df = 2, 18$; $P \leq 0.05$). Tukey's test results are a posteriori comparisons of each variable in treatments with different numbers of trophic levels: (1) plants only; (2) plants and herbivores; (3) plants, herbivores, and spiders. Parentheses around numbers in the table identify sets of treatments that do not differ from one another ($P > 0.05$).

unpublished data), leading to less aboveground plant biomass than in the one-level treatment. Thus, weak net effects on total plant biomass propagated by strong compensatory effects on species composition cause strong changes in ecosystem properties. This effect, defined as a cryptic cascade (Tessier and Woodruff 2002), means that we need to rethink the rich ways that trophic control can influence ecological systems.

Much of the research on the link between biodiversity and ecosystem function has focused on horizontal diversity, viz. diversity within the plant trophic-level (Hooper et al. 2005). The main purpose has been to understand how species' identity and functional attributes, individually and collectively, contribute toward ecosystem functioning. As such, field experiments typically control for confounding productivity effects of a few highly dominant plant species (Loreau and Hector 2001). Yet, dominance effects can be important drivers of natural ecosystem structure and function (Tilman 1988, Chapin et al. 2000, Smith et al. 2004, Wilsey et al. 2005), and can be mediated by trophic interactions (Wootton 1995, Chapin et al. 2000, Duffy 2002, Paine 2002, Schmitz 2003). So, tightly controlled biodiversity experiments that ignore higher trophic-level effects on plant dominance may distort our understanding of the chain of causality between biodiversity and ecosystem function. Indeed, in this system, change in horizontal diversity (plant species evenness) seems to arise as a by-product of altered vertical diversity affecting a competitive dominant plant species. Thus, plant diversity does not control ecosystem function directly. Rather, control of ecosystem function is determined by cascading effects passing along a chain from top predators through herbivores to the competitive dominant plant *S. rugosa*; these effects in turn strongly influence biophysical properties. As a consequence, in this system the top-down cascade strengthens

from the community to the ecosystem level. It is, therefore, not possible to conclude that only because top-down effects on terrestrial plant community biomass are weak, that top-down effects on ecosystem function should likewise be weak, without knowledge about species-specific effects on ecosystem processes.

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