

REPORT

Perturbation and abrupt shift in trophic control of biodiversity and productivity

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Abstract

Ecology is founded on the view that ecosystem properties like biodiversity and productivity change smoothly with changing environmental conditions. However, emerging theory predicts that environmental change may cause abrupt shifts to alternate states. In many ecosystems, top predators play a pivotal role in controlling plant productivity and diversity. Yet it remains uncertain if altering this control shifts systems to alternate states. I report on a test of the hypothesis that loss of predator control of ecosystem function causes abrupt state changes in diversity and productivity. In this meadow ecosystem, predators enhance plant diversity by causing a highly productive, competitively dominant plant species to be suppressed by herbivores. Experimental predator removal caused rapid proliferation of the competitively dominant plant. Moreover, temporally staggered predator reintroductions failed to restore the ecosystem. This loss of resilience confirmed that the ecosystem crossed a critical threshold and entrained into an alternate state.

Keywords

Alternate states, ecosystem function, ecosystem recovery, plant diversity, productivity, regime shift, resilience, trophic interactions.

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INTRODUCTION

Ecologists have been perennially engaged in studying the mechanisms underlying two fundamental ecosystem properties: pattern in the diversity and abundance of species; and quantity and rate of production of species biomass (Worm & Duffy 2003). These endeavours have culminated in attempts to understand how these properties are related (Johnson *et al.* 1996; Chapin *et al.* 1997; Loreau *et al.* 2001; Kinzig *et al.* 2002; Naeem & Wright 2003; Worm & Duffy 2003). Much of the research has focused solely on plant species. A strictly plant-based focus may, however, be insufficient to understand the full spectrum of relationships for two reasons. First, consumers in higher trophic levels of ecosystems can have important effects on diversity–productivity relationships (Gutierrez *et al.* 1997; Duffy 2002, 2003; Paine 2002; Worm *et al.* 2002; Dyer & Letourneau 2003; Schmitz 2003; Thébault & Loreau 2003). Second, disrupting consumer control of ecosystem function theoretically may cause systems to shift abruptly to alternate states (Scheffer *et al.* 2001; Scheffer & Carpenter 2003). Limited experimental evidence from aquatic systems shows that such disruption can indeed cause ecosystems to

shift to alternate states of species diversity or productivity (Paine *et al.* 1985; Straile 2002; Chase 2003).

I report here on a long-term study designed expressly to test the hypothesis that manipulating top predators causes abrupt state changes in a terrestrial ecosystem. This study complements the finding (Schmitz 2003) that levels of plant diversity and productivity in this ecosystem are governed largely by interactions among the top spider predator that causes a generalist grasshopper herbivore to forego feeding on preferred grass and hide in and forage on a competitively dominant herb species. Grasshopper suppression of the dominant plant alters plant productivity and enhances plant species diversity.

Productivity and diversity responses to changing environmental conditions can be linear, nonlinear or discontinuous, the latter being indicative of alternative states (Scheffer & Carpenter 2003). I tested for discontinuities in two ways. I examined data from prior research (Schmitz & Sokol-Hessner 2002; Schmitz 2003) to identify any pattern between abundance of the competitively dominant plant and two ecosystem properties: plant species evenness and strength of top–down control by predators. While sample data may reveal a discontinuity, they cannot rule out the alternative hypothesis

that ecosystem properties merely vary in a continuous, nonlinear way (Connell & Sousa 1983; Scheffer & Carpenter 2003). A full demonstration of alternate states requires executing a perturbation and recovery experiment. Such an experiment must disrupt a factor controlling ecosystem function to effect a change in state and then demonstrate that the original state cannot be recovered once the factor is restored (May 1977; Sinclair 1989; Schmitz & Sinclair 1997). That is, the experiment must cause the system to undergo a regime shift by crossing a critical threshold (May 1977; Sinclair 1989). I report here on such an experiment.

METHODS

Natural history

The study was conducted in north-eastern Connecticut, USA in a 1.5 ha meadow completely surrounded by hardwood forest. Sampling vegetation in 50, 1 m² plots prior to the start of the experiment revealed that 18 species of herbaceous plants coexist in the field. I sorted vegetation in each plot by species, dried the samples at 60 °C and weighed them. The dominant (collectively >90.6% biomass per plot) species were the biennial or perennial herbs *Solidago rugosa*, *S. graminifolia*, *Potentilla simplex*, *Daucus carota*, *Trifolium repens*, and the perennial grass *Poa pratensis*. Other herb species include *Asclepias syriaca*, *S. altissima*, *S. canadensis*, *T. agrarium*, *Chrysanthemum leucanthemum*, *Aster novaeangliae*, *Fragaria canadensis*, *Erigeron canadensis*, *Hieracium aurantiacum*, *Rhynchospora hirta* and the grasses *Phleum pratense* and *Holcus* sp. The field contains two main herbivore-feeding guilds. Sap feeders are present during early June to mid-late July and leaf chewers begin in early mid-July and persist until late September when they and their plant resources succumb to frost. Mammalian herbivores such as woodchucks (*Marmota monax*), deer (*Odocoileus virginianus*) and meadow voles (*Microtus pennsylvanicus*) have no observable impacts in the field (Schmitz 2003). The insect herbivores face species of hunting spider predators which exist in the vegetation layer of the field during the entire summer period (Schmitz 2003). Predators such as passerine birds do not appear to be important in this system. During the course of 10 years of field research they have rarely been observed feeding in the field and no nests were ever found in the field vegetation (O.J. Schmitz, personal observation).

Despite the complexity of this system, long-term research (reviewed in Schmitz 2004) has shown that ecosystem structure and function is controlled primarily by direct and indirect interactions among a few dominant species: the top spider predator *Pisaurina mira*, the generalist grasshopper *Melanoplus femurrubrum*, the grass *P. pratensis*, and a competitively dominant herb *S. rugosa* which suppresses the abundance of other herb species. *M. femurrubrum* eats both

P. pratensis and *S. rugosa*. But, it prefers *P. pratensis* in the absence of predators and can inflict considerable damage to it. Thus, *S. rugosa* is a key species that mediates external and internal drivers of ecosystem function in my system.

Field patterns

I used the dry mass data from the initial plant survey involving 50, 1 m² sampling plots to evaluate the relationship between *S. rugosa* relative abundance and plant species diversity. Plant diversity can be quantified as species richness and evenness. Although species richness (S) is the standard measure in diversity–productivity studies (Tilman *et al.* 2001) it does not adequately account for diversity effects arising from changing competitive dominance. In my system, richness is a less robust diversity measure than is evenness (Schmitz 2003). Species evenness combines plant species dominance and abundance, two important factors in this and other meadow systems (Wilsey & Potvin 2000). Indeed, variation in plant diversity because of biotic interactions among plant species often results from evenness effects (Chapin *et al.* 2000). I calculated evenness using the Shannon index, $J' = (-\sum p_i \log p_i) / \log S$, where p_i is the abundance (% of total biomass) of species i in a plot. Low evenness values indicate one or a few species dominate; values close to 1 reflect equitable species abundances.

I used two sets of plant data from a predator manipulation experiment conducted in 1 m² enclosure cages (Schmitz & Sokol-Hessner 2002; O.J., Schmitz, unpublished data) to reveal how the strength of top–down control varied with *S. rugosa* abundance. We measured the % of the ground surface covered by herb or grass species within each cage just before the start of experimentation in early July of each year. At the end of the experimentation in September, we clipped and sorted all vegetation within each cage by species, dried the samples at 60 °C and weighed them.

I calculated interaction strength as the log ratio [$\ln(N_{p+}/N_{p-})$] of total dry plant biomass in the presence (N_{p+}) and absence (N_{p-}) of predators (Shurin *et al.* 2002). I used specifically data from treatments involving *P. mira* spiders, *M. femurrubrum* grasshoppers and plants (N_{p+}), and the matching treatment within an experimental block involving *M. femurrubrum* grasshoppers and plants (N_{p-}). Schmitz & Sokol-Hessner (2002) report on trophic interactions under comparatively low levels of *S. rugosa* ($c. \leq 35\%$ dry biomass in a cage) in which treatments were replicated six times in each of two years. This was part of a larger experiment blocked on an *S. rugosa* gradient that included three additional yearly replicates involving high (>35%) *S. rugosa* biomass (O.J. Schmitz, unpublished data). All treatments in that experiment were randomly allocated to cages within a block each year. Thus, I combined the yearly data giving $n = 18$ independent samples for the analysis reported here. I

Table 1 Comparison of statistical fits of linear and cubic polynomial (sigmoid) regressions of two ecosystem properties on the abundance of a dominant plant *Solidago rugosa*. Model fit is judged by Akaike Information Criteria (AIC) that penalizes models with higher parameter values. In each case, the best model is the one with the smallest AIC value

Variables	Regression model	AIC
Evenness (E)	$E = 0.92 - 0.76SR$	0.29
vs. <i>S. rugosa</i> (SR)	$E = 0.83 + 0.55SR - 4.28SR^2 + 3.39SR^3$	-0.11
Interaction strength (IS)	$IS = -0.85 + 1.32SR$	1.51
vs. <i>S. rugosa</i> (SR)	$IS = -1.44 + 2.32SR + 2.42SR^2 - 3.12SR^3$	0.96

plotted the average initial *S. rugosa* relative abundance for each paired N_{p+} and N_{p-} cage against the corresponding measure of interaction strength.

Using least squares methods I fit to each of the data sets a simple linear model and a cubic polynomial to generate a sigmoid curve. Prior graphical analysis using splines in SYSTAT 9 for Windows revealed that a sigmoid model was appropriate. I compared each linear and nonlinear regression by penalizing the nonlinear model for multiple parameters using the Akaike Information Criterion (AIC) applied to the residual sum of squares. All regressions gave significant fits to the data ($P < 0.05$). AIC revealed that the nonlinear model was a much better descriptor for both relationships (Table 1). Given this finding, I next ascertained the potential location of a threshold in the data in two ways. First, I identified the inflection point in the nonlinear equations by taking the second derivative of each empirically fit cubic polynomial $y = f(x, x^2, x^3)$ and solving for x . Second, I fit piecewise linear regressions to the data to identify putative lower and upper regimes in the data. Selection of these regimes was based on the maximum data range that produced a regression equation with a significant intercept but zero slope. I next fit linear regressions to data lying between the regimes and solved for x whenever the regression resulted in a significant fit (at $P \leq 0.05$).

Field experiment

I initiated the field experiment during summer 1998. The experiment comprised 60, 2 m × 2 m field plots arrayed in a randomized-block design to randomize effects of slope and soil moisture. I measured initial plant species abundance as % cover in each plot site in June 1998 using a 1.6 m × 1.6 m sampling quadrat, with a 0.2 m grid. This confirmed that initial *S. rugosa* abundance and plant species evenness was statistically similar among treatment plots (ANOVA $P > 0.25$). The entire experiment was completely set-up and running by late July 1998.

The experiment comprised a perturbation and a recovery component. The perturbation component consisted of two treatments and a control randomly assigned to each of 10 blocks, each lasting the full duration of the experiment. The control contained natural levels of plants, herbivores and predators (three-level treatment). Predators were excluded (two-level treatment containing herbivores and plants) by surrounding the treatment plots with a 45 cm wide aluminium 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. Semi-weekly inspections of plots ensured the persistent absence of arthropod predators. Damaging herbivory (one-level treatment containing only plants) was prevented by applying with a backpack sprayer organic pyrethroid insecticide every 15 days. A 0.21 l m⁻² concentration of pesticide was applied in each period. The recovery component comprised three, two-level treatments that were sequentially returned to three-level conditions at the end of the 1999, 2000 and 2001 growing seasons. Removing aluminium barriers surrounding two-level plots effected natural re-invasion.

Each year (1999–2003), individual plant species % cover was sampled non-destructively once per month between May and September using the 1.6 m × 1.6 m sampling quadrat. For purposes of analysis, I averaged the monthly % cover data for each year.

I evaluated treatment effects on plant species evenness and productivity using randomized block ANOVA. I estimated evenness using the Shannon index on July 2003 data. I estimated dry plant biomass production (g plot⁻¹ day⁻¹). This index of productivity was estimated by calculating the difference in total plant biomass in each plot between 31 May 2003 and 16 July 2003 (the main growing season) and dividing the difference by the intervening number of days. I converted non-destructive sample estimates of all species % cover into estimates of dry biomass using regression equations. To do this, mean height of a species in a plot was measured using a meter stick on five random plants of a species when sampling species cover. Plant species biomass was estimated using regressions of plant species dry mass on species % cover and species height (Schmitz 2003).

RESULTS

Field patterns

Plant species evenness and the strength of top-down control seem to vary discontinuously with the abundance of

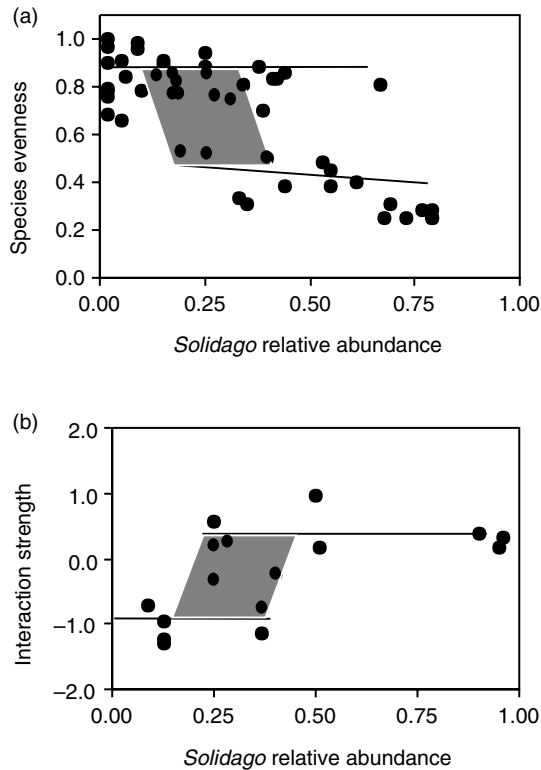


Figure 1 Relationship between a dominant plant *Solidago rugosa* and two properties of a meadow ecosystem. (a) Plant species evenness quantifies the relative representation of plant species in the ecosystem. (b) Interaction strength quantifies the strength of top predator control on plants. Upper and lower solid lines are hypothesized alternate states based on piece-wise regression. The shaded regions represent hypothesized thresholds based on piecewise and nonlinear regression.

S. rugosa (Fig. 1). Plant species evenness is highest below a threshold region of 20–45% (Fig. 1a). Within the threshold region, evenness appears to bifurcate into a high and low level rather than change gradually with *S. rugosa* abundance. Evenness remains low at high *S. rugosa* abundance. Interaction strength exhibits a similar discontinuous pattern (Fig. 1b). Below the threshold, top-down control is strong by comparative standards (Shurin *et al.* 2002). Within the narrow threshold region, the strength of top-down control drops sharply and remains weak at high *S. rugosa* abundance (Fig. 1b).

Field experiment

Solidago rugosa relative abundance began below 25% relative abundance in all experimental treatments and controls (Fig. 2). The one-level plant-only treatment confirmed that *S. rugosa* abundance would erupt in the absence of consumers (Fig. 2). *Solidago rugosa* abundance rose above

25% in the 6-year predator exclusion (two-level) treatment and remained below 25% in the 6 year control (three-level).

The staggered predator reintroductions revealed that *c.* 25% *S. rugosa* abundance was a critical threshold. After one full year of exclusion (all of 1999; Fig. 2) *S. rugosa* abundance had not yet crossed the threshold in most cases. Removing barriers to predators at the end of 1999 caused *S. rugosa* abundance to decline in the following year and approach the natural three-level control state. Two or more full years of predator exclusion allowed *S. rugosa* abundance to cross the threshold. Now, predator reintroduction failed to prevent *S. rugosa* abundance from rising to levels matching the long-term two-level treatment. ANOVA on 2003 data (selected because the time series had stabilized) revealed that the treatment effects were significant ($P = 0.05$, d.f. = 5, 49). A Tukey test revealed that treatments constraining *S. rugosa* abundance below the threshold (i.e. the three-level control and the 1-year predator exclusion/recovery) were similar to each other but differed significantly from the other treatments.

ANOVA revealed a significant treatment effect on plant species evenness ($P = 0.05$, d.f. = 5, 49) and on plant productivity ($P < 0.05$, d.f. = 5, 49). A Tukey test revealed that plant species evenness in the three-level control matched the 1-year predator exclusion/recovery treatment but both differed significantly from the other treatments (Fig. 3a). Plant species evenness was significantly lower in the plant-only treatment, in which *S. rugosa* erupted, than in all other treatments (Fig. 3a). A Tukey test revealed that productivity was highest in the plant-only treatment, intermediate in the long-term predator exclusion and the 3-year exclusion/recovery treatments, and it was lowest in the three-level control, and the 1- and 2-year predator exclusion/recovery treatment (Fig. 3b).

DISCUSSION

The idea that communities can entrain into alternate states following disturbances is an intriguing but contentious one that is deeply rooted in the history of ecology (Connell & Sousa 1983; Sinclair 1989; Chase 2003; Scheffer & Carpenter 2003). Many putative cases of alternate states are equivocal because the studies failed to meet stringent evidentiary criteria (Connell & Sousa 1983). First, one must demonstrate that the ecosystem follows different trajectories over time consequent to altered initial conditions (Connell & Sousa 1983; Chase 2003). This can be achieved by executing a perturbation experiment that disrupts at factor controlling ecosystem structure and function long-enough to allow the system to reach an alternate state (May 1977; Sinclair 1989; Schmitz & Sinclair 1997). One must then demonstrate that the original state cannot be recovered once the controlling factor is restored (May 1977; Sinclair 1989;

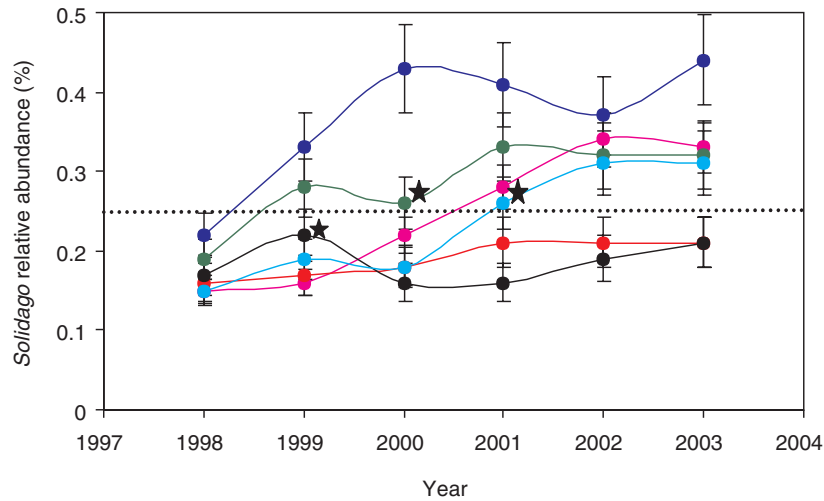


Figure 2 Time series of mean and standard errors in annual *Solidago rugosa* abundance in response to systematic perturbation and restoration of top predators. The lines connect treatment values among years. Perturbation involves three treatments: a three-trophic level control (three-level) that includes top predators, herbivores and plants (red), a predator exclusion (two-level) that contains only plants and herbivores (magenta), a predator and herbivore exclusion (one-level) that contains only plants (dark blue). Three attempts to restore the system from two-level to the three-level conditions were staggered over 3 years from 1999 to 2001 (black, green, light blue). Year in which restoration was initiated is represented by a star. The hypothesized critical threshold is indicated by the dotted line. Values are based on 10 replicates for each treatment in each time period.

Schmitz & Sinclair 1997). Finally, one must also show that alternate states persist under identical abiotic environmental conditions for at least one complete turnover of all individuals in the system (Connell & Sousa 1983).

Ten years of systematic examinations of species interactions within the study system revealed that ecosystem structure and function is controlled largely by interactions among a few dominant species (Schmitz 2004): *P. mira* spiders, *M. femurrubrum* grasshoppers, *P. pratensis* grass, and *S. rugosa* herb. *P. mira* has a strong indirect effect on plant species diversity and productivity by causing *M. femurrubrum* to switch from feeding on preferred *P. pratensis* to seeking refuge from predation in *S. rugosa* and thus feeding on this less preferred plant species. Suppression of *S. rugosa* abundance by herbivory has, over the long-term, caused other less productive herb species that are intolerant to shading by *S. rugosa* to proliferate (Schmitz 2004). This amounts to a multi-trophic level variant of the keystone predation hypothesis (Paine 1966; Leibold 1996) in which *P. mira* acts as an indirect keystone predator on the dominant herb species *S. rugosa* (Schmitz 2004). Alteration of *S. rugosa* abundance by manipulating the indirect keystone effect causes predictable changes in plant species evenness and productivity (Schmitz 2003).

This study tested whether or not long-term disruption of the indirect keystone effect causes the system to entrain to alternate states by experimentally removing spider predators and then staggering their reintroduction over protracted

periods. All experimental treatments began with statistically identical abiotic conditions and *S. rugosa* abundance (Fig. 2). Moreover, the randomized block design ensured that all treatments, on average, experienced similar abiotic conditions for the duration of the study. The experiment involved two long-term reference treatments (an unmanipulated field state, and a persistent absence of top predators) and three recovery treatments that restored top predators. The reference treatments were designed to identify potential alternate states in the system. The recovery treatments, staggered temporally, were designed to test whether the system would always return to the baseline natural state – which would lead to rejection of the multiple states hypothesis (Connell & Sousa 1983; Scheffer & Carpenter 2003) – or entrain to an alternate state.

The experiment showed that reintroducing predators after 1 year of exclusion caused *S. rugosa* abundance to return to levels matching the baseline natural state (Fig. 2). Such resilience confirmed that predators regained control over ecosystem structure and function. However, the system did not return to the natural state when predators were reintroduced following two or more years of exclusion. Instead, *S. rugosa* abundance continued to rise to levels matching the long-term reference that excluded predators. Thus, top predator control was lost and the system entrained into an alternate state. Treatments that reached this alternate state consistently had lower levels of plant species evenness than treatments in which top predator

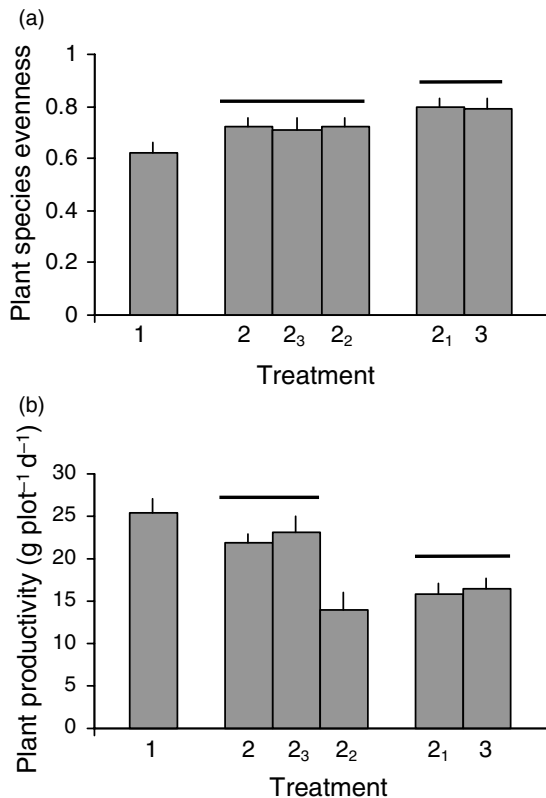


Figure 3 Mean and standard error in plant species evenness and plant productivity in relation to long-term manipulation of trophic structure. Experimental treatments are long-term predator and herbivore exclusion (1), long-term predator exclusion (2), and natural field state (3). Treatments 2₁, 2₂, and 2₃ represent predator restoration after 1, 2 and 3 years of exclusion respectively. Bars identify statistically similar treatment groups ($P \leq 0.05$). Values are based on 10 replicates for each treatment.

control persisted (Fig. 3a). Treatments with lower evenness tended to have higher plant productivities than treatments with higher species evenness (Fig. 3b), consistent with earlier observations (Schmitz 2003). The one exception is the unexpected low productivity in the 2-year exclusion/recovery treatment. This outcome stems from anomalously low plant height growth in two of 10 plots; otherwise, the productivity would match the others in the treatment group.

The different states persisted anywhere from 2 to 4 years once the time series reached a steady-state (Fig. 2). All of the arthropod species in the system have annual life-cycles, so adults of these species turned over multiple times. The plants are either biennials or perennials. These plants die back to their root stocks at the end of each growing season and produce new individual ramets the following growing season. Thus, an individual plant may not turn over within the duration of the field experiment, but aboveground ramet production (which can vary annually depending on environmental conditions) turned over annually.

The differences in species evenness and productivity among the treatment groups (Fig. 3) are comparatively small which could give the impression that these ecosystem properties vary more or less continuously with changes in environmental conditions. However, the time series from the perturbation and recovery experiment offers a mechanistic explanation for the small differences. Essentially, perturbation caused the system to shift abruptly at a very narrow, knife-edge breakpoint *c.* 25% *S. rugosa* abundance. This experimental outcome differs somewhat from the broader threshold regions identified in the field patterns (Fig. 1). The field data were gathered either by sampling along an established *S. rugosa* gradient under natural field conditions in which predator abundance was not systematically controlled or from shorter-term (1 year) experiments which may not have reached a long-term steady-state. Thus, the threshold may not be as clear-cut in these data because they may reflect transitory local conditions. Nevertheless, the fact that the experimentally determined breakpoint (Fig. 2) falls within the threshold regions identified statistically (Fig. 1) suggests that the hypothesis of alternate states might be tenable.

Perturbation of the field system not only altered *S. rugosa* abundance but the effects cascaded to influence plant diversity and productivity. This result adds to a growing body of evidence that modest predator manipulations can have ecosystem level impacts similar to those arising merely from large experimental changes in plant diversity (Gutierrez *et al.* 1997; Duffy 2003; Dyer & Letourneau 2003; Schmitz 2003). Moreover, the observation that multiple states may arise at very sharp breakpoints can help to explain variation in the strength of trophic cascades among local field sites facing the same abiotic environmental conditions (Chase 2003).

It is often unclear if ecosystem experiments such as this, conducted within a comparatively small scale (within 4 m² plots), can indeed inform real-world landscape-level management that is routinely conducted at 10⁶ m² or larger scales (Kareiva & Anderson 1988; Scheffer & Carpenter 2003). In this case it may. Insight about the mechanism controlling ecosystem structure and function (*viz.* herbivore foraging trade-off) has been used to explain dynamics of larger-scale mammalian dominated ecosystems such as aspen parkland (Ripple *et al.* 2001) and northern forests (Post *et al.* 1999). In particular, external forcing such as small temperature changes arising from global warming may disrupt predator control of northern forest ecosystem functioning and potentially cause an abrupt switch in state (Schmitz *et al.* 2003). My study shows that it can be difficult to reverse the effects of such perturbations, especially when their effects propagate through several trophic levels. If this is generally true then this study and others (Paine *et al.* 1985; Straile 2002; Chase 2003) provide a cautionary tale that ecosystem management which alters predator abundances could cause surprising and irreversible shifts in ecosystem productivity and diversity.

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