Perturbation and abrupt shift in trophic control of biodiversity and productivity

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.

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 efforts 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; Naem & 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 virginiana, Erigeron canadensis, Hieracium aurantiacum, Rhod obeckia birta 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 choppers begin in early mid-July and persist until late September when they and their plant resources succumb to frost. Mammalian herbivores such as woodducks (Marmota monax), deer (Odocoileus virginianus) and meadow voles (Microtus pennsylvaniae) 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. ≤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.
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 effect 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 $\times$ 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...
**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;
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 control was maintained.

![Figure 2](image-url)

**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.
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.
ACKNOWLEDGMENTS

I thank A. Beckerman, C. Burns, L. DeMarchis, E. Kalies, L. Sokol-Hessner, B. Suttle, and M. Young for help with the field work. J. Balch, M. Booth, C. Burns, J. Chase, O. Ovadia, E. Post, P. Raymond, D. Skelly and A. Walters provided helpful discussion and comments. The work was supported by NSF grants DEB-9508604 and DEB-01077780.

REFERENCES


Editor, M. Loreau

Manuscript received 28 January 2004
First decision made 19 February 2004
Manuscript accepted 4 March 2004

©2004 Blackwell Publishing Ltd/CNRS