Alternative Dynamic Regimes and Trophic Control of Plant Succession

Oswald J. Schmitz,[1,2]* Elizabeth L. Kalies,[1,3] and Michael G. Booth[1,4]

[1]School of Forestry and Environmental Studies, Yale University, 370 Prospect Street, New Haven, Connecticut 06511, USA;
[2]Department of Ecology and Evolutionary Biology, Yale University, New Haven, Connecticut 06511, USA; [3]School of Forestry,
Northern Arizona University, Flagstaff Arizona 86011, USA; [4]Institute of Arctic Biology, University of Alaska, Fairbanks,
Alaska 99775, USA

ABSTRACT

Ecological succession has been the subject of intense study and debate throughout the history of ecology as conceptualizations of process were proposed and refined. Modern concepts view ecological succession as largely driven by bottom-up resource competition for light and nutrients. However, growing evidence shows that top–down effects of consumers can govern succession. These contrasting perspectives require synthesis. We offer such a synthesis by revitalizing the hypothesis that succession proceeds by abrupt transitions to alternative states or dynamic regimes. We present evidence from field sampling along two successional gradients in a New England old field aimed at identifying pattern, and from experimentation in the same field aimed at identifying process. Field sampling revealed that a competitive dominant plant existed in a mosaic with two distinct patch types of relative abundances (≤ 25% and > 30%). Competitive dominant plant abundance varied systematically with plant species diversity (evenness), and resource supply (light and soil nitrogen). The six-year field experiment tested for alternative regimes by systematic removal and staggered reintroduction of top predators. Long-term predator removal caused an abrupt and irreversible shift from a top–down to a bottom–up controlled regime with a breakpoint at approximately 25% relative abundance of the competitive dominant plant. This caused significant shifts in plant species evenness and resource supply (solar radiation and N mineralization rate). Moreover, the competitive dominant abundance, species evenness and resource supply in the two dynamic regimes matched levels in the different patch types in the field. We conclude that a single ecosystem can display both top–down and bottom–up control. Abrupt shifts in trophic control lead to abrupt changes in the rate of development of ecosystems consistent with a working hypothesis that succession proceeds via abrupt regime shifts.

Key words: tropic cascade; secondary succession; food webs; indirect effects; keystone effects; alternative states.

INTRODUCTION

Terrestrial ecosystems recovering from disturbances undergo chronologically distinct changes in their species composition (viz. diversity). This recovery process, called ecological succession, has been the subject of intense study and debate as conceptualizations of the driving mechanisms were developed and refined (for example, Cowles 1899; Cooper

1913; Clements 1916; Gleason 1927; Elton 1927; Tansley 1935; Lindeman 1942; Connell and Slatyer 1977; Bazzaz 1979; Peet and Christensen 1980; Pickett and others 1987; Tilman 1988).

Modern conceptions of secondary succession largely view it as a process dominated by competitive replacement of colonizing plant species (Connell and Slatyer 1977; Bazzaz 1979; Peet and Christensen 1980; Pickett and others 1987; Tilman 1988). It is argued that fast-growing, short-lived species that best cope with high light and low nutrient conditions are typically the first to invade

(Tilman 1988; Smith 1996; Foster and Tilman 2000). Those species ameliorate these biophysical conditions through altered nutrient cycling and shading thereby facilitating invasion of slower-growing, longer-lived plant species that better compete under newly created light and nutrient regimes (Tilman 1988; Smith 1996; Foster and Tilman 2000). The new competitors eventually supplant opportunistic species but then transform ratios of light and nutrient availability in ways that lead to their own replacement by other competitors (Tilman 1988; Smith 1996).

This concept accords with a long-held view that terrestrial ecosystem productivity and trophic structure is governed largely from the bottom-up by limiting supplies of nutrients and light to plants (Lindeman 1942; Hutchinson 1959; Odum 1969; White 1978; Polis and Strong 1996; Loreau and others 2001). The view is strengthened by two additional observations. Namely, the diversity and identity of species in higher trophic levels may often be determined by plant diversity within specific sites or along successional gradients (Southwood and others 1979; Lawton 1983; Corbett 1995; Tscharntke and Greiler 1995; Siemann and others 1998, 1999); and, herbivore species can have little or no measurable effect on total plant biomass or net primary production (Crawley 1983; Strong 1992; Hairston and Hairston 1993; Polis and Strong 1996).

Accumulating evidence, however, shows that species in higher trophic levels exert strong top–down control over plant species productivity and diversity (Gutierrez and others 1997; Fraser and Grime 1998; Ritchie and others 1998; Duffy 2002; Paine 2002, Schmitz 2003; Seabloom and Richards 2003; Carson and others 2004). Moreover, such top–down effects can govern the successional trajectories of terrestrial ecosystems (Harper 1969; Sutherland 1974; Brown and others 1988; Brown and Gange 1992; Pastor and Naiman 1992; Davidson 1993; Bach 1994; Carson and Root 1999; Wootton 2002; Seabloom and Richards 2003; Kuijper and others 2004). In particular, selective foraging by herbivores in response to plant nutrient quality or predators can alter the identity and rate of spread of the colonizing species: effects that cascade further downward to influence nutrient cycling (Pastor and Naiman 1992; Davidson 1993; Carson and Root 2000, Uriarte 2000).

Such contrasting perspectives about the mechanism driving secondary succession begs explanation. To this end, we offer here a conceptualization that attempts to reconcile when bottom–up and top–down processes might govern secondary successional dynamics. Our conceptualization revitalizes the hypothesis that succession proceeds by changes in the nature of trophic control of ecosystem function that leads to abrupt transitions to alternative states (Sutherland 1974; Holling 1986; Gunderson 2000). The view is supported by recent experimental evidence for alternative states in a terrestrial old-field ecosystem (Schmitz 2004b). In our view, alternative states represent different dynamic regimes (sensu Scheffer and others 2001) in which the dominant factor controlling succession varies. Thus, during one phase of succession, development is slowed or arrested by top–down trophic interactions between plants and their associated fauna. Eventually, environmental conditions cause the system to reach a breakpoint in which top–down control is rapidly lost and the system abruptly transitions to an alternative, bottom–up controlled regime.

We present here two lines of evidence—one from field sampling aimed at identifying pattern; and the other from a field experiment aimed at identifying process—that together bolster the hypothesis (Holling 1986) that succession proceeds via abrupt transitions to alternative regimes in response to alteration of trophic control of ecosystem function. We first present our evidence in two stand-alone sections dealing separately with the field survey and the field experiment. The sections each present methods, results and a brief summary of the results. We use this approach deliberately to provide appropriate background and rationale for the separate phases of this study and their associated methodologies. These sections are followed by a third that synthesizes the field sampling and experimental data to infer the process underlying the field pattern. We close the paper with a general discussion of the implications of our findings for understanding terrestrial plant succession in the context of alternative dynamic regimes theory.

FIELD SURVEY: IDENTIFICATION OF PATTERN

Background

The temporal progression of species change in old fields is often proffered as a textbook example of succession (for example, Morin 1999; Smith 1996). It involves clonal spread of grasses and herbs, especially *Solidago* (goldenrod) species (Bazzaz 1996; Smith 1996; Carson and Root 1999). *Solidago* species can dominate by preempting less competitive herb species through shading (Cain and others

1991; Bazzaz 1996; Uriarte and Schmitz 1998; Schmitz 2003) and altering soil N availability and cycling (Uriarte 2000).

Old field successional dynamics are ideally studied by following the chronological progression of species change at a specific location (Smith 1996). But, this requires long-term study because succession requires decades to play itself out completely. This limitation can be overcome by swapping space for time (Pickett 1989) and comparing patterns among different locations that represent different stages of succession (for example, Uriarte and Schmitz 1998; Foster and Tilman 2000; Uriarte 2000). Such comparisons are usually made at the whole field scale based on the implicit reasoning that the post-disturbance age of a field is a good approximation of its successional stage; and that entire fields are uniformly affected by a disturbance (for example, agriculture).

Examining succession at the whole field scale is appropriate whenever the species composition of a field is comparatively uniform. However, there may be considerable spatial heterogeneity in relative abundance of a competitive dominant within fields because plant species may be organized into patchy mosaics (Peterson 1984; Petraitis and Latham 1999; Seabloom and Richards 2003). In such cases, field age may not be an appropriate surrogate for successional state. Rather, several successional states may co-occur in a field; so whole-field comparisons may be too crude to reveal important mechanisms governing the successional processes. Moreover, the existence of patchy mosaics with sharp boundaries is a necessary precondition for any argument that alternative dynamic regimes explain dynamics (Sutherland 1974; Seabloom and Richards 2003).

We illustrate this case in point using insights from long-term research in a New England old field ecosystem (reviewed in Schmitz 2004a). The study system includes 18 species of herbaceous plants and numerous arthropod predators and herbivores that are linked in a highly interconnected food web (Schmitz 2004a). The five most abundant plant species (species comprising > 95% of the total plant biomass) are the perennial grass *Poa pratensis*, and the perennial herbs *Solidago rugosa, Solidago graminifolia, Potentilla simplex*, and *Trifolium repens* (Schmitz 2004a).

Methods

During summer 2003, we sampled two locations (Upper and Lower) of an old field ecosystem that was the focus of past research on trophic interactions (Schmitz 2004a). We arrayed an 8 m × 20 m sampling grid in each location. Grid points were marked at 2 m intervals using wooden stakes. Both sampling grids were located along an *S. rugosa* abundance gradient.

Plant Sampling. We sampled the % cover of all plant species within a 0.5 m^2 sampling quadrat centered at each 2 m grid point four times during the summer (mid May, late June, late July and late August). These periods represented different growing conditions in the field system (Schmitz 2004a).

Resource Sampling. According to the Resource-Ratio hypothesis of plant succession (Tilman 1988), plant dominance is controlled from the bottom–up by resource supply. Different plant species should dominate at different supply ratios of limiting nutrients based on a trade-off in their physiological capacities to exploit different resources. Old field systems tend to be limited most by the amount of light penetrating the vegetation canopy to the ground storey, and by soil nitrogen (Tilman 1988; Cain and others 1991; Uriarte 2000). We therefore sampled photosynthetically active solar radiation (PAR) striking the ground and soil nitrogen content along each gradient concurrently with plant species sampling. We measured PAR (μ mol s^{-1} m^{-2}) by placing a LI-190SA quantum sensor coupled to a LI-250 Light Meter (Li-Cor Inc., Lincoln, Nebrasea, USA) on the ground surface in the center of each 0.5 m^2 sampling quadrat. We allowed the readings to stabilize for 10 s before recording a measurement. For logistical reasons, we sampled nitrogen at fewer locations along the grid. We treated each 2 m × 8 m section of the 20 m sampling area as a block and subdivided each section into four, 2 m × 2 m plots. We randomly select two of four plots in each block and extracted soil cores (10 cm long × 5.08 cm diameter metal corer) below the litter layer to estimate soil N (ammonium and nitrate) content (mg g^{-1} soil). We extracted N in 2 M KCl using standard procedures (Hart and others 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 facility. We also measured, at each 2 m grid point, soil surface temperature using a Digi-Sense 8523 thermistor thermometer (Cole-Parmer Instrument Company, Chicago, Illinois, USA), coupled to a surface probe accurate to 0.1°C; and soil moisture (% water content) using a Dynamax ML2x Theta Probe (Dynamax, Inc., Houston, Texas, USA).
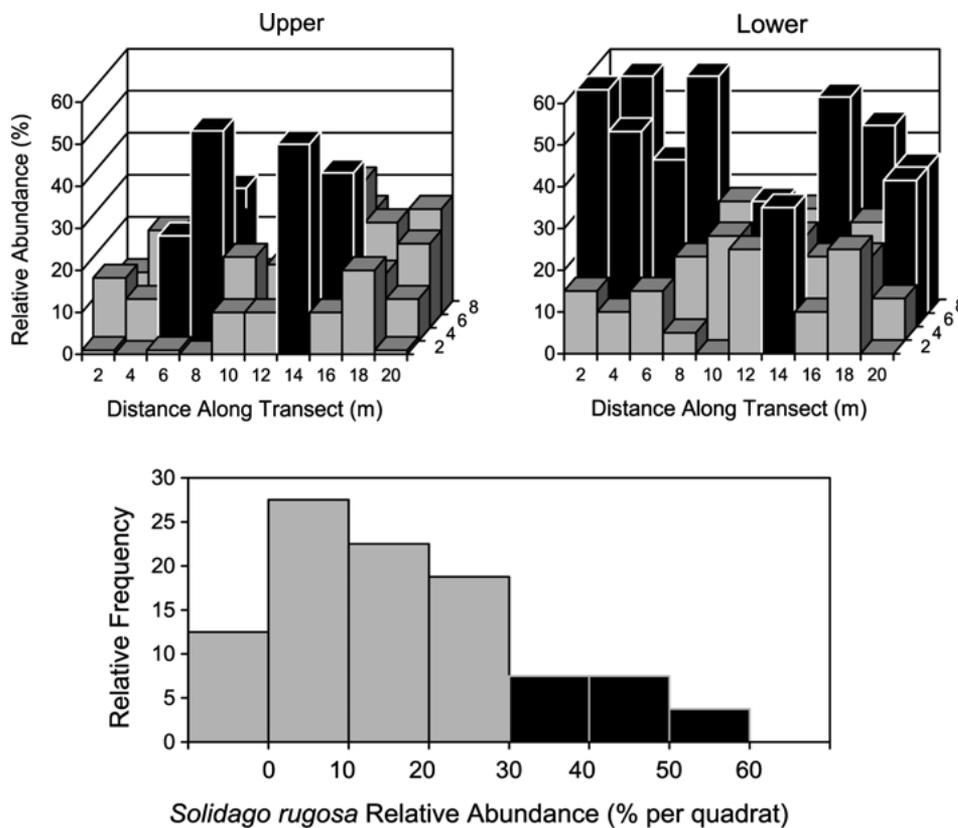
Figure 1. Relative abundance (% cover) of a competitively dominant herb species *Solidago rugosa* in two 8 m × 20 m sampling locations (Upper and Lower) in the old-field study system. The *top two figures* show that *S. rugosa* is organized into patchy mosaics in space. It also tends to aggregate into patches containing ≤ 25% (*gray*) or > 30% (*black*) *S. rugosa*. The *bottom figure* presents the frequency distribution of *S. rugosa* abundance among sampling quadrats (*n* = 80) demonstrating a negative binomial-like pattern.

Results

We report here on the July 2003 sampling period because this represents the height of the growing season (Schmitz 2003), but conclusions are qualitatively similar for earlier and later sampling.

Plant Sampling. Sampling in both field locations revealed that relative abundance of the competitive dominant herb *S. rugosa* consistently varied between zero and 60% (Figure 1). Moreover, *S. rugosa* appeared to be spatially distributed in a highly patchy mosaic at both sampling locations (Figure 1). The frequency distribution of *S. rugosa* abundance among plots, generated by aggregating sampling data from both grids, appears to approximate a negative binomial distribution (Krebs 1989). We tested for the significance of negative binomial clumping (as opposed to lognormal or random distribution) by calculating an index of dispersion based on this distribution (I = variance/ mean), and associated test statistic χ^2 = I(n-1), where n = 80 samples (Krebs 1989). That value (I = 15.66) revealed a highly significant deviation from random (Poisson) in favor of clumping or distinct patchiness, based on a normal approximation to the chi-square for large sample sizes (z = 32.2 > $z_{\alpha=0.05}$ = 1.96: Krebs 1989). Nevertheless, conclusions about such a clumped pattern

could simply be an artifact of very fine-scale sampling relative to the size of a vegetation patch. This possibility is unlikely in our case however. Analysis of data collected in a survey of 24, 5 m × 5, m connected plots in the same field (O.J. Schmitz, unpublished data) revealed a similar deviation from random (Poisson) in favor of clumping (χ^2 = 146.74 > $\chi^2_{\alpha=0.05}$ = 40).

We calculated plant species evenness for each sampling quadrat using the Shannon index, J' = ($-\Sigma p_i \log p_i$)/ log S, where p_i is the abundance (% cover) of species *i* in a plot. Plant evenness is the most appropriate measure of diversity in our case because it combines two key mechanistic factors—dominance and plant species abundance—that determine plant diversity patterns in old-field systems (Wilsey and Potvin 2000; Schmitz 2003; Wilsey and others 2005). Linear and polynomial (second order) regression using SYSTAT 9 for Windows revealed that the relationship between *S. rugosa* relative abundance and plant species evenness (Figure 2) was decidedly hump-shaped (second order *F* = 1,677, *df* = 3, 76, *P* < 0.001: vs. linear *P* > 0.50).

Resource Sampling. We detected an inverse relationship between PAR and soil N content in both sampling grids (Figure 3A), consistent with the idea that supply ratios of limiting resources
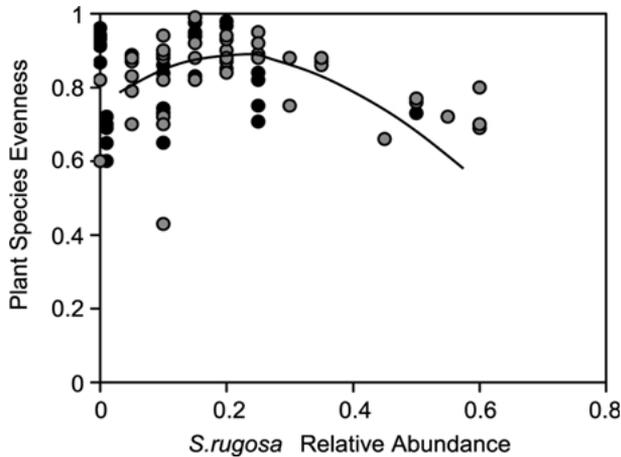
Figure 2. Relationship between the abundance (% cover) of a competitively dominant herb species *S. rugosa* and plant species evenness measured in two 8 m × 20 m sampling locations. *Black circles* represent the Upper field sampling site and *gray circles* represent Lower field sampling site. The curve through the data is derived from fitting a second order polynomial regression to the data.

Figure 3. **A** Relationship between soil nitrogen content (mg g soil^{-1}) and photosyntheitically active radiation at ground surface (PAR, μ mol s^{-1} m^{-2}) measured along two sampling transects in the field. (Upper *black circles*; Lower *gray circles*) The curve through the data is derived from fitting an exponential regression to the data. **B** Relationship between PAR and abundance (% cover) of a competitively dominant herb species *S. rugosa*. **C** Relationship between soil N content and *S. rugosa* abundance (% cover). These figures demonstrate that *S. rugosa* dominates under low light and low soil N.

should vary inversely along a successional gradient (compare. Figure 8.13 in Tilman 1988). We fit a linear regression and the exponential model $Y = a \ e^{b/X}$ to these data using linear and nonlinear regression in SYSTAT 9 for Windows. The linear regression was not significant ($P > 0.25$) but the exponential model was ($F = 20.92$, $df = 2$, 36, $P < 0.01$, $R^2 = 0.54$). Plots of PAR and N mineralization in relation to the *S. rugosa* abundance (Figure 3B, C) revealed that *S. rugosa* dominated when both biophysical variables were at their lowest levels. We found no significant relationship between *S. rugosa* abundance and either soil surface temperature or soil moisture (both regression $P > 0.65$).

Summary

Field sampling revealed that *S. rugosa* is indeed organized into a patchy mosaic. Under an hypothesis of alternative regimes, one might, however, expect that the frequency distribution of *S. rugosa* abundance should be bimodal rather than unimodal. However, succession is a temporally sequenced process and the frequency of the two regimes depends on the time a field is sampled. A bimodal distribution may eventually occur during later succession and indeed the entire system may eventually be overwhelmed by *S. rugosa* and completely flip to the single bottom–up controlled regime in late succession, giving again a unimodal dis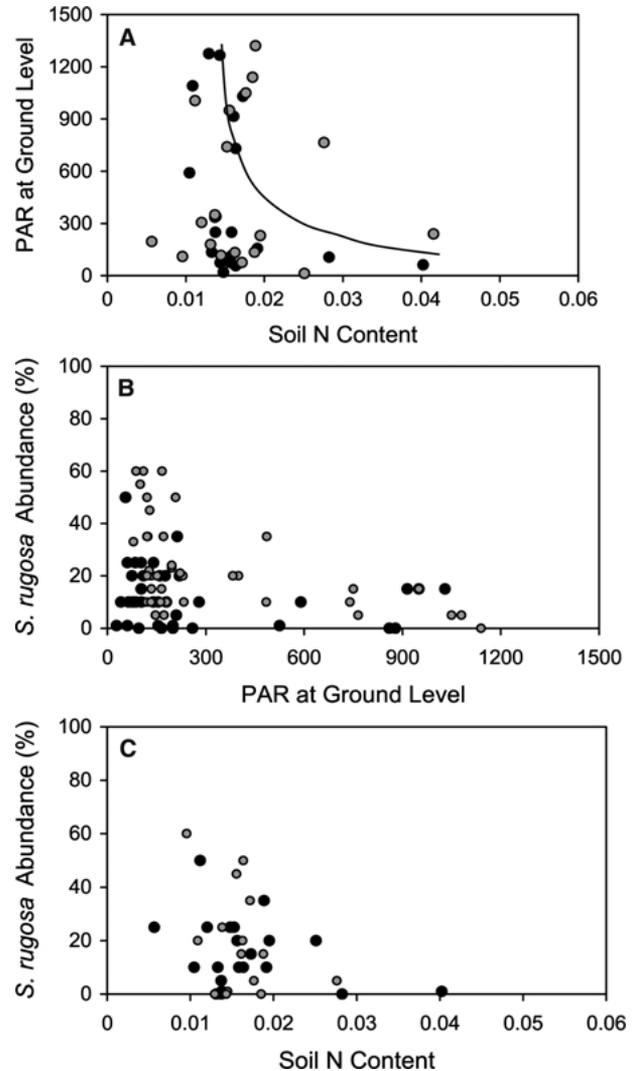tribution. We suggest that such a temporal transition is akin to shifts from murky to clear water regimes in freshwater systems (Scheffer and others 2001) but that it requires a considerably longer period of time to manifest itself in the old-field system.

The humped-shaped species evenness curve is consistent with the way species diversity is expected to change as competitive dominant species gradually replace one another along a successional

gradient (Tilman 1988). However, the dominance of a single competitor species (*S. rugosa*) at both extremes of a resource ratio gradient is inconsistent with the predictions of the resource ratio hypothesis of plant succession (Tilman 1988). Consumer-resource competition theory (Tilman 1988) predicts that a species can only dominate at both extremes of the resource ratio gradient if it is a superior competitor for both resources (that is, draws down both resources to lower levels than other plant species). If this were the case here, then the zero net growth isocline (ZNGI) should fall below that of other plant species; and the competitive dominant plant should preempt other plant species from the system. The fact that multiple plant species coexist across the gradient implies that the system may not be altogether bottom–up controlled. One candidate explanation for the pattern in our field system is that *S. rugosa* dominance is modified by keystone predation (Holt and others 1994; Leibold 1996), which has attendant affects on light and soil nutrient supply via altered N mineralization rates. We now describe a field experiment that addresses this possibility.

## FIELD EXPERIMENT: IDENTIFICATION OF PROCESS

Background

Long term research (Schmitz 2003, 2004a) revealed that an important controlling factor of plant diversity and productivity in the old field ecosystem is an indirect keystone predation effect among a dominant hunting spider *Pisaurina mira*, its grasshopper herbivore *Melanoplus femurrubrum* prey, and the grass *P. pratensis*, and the competitive dominant herb *S. rugosa*. *M. 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. Mortality risk due to predator presence causes 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. Suppression of the competitive dominant *S. rugosa* allows less competitive herb species to proliferate, leading to increased plant species diversity but lowered productivity (Schmitz 2003).

Furthermore, long-term disruption of the indirect keystone effect (top–down control) can cause the system to entrain to an alternative bottom–up controlled regime once *S. rugosa* relative abundance exceeds 25–30%. Such evidence comes from a long-term field experiment designed expressly to test for alternative regimes (Schmitz 2004b). Demonstrating the existence of alternative regimes requires three pieces of evidence (May 1977; Connell and Sousa 1983; Sinclair 1989; Scheffer and Carpenter 2003). There must be experimental demonstration that patches with high and low *S. rugosa* abundance present alternative regimes of plant diversity and biophysical properties. There must be experimental demonstration that a discontinuity separates the alternative regimes. There must be experimental demonstration that perturbation of an important controlling factor of ecosystem function causes an abrupt and irreversible shift across the discontinuity (that is, no recovery to initial conditions). We now briefly review a previous field experiment—conducted in the same field as the field survey—that fulfilled these criteria. We then describe methodology and results of sampling aimed at measuring the same biotic and biophysical variables as in the field survey.

The field experiment, which ran between 1998 and 2003, was deployed in 2 m × 2 m field plots arrayed in ten blocks of six plots each with each of five treatments or control assigned randomly to each block (Schmitz 2004b). Initial *S. rugosa* abundance was below 25% in all plots and did not differ systematically among treatments and the control (Figure 4). Trophic control of ecosystem function was systematically altered by manipulating the trophic structure in different perturbation and recovery phases of the experiment. The perturbation comprised two treatments and a control randomly assigned to plots once in each of ten blocks. The control contained natural levels of plants, herbivores, and predators (3-level treatment). Predators were excluded (2-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. Herbivory was prevented (1-level treatment containing only plants) by applying an organic pyrethroid insecticide every 15 days with a backpack sprayer. The recovery component comprised three 2-level treatments that were sequentially returned to 3-level conditions in 1999, 2000 and 2001. Removing aluminum barriers surrounding 2-level plots effected natural re-invasion. Details of sampling protocol are presented in Schmitz (2004b).

Long-term time series (Figure 4A) and mean treatment values for 2003 (Figure 5A) confirmed that *S. rugosa* abundance in the 1-level plant-only treatment would increase in the absence of any consumer top–down control. *S. rugosa* abundance
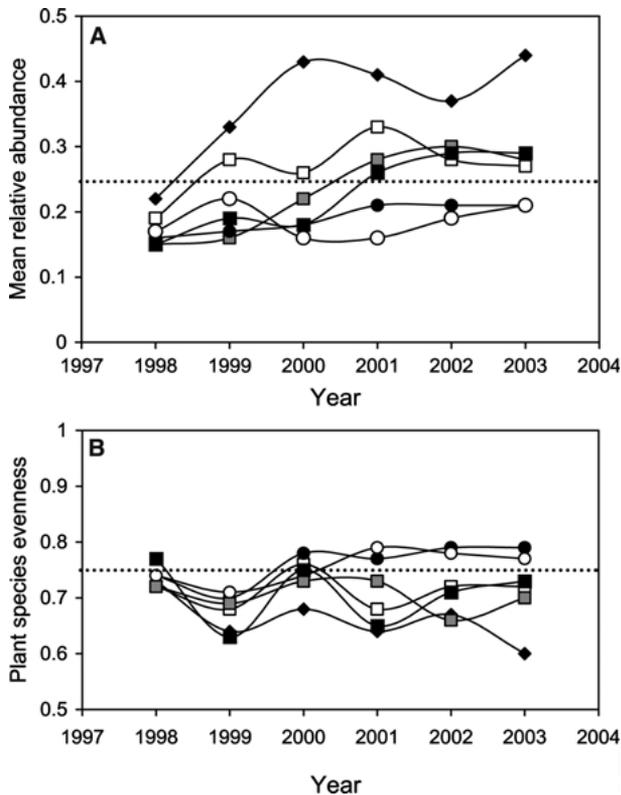
Figure 4. Time series of mean annual *Solidago rugosa* abundance (**A**) and plant species evenness (**B**) in response to systematic perturbation and restoration of top-predators. The lines connect treatment values among years. Perturbation involves three treatments: a 3-trophic level control (3-level) that includes top predators, herbivores and plants ●, a predator exclusion (2-level) that contains only plants and herbivores ■, a predator and herbivore exclusion (1-level) that contains only plants ◆. Three attempts to restore the system from 2-level to the 3-level conditions were staggered over three years from 1999 to 2001 (reintroduction: after 1999 ○, after 2000 □, after 2001 ▨). The hypothesized critical threshold is indicated by the *dotted line*. Values are based on ten replicates for each treatment in each time period. Figure 4A is modified from Schmitz (2004b) and is reproduced with permission from Blackwell Scientific.

rose above 25% in the 6-year predator exclusion (2-level) treatment and remained below 25% in the 6-year control (3-level) (Figures 4A, 5A). The staggered predator reintroductions revealed the existence of a sharp discontinuity or break point (approximately 25% *S. rugosa*, Figure 4A). Removing barriers to predators at the end of 1999 in one recovery treatment in which *S. rugosa* abundance was below 25% caused *S. rugosa* abundance to decline (Figure 4A) and approach the natural 3-level top–down controlled regime (Figure 4A). Two or more full years of predator

exclusion allowed *S. rugosa* abundance to exceed 25% (Figure 4A). Now, predator reintroduction failed to prevent *S. rugosa* abundance from rising further to levels matching the long-term 2-level treatment—an irreversible shift to a new bottom-up controlled regime (Figure 4A). ANOVA on 2003 data (selected because the time series had stabilized for 2 years) revealed that the treatment effects on *S. rugosa* biomass (Figure 5A) were significant ($P = 0.05$, $df = 5, 49$). A Tukey test revealed that treatments constraining *S. rugosa* abundance below the discontinuity (that is, the 3-level control and the one year predator exclusion and recovery) were similar to each other but differed significantly from the other treatments.

The perturbations also affected plant species evenness (Figure 4B), but it typically lagged treatment effects on *S. rugosa* abundance by 1 year (Figure 4B). Nevertheless, treatments resulted in an irreversible shift in plant species evenness (Figure 4B). ANOVA ($P = 0.05$, $df = 5, 49$) followed by a Tukey test revealed that 2003 plant species evenness in the 3-level control matched the one year predator exclusion/recovery treatment but both differed significantly from the other treatments (Figure 5B). Plant species evenness was significantly lower in the plant-only treatment, in which *S. rugosa* reached its highest abundance, than in all other treatments (Figure 5B). Plant evenness in the top–down and bottom-up controlled regimes was separated also by a sharp break (midpoint approximately 0.79, Figure 5B).

Methods

Concurrent with the field survey during summer 2003, we measured PAR, N mineralization rate, soil surface temperature and soil moisture in the center of each experimental 2 m × 2 m plot once per month between May and September 2003. We measured soil temperature and moisture, and PAR using the protocols described above for the field survey. We used a modified buried-bag method (Hart and others 1994) to estimate soil N mineralization rate (mg g^{-1} m^{-1}). Within the center of each 2 m × 2 m plot one soil core (10 cm long × 5.08 cm 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. We extracted soil cores in 2
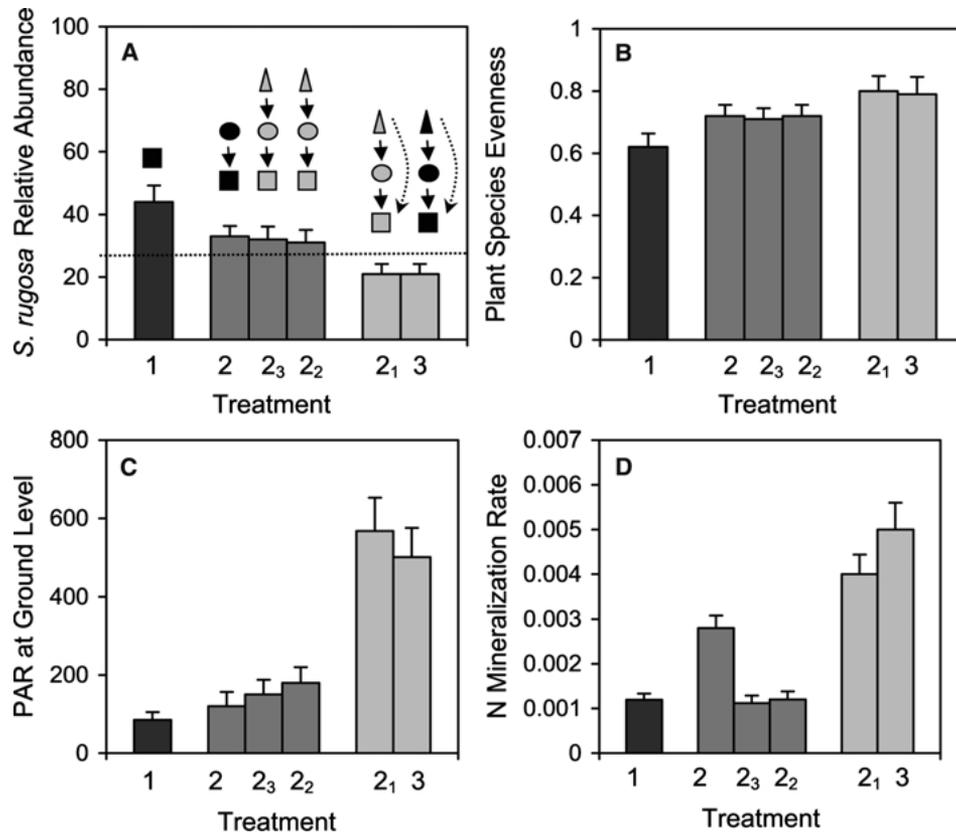
Figure 5. Mean and standard error in: (**A**) steady state abundance of *Solidago rugosa* (% cover); (**B**) plant species evenness (from Schmitz 2004b); (**C**) photosyntheitically active radiation at ground surface (PAR, μ mol s^{-1} m^{-2}); and (**D**) nitrogen mineralization rate (mg g^{-1} month^{-1}) in response to experimental removal and restoration of top predators. Treatments are long-term predator and herbivore exclusion (1), long-term predator exclusion (2), and natural (control) field state (3). Treatments 2_1, 2_2, and 2_3 represent predator restoration after 1, 2 and 3 years of exclusion, respectively. $N = 10$ replicates for each treatment. The food web diagrams (Figure 4A) depict trophic linkages (*solid arrows*) among predators (*triangle*), herbivores (*circles*), and plants (*squares*) in each treatment. In the natural field state (3), top predators exert an indirect negative effect on *S. rugosa* (*dotted arrow*). This effect was re-established upon reintroducing predators after 1 year of exclusion (2_1) but not after 2 and 3 years (2_2, and 2_3). The *dotted lines* (A and B) represent breakpoints between alternative regimes.

M KCl using standard procedures (Hart and others 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 facility. We calculated N mineralization rate using standard methodology (Hart and others 1994), which converts wet mass concentrations of nitrate and ammonium in samples to dry mass concentrations. Net mineralization rate is expressed as the difference in the sum of dry mass nitrate and ammonium concentration between consecutive monthly (28 days) sampling periods.

Results

We report here on the July 2003 sampling period because this represents the height of the growing season (Schmitz 2003), but conclusions are qualitatively similar for earlier and later sampling. ANOVA's ($P = 0.05$, $df = 5$, 49) followed by Tukey tests revealed that in general treatment effects on N mineralization rate and PAR were parallel to treatment effects on *S. rugosa* abundance and on plant species evenness (Figure 5C, 5D). Namely, the 3-level control and 1-year perturbation and recovery treatment were similar to each other but differed from the other treatments (Figure 5). There was one outlier: N-mineralization for the 6-year 2-level treatment was significantly intermediate to the other treatments (Figure 5D). (This bias was determined by two of ten plots with consistently (all sampling periods) high estimates of N mineralization rate.) There was no systematic treatment effect on either soil surface temperature or soil moisture (ANOVA, both $P > 0.15$).

Summary

The field experiment revealed that relationships among *S. rugosa* relative abundance, plant species evenness, PAR and N mineralization rate are influenced by an indirect top–down keystone effect between a top predator and the competitive dominant plant *S. rugosa*. Long-term suppression of top–down control led to a regime shift in trophic control of ecosystem function and the level of associated biophysical variables (plant species evenness, PAR, N-mineralization rate).

SYNTHESIS OF FIELD RESEARCH: RELATING PROCESS TO PATTERN

In the field, *S. rugosa* is organized into a patchy mosaic (Figure 1) in which it is comparatively rare (approximately 5%–20%) or comparatively abundant (approximately 35%–60%). There also appears to be a sharp change (transition) between theses patches at approximately 25–30% (Figure 1). The existence of patchy mosaics with sharp boundaries has been regarded as evidence that local history might determine community state (Sutherland 1974; Seabloom and Ricahrds 2003) in which case alternative dynamic regimes could be the appropriate explanation for such pattern (Sutherland 1974; Seabloom and Richards 2003). To examine this more closely, we now use the results of the field experiment demonstrating alternative regimes to infer process in the pattern observed in the field survey.

In Figure 3, we treated PAR and soil N content as independent variables and *S. rugosa* abundance as a dependent variable—an appropriate relationship if the line of dependency is from resource-supply up to the organism (that is, bottom–up control of pattern and function). However, the field experiment revealed that *S. rugosa* was important in mediating top–down direct and indirect effects among predators, herbivores and resource supply (PAR and N mineralization rate). That is, resource supply is dependent on *S. rugosa* abundance. Species evenness then becomes dependent upon resource supply. We thus reinterpret the field pattern by switching dependent and independent variables (Figure 6). We also superimpose on these graphs the breakpoints observed in the field experiment and the mean and standard errors of the treatment response variables in the field experiment. This comparison demonstrates strong congruence between the pattern observed in the field and in the experiment.

Below 25% *S. rugosa* abundance (that is, the top–down controlled regime) both PAR and N mineralization rates vary widely with *S. rugosa* abundance and this is reflected in treatment values for the field experiment (Figure 6A, B). Beyond 25% *S. rugosa*, (the bottom-up controlled regime) PAR and N mineralization vary tightly with *S. rugosa* abundance. This same pattern of variation in response variable with the nature of trophic control is observed in the relationship between resource supply and plant species evenness (Figure 6C, D).

In light of the correspondence between the field survey and the experiment, we expect to see wide variation in plant species evenness and *S. rugosa* abundance when top–down control should prevail (that is, less then or equal to 25% *S. rugosa*) and a tight relationship between plant species evenness and *S. rugosa* abundance when bottom-up control is expected to prevail (that is, greater than 25%). Reanalysis of the data in Figure 2 bears this out. Linear regression using Systat 9.0 for Windows revealed a significant positive relationship over the range 0–25% *S. rugosa* abundance ($F = 10.53$, df 1, 57, $P < 0.01$). Moreover, little of the variation in the data is explained by this regression ($R^2 = 0.39$). The data beyond 25% *S. rugosa* reveal a different pattern. There is a significant negative relationship between evenness and *S. rugosa* abundance ($F = 13.78$, $df = 1$, 21, $P < 0.01$) and the regression explains almost 2 times more variation in the data ($R^2 = 0.63$).

Our synthesis thus suggests that hump-shaped diversity curves (Figure 2) and inverse relationships between limiting resources (for example, Figure 3; Figure 8.13 in Tilman 1988) derived from field surveys offer equivocal evidence for the resource ratio hypothesis (and alternative regime hypothesis for that matter) primarily because they cannot resolve sharp breakpoints if they exist. Rather, it is critical to deploy companion field experiments to elucidate whether or not alternative regimes exist and if so where the breakpoints in the system lie.

DISCUSSION

Evidence from the field experiment and field sampling revealed that a competitive dominant plant species, *S. rugosa*, transformed important biotic (diversity) and biophysical (N-mineralization rate, photosynthetically active radiation) properties of an old-field ecosystem as it increased in abundance. Such ecosystem transformation could be consistent with long-held views of plant succession progressing entirely via competitive (bottom–up controlled) processes. However, the identification of alternative regimes, thresholds, and abrupt shifts
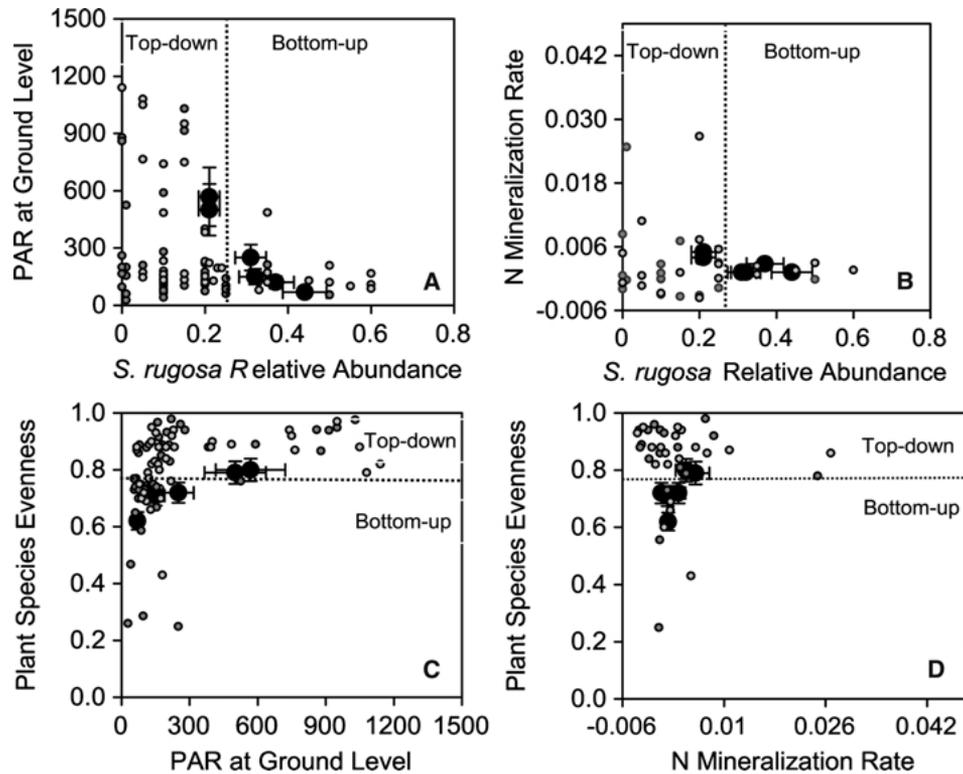
Figure 6. Relationships between biophysical properties (**A**: Photosyntheitically active radiation at ground surface PAR, μ mol s^{-1} m^{-2}; **B**: N-mineralization rate mg g^{-1} month^{-1}) and relative abundance (% cover) of a competitive dominant plant species *S. rugosa*, and between biophysical properties and plants species evenness (**C**, **D**). The figures superimpose values sampled at two locations (Upper *black circles*; Lower *gray circles*) with treatment values measured in the field experiments (*large black circles* with standard errors). The *dotted lines* represent breakpoints between the top–down and bottom–up controlled regimes revealed by the field experiment.

in abundance of the competitive dominant suggests that successional development and corresponding ecosystem change is not solely competition-driven. Instead, we offer that succession can proceed via abrupt transitions to alternative regimes in response to alteration of trophic control of ecosystem function, consistent with the idea proposed by Holling (1986).

Early proposals that succession proceeds via transitions to alternative regimes (Matthews 1979; Sutherland 1974) were criticized for failing to meet specific criteria (Connell and Sousa 1983). Namely: (1) One must demonstrate threshold relationships between ecosystem properties (for example, productivity, species diversity) and associated biotic or abiotic factors controlling those properties; (2) One must show that manipulating the controlling factor leads to irreversible regime changes by causing the system to cross a breakpoint (sensu May 1977); (3) One must show that different regimes propagate from similar initial conditions and that they persist under similar abiotic conditions. (4) Finally, one must also show that alternative regimes persist

under identical abiotic environmental conditions for at least one complete turnover of all individuals in the system.

Our evidence is largely consistent with these criteria. Experimental predator removal disrupted an important controlling factor of ecosystem function—an indirect keystone predation effect that arrested the progression of the competitive dominant plant *S. rugosa*. This allowed *S. rugosa* to proliferate (Figure 4). Temporally-staggered predator reintroductions eventually failed to re-establish the keystone effect because *S. rugosa* abundance crossed a critical threshold and entrained into an alternative regime (Figure 4). The different regimes persisted anywhere from two to four years once the time series reached a steady state. The more striking feature is that all reintroduction treatments entrained to the bottom–up controlled regime once *S. rugosa* exceeded 25%. 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 stems the following growing season. Moreover, the rhizomes from which *Solidago* stems are produced persist up to 5–6 years (Cain and others 1991). Thus, much of the turnover of vegetative production by an individual *S. rugosa* plant potentially occurred within the duration of the field experiment.

Holling (1986) proposed three additional evidentiary criteria were needed to conclude that succession may proceed via transitions to alternative regimes. First, the ecological system has to build up into a complex network of trophic interactions. Second, the boundary between alternative dynamic regimes must be narrow so disturbances can easily push the system abruptly from one regime to another. Third, the shift between regimes can be internally or externally driven. Long-term research (Schmitz 2004a) has revealed that the old-field system is comprised of many consumer species connected by a large network of direct and indirect interactions. The field experiment revealed a narrow transition zone separating the top–down and bottom–up controlled regimes (Figure 4A) and plant species evenness (Figure 4B). *S. rugosa* abundance in the ecosystem was experimentally pushed across the threshold after a short 2 years following initial perturbation (Figure 4) and led to different values of ecosystem variables like solar radiation striking the soil surface and nitrogen mineralization rate (Figure 5C, 5D). Finally, experimental disruption of the internal factor (the indirect keystone effect) resulted in the abrupt regime shift.

The Exploitation Ecosystems Hypothesis, which predicts that top–down control weakens as plant nutrient supply or standing plant biomass—surrogates for productivity—increase (Oksanen 1990) proposes a potential alternative explanation for our results. Under this hypothesis, the strength of top–down control should vary in a continuous, hump-shaped manner along a gradient of nutrient supply or plant biomass, viz., top–down control should be strongest in the middle of the gradient and weakest at either end of the gradient (Schmitz 1992). Moreover, the shift from top–down to bottom-up control should be gradual (Schmitz 1992). In our system, however, the strength of top–down control along a *Solidago rugosa* biomass gradient is z-shaped rather than hump-shaped (see Figure. 1 in Schmitz 2004b), suggesting consistently strong top–down control over part of the gradient and an abrupt shift to weak top–down control over the remainder of the gradient.

The switch from the top–down to the bottom-up controlled regime in our experiment was induced by complete removal of the top predator trophic level. Such complete loss of a trophic level is unlikely to occur in natural settings however. Nevertheless, top predator control of ecosystem function can be systematically altered by exogenous climatic factors that alter the strength of the indirect keystone effect. In the study system, grasshopper survival changed by 88% between years with a small (3–4°C) difference in temperature (Ovadia and Schmitz 2003). Such a small, but season-long temperature increase can decouple predator–herbivore interactions leading to an abrupt shift from top–down to bottom–up control (Chase 1996). An increase in rainfall also can cause a shift from top–down to bottom–up control. A 20% rainfall increase was shown to decrease the strength of top–down control by 80%, because wetter conditions lower grasshopper survival and cause plants to become more productive and compensate for herbivory (Ovadia and Schmitz 2004).

The idea of alternative regimes may seem incompatible for systems with clonally growing species like *Solidago*. After all, there is potential for a single individual to exist in 2 different regimes, given the adjacency of different patches (Figure 1) and our definition of regimes based on patch structure. However, previous research (Cain and others 1991) has shown that the mean length of *Solidago* rhizomes is on the order of 11–13 cm and that rhizome growth involves considerable random advancing and backtracking. Thus the linear extent of a clone is restricted to a locally narrow domain because of the low net displacement of the rhizomes from a point of origin (Cain and others 1991). Moreover, consumers can limit the production and growth of both rhizomes and associated emergent aboveground shoots (Cain and others 1991) and consumer effects may be quite local. Field mark-release experiments in our system (O.J. Schmitz, unpublished) revealed that *M. femurrubrum* grasshoppers undergo a net displacement of 111.2 cm ± 24.4 cm (1 SE, $n = 14$) from their point of release over the course of 2 days. This displacement compares with that found for this species at other locations (Narisu and others 1999) and falls well within the area of the 2 m × 2 m experimental field plots and the 4 m × 4 m or greater patches of natural vegetation within the field (Figure 1). We propose therefore, that alternative regimes and clonal growth can be consistent whenever species clones exist in local patches. In our case, as *S. rugosa* relative abundance approaches 20–25%, climate-altered strength of top–down control may allow *S. rugosa* to rapidly increase in abundance via above- and below-

ground expansion outward into space along a wave front at the patch boundaries, giving rise to the patchy mosaics observed in the field.

We also propose that the patchy mosaic in the field is maintained over the long-term because succession may not proceed by continuous proliferation of the competitive dominant once the bottom–up controlled regime is reached. This is because an alternative mechanism of top–down control may emerge as a consequence of *Solidago* reaching high field densities. In many old-field systems, dense concentrations of *Solidago* species attract specialist insect species and foster their outbreak which in turn causes *Solidago* to be devastated (Carson and others 2004). This feedback frees resources for subordinate plant species (Carson and others 2004) to the extent that the stage of successional development can be reset. We suggest further that such severe damage may push the ecosystem from a bottom–up back to a top–down controlled regime. The cyclic transition from a top–down to bottom-up controlled regime followed by resetting to a top–down controlled regime may explain why old-field succession persists for 50–60 or more years despite many *Solidago* species' capacities to rapidly increase in abundance, reduce resource levels and thus preempt other plant species when top–down control is altogether absent (for example, Figure 4).

This study contributes to growing evidence that top–down effects of consumers can have major effects on succession by altering light and soil nutrient levels (Pastor and Naiman 1992; Pastor and others 1993; Kielland and Bryant 1998; Carson and Root 1999). In our system, top–down effects likely prolong early succession by arresting *S. rugosa* abundance at or below 25%. However, top–down control can be disrupted thus allowing the system to cross a critical breakpoint and entrain into a bottom–up controlled regime. We therefore do not suggest here that the resource ratio hypothesis of plant succession should be discarded altogether. Rather, the resource ratio hypothesis can be nested within the alternative regime framework. Thus, consumer effects dominate by mediating resource ratio competition in the top–down controlled regime as shown in theoretical analyses (Holt and others 1994; Leibold 1996). This may explain the weak coupling between *S. rugosa* abundance and plant species evenness uncovered over the domain 0–25% *S. rugosa* abundance in Figure 2. We expect resource ratio competition to dominate once the system entrains into the bottom-up controlled regime. This would explain the rapid proliferation of *S. rugosa*—a superior competitor for light and soil

N—when consumers are removed from the system (Treatment 1: Figure 4A) and the tighter coupling between *S. rugosa* abundance and evenness beyond 25% *S. rugosa* (Figure 2).

Our interpretation of the collective body of evidence presented here is that a single ecosystem can display both top–down and bottom–up control. These shifts in trophic control are mirrored by abrupt changes in ecosystem properties such as plant species diversity and resource supply (solar radiation at soil surface and nitrogen mineralization rate), consistent with a working hypothesis that succession proceeds via abrupt regime shifts (Holling 1986).

ACKNOWLEDGEMENTS

REFERENCES

Bach CE. 1994. Effects of a specialist herbivore (*Altica subplicata*) on *Salix cordata* and sand dune succession. Ecol Monogr 64:423–45.

Bazzaz FA. 1979. The physiological ecology of plant succession. Ann Rev Ecol Syst 10:351–71.

Bazzaz FA. 1996. Plants in a changing environment. Cambridge (UK): Cambridge University Press.

Brown VK, Gange AC. 1992. Secondary plant succession: how is it modified by herbivory? Vegetatio 101:3–13.

Brown VK, Jepson M, Gibb CWD. 1988. Insect herbivory: effects of early old-field succession demonstrated by chemical exclusion methods. Oikos 52:293–302.

Cain ML, Carson WP, Root RB. 1991. Lon-term suppression of insect herbivores increase the production and growth of Solidago altissima rhizomes. Oecologia 88:251–7.

Carson WP, Cronin JP, Long ZT. 2004. A general rule for predicting when insects will have strong top–down effects on plant communities: on relationship between insect outbreaks and host concentration. In: Weisser WW, Siemann E, Eds. Insects and ecosystem function. Springer series in ecological studies. Berlin: Springer-Verlag. p 193–211.

Carson WP, Root RB. 1999. Top–down effects of insect herbivores during early succession: influence of biomass and plant dominance. Oecologia 121:260–72.

Carson WP, Root RB. 2000. Herbivory and plant species coexistence: community regulation by an outbreaking phytophagous insect. Ecol Monogr 70:73–100.

Chase JM. 1996. Abiotic controls of trophic cascades in a simple grassland food chain. Oikos 77:495–506.

Clements FE. 1916. Plant succession: an analysis of the development of vegetation. Carnegie Institute Washington Publication 242.

Connell JH, Slatyer RO. 1977. Mechanisms of succession in natural communities and their role in community stability. Am Nat 111:1119–44.

Connell JH, Sousa WP. 1983. On the evidence needed to judge ecological stability or persistence. Am Nat 121:789–824.

Cooper WS. 1913. The climax forest of Isle Royale, Lake Superior, and its development. Botanical Gazette 55:1–44.

Corbett SA. 1995. Insects, plants and succession: the advantage of long-term set aside. Agric, Ecsosys Environ 53:201–17.

Cowles HC. 1899. The ecological relations of the vegetation on the sand dunes of Lake Michigan. Botanical Gazette 27:95–117.

Crawley MJ. 1983. Herbivory: the dynamics of animal–plant interactions. Oxford (UK): Blackwell Scientific.

Davidson DW. 1993. The effects of herbivory and granivory on terrestrial plant succession. Oikos 68:23–35.

Duffy JE. 2002. Biodiversity and ecosystem function: the consumer connection. Oikos 99:201–19.

Elton C. 1927. Animal ecology. London: Sidgwick and Jackson.

Foster BL, Tilman D. 2000. Dynamic and static views of succession: testing the descriptive power of the chronosequence approach. Plant Ecol 146:1–10.

Fraser LH, Grime JP. 1998. Top–down control and its effect on biomass and composition of three grasses at high and low soil fertility in outdoor mesocosms. Oecologia 113:239–46.

Gunderson LH. 2000. Ecological resilience—in theory and application. Ann Rev Ecol Syst 31:425–39.

Gleason HA. 1927. Further views on the succession concept. Ecology 8:299–326.

Gutierrez J, Meserve PL, Herrera S, Contreras LC, Jaksic FM. 1997. Effects of small mammals and vertebrate predators on vegetation in the Chilean semi-arid zone. Oecologia 109:396–406.

Hairston NG, Hairston NG. 1993. Cause–effect relationships in energy flow, trophic structure and interspecific interactions. Am Nat 142:379–411.

Harper JL. 1969. Role of predation in vegetational diversity. Brookhaven Symposia in Biology 22:48.

Hart SC, Stark JM, Davidson EA, Firestone MK. 1994. Nitrogen mineralization, immobilization, and nitrification. Methods of soil Analysis, Part 2. Microbiological and biochemical properties. Soil Science of America Book Series, no. 5. p 985–1018.

Holling CS. 1986. The resilience of terrestrial ecosystems: local surprise and global change. In: Clark WC, Munn RE, Eds. Sustainable development of the biosphere. Cambridge, UK: Cambridge University Press. p 292–317.

Holt RD, Grover J, Tilman D. 1994. Simple rules for interpspecific dominance in systems with exploitative and apparent competition. Am Nat 144:741–71.

Hutchinson GE. 1959. Homage to Santa Rosalia, or why are there so many kinds of animals? Am Nat 93:145–59.

Kielland K, Bryant JP. 1998. Moose herbivory in taiga: Effects on biogeochemistry and vegetation dynamics in primary succession. Oikos 82:377–83.

Krebs, CJ. 1989 Ecological methodology New York (NY): Harper and Row.

Kuijper DPJ, Nijhoff DJ, Bakker JP. 2004. Herbivory and competition slow down invasion of a tall grass along a productivity gradient. Oecologia 141:452–9.

Lawton JH. 1983. Plant architecture and the diversity of phytophagous insects. Annu Rev Entomol 28:23–39.

Leibold MA. 1996. A graphical model of keystone predators in food webs: trophic regulation, of abundance, incidence, and diversity patterns in communities. Am Nat 147:784–812.

Lindeman R. 1942. Trophic-dynamic aspect of ecology. Ecology 23:399–418.

Loreau M, Naeem S, Inchausti P, Bengtsson J, Grime JP, Hector A, Hooper DU, Huston MA, Raffaelli D, Schmid B, Tilman D, Wardle DA. 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. Science 294:804–8.

Matthews JA. 1979. A study of the variability of some successional and climax plant assemblage-types using multiple discriminant analysis. J Ecol 67:255–71.

May RM. 1977. Thresholds and breakpoints in ecosystems with a multiplicity of stable states. Nature 269:471–7.

Morin PJ. 1999. Community ecology. Oxford: Blackwell Science.

Narisu , Lockwood JA, Schell SP. 1999. A novel mark-recapture technique and its application to monitoring the direction and distance of local movement of rangeland grasshoppers (Orthoptera: Acrididae) in the context of pest management. J Appl Ecol 36:604–17.

Odum EP. 1969. The strategy of ecosystem development. Science 164:262–70.

Oksanen L. 1990. Predation, herbivory and plant strategies along gradients of primary productivity. In: Grace JB, Tilman D, Eds. Perspectives on plant competition. New York: Academic Press. p 445–74.

Ovadia O, Schmitz OJ. 2004. Weather variation and trophic interaction strength: sorting the signal from the noise. Oecologia 140:398–406.

Paine RT. 2002. Trophic control of production in a rocky intertidal community. Science 296:736–9.

Pastor J, Naiman RJ. 1992. Selective foraging and ecosystem processes in boreal forests. Am Nat 139:690–705.

Pastor J, Dewey B, Naiman RJ, McInnes F, Cohen Y. 1993. Moose browsing and soil fertility in boreal forests of Isle Royale National Park. Ecology 74:467–80.

Peet RK, Christensen NL. 1980. Succession: a population process. Vegetatio 43:131–140.

Peterson CH. 1984. Does a rigorous criterion for environmental identity preclude the existence of multiple stable points? Am Nat 124:127–33.

Petraitis PS, Latham RE. 1999. The importance of scale in testing the origins of alternative community states. Ecology 80:429–42.

Pickett STA. 1989. Space for time substitution as an alternative to long-term studies. In: Likens GE, Ed. Long-term studies in ecology. Chichester: Wiley. p 71–88.

Pickett STA, Collins SL, Armesto JJ. 1987. Models, mechanisms and pathways of succession. Bot Rev 53:335–71.

Polis GA, Strong DR. 1996. Food web complexity and community dynamics. Am Nat 47:813–46.

Ritchie ME, Tilman D, Knopps JM. 1998. Herbivore effects on plant and nitrogen dynamics in oak savanna. Ecology 79:165–77.

Scheffer M, Carpenter SR. 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. TREE 18:648–656.

Scheffer M, Carpenter SR, Foley JA, Folke C, Walker B. 2001. Catastrophic shifts in ecosystems. Nature 413:591–6.

Schmitz OJ. 1992. Exploitation in model food chains with mechanistic consumer-resource dynamics. Theor Population Biol 41:161–83.

Schmitz OJ. 2003. Top predator control of plant biodiversity and productivity in an old field ecosystem. Ecol Lett 6:156–63.

Schmitz OJ. 2004a. From mesocosms to the field: the role and value of cage experiments in understanding top–down effects in ecosystems. In: Weisser WW, Siemann E, Eds. Insects and ecosystem function. Springer series in ecological studies. Berlin: Springer-Verlag. p 277–302.

Schmitz OJ. 2004b. Perturbation and abrupt shift in trophic control of biodiversity and productivity. Ecol Lett 7:403–9.

Seabloom EW, Richards SA. 2003. Multiple stable equilibria in grasslands mediated by herbivore population dynamics and foraging behavior. Ecology 84:2891–904.

Siemann E, Tilman D, Haarstad J, Ritchie ME. 1998. Experimental tests of the dependence of arthropod diversity on plant diversity. Am Nat 152:738–50.

Siemann E, Haarstad J, Tilman D. 1999. Dynamics of plant and arthropod diversity during old field succession. Ecography 22:406–14.

Sinclair ARE. 1989. Population regulation in animals. In: Cherett JM, Ed. Ecological concepts. Oxford: Blackwell Scientific. p 197–241.

Smith RL. 1996. Ecology and Field biology. 5th ed. New York: Harper and Collins Publishers.

Southwood TRE, Brown VK, Reader PM. 1979. The relationship of plant and insect diversities in succession. Biol J the Linnean Society 12:327–48.

Strong DR. 1992. Are trophic cascades all wet? Differentiation and donor control in a speciose system. Ecology 73:747–54.

Sutherland JP. 1974. Multiple stable points in natural communities. American Naturalist 108:859–73.

Tansley AG. 1935. The use and abuse of vegetational concepts and terms. Ecology 16:284–307.

Tilman D. 1988. Plant strategies and the dynamics and structure of plant communities. Princeton (NJ): Princeton University Press.

Tscharntke T, Greiler H. 1995. Insect communities, grasses, and grasslands. Ann Rev Entomol 40:535–58.

Uriarte M. 2000. Interactions between goldenrod (*Solidago altissima L.*) and its insect herbivore (*Trirhabda virgata*) over the course of succession. Oecologia 122:521–8.

Uriarte M, Schmitz OJ. 1998. Trophic control across a natural productivity gradient with sap-feeding herbivores. Oikos 82:552–60.

White TCR. 1978. The importance of relative shortage of food in animal ecology. Oecologia 33:71–86.

Wilsey BJ, Potvin C. 2000. Biodiversity and ecosystem functioning: Importance of species evenness in an old field. Ecology 81:887–92.

Wilsey BJ, Chalcraft DR, Bowles CM, Willig MR. 2005. Relationships among indices suggest that richness is an incomplete surrogate for grassland biodiversity. Ecology 86:1178–84.

Wootton JT. 2002. Mechanisms of successional dynamics: consumers and the rise and fall of species dominance. Ecol Res 17:249–60.