

Oswald J. Schmitz

## Scaling from plot experiments to landscapes: studying grasshoppers to inform forest ecosystem management

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**Abstract** Ecologists studying food web interactions routinely conduct their experiments at scales of 1–10 m<sup>2</sup> whereas real-world landscape-level management problems exist on scales of 10<sup>6</sup> m<sup>2</sup> or larger. It is often asserted that the experimental tradition in ecology has little to offer to environmental management because small scale empirical insights are not easily, if at all, translatable to the large scale problems. Small scale experiments are very local in nature and they are conducted in ways that tend to homogenize background environmental variation. Real world management is conducted across vast landscapes. Managers routinely must wrestle with complexity that is introduced by the heterogeneous structure of those landscapes and they often have limited recourse to do careful experimentation. How then is empirical ecological science ever to inform landscape-level management? The solution to this dilemma lies in arriving at good working conceptualizations of ecosystem structure and function that embody principles that are relatively scale independent. In this paper, the evolutionary ecological principle of foraging versus predation risk avoidance trade-offs is proffered as one central organizing conceptualization for plant-herbivore interactions across all systems. The utility of this conceptualization is first illustrated by presenting results of detailed experiments involving spider predators, grasshopper herbivores, and two classes of plant resources that afford grasshoppers differential protection from predators: nutritionally superior but risky grasses and less nutritious but safer herbs. The paper then shows how the foraging versus predation risk avoidance conceptualization in the context of a “landscape of fear” can be applied to manage large herbivore

impacts of forest regeneration following forest harvesting. I present results of landscape-scale experiments that mediate predation risk of the herbivores through manipulation of safe habitat in order to enlist herbivores to facilitate boreal forest mixed species regeneration through preferential foraging of certain woody species.

### Introduction

Ecologists have been perennially engaged in seeking ways to illuminate and solve environmental problems that result from human impacts on ecosystems (Worster 1994). Indeed, numerous success stories have been celebrated (e.g. Likens and Bormann 1974; Schindler 1974; Carpenter et al. 1987). Yet, as the scale and magnitude of human impacts continues to increase, ecologists are continually challenged to find tractable solutions at these ever increasing scales of impact. For example, large scale landscape disturbance consequent to land use clearing, intensive forest management or climate change can disrupt linkages among species in several trophic levels propagating a host of direct and indirect effects that may require decades to fully manifest themselves (Fig. 1). It is often difficult and expensive to conduct fully replicated factorial experiments with sufficient statistical power to explore precisely alternative hypotheses about the causal drivers of trophic dynamics at such scales (e.g., Sinclair et al. 2000; Krebs et al. 2001). So, ecologists usually try to extrapolate insights about the nature and strength of trophic interactions from study systems that can be made to conform more closely to the norms of experimental research (i.e., studies having good control, replication, and high precision [Hairston 1990]). By necessity, such research is conducted within plots or enclosures on spatial scales of meters to hectares over periods of weeks to months (Fig. 1). This mismatch of scale makes the transfer of scientific insights to management somewhat challenging because the

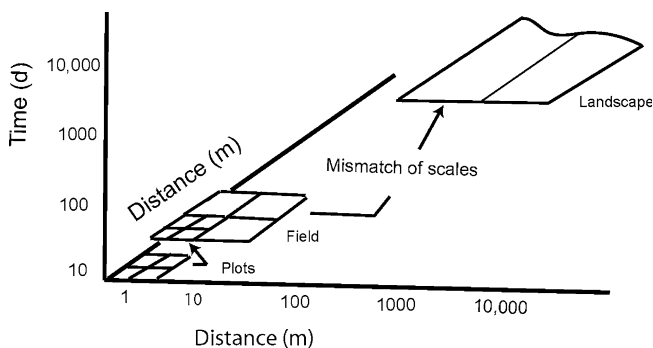
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O. J. Schmitz  
School of Forestry and Environmental Studies and  
Department of Ecology and Evolutionary Biology,  
Yale University, 370 Prospect Street,  
New Haven, CT, 06511 USA  
E-mail: oswald.schmitz@yale.edu

dynamics of small organisms, confined within small plots, may be quite different from dynamics that involve large organisms that move freely over landscapes (Kareiva and Anderson 1988; Morales and Ellner 2002). The question that then emerges is this: How might we use small-scale experimental research to inform management that operates on large spatial scales?

I begin to answer this question using a case study of my own attempts to extrapolate research findings in New England meadows to management of boreal forests. For both systems, the fundamental challenge is to know whether or not trophic interactions among species (top-down control) or plant-soil interactions (bottom-up control) is the dominant driver of species composition and productivity of the ecosystems. It may seem to be inconceivable that insights about ecosystem function derived from experiments involving spiders, grasshoppers and herbaceous plants can be applied directly to guide the management of forest ecosystems comprised of woody plants and widely ranging mammalian predators and herbivores. I argue that this is merely a technicality arising from a strict taxonomic view of the different systems. From a functional standpoint, both meadow and boreal systems can be viewed as systems of interacting carnivores, herbivores and plants (Fig. 2) making the exact spatial scale and taxonomic composition of each system only *proximally* relevant. The ability to scale from one system to another, in turn, rests on identifying fundamental effects or mechanisms: effects that are evident among systems regardless of spatial scale (Petersen et al. 2003).

In the following, I provide an overview of small-scale experimental research conducted within plots in a New England meadow and show how I have arrived at a working conceptualization of the mechanism driving trophic interactions in this system. I next detail the



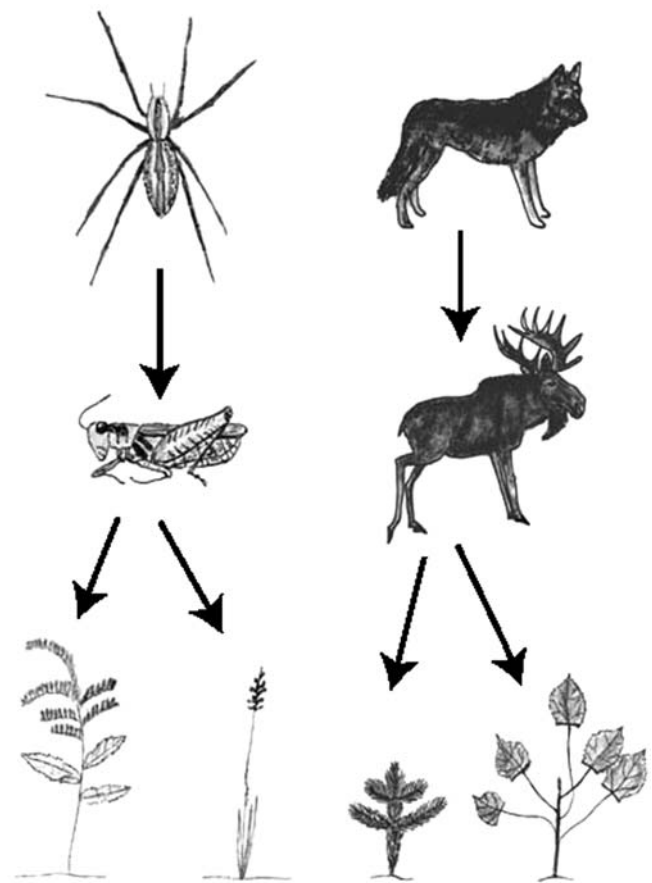
**Fig. 1** Graphical representation of the temporal scale and spatial extent (depicted as area defined by two length dimensions) at which basic ecological research and management operate. The *lower left corner* depicts small plots within which small-scale, well replicated field experiments are conducted. It is possible to scale up results from plots to the field level, as depicted by the plot level grid nested within the whole field level grid. Ecologists encounter a mismatch of scales when translating insights from plot experiments at the field level to management at the landscape level because of difference in spatial and temporal extent of the respective systems and differences in focal taxa. After Holling (1992)

reasoning used to claim that this should be considered a fundamental mechanism. I then show how application of the mechanistic understanding can lead to productive change in forest management.

### Small scale research: mechanisms of trophic interactions in a New England meadow system

Over the past 10 years, I have been conducting research on trophic interactions among predators, herbivores and plants in a New England meadow ecosystem. Specific natural history details of that system and an overview of the various experiments and protocols used are presented in Schmitz (2003, 2004).

There is considerable plant, herbivore and carnivore species complexity in the ecosystem (Schmitz 2004). Nevertheless, the key observation is that there are two fairly distinct insect herbivore feeding guilds (sap-feeders



**Fig. 2** Common conceptualization of interactions among dominant species in two ecosystems. On the *left* is an old-field ecosystem comprised of the hunting spider predator (*Pisaurina mira*), the generalist grasshopper herbivore (*Melanoplus femurrbrum*), and two distinct classes of herbaceous plants: grasses and herbs. On the *right* is a boreal forest ecosystem comprised of wolves (*Canis lupus*), the generalist herbivores such as moose (*Alces alces*) and two distinct classes of trees: deciduous aspen (*Populus tremuloides*) and coniferous white spruce (*Picea glauca*)

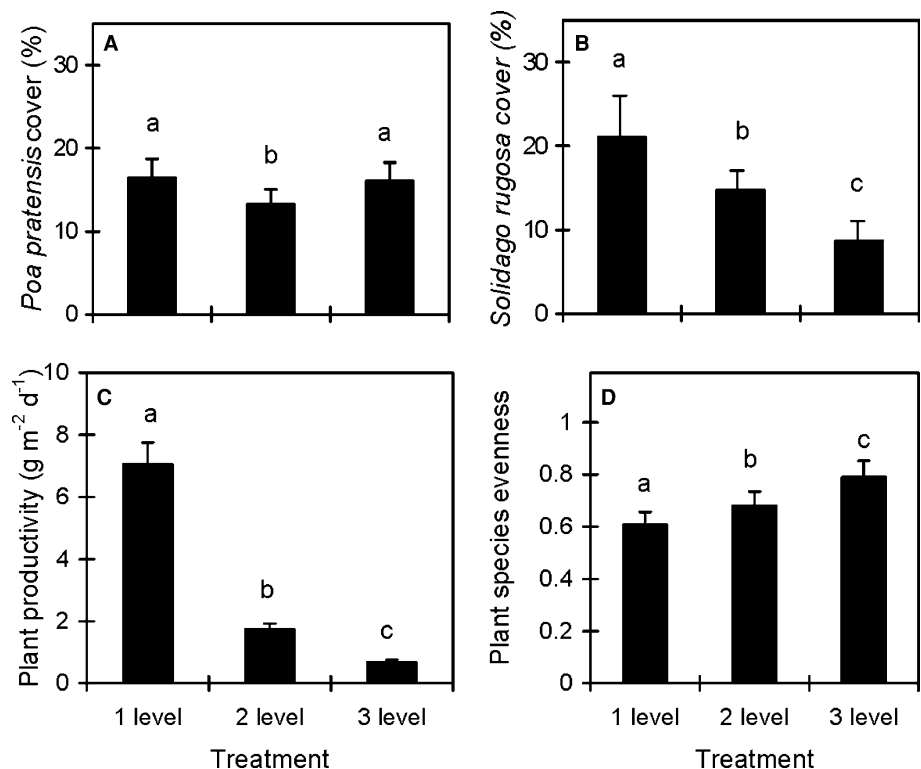
and leaf-chewers) present each year. These guilds may have widely different effects on plant species because of their feeding ecology and the degree to which predators influence their abundance. Top predator effects could transmit through the herbivore guilds to influence the abundance of plants and ecosystem function in several contingent ways. First, neither guild could have any net effect on ecosystem structure and function, in the presence or absence of predators, in which case one concludes that the field system is entirely bottom-up controlled. Second, strong top-down effects might be transmitted through only one feeding guild but not the other. In this case, one of the feeding guilds will play a dominant role in shaping ecosystem structure and function. Finally, top-down effects could be transmitted through both feeding guilds. However, those effects could be antagonistic, i.e., one guild could influence a particular group of plant species and the other guild influences another group. If groups of plants compete for resources then the effects due to one feeding guild could be reversed by the other feeding guild. In this case, there may be no net measurable effect of top-down manipulations on the ecosystem in the aggregate. However, it would be incorrect to conclude that the system was bottom-up controlled in this case. Finally, top-down effects might be transmitted through both feeding guilds in the same way. Hence, the top-down effects involving one feeding guild could synergistically enhance those of the other feeding guild.

Field research systematically addressing these contingencies (summarized in Schmitz 2004) revealed that the structure and short-term dynamics in this system is

largely determined by top-down interactions among four species: the hunting spider *Pisaurina mira*, the grasshopper herbivore *Melanoplus femurrubrum*, the grass *Poa pratensis*, and the competitive dominant herb *Solidago 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 (Beckerman et al. 1997; Schmitz et al. 1997; Schmitz and Suttle 2001). Mortality risk caused by predator presence forces grasshoppers largely to forego feeding on grass and to seek refuge in and forage on leafy *S. rugosa*, thereby causing high damage levels to this species (Beckerman et al. 1997; Schmitz 1998). Thus, *P. mira* spiders exert strong control by having a positive indirect effect on *P. pratensis* abundance and a negative indirect effect on *S. rugosa* abundance.

This insight leads to predictions about long-term top-predator effects on plant diversity and productivity in this field system. In particular, the dominant interaction shaping the structure of the ecosystem is a behavior-mediated interaction involving *P. mira* spiders, *M. femurrubrum* grasshoppers, *P. pratensis* grass, and *S. rugosa* herb. The emerging hypothesis is that *P. mira* should have a strong diversity-enhancing effect on herb species via a shift in plant species abundance (an evenness effect) caused by *M. femurrubrum* grasshoppers switching from feeding on *P. pratensis* to feeding heavily on the competitively dominant herb *S. rugosa*. Over the long term, such competitive release should cause many of the 18 other less productive herb species to proliferate. This amounts to a multi-trophic level variant of the classic keystone predation hypothesis (Paine 1966;

**Fig. 3** Consequences of 3-years of sustained meadow trophic level manipulations on the plot area covered by *Poa pratensis* and *Solidago rugosa*. Positive and negative indirect effects of predators on **a** *P. pratensis* and **b** *S. rugosa* mediated by grasshopper antipredator behavior. Effect of shifts in dominant plant species abundance on average yearly **c** plant productivity and **d** plant species evenness. Values shown are mean and 1 SE ( $n=10$  replicate plots). Bars with different lower case letters indicate significant differences based on a Tukey test at  $P < 0.05$  following a Randomized block ANOVA. Treatments: 1 level = plants only, 2 level = plants and herbivores, 3 level = plants, herbivores, and carnivores. After Schmitz (2003)



Leibold 1996) in which *P. mira* acts as an *indirect* keystone predator (Schmitz 2003).

This hypothesis was tested with a multiyear (1999–2001) field experiment that systematically manipulated the number of trophic levels in 2×2 m open field plots and measured the response of each manipulation on plant diversity and productivity. The experiment consisted of two treatments (a predator exclusion and a predator and herbivore exclusion) and a control (natural field state) replicated ten times using a randomized blocks design (Schmitz 2003). The experiment revealed significant, cumulative treatment effects on % *P. pratensis* cover and % *S. rugosa* cover (Fig. 3). Three years of predator exclusion resulted in significantly lower *P. pratensis* and *S. rugosa* cover relative to the one-trophic level, plant-only treatment (Schmitz 2003). Sustained predator presence (three trophic level treatment) resulted in increased *P. pratensis* cover and decreased *S. rugosa* cover relative to the predator exclusion treatment (Schmitz 2003). Manipulation of trophic structure also caused significant shifts in plant species evenness (Schmitz 2003). Evenness was significantly higher in three trophic level plots than in either the two-trophic level or one trophic level treatments (Fig. 3). In addition, there was a significant decrease in estimated plant productivity with increasing number of trophic levels in both sampling periods, owing largely to the suppression of the highly productive, and competitive dominant plant *S. rugosa* (Fig. 3).

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### Fundamental mechanism

Despite the high species richness in all trophic levels in this system, top-down effects appeared to transmit fairly linearly down a chain comprised of a dominant predator and herbivore species to the plant species. The emerging mechanistic insight from the highly replicated experiment was that the top predator controlled the structure and functioning of the natural ecosystem by causing the generalist grasshopper to trade-off foraging with hiding to avoid predation risk. This trade-off behavior altered the ability of a highly competitive plant species to dominate the meadow ecosystem.

Evolutionarily, any species that is subject to predation risk ought to respond flexibly to balance fitness gains from foraging against fitness losses from predation risk (Mangel and Clark 1988; Lima and Dill 1990; Lima 1998). There is evidence that species do respond to predation risk (Lima 1998). This reasoning then leads to the identification of a fundamental mechanism driving trophic interactions that can transcend spatial and temporal scales, and taxa. In essence, one could view ecological systems as “landscapes of fear” (Brown et al. 1999) in which species trade-off foraging against being consumed by their predators. Such a disarmingly simple conception has far-reaching implications for predicting trophic interactions among systems (Abrams 1984, 1992, 1995; Werner and Peacor 2003; Schmitz et al. 2004). In

the present case, understanding the motivation for the trade-off by the middle herbivore species in the food web is the core knowledge that should facilitate the application of scientific insights from the meadow system to the boreal forest.

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### Scaling the insight: management of boreal forest ecosystems for diversity and productivity

The dynamics of boreal forest ecosystems are driven by many factors including fire, insects and mammalian herbivores (Shugart et al. 1992). A large body of evidence shows that among those factors, interactions between large mammalian predators, herbivores and plants may play an important role in shaping ecosystem structure and function (McLaren and Peterson 1994; Pastor and Naiman 1992; Krebs et al. 2001; Post et al. 1999; Pastor and Cohen 1997; Niemelä et al. 2001; Sinclair et al. 2000).

An important, large-scale (25 ha or larger) disturbance in boreal systems is forest harvesting for timber and pulpwood. A limiting factor in long-term sustainability of boreal forests, and a central challenge to forest ecosystem management, is a forest’s capacity to regenerate following harvesting. My research has been part of a collaborative effort (P.M.S. Ashton, B. Larson, R. Neshody, O.J. Schmitz, unpublished) aimed at identifying ecologically compatible ways of regenerating southern boreal mixed-wood forests—forests dominated by aspen (*Populus tremuloides*) and white spruce (*Picea glauca*)—following harvesting in northwestern Saskatchewan, Canada. Below, I provide a brief sketch of that research to demonstrate proof-of-scaling-concept.

Southern boreal mixed-wood is the most economically important to the forest industry and its successful regeneration is the most problematic management issue for many companies.

Historically, attempts by the forest industry to regenerate boreal mix-woods after harvesting have largely met with failure because aspen, a competitive dominant, suppresses regeneration of spruce (Yang 1991) leading often to aspen monocultures with low understorey plant species diversity.

One potential reason for the failure to regenerate mixed wood forests is that management has not developed the appropriate conceptualization of the functional ecosystem. The traditional view, signified by the management practice of large-scale harvesting, extensive site preparation after harvesting followed by intensive replanting of spruce seedlings, is that forest ecosystem structure and function is driven largely by bottom-up local soil-plant interactions. There is some recognition that top-down effects might also play a role, but it is largely viewed that they lead to undesirable outcomes. Specifically, ecosystems are viewed as having two functional trophic levels: herbivores and plants. In this conception, herbivores damage regeneration so their population numbers should be reduced to prevent



regeneration failure (Alverson et al. 1988; Tilghman 1989; Sullivan et al. 1990; Anderson and Katz 1993; Andren and Angelstam 1993).

I argue that extending the conception of an ecosystem by considering three functional trophic levels in the context of landscapes of fear offers ways to utilize ecological interactions among species, rather than intensive mechanical site preparation or herbivore exclusion, to create environmental conditions that foster mixed wood regeneration.

In forest ecosystems, large herbivores such as white-tailed deer *Odocoileus virginianus*, and moose *Alces alces*, like grasshoppers, respond to predation risk by seeking refuge habitats or shifting the spatial location in which they forage (Edwards 1983; Andren and Angelstam 1993; White et al. 2001; Lingle 2002). In the study system, both herbivore species prefer aspen (O.J. Schmitz, unpublished). So, each species conceivably could reduce the abundance of the competitive dominant and thus release spruce to regenerate. However, forest harvesting, especially clear-cutting, fragments the forest landscape in ways that have a profound influence of herbivore foraging. In particular, large openings increase the vulnerability of large herbivores such as deer, and moose to predation by both wolves *Canis lupus* and humans. Consequently, these herbivore species select habitats to decrease risk, and accordingly have weak or much localized impacts on plant species (Andren and Angelstam 1993). If they do forage in the open risky areas, they tend to be less selective owing to heightened vigilance (Molvar and Bowyer 1994). Moreover, they tend to congregate in higher densities in riskier areas leading to increased frequency of antagonistic interactions, which in turn reduces foraging efficiency (Molvar and Bowyer 1994). Thus, management can create conditions that impact several aspects of large herbivore behavior that accordingly enables aspen to proliferate on the landscape.

I now illustrate how managing forests in ways that alter herbivore foraging preferences through predation risk (landscapes of fear) can lead to management strategies that successfully regenerate boreal mixed woods.

We examined herbivore-mediated effects in two stages by enlisting management as a scientific experiment (*sensu* Walters and Holling 1990; Sinclair 1991). The first stage involved stand-level experiments aimed at understanding herbivore-mediated plant–plant interactions. The second stage involved experiments that manipulated landscape-scale “fear” to alter habitat use by herbivores.

#### Stand-level experiment: herbivore mediation of aspen-spruce competition

Herbivores may single-handedly shape community structure and function via direct interactions with their plant resources. There are two ways of viewing that role. The traditional view holds that herbivores are damaging

to regeneration. An alternative view recognizes that plant species compete for resources and that herbivores shape the outcome of that interaction by preferentially feeding on competitively dominant species (Louda et al. 1990; Huntly 1991; see De Steven 1991 and Schmitz and Sinclair 1997 for focus on tree species). Indeed, theory suggests that in boreal forests, the successional pathway during stand development (and eventual composition of spruce or aspen in the overstory) may be quite different when herbivores are present than when they are absent (Pastor and Naiman 1992). Herbivores may have strong direct effects by selectively feeding on plant species but the trajectory taken during stand development is largely an indirect consequence of herbivores mediating plant–plant interactions (Brandner et al. 1990). Theory (Pastor and Naiman 1992; Pastor and Cohen 1997) also suggests that in boreal systems, the effects of herbivores on the successional trajectory taken by a stand may persist long after herbivory has stopped (when trees have grown beyond the herbivore’s reach).

In partnership with a local forest management company, we established and monitored a large-scale field experiment between 1997 and 2000. We studied stand development in an aspen-spruce mixed wood forest within sites that had similar soil type, successional stage and fire disturbance origin. The experiment was initiated by carefully harvesting all timber and vegetation exceeding 2.5 cm diameter-at-breast height (dbh) within four replicate 340×80 m strips (~2.7 ha) whose long axes are oriented in an east-west direction. Harvesting was done using a mechanical harvester that minimized impacts to the ground story vegetation.

The east-west orientation of the strips served two purposes. First, the width of this gap resembles a large natural canopy disturbance like that of several tree-falls (Ashton and Larson 1996). Second, boreal herbivores may differentially browse plant species at different distances from the edge of a strip owing to predation risk (reviewed in Andren and Angelstam 1993). However, sun-exposed woody plants tend to have higher nutritional quality than do plants growing in shadier conditions (Robbins 1983). Thus there may be a predation-risk/food value trade-off that may cause variation in the strengths of top-down control across an opening.

We crossed a silvicultural treatment, commonly employed by management, with a herbivore exclusion in a 2×2 design. Treatments were imposed on 5×20 m plots. Each treatment was randomly assigned to each transect in each of the four strips. The north-south oriented transects run across the width of each strip. The treatments were imposed in three plot locations in each transect: north edge, center and south edge to control for confounding effects of plot location on plant production.

We compared with an unmanipulated control a silvicultural treatment that emulated a ground story disturbance used by the forest industry to prepare sites for planting. The control preserved all vegetation below 2.5 cm dbh thus releasing advanced regeneration (*full*

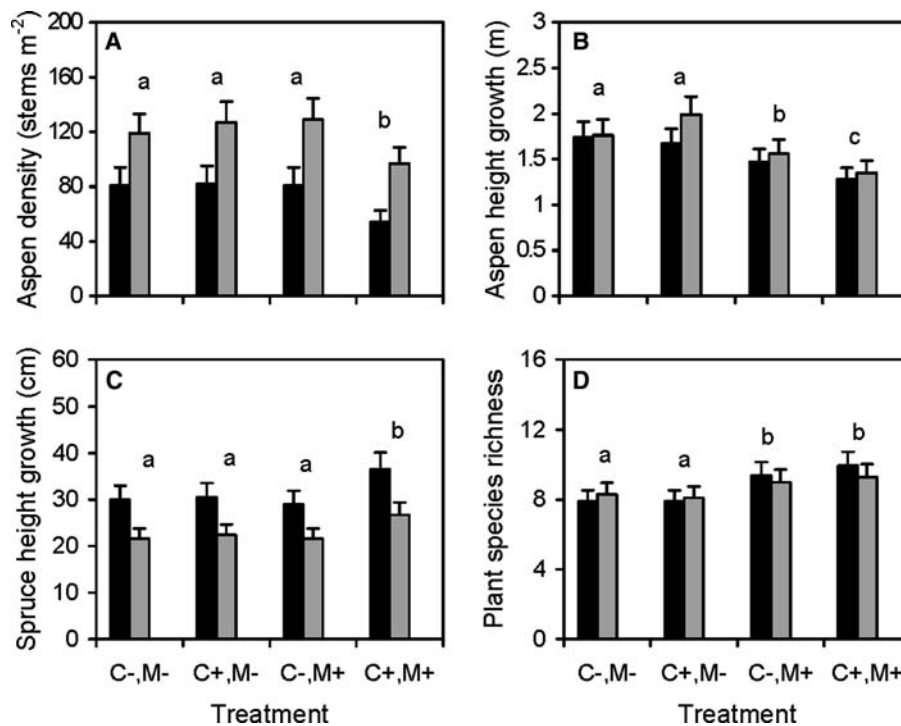
plant competition, hereafter C+). The treatment was a mechanical eradication of all aboveground vegetation below 2.5 cm dbh. This removed advanced regeneration (*removal of above-ground competition*, hereafter C-) but released root suckering of aspen. In each 5×20 m plot, we randomly selected one half-side (split plot design) in which we planted nine spruce seedling in each of six, 2×2 m subplots. The other half-side was left as a natural regeneration control.

The herbivore treatments were ultimately designed to separate smaller mammal (snowshoe hare, *Lepus americanus*) effects from large mammal (moose and deer) effects, but we did not detect differential effects of these large and small mammals during the course of the experiment (O.J. Schmitz, unpublished). Thus, I describe here treatments that manipulated mammalian herbivory generally. The control (hereafter M+) allowed herbivorous mammals full access to the 5×20 m plots. The treatment excluded all mammals (hereafter M-) from replicate 5×20 m plots using 2.5 m high 5×5 cm grid page wire fencing. We were concerned that the large enclosure pens themselves might deter herbivores from entering the experimental area. We therefore cut companion 80×340 m strips 80 m adjacent to each experimental strip and left them unmanipulated (unmanipulated control strips). We used the same criteria for site selection as those for the experimental strips. We then conducted browse surveys along 1.5 m-wide swaths

in eight transects running the full 340 m length of the strips in the experimental and unmanipulated control strips (in experimental strips, enclosure pens did not fall along a transect line). We did not find any significant differences in browsing (number of stems browsed per m<sup>2</sup>) between experimental and control strips at different distances along the sampling transects (All *t*-tests,  $P > 0.65$ ).

We measured two woody plant response variables and one total (woody and herbaceous) plant response in the experiment. We measured aspen stem density (a measure of abundance: note, spruce density was fixed by planting seedlings) and aspen and spruce height growth (an index of productivity) by subdividing each 5×20 m plot into twelve, 2×2 m subplots and then systematically sampling every other plot. Height growth was measured using a meter stick. We measured the maximum height of each clonal clump of aspen within each subplot (usually there were 2–3 clumps per subplot). To avoid pseudoreplication, we aggregated all subplot measures to a plot average. We estimated stem density by counting all emergent stems in sampling subplots and then scaling the subplot total to the entire plot to estimate plot density. In the same 2×2 m subplots, we counted all plant species to estimate plant species richness.

Aspen and spruce plants grew differently (All Randomized Block Anova's,  $P < 0.05$ ,  $df = 3,9$ ) when exposed to natural conditions (herbivory and competition)



**Fig. 4** Effect of stand-level manipulations on **a** aspen density, **b** aspen height growth, **c** spruce height growth and **d** understorey plant species richness. The experiment included the following treatments: C-, M-plant competition mediated mechanically and mammalian herbivores excluded; C+, M-plant competition not manipulated and mammalian herbivores excluded; C-, M+ plant competition mediated mechanically and mammalian herbivores not

excluded; and C+, M+ plant competition not manipulated and mammalian herbivores not excluded (natural control state). The *dark bars* represent plant responses along edges, *lightly shaded bars* represent plant responses in the center of the harvested strips. *Bars with different lower case letters* indicate significant differences based on a Tukey test at  $P < 0.05$  following a Randomized block ANOVA. Values shown are mean and 1 SE ( $n = 4$  replicate plots)

than under any of the other classical management-type treatments, especially ones which excluded the herbivores (Fig. 4). The qualitative pattern of effect was similar in edge and in open plots. Tukey tests revealed that aspen stem density and height growth was significantly lower in natural plots than in managed plots. Alternatively, spruce height growth was significantly higher in natural plots than in managed plots. This combined evidence indicates that after 4 years, herbivores were capable of mediating the abundance of aspen and spruce in desired ways much better than the more traditional management systems (i.e., mechanical site manipulation and herbivore exclusion). There was also a slight tendency for plots exposed to herbivory to have higher understory plant species richness than plots that excluded herbivores at both edge and center locations (Fig. 4, both Randomized Block Anova's,  $P < 0.09$ ,  $df = 3,9$ , followed by Tukey Tests).

The stand level experiment revealed that mammalian herbivores are capable of mediating plant species abundance, productivity, and richness in ways that are predicted by a priori principles of trophic interactions. The limitation of this experiment, however, is that it remains uncertain if herbivore impacts uniformly scale to the landscape level where clear-cut harvesting routinely removes timber within 25–100 ha areas. Such a scale is at least an order of magnitude larger than the strip cuts. Herbivores may not affect plants uniformly across such vast open spaces because of predation risk. Feeding in the middle of such large openings requires that herbivores move long distances away from escape cover afforded by the intact forest stands surrounding the clear-cuts (Rothley 2002). Herbivores will instead forage near the perimeter of the harvested area, despite the high nutritional value of browse in the open, leading to exponential declines in browsing impacts from the edge to the center of the harvested area (Drolet 1978; Tomm et al. 1981; Andren and Angelstam 1993). Such trade-off behavior will cause an uneven pattern of regeneration. Mix-wood regeneration will proliferate around the perimeter of the harvested area; aspen monocultures will proliferate in the center. One potential solution then is to harvest the landscape in ways that alter the herbivores' perceived risk of predation.

Landscape-level experiment: predation risk-mediated herbivore use of harvested areas

Use of harvested areas by large mammalian herbivores varies with the size, shape and distribution of cut-over areas on the landscape (Tomm et al. 1981; Rothley 2002) as well as with the spatial pattern of overstorey remaining in residual patches (Forman and Godron 1981; Hunter 1990; Rothley 2002). Changing landscape-scale patch structure should thus cause deer to change their use of the land matrix. Specifically, altering the degree of openness of harvested areas may

be one way to mitigate the risk of predation they perceive.

Our goal during this stage of the research was to test whether or not the herbivores could be drawn out to the center of the harvested areas and thus mediate aspen-spruce interactions more evenly across the harvested areas. We therefore compared herbivore foraging impacts under two harvesting treatments relative to an unharvested control. The first harvesting treatment was a classic overstorey removal (COR) or clear-cut. The second treatment was a new harvesting strategy called a partial overstorey removal (POR) that retained habitat patches within a harvested area. In a POR strategy, 10–20 small patches (~1 ha) of uncut timber are left throughout the middle of a harvested area (~50–100 ha). The patches are arrayed to reduce the distance between open feeding areas and escape cover, thereby foreshortening the herbivore's perception of predation risk in the center of a harvested area.

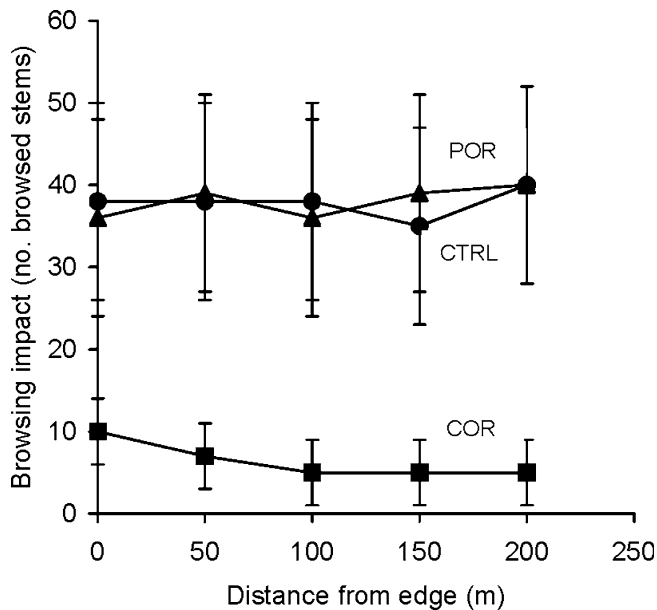
We selected three harvesting areas and matched, in each area, a COR, POR and control site that had similar site conditions (as described in the Stand-level experiment section above). Harvested areas ranged in size from 55 ha to 90 ha. We delineated a 250×250 m sampling grid that extended from the edge to the center of each treatment area or from the edge/forest margin to the interior forest in the control. As an index of large herbivore spatial use and impacts, we sampled the number of stems browsed along the entire length of five, 1×250 m transects spaced at 50 m intervals within each sampling grid.

This experiment revealed that browsing activity by large herbivores in the patch retention (POR) areas was similar to unharvested controls (Fig. 5). Browsing activity was fairly uniform from the edge of the patches toward the center. However, herbivore activity in traditional clear cuts (COR) was quite different than in either the POR or control. Browsing activity rapidly declined a short distance from the perimeter into the harvested area and remained low out to the center (Fig. 5), consistent with earlier findings (Drolet 1978; Tomm et al. 1981; Andren and Angelstam 1993). It would appear that harvesting the landscape in ways that protect values sought by herbivores (food and escape cover) will result in more even use of the harvested landscape. Thus, management can enlist the fear-factor associated with herbivore habitat selection to regenerate forest stands in desired ways.

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## Discussion

The aim of this paper was to illustrate how one might successfully apply insights from field research that is normally conducted at scales of 1–10 m<sup>2</sup> to landscape-level management that occurs on scales of 10<sup>6</sup> m<sup>2</sup> or larger. The success of this application rests on deriving an appropriate conceptualization of species interactions within an ecosystem and then identifying a scaling



**Fig. 5** Effects of landscape-scale forest harvesting strategy on large herbivore habitat use measured as browsing impacts along a gradient from forest edge to the center of the cut-over area. Treatments are classic overstorey removal (*COR*), partial overstorey removal (*POR*) and unharvested control (*CTRL*). Values are mean and 95% CI

principle (i.e., fundamental effect or mechanism [Petersen et al. 2003]) that transcend spatial scales. In the present case, that conceptualization was simply viewing an ecosystem as an interacting set of dominant carnivore, herbivore and plant species (Fig. 2) whose interactions are mediated by herbivore trade-offs to balance foraging against avoiding contact with predators. At the same time, scaling from the meadow research to forest management did not involve, and indeed could not involve, an explicit consideration of space.

For example, grasshoppers in the small scale research avoided predators by switching from locations with highly nutritious resources to locations containing safe plants. This resource switching mediated competitive interactions among plants in predictable ways. But, from the grasshoppers' perspective, grasses and herbs are simultaneously separate foods and habitats. Large herbivores such as moose and deer, on the other hand, encounter both aspen and spruce plants fairly evenly within the same habitat. In this case, food resources are nested within a single habitat. But, they still mediate competitive interactions among the plants through preferential foraging. Escape cover is afforded to large herbivores by an altogether different habitat structure which determines the degree to which the herbivores mediate competitive interactions in large openings. Thus, it is the foraging-predation risk trade-off mechanism that is preserved across spatial scales and taxa. The specific way each herbivore species uses resources and habitats to resolve the trade-off comes down to the old idea of environmental grain (Hutchinson 1965; Pianka 1978, see also Abrams and Schmitz 1999).

There is nothing novel about the individual elements of the forest management research describe here. The ecology of aspen and spruce regeneration, aspen-spruce interactions, and herbivore damage on forest plants is certainly well known in the silviculture literature. Moreover habitat selection and foraging by large mammalian herbivores is well described in the wildlife management literature. It is the way the elements are packaged in a unifying conceptualization of ecosystem function that differs from that presented in previous management literature. This is because forest management and wildlife management have often operated at cross-purposes.

The goal of forest management and harvesting typically is to maximize the production of wood fiber. The goal of wildlife management is to manage habitat in ways that maximize deer and moose species production. Accordingly, forest harvesting has been viewed as antithetical to wildlife management goals. Harvesting has fragmented the forest landscape and it has introduced anthropogenic disturbances to the extent that habitat quality has become unsuitable for species to remain within the ecosystem. In contrast, successful wildlife management creates conditions—high abundances of herbivores—that are viewed by forest management as detrimental to forest regeneration. The conceptualization presented here integrates those factors that have in the past been investigated separately and often without properly controlled experiments. Such integration shows how forest ecosystem management can enlist wildlife habitat management that mediates predation risk and the capacity of herbivore species to damage vegetation selectively as strategic management tools. The inspiration for applying this idea, however, comes from detailed, fully replicated mechanistic examination of small-scale systems comprised of arthropod predators and herbivores and plants.

Our ability to develop tools that facilitate reliable application of basic ecological insights to management requires that we develop conceptualizations that account for the important links and feedbacks among biotic components of ecosystems as a whole. The “landscape of fear” concept is one such candidate. Indeed, it is also being applied to understand ecosystem dynamics at other spatial scales, involving other taxa including elk (*Cervus canadensis*) impacts on woody vegetation in the Yellowstone Park ecosystems before and after wolf reintroduction (Laundre et al. 2001; Ripple et al. 2001, 2003), and interactions among lynx (*Lynx Canadensis*), snowshoe hare, and woody vegetation in northern boreal ecosystem (Krebs et al. 2001). And so, creative solutions to emerging environmental problems can be developed by identifying fundamental mechanisms of species interactions that transcend spatial scales of ecological organization and function.

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