

## PRESS PERTURBATIONS AND THE PREDICTABILITY OF ECOLOGICAL INTERACTIONS IN A FOOD WEB

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**Abstract.** Press perturbations, in which one or more species densities are experimentally altered and held at higher or lower levels, are common field approaches used to understand community dynamics. The outcomes of such experiments are often difficult to anticipate solely on the basis of intuition. This is because the effects of a perturbation may pass through a complex network of direct and indirect pathways in a food web, and the outcome may be highly sensitive to the strength of interactions among species. One solution to understanding outcomes of press experiments is to quantify first the community matrix, the matrix of measured direct interactions between all species in a food web, and then obtain the inverse of this matrix. The inverse of the community matrix predicts the effect of all species presses on all other species. I evaluated the utility of the inverse community matrix in predicting the outcomes of press experiments in an old-field food web. I used data from field and laboratory experiments to quantify the interaction strengths between grasshoppers, four old-field plants, and nitrogen supply. These values were used to parameterize the community matrix and obtain its inverse in a Monte Carlo simulation. The simulation was used to predict the mean and standard error in the outcome of a simultaneous nitrogen and herbivore press on food-web structure and dynamics. The predictions were compared with data from an enclosure experiment in the field in which I manipulated nitrogen supply and herbivore abundance. There was a high degree of uncertainty predicted and observed in the study system. Despite this, I show that the degree and the sources of uncertainty were predictable for each species. This suggests that the inverse community matrix offers a useful theoretical benchmark for understanding the outcome of field press experiments.

**Key words:** *community matrix and inverse; ecological interactions, predictability of; field experiment; food-web dynamics; grasses, grasshoppers, and nitrogen; manipulative experiments; old-field food web; Parry Sound, Ontario, Canada; press perturbation experiment; top-down vs. bottom-up control.*

### INTRODUCTION

Community ecology has enjoyed a long empirical tradition in which individuals have gathered valuable, detailed information on natural systems and then devised explanations for their observations (Hairston 1990). More recently, this approach has given way to increased use of manipulative experiments in which one or more components of a natural community are systematically altered to gauge the response of other members of the community (Bender et al. 1984, Diamond 1986, Yodzis 1989, Hairston 1990). The advantage of the experimental approach over field observation studies is that it establishes causal linkages between different components of natural communities.

Often, however, the outcome of experimental manipulations are not clear-cut. Consequently, ecologists have appealed to the complexity of natural systems when explaining discrepancies between predictions and experimental outcomes (Hairston 1990). These appeals certainly are not without justification. Field experi-

ments have established the importance of comparatively direct species interactions such as predation, competition, parasitism, and mutualism in structuring natural communities (Connell 1983, Schoener 1983, Sih et al. 1985, Hairston 1990). They have also shown that there may be a variety of indirect species interactions whose importance in structuring ecological communities may equal or exceed the importance of direct interactions (Yodzis 1988, Pimm 1991, Abrams 1993, Schoener 1993, Wootton 1994c). When the strength of indirect interactions swamps out any direct effects, theory tells us that we may expect to have some trouble explaining the dynamics of natural systems (Yodzis 1988, Schoener 1993).

Satisfactory explanations of community dynamics require knowing which species are dynamically coupled, either directly or through intermediary species, and the signs and strengths of the species interactions (Bender et al. 1984, Schoener 1993). The issue of using field experiments to quantify the dynamical couplings and the form and strengths of species interactions is a current focal point of food-web ecology (Bender et al. 1984, Paine 1988, 1992, Yodzis 1988, 1995, Schoener

1993, Wootton 1994a, b, deRuiter et al. 1995). The roots of the approach can be traced back to classical community-ecology theory in which species interactions are described mathematically by a dynamical system of the form (e.g., May 1973, Yodzis 1989)

$$dN_i/dt = f_i(N) \quad i = 1, 2, \dots, n \quad (1)$$

where  $N_i$  is the density of species  $i$ , and  $N$  represents a vector of species ( $N_1, N_2, \dots, N_n$ ) in an  $n$ -species community. This formalism assumes that the population growth rate of species  $i$  is a function  $f_i$  of some set of all species in the community. In community-ecology theory, interaction strengths between species  $i$  and  $j$  are determined by calculating the per capita effect of species  $j$  on the growth rate of species  $i$  ( $\partial f_i / \partial N_j$ ) at equilibrium. This produces a "community" matrix (May 1973, Yodzis 1988) with elements

$$A_{ij} = (\partial f_i / \partial N_j) | N_e \quad (2)$$

where  $N_e$  is the equilibrium density. The interaction-strength approach quantifies the direct effect of one species, at equilibrium, on all other species with which it is directly linked in a food web (e.g., trophic interactions, interference competition). The power of this approach is that we can now quantify the importance of different species in community dynamics and separate out those species that are likely to have strong effects from those species that exert weaker effects (Paine 1988, 1992).

The interaction-strength approach requires that one conduct perturbation experiments to quantify the dynamical interactions among species (Bender et al. 1984, Paine 1992). The utility of the community matrix ( $A_{ij}$ ) for explaining the results of perturbation experiments depends critically on the specific design employed (Bender et al. 1984). There are two basic designs for perturbation experiments. The first design, called "pulse experiments," perturbs one or more species slightly away from equilibrium and then lets the community return to that equilibrium (Bender et al. 1984, Yodzis 1988, 1995). The second, called "press experiments," pushes the system to alternative equilibria by altering one or more species densities and holding those densities at higher or lower levels through experimental methods including enclosures or nutrient additions (Bender et al. 1984, Yodzis 1988, 1995). In pulse experiments the interaction strengths (measured as population growth rates) are directly tied to the elements of the community matrix (Bender et al. 1984). In press experiments, however, interaction strengths are based on the measured difference between initial equilibrium density and equilibrium density under press conditions (Bender et al. 1984). In this case, it can be shown mathematically that interaction strengths are directly tied to elements of the negative of the inverse of the community matrix (i.e.,  $-[A^{-1}]_{ij}$ ) (Bender et al. 1984, Yodzis 1988). The elements of  $-[A^{-1}]_{ij}$  summarize the total effect of species  $j$  on species  $i$  due to the direct

linkage with species  $i$  (e.g., predation or interference competition) and all possible indirect pathways through which species  $i$  and  $j$  are connected via linkages with intermediary species.

The use of the inverse of the community matrix to quantify interaction strength is important for several reasons. First many natural (sensu Diamond 1986) and manipulative field experiments in community ecology amount to press experiments (Hairston 1990). Second, the importance in community dynamics of indirect interactions between two species, via intermediary species, increases with the duration of a perturbation on a system, at least theoretically (Yodzis 1988, 1995). Finally, the results of press experiments may not be clear-cut because of the potential indeterminacy in the directional outcome associated with a press experiment. Indeterminacy results from mediation of the direct effects of one species on another by intermediate species in a food web (Yodzis 1988). A high degree of directional indeterminacy means, for example, that the addition of predators to a community will not necessarily result in fewer prey species (Yodzis 1988). The inverse of the community matrix offers a useful theoretical benchmark to begin assessing the likelihood of indeterminacy in the outcome of a field experiment.

One of the potential difficulties with using the inverse community matrix as a theoretical benchmark is that it may be difficult in practice to define the appropriate mathematical model of dynamics, especially for complex systems involving many species in several trophic levels. Moreover, predictions based on inverse community matrices may be sensitive to values of interaction strengths among species in the community and the variability associated with each measure of interaction strength (Yodzis 1988, Pimm 1993). These issues have yet to be evaluated empirically. I present here a quantitative, empirical evaluation of the inverse community-matrix approach in helping to understand the outcome of press experiments in an old-field food web. This system was sufficiently simple to derive an appropriate mathematical model of food-web interactions among grasses, herbs, and insect herbivores and to parameterize the model using data from field and laboratory experiments (Schmitz 1994).

This paper is divided into four major sections. The first section provides the contextual basis for this study by presenting the natural history of the study area and an overview of previous work on food-web interactions with the study system. The second section presents the derivation of the community matrix and its inverse that is used to predict the outcome of press experiments. The third section details the field press experiments that are used to evaluate the utility of the inverse community-matrix approach. The final section provides a discussion of the implications of the inverse matrix approach in food-web ecology.

## NATURAL HISTORY AND BACKGROUND

All field work on food-web interactions was conducted during the summers of 1991 through 1993 in a 5-ha old field near Parry Sound, Ontario, Canada (46° N, 80° W). The study site was in the midst of a temperate hardwood forest that had been abandoned from farming since 1954 and was still in an early to middle successional state. The site was dominated by perennial dicots and grasses with a mean species richness of  $4.6 \pm 1.1$  species per 0.5-m<sup>2</sup> quadrat ( $n = 25$  plots). Average relative abundance (mean  $\pm 1$  SE) and the rank order of abundance of the four dominant species (>2% of biomass in plots), measured in 10, random 0.5-m<sup>2</sup> field plots prior to the onset of field experiments were: *Hieracium aurantiacum*,  $0.37 \pm 0.05$  g dry mass; *Solidago altissima*,  $0.33 \pm 0.03$  g dry mass; *Phleum pratense*,  $0.21 \pm 0.04$  g dry mass; and *Fragaria canadensis*,  $0.09 \pm 0.03$  g dry mass.

Field surveys indicated that the site supported three species of phytophagous insects (the grasshopper *Melanoplus borealis*, the katydid *Orchelimum vulgare*, and the grasshopper *Dissosteira carolina*). I used a standard catch-effort method (Krebs 1989) to estimate grasshopper density. Grasshoppers were caught in a 10-m<sup>2</sup> open-top enclosure made of aluminum screening. I sampled for consecutive 5-min periods, separated by 5-min rest periods, until grasshoppers were no longer caught in the enclosure. A plot of catch per 5 min vs. cumulative catch based on this sampling resulted in a linear decrease in numbers caught vs. sampling effort (O. J. Schmitz, unpublished data). The  $x$  intercept of this plot provided an estimate of the population density in the enclosure. This revealed that the grasshopper *M. borealis* was far more abundant (average density  $5.5 \pm 1.2$  adults/m<sup>2</sup>,  $n = 10$ ) than *O. vulgare* and *D. carolina* (both species had adult densities <1 insect/m<sup>2</sup>). Larger herbivores such as *Microtus pennsylvanicus*, *Lepus americanus*, or *Odocoileus virginianus*, which may have visited the site, had no measurable impact on the plant trophic level as revealed by previous field experiments (Schmitz 1994).

All field work was conducted within a time period relevant to the biology of the major players in the community. The plant species are early season perennials, which dominate the community after the last frost in late May until late July, when they begin to senesce (Britton and Brown 1970). Correspondingly, nymphs of the dominant grasshopper, *M. borealis*, the focal herbivore species in the food-web studies, emerge in early June, become adults in early July, and begin to die off in early August. This grasshopper species was present during the  $\approx 80$ -d temporal window when the dominant plants were abundant. Moreover, the grasshoppers reproduce once a year, matching the perennial seasonality of the plant species. Plants and herbivores in such systems also reach steady state within a field season (Schmitz 1993, 1994). This satisfies an impor-

tant assumption of the inverse community matrix approach.

Previous experiments at the field site explored how environmental productivity (soil nitrogen supply) and Lycosid hunting spiders (*Hogna helluo*) mediated interactions among a dominant grasshopper (*M. borealis*), edible perennials (*Solidago altissima*, *Phleum pratense*, and *Fragaria canadensis*) and a comparatively inedible perennial, *Hieracium aurantiacum*, which was resistant to herbivory because of protection by pubescent leaves and stems (Schmitz 1994). Those experiments revealed that nitrogen supply was limiting in the system; increasing nitrogen supply directly enhanced net primary productivity, and plant and herbivore biomass. Moreover, edible and resistant plants were competitors for nitrogen, and herbivores mediated this competitive interaction in ways consistent with assumptions of Leibold's (1989) edibility hypothesis (Schmitz 1994). In cages without nitrogen addition, experimentally changing spider abundance caused a classic "trophic cascade" where herbivore biomass increased and edible plant biomass decreased. Resistant plant biomass increased. This result was entirely consistent with predictions of Leibold's (1989) edibility hypothesis (Schmitz 1994).

Contrary to predictions of Leibold's (1989) hypothesis, a trophic cascade was not observed under enriched conditions. Indeed, the abundance of plants in one-, two-, and three-trophic-level webs was identical despite the fact that carnivores significantly reduced grasshopper abundances (Schmitz 1994). This curious outcome in nitrogen-enriched conditions was, in part, the motivation for the present study.

In the unenriched treatments, the field experiments approximated natural field conditions as the abundances of plants and herbivores in enclosures, in the presence of spiders, were not statistically different from natural field levels (Schmitz 1994). This represents a pulse experiment because the natural field densities were recovered during the course of the experiment. In treatments with nitrogen enrichment, there was a net increase in plant and herbivore biomass (Schmitz 1994). Nitrogen-enriched treatments qualify as a press experiment for two reasons. First, nitrogen enrichment was a bottom-up press as it increased the abundances of all higher trophic levels (Schmitz 1994). Second, the higher abundances of herbivores, relative to natural field conditions, can be considered a top-down press as the effects of higher herbivore abundances are expected to cascade back down the food web. It now remains to identify the degree to which the nitrogen and herbivore presses simultaneously influence food-web dynamics.

I next describe a series of experiments designed to quantify per capita interaction strengths among the herbivore *M. borealis* and the four dominant plant species and the plants and soil nitrogen supply in the old-field study system. I use these data to generate the com-

munity matrix and its inverse in order to derive predictions for the outcome of nitrogen and herbivore press experiments on the plant community. These predictions are then used in the subsequent section to evaluate the results of field experiments in which the plant community was subject to nitrogen and herbivore presses.

#### QUANTIFYING THE COMMUNITY AND INVERSE COMMUNITY MATRICES

The purpose here is to derive a benchmark that can be used to quantify net direct and indirect interactions and identify the directional outcome of the field experiments (i.e., net increase or decrease in species biomass), based on a hypothesized set of species interactions in the experimental old-field system. In essence, the inverse community matrix serves as a tool that can suggest how direct and indirect species interactions shape the dynamics and structure of a food web.

Although it is theoretically possible to derive the inverse community matrix entirely through experimental means (Bender et al. 1984), it can be difficult in practice for multiple species communities. To quantify the inverse matrix experimentally, one must selectively alter the carrying capacities of each species and then measure the net changes in all other species abundances after they have reached a new equilibrium (Bender et al. 1984). The problem is that one cannot know each species' carrying capacity a priori (Bender et al. 1984). Moreover, for an  $n$ -species community, one must conduct  $n$  independent single-species press experiments to derive the entire matrix (Bender et al. 1984). This series of experiments is usually impossible due to logistical limitations.

One empirical solution is to derive an appropriate set of equations that describes the hypothesized species interactions in the food web. The equations can then be parameterized with data from laboratory and field experiments. One then applies conventional analytical techniques (May 1973, Yodzis 1989) to generate the matrix of partial derivatives, i.e., the community matrix ( $A_{ij}$ ), and its inverse from the parameterized set of equations. This is, in effect, a variation of the approach used by Yodzis (1988) to parameterize and obtain the inverses of "plausible" community matrices describing trophic linkages in a collection of published food webs.

#### Hypothesized species interactions

A working hypothesis (Schoener 1993) for interactions in my study system is presented in Fig. 1. I propose that three major types of direct interaction occur among the component species: (1) consumer–resource, or trophic, interactions (i.e.,  $+/-$  interactions); (2) intraspecific interference competition (negative feedback); and (3) interspecific interference competition (i.e.,  $-/-$  interactions). Intra- and interspecific exploitative (consumptive) competition, which are im-

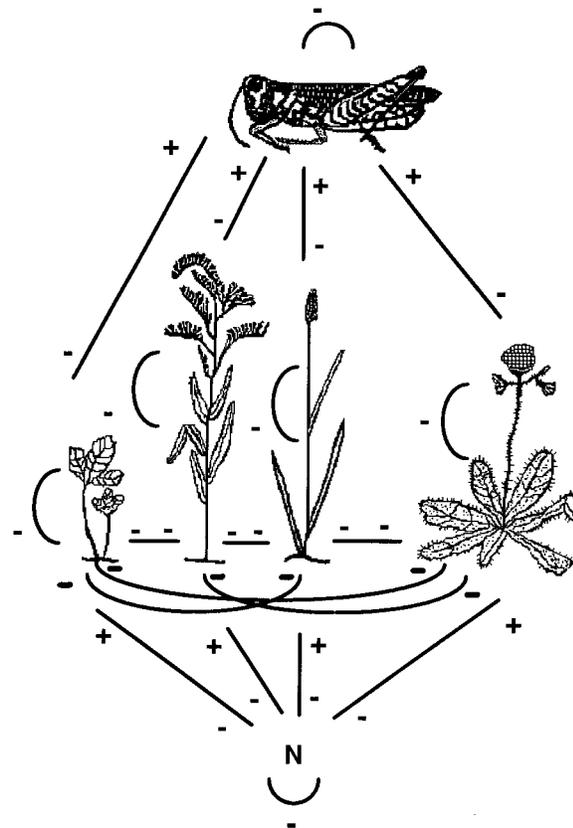


FIG. 1. Hypothesized interactions among grasshoppers (*Melanoplus borealis*), four perennial plants (in order from left to right: *Fragaria canadensis*, *Solidago altissima*, *Phleum pratense*, and *Hieracium aurantiacum*), and nitrogen supply in an experimental old-field food web (Parry Sound, Ontario). Lines joining two species with + and - signs represent consumer–resource interactions. Curved lines with a - sign represent self damping or negative feedbacks.

portant indirect interactions (Yodzis 1988, Connell 1990, Schoener 1993), are implicit among plants in this system as a consequence of each plant species' direct consumer–resource interaction for limiting nitrogen.

The hypothesized food-web linkages can be formalized by a system of equations describing the biomass growth rates of nitrogen ( $N$ ), plant species  $i$  ( $V_i$ ), and herbivores ( $H$ ). I predicted dynamics in terms of population biomass rather than population numbers for practical reasons. Some of the plant species in the study (*Solidago*, *Fragaria*) are clonal or ruderal and it is thus difficult to identify unique individuals in order to assess population numbers.

Given its initial success in predicting some of the dynamics in my study system, I generalized Leibold's (1989) model for herbivore mediation of competition between two plant species to an  $n$ -species case. Moreover, I included an explicit equation for nitrogen dynamics (Abrams 1988, Tilman 1988, Schmitz 1992) as Leibold's (1989) model only embodies nutrient dynamics implicitly through the assumption that nutrients ef-

TABLE 1. Definitions and notation of parameters used in the model to describe food-web dynamics in the old-field study system.

Parameter	Description
$S_N$	Supply rate of soil nitrogen (grams of N per day)
$\mu_i$	Per capita uptake rate of nitrogen by plant species $i$ (fraction of N taken up per gram of plant species $i$ per day)
$a_i$	Conversion of nitrogen into plant biomass (fraction of plant biomass produced per g N taken up)
$\beta_i$	Per capita loss rate of plant biomass due to intraspecific interference competition (fraction of biomass per day)
$\alpha_{ij}$	Per capita loss rate of plant biomass due to interspecific interference competition with members of plant species $j$ (fraction of biomass per plant species $j$ per day)
$f_i$	Per capita loss rate of plant biomass due to herbivory (fraction of plant biomass lost per time per herbivore)
$e_i$	Conversion of plant biomass into herbivore biomass (grams of herbivore biomass produced per gram of plant biomass consumed)
$\beta_H$	Per capita loss rate of herbivores due to herbivore density (fraction of herbivore production lost per day per herbivore)

fect the intrinsic growth rate of plants ( $r$ ) and the level of carrying capacity ( $K$ ). The following set of equations describe the hypothesized (Fig. 1) set of food-web interactions:

$$dN/dt = S_N - N \sum \mu_i V_i \quad (3a)$$

$$dV_i/dt = V_i [a_i \mu_i N - \beta_i V_i - \sum \alpha_{ij} V_j - f_i H] \quad (3b)$$

$$dH/dt = H [\sum e_i f_i V_i - \beta_H H] \quad (3c)$$

where  $S_N$  is the supply rate of soil nitrogen,  $\mu_i$  is the per capita uptake rate of nitrogen by plant species  $i$ ,  $a_i$  is the conversion of nitrogen into plant biomass,  $\beta_i$  is the per capita loss rate of plant biomass due to intraspecific interference competition,  $\alpha_{ij}$  is the per capita loss rate of plant biomass due to interspecific interference competition with members of plant species  $j$ ,  $f_i$  is the per capita loss rate of plant biomass due to herbivory,  $e_i$  is the conversion of plant biomass into herbivore and  $\beta_H$  is the per capita loss rate of herbivores due to herbivore density. For reference, all the parameters used and their definitions are summarized in Table 1. I assume that there is a fixed  $f_i$  for each plant species. This assumes that grasshoppers have a fixed rate of plant consumption across the range of available plant species biomass. This assumption is supported for the grasshopper species as their functional responses for multiple plant resources saturate at very low levels of plant biomass (M. Uriarte, A. P. Beckerman, and O. J. Schmitz, unpublished data).

The model described by Eqs. 3a, b, and c is, at best, a first-order approximation of species interactions in a

food web (Wilbur and Fauth 1990). It is not at all self-evident that this system of equations adequately predicts dynamics even of this comparatively simple food web as quantitative empirical tests of such models are rare. This study represents an opportunity to evaluate the predictive success of such models.

An appropriate first step in using the model to understand press experiments is to parameterize it with field and laboratory data, construct the community matrix, and take its inverse to generate predictions about individual species responses to a press. The next section details how the community matrix was derived empirically and how it was used to provide insight into the outcome of field press experiments at the study site.

#### Quantifying species interactions

According to the working hypothesis of species interactions (Fig. 1) I needed to quantify the following four kinds of interaction in order to predict the outcome of nitrogen and herbivore press experiments: (1) plant–nitrogen interactions, (2) plant–plant interactions, (3) plant–herbivore interactions and (4) herbivore–herbivore feedback.

*Plant–nitrogen interactions.*—I conducted laboratory experiments following the protocol in Schmitz (1994) to quantify the effect of nitrogen supply on plant biomass in the absence of consumers and to quantify the loss of N from the soil. Seedlings of *Hieracium*, *Solidago*, *Phleum*, and *Fragaria* were transplanted from the field to polystyrene containers containing a 2:1 mixture of sterile potting soil and cleaned sand. All seedlings were weighed on an electronic balance prior to planting in the pots. I converted seedling wet mass to dry mass using predetermined wet mass/dry mass ratios for each seedling species. These masses were also converted to masses of above- and below-ground parts based on predetermined calibrations for each species.

Seedlings were planted one per container and were grown under ambient light and with unlimited water. I measured plant growth in pots supplied with nitrogen fertilizer (Treatment) relative to plants that received no fertilizer (Control). An equal amount of  $\text{NaNO}_3$  fertilizer was delivered in each week of a 6-wk growing period to provide each plant the equivalent of a total supply rate of  $15 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$  (see *Field press perturbation experiments*, below). I randomly assigned seedlings to a particular treatment. The treatment and control were each replicated 8 times. The seedlings were grown until they reached a steady-state height. I measured height growth in each cup every 2 d using a ruler placed at the soil surface. The experiment was terminated once there was no increase in seedling height growth in three consecutive sampling periods. Seedlings were then removed from the pots, dried at  $60^\circ\text{C}$ , clipped to separate above- and belowground parts, and weighed. Seedling biomass growth rate was measured as the difference between aboveground seedling mass

TABLE 2. Parameter estimates for the equations describing the hypothesized direct food web interactions in the Parray Sound, Ontario, Canada, old-field study system. Values are mean  $\pm$  1 SE,  $n = 8$  replications. For parameter definitions, see Table 1.

Species $i$	$\mu_i$	$a_i$	$\beta_i$	$\alpha_{ij}$		
				$j = Hieracium$	$j = Solidago$	$j = Phleum$
<i>Hieracium</i>	0.183 $\pm$ 0.025	1.02 $\pm$ 0.13	0.002 $\pm$ 0.0002	...	0	0
<i>Solidago</i>	0.042 $\pm$ 0.0003	1.05 $\pm$ 0.196	0.003 $\pm$ 0.0007	0	...	0
<i>Phleum</i>	0.095 $\pm$ 0.013	1.03 $\pm$ 0.42	0.005 $\pm$ 0.0007	0.012 $\pm$ 0.0016	0.017 $\pm$ 0.0025	...
<i>Fragaria</i>	0.336 $\pm$ 0.025	1.03 $\pm$ 0.009	0.003 $\pm$ 0.0004	0.018 $\pm$ 0.0024	0.029 $\pm$ 0.0065	0.010 $\pm$ 0.002

at the beginning of the experiment and at steady-state height divided by the time to reach steady state. I quantified growth of only the aboveground parts because this quantity was the response variable measured in the field experiments.

I also collected soil samples from each of the polystyrene containers receiving N fertilizer. The samples were analyzed with an HCN autoanalyzer to quantify the concentration of N remaining in the soil after each seedling reached its steady-state height.

*Plant-plant interactions.*—The within- and between-plant species interactions assumed by the hypothesis must be due to direct interference competition if they appear as an element of the community matrix. The interaction strengths must be quantified in the absence of N fertilizer, otherwise the measurement would be confounded by consumptive competition for soil N, an indirect effect that does not appear as an element of the community matrix.

I used a laboratory experiment to quantify the strength of negative feedback, in the absence of N enrichment, in each of the four dominant plant species. I conducted a target-neighbor experiment (Goldberg 1987, Goldberg and Barton 1992) in which seedlings of *Hieracium*, *Solidago*, *Phleum*, and *Fragaria* were weighed and transplanted using the protocol described above. Target seedlings either were planted individually, with an individual conspecific or with an individual heterospecific and they were grown under ambient light and with unlimited water. I assigned seedlings randomly to a particular treatment. Each target-neighbor combination was replicated 8 times. The seedlings were grown until they reached a steady-state height and the experiment was terminated following the protocol described above.

This measure of negative feedback represents a conservative estimate of per capita reduction in plant performance due to a neighbor as it only focuses on one component of plant growth, plant biomass production. Another component, seed production, could not be measured because most individuals did not produce flowers during the course of the experiment. This is not a pathological problem, however, as the field press experiments were conducted within only one season of each year. I explored only within-season dynamics because previous experiments (Schmitz 1993, 1994) indicated that plant biomass reaches an equilibrium with-

in this temporal window satisfying an important assumption of the inverse-community-matrix approach. Carrying out longer term press experiments across seasons would have required an understanding of seed production dynamics. I opted to examine dynamics within a shorter term because the objective was to evaluate the outcome of press experiments in conditions where I could disregard potential interannual variation unrelated to the press. This approach still lends itself to studying effects of interspecific interactions in a moderately complicated network by focusing on within-season interactions even though the range of the effects of those interactions are simplified. If the inverse-matrix approach offers sufficient insight into food-web interactions, a logical next step would be to conduct such experiments over the longer term.

*Plant-herbivore interactions.*—I conducted a series of feeding trials following the protocol in Schmitz (1994) to estimate the loss rate of plant tissue to herbivores. A known quantity of plant leaves was presented to 16 adult *M. borealis* housed individually in 1-L glass jars covered with nylon screening. I presented each grasshopper a sample of each plant species separately. Grasshoppers were allowed to feed on plant samples for a 20-min period. I then measured the area of plant tissue removed by the herbivore during this period. This area was converted to dry-mass consumption based on previously determined dry mass-plant tissue area relationships for each plant species. I used the area of plant tissue consumed rather than wet mass to avoid biases due to leaf desiccation during the feeding trials. The feeding trials were replicated 3 times for each individual grasshopper to obtain a representative average for each individual.

Plants benefit herbivore populations among seasons by providing them with the nutrition needed for maintenance, growth, and reproduction; the conversion of food intake into herbivore biomass must be estimated. In this study, I was concerned only with herbivore impacts within a season. The grasshopper species used in this study reproduces at the end of the plant growing season (Helfer 1987) so, because of the time span of the press experiment, and trophic impacts within that time period, the only life-history components of concern were body growth and survival. Data for conversion of plant biomass into herbivore biomass were obtained from a previous experiment (Schmitz 1994). In

TABLE 2. Continued.

$\alpha_{ij}$		
$i = \textit{Fragaria}$	$f_i$	$e_i$
$0.002 \pm 0.0003$	$0.08 \pm 0.02$	$0.0034 \pm 0.0001$
0	$0.13 \pm 0.07$	$0.0030 \pm 0.0001$
$0.002 \pm 0.0002$	$0.10 \pm 0.09$	$0.0031 \pm 0.0001$
...	$0.05 \pm 0.02$	$0.0028 \pm 0.0001$

that study, I measured both the net increase in herbivore biomass due to nitrogen enrichment (g herbivore biomass/g N) and the net nutritional value of each plant species (g digestible N per 100 g of dry plant tissue) following a nitrogen enrichment experiment in which plants were provided with the equivalent of  $15 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$  of  $\text{NaNO}_3$ . The nutritional values for each species were multiplied by the herbivore growth response to estimate the conversion of a unit of plant-species- $i$  biomass into herbivore biomass.

*Herbivore negative feedback.*—The grasshopper genus used in this study exhibits seasonal life cycles in which nymphs emerge in spring and grow through 4–5 instar stages to adulthood during the course of the summer (Vickery and Kevan 1967, Helfer 1987). Adults mate in late summer and lay eggs that diapause over the winter (Vickery and Kevan 1967, Helfer 1987). In most cases the adult grasshoppers produce more individuals than can be supported in the environment the following spring (Belovsky and Slade 1993, 1995). Consequently, the grasshoppers exhibit significant declines in abundance throughout the summer, reaching distinct steady-state densities at specific instar stages, e.g., instar I–III, instar IV–V, and adults (Ritchie and Tilman 1992, Belovsky and Slade 1993, 1995, Schmitz 1993, 1994). Thus, mortality due to intraspecific competition seems to be an important dynamical interaction during the spring-summer season (Belovsky and Slade 1995).

I also extensively sampled grasshopper abundances in relation to food resources at the field site. This was followed by a census regression analysis (Schoener 1974, Crowell and Pimm 1976, Rosenzweig 1987) in which I fit to the data mechanistic logistic and non-logistic growth equations that describe the relationship between food resources and consumer population density (Schoener 1973). The analysis indicated that the population growth of *M. borealis* was most consistent with a logistic growth model, which indicates that there is indeed a negative feedback on the population resulting from increased grasshopper density (O. J. Schmitz, unpublished data) as hypothesized (Fig. 1).

I conducted an experiment to quantify the magnitude of the density-dependent feedback on a per capita basis. The experiment was conducted in a  $50 \times 50 \text{ m}$  area within the field site using standard  $0.1 \text{ m}^2 \times 1 \text{ m}$  enclosure cages (Ritchie and Tilman 1992, Belov-

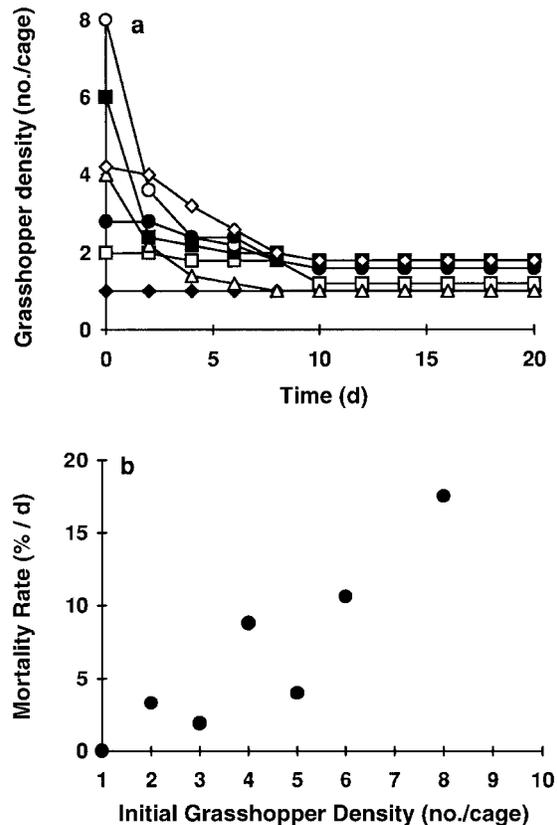


FIG. 2. (a) Decline in grasshopper abundances to steady state for different starting densities in experimental cages in the old-field environment. (b) Mortality rate of grasshoppers to the steady state in relation to different starting densities. The data indicate linear density-dependent mortality within the grasshopper population. The data are used to estimate the strength of the negative feedback in the herbivore population.

sky and Slade 1993, 1995, Schmitz 1993, 1994). Cages were constructed with aluminum screening and fastened at the base to a  $126 \times 10 \text{ cm}$  strip of aluminum sheet metal. Cages were secured by sinking the sheet metal beneath the soil surface and by fastening the sides of the cages to wooden stakes. The cages were separated by  $\approx 1.5 \text{ m}$  and were arrayed in a randomized-block experimental design consisting of five blocks with seven cages per block. I stocked late-instar and adult grasshoppers (the stages most likely to have an effect on plant biomass [Onsager 1983] and therefore the stages stocked in the field press experiments) to the cages at the following initial densities: 1 (density-independent control), 2, 3, 4, 5, 6, and 8 grasshoppers. Each of the seven starting density treatments was replicated 5 times, with one replicate per block. Mortality of grasshoppers was measured every 2 d by censusing all grasshoppers in each enclosure cage.

TABLE 3. Empirically derived community matrix for the Parry Sound, Canada, old-field study system based on estimated per capita interaction strengths among soil nitrogen supply, the four dominant old-field plant species, and the dominant grasshopper herbivore. Values are mean  $\pm$  1 SE,  $n = 8$  replicates.

	Nitrogen	<i>Hieracium</i>	<i>Solidago</i>	<i>Phleum</i>
Nitrogen	-1.13	-1.72 $\pm$ 0.24	-0.55 $\pm$ 0.056	-1.25 $\pm$ 0.0169
<i>Hieracium</i>	0.541 $\pm$ 0.068	-2.41 $\pm$ 1.61	0	0
<i>Solidago</i>	0.124 $\pm$ 0.023	0	-0.51 $\pm$ 0.042	0
<i>Phleum</i>	0.117 $\pm$ 0.042	-0.0144 $\pm$ 0.003	-0.0204 $\pm$ 0.0017	-1.15 $\pm$ 0.17
<i>Fragaria</i>	0.369 $\pm$ 0.034	-0.0198 $\pm$ 0.0018	-0.0319 $\pm$ 0.0033	-0.011 $\pm$ 0.001
<i>Melanoplus</i>	0	0.00781 $\pm$ 0.0002	0.0109 $\pm$ 0.0029	0.0003 $\pm$ 0.0001

### Data analyses and results

Statistical analyses of all data were performed using SYSTAT for Windows version 5 (Wilkinson 1992). I used one- and two-sample  $t$  tests to test for significance of treatments on species interactions. All proportional data were subject to an arcsine-square-root transformation prior to statistical analyses. Analyses of the significance of treatment effects was a crucial first step because it is not appropriate to parameterize the community matrix without such an assessment. This requirement is because any failure to detect a significant species interaction would require updating the working hypothesis (Fig. 1) before the community matrix could be parameterized with appropriate estimates of per capita interaction strengths.

Parameter values for Eqs. 3a–c are presented in Table 2. These values quantify plant–nitrogen interactions, intra- and interspecific interference among plants, and plant–herbivore interactions. Data are presented for those interactions that were found to be statistically significant, i.e., either significantly different from zero or a significant difference between treatment means at  $P < 0.05$ . This analysis revealed that several interspecific interference interactions among plants that were originally hypothesized to occur (Fig. 1) were not statistically significant (Table 2).

*Within-herbivore population interactions.*—All grasshopper populations in the experimental cages, save the density-independent control, declined to a similar steady-state density ( $1.4 \pm 0.13$  [mean  $\pm$  1 SE],  $n = 6$  treatments). This steady-state density was independent of starting conditions (Fig. 2a).

I estimated the mortality of grasshoppers in consecutive sampling periods during the course of their decline to steady state using the formula  $1 - p(s)$ . The probability of survival,  $p(s)$ , was estimated by dividing the density in time period  $t$  by the density in time  $t - 2$  (Fig. 2). I used percentage survival to standardize for different starting densities. Percentage mortality was regressed on time for each initial density treatment respectively to generate a regression coefficient that quantified mortality rate to the steady state (percentage mortality per unit time). I then regressed these coefficients against starting density to quantify the relationship between mortality rate and starting density.

Mortality rate was found to be linearly related to starting density ( $y = 0.023x - 0.026$ ,  $r^2 = 0.83$ ,  $P \leq 0.01$ ,  $df = 1, 5$ ), confirming that there was density-dependent mortality in the caged populations (Fig. 2b). The slope of this equation (0.023) yields an estimate of the average per capita loss rate of herbivores due to herbivore density ( $\beta_H$ ).

### Per capita interaction strengths and the community matrix

Once parameterized, Eqs. 3a–c were solved analytically to estimate (1) equilibrium nitrogen concentration, plant species biomass, and herbivore biomass and (2) the partial derivatives that incorporate the equilibrium values to create the community matrix. The parameterized community matrix is presented in Table 3. The values are a quantitative representation of all direct food web linkages and negative feedback. It appears that no single species is expected to have a dominant direct effect on the food web as the magnitude of trophic linkages and interference interactions, respectively, are similar for all species (Table 3).

### Inverse community matrix

The negative inverse of the parameterized community matrix summarizes the outcomes of all possible press experiments in the food web described in Fig. 1. The elements of the inverse community matrix give the net change in equilibrium density of a particular species, the difference between equilibrium density before and after the press (Bender et al. 1984). The signs of the inverse matrix elements indicate the direction of the outcome of the press; e.g., if  $-(A^{-1})_{ij} > 0$  then the press will cause an increase in the target species. The elements of the negative inverse matrix also quantify the net effects of species  $i$  on species  $j$  given the host of direct and indirect interaction pathways that link the two species. It is important to realize that predictions about experimental outcomes based on the inverse matrix must account for *all* interaction pathways in the hypothesized food web (Fig. 1), regardless of which single component is being pressed. For instance, the effect of nitrogen on each plant species must account for the indirect pathways through the herbivore trophic level. The effect of a herbivore press on plants must account for interaction pathways that pass through the

TABLE 3. Continued.

<i>Fragaria</i>	<i>Melanoplus</i>
$-4.44 \pm 0.325$	0
$-0.0058 \pm 0.0001$	$-0.230 \pm 0.06$
0	$-0.364 \pm 0.20$
$-0.0024 \pm 0.0002$	$-0.12 \pm 0.14$
$-4.31 \pm 0.071$	$-0.055 \pm 0.02$
$0.0002 \pm 0.00001$	$-0.0373 \pm 0.002$

soil nitrogen node of the food web. This requires using the entire set of community-matrix elements to predict the outcome of separate nitrogen and herbivore press experiments.

The elements of the community matrix contain a degree of random variation (Table 3) that could lead to uncertainty in the predicted outcome of an experiment. The implication of this is that the outcome of a press in any single replicate or experiment could be opposite to the expected (mean) direction (Yodzis 1988, Schoener 1993). More importantly, if the variation is sufficiently large and the mean response is weak, i.e., a high proportion of replicates are predicted to respond opposite to the mean direction, one would predict that there will be little or no statistically significant effect of a press. Consequently, the inverse community matrix potentially can lend tremendous insight into why a particular treatment may have failed to elicit a statistically detectable response.

I conducted a Monte Carlo simulation to generate the mean and standard error for each element of the inverse community matrix. I used an algorithm programmed in Mathematica for Windows version 2.2.3 (Wolfram 1993). The algorithm generated a normal distribution for each element of the community matrix respectively using the means and standard errors (converted to standard deviation) presented in Table 3. In each run of the Monte Carlo simulation, a single value was randomly sampled from the distribution for each community-matrix element. The set of values was used to construct a new community matrix. The negative of the inverse of the community matrix was then taken. This was repeated 100 times to generate the mean and standard error for each element of the inverse matrix.

#### *Predictions for press experiments*

The predicted outcomes of a nitrogen- and herbivore-press experiment, generated by the Monte Carlo simulation, are presented in Table 4. The predictions are represented by the mean and standard error corresponding to the effect on each of the four plant species of an increase in nitrogen supply only (nitrogen press) and the effect of an increase in herbivore abundance only (herbivore press).

*Nitrogen-press predictions.*—The values of the negative inverse matrix predict that a fixed, elevated nitrogen supply should, on average, increase (have a net

positive effect on) the biomass of plant species in the food web (Table 4). All plant species, save *Hieracium*, are expected to have statistically significant responses to a nitrogen press.

*Herbivore-press predictions.*—The negative inverse matrix predicts that a herbivore press should, on average, decrease the biomass of *Hieracium*, *Solidago*, and *Phleum* as expected from consumer–resource interactions (Table 4). The net effects of a grasshopper press on *Fragaria* is an increase in biomass, indicating that herbivores in this system are predicted to act as net indirect mutualists to *Fragaria*. This is an example of directional indeterminism discussed by Yodzis (1988), i.e., addition of a consumer results in an increase rather than decrease in prey abundance. In all cases, however, a grasshopper press is predicted not to have a statistically significant effect on the plant species (Table 4).

#### FIELD PRESS PERTURBATION EXPERIMENTS

The effects of nitrogen supply and herbivory on plants were examined by a factorial experiment that manipulated N supply rates and selectively excluded herbivores. It is noteworthy that in order to test the predictions of the inverse matrix one must use the proper experimental controls. The logical control in a conventional factorial enclosure experiment that manipulates N supply and herbivory is a set of enclosures that receive neither nitrogen nor herbivores. However, a systematic evaluation of the effects of nitrogen and herbivore presses requires that one account for the interaction pathways through the nutrient and herbivore trophic levels, so one or the other trophic level must be included in the control treatment, depending on the type of press. Thus, a control that excludes both treatments (i.e., both trophic levels) is inappropriate for the present evaluation.

The appropriate controls for evaluating predictions must keep the effects of nitrogen constant in a herbivore press and the effects of herbivores constant in a nitrogen press. These controls then become: (1) Control for the herbivore press—one conducts a nitrogen press and completely excludes herbivores and (2) Control for the nitrogen press—herbivores are allowed to exist at equilibrium levels; nitrogen is not added to the experimental cages. The treatment in this case is a simultaneous nitrogen and herbivore press where nitrogen is added to the system and herbivores and plants are allowed to reach a new equilibrium.

#### *Methods*

I conducted independent press experiments in 1992 and 1993 in a 50 × 50 m area within the field site using the standard 0.1 m<sup>2</sup> × 1 m enclosure cages described above. The cages were separated by ≈1.5 m and were arrayed in a randomized-block experimental design consisting of eight blocks with three cages per block. Each cage within a block was randomly assigned to

TABLE 4. Predicted outcome of nitrogen- and herbivore-press experiments on plant species biomass in the Parry Sound, Canada, old-field study system. Predictions represent the net difference between steady-state plant species biomass in the absence and presence of a nitrogen or herbivore press. Predicted responses were derived by a Monte Carlo simulation that generated 100 inverse community matrices.

Experiment	Species	Predicted response ( $\bar{X} \pm 1 \text{ SE}$ )	<i>t</i>	df	<i>P</i>
Nitrogen press	<i>Hieracium</i>	0.033 ± 0.107	0.31	99	NS
	<i>Solidago</i>	0.111 ± 0.036	3.08	99	<0.01
	<i>Phleum</i>	0.088 ± 0.023	3.82	99	<0.01
	<i>Fragaria</i>	0.050 ± 0.007	7.14	99	<0.01
Herbivore press	<i>Hieracium</i>	-3.40 ± 2.23	1.52	99	NS
	<i>Solidago</i>	-7.37 ± 25.31	0.29	99	NS
	<i>Phleum</i>	-3.66 ± 3.15	1.16	99	NS
	<i>Fragaria</i>	0.45 ± 0.47	0.95	99	NS

either a nitrogen press (herbivore control), a herbivore press (nitrogen control) or a simultaneous nitrogen-herbivore press.

**Nitrogen supply.**—Based on previous experiments at the study site (Schmitz 1994) that found that nitrogen was limiting old-field plants, I supplied nitrogen fertilizer at a rate of 1.5 g·cage<sup>-1</sup>·yr<sup>-1</sup>. I used commercial NaNO<sub>3</sub> fertilizer, applied by broadcasting it dry onto the cage bottoms four times at 7-d intervals. The fertilizer supply equaled an application rate of 15 g·m<sup>-2</sup>·yr<sup>-1</sup>. This was within the range utilized in previous studies on old-field plant communities (Tilman 1984, Berendse and Elberse 1990, Wilson and Tilman 1991).

**Herbivore stocking density.**—I stocked five late-instar *Melanoplus borealis* per cage. Grasshoppers were caught within the field site and stocked into the cages within 1 h of capture to minimize stress due to handling. Grasshoppers were stocked at levels higher than the expected cage density (e.g., 5.5 grasshoppers/m<sup>2</sup>) because this would cause their numbers to decline toward a steady state set by the nutrient supply rate and, accordingly, abundance of vegetation (Ritchie and Tilman 1992, Schmitz 1993, 1994). This method of stocking was essential for two reasons. First, a requirement of the inverse-community-matrix approach is that the system reach a steady state. Second, there was no a priori way of knowing appropriate grasshopper densities for the background conditions in each cage. Stocking all cages at predetermined average field or cage levels and maintaining densities there is not appropriate because it could cause artificially high resource limitation in some cages and unrealistically low levels in others. The consequence of stocking at fixed average field densities could be that the plant and herbivore communities might never reach a steady state in the enclosures.

All caged grasshoppers were censused every 2 d to monitor natural survivorship over the course of the field experiment. I terminated the experiment once adult grasshoppers began to die off rapidly due to senescence. The onset of senescence (as opposed to mortality

due to cage effects) was confirmed by comparing changes in grasshopper densities in cages with changes in densities in the field. Field densities were measured using periodic catch-effort surveys (Krebs 1989) in which grasshoppers were caught, within a portable 10 × 10 m enclosure in the vicinity of the experimental site, using a sweep net. This ensured that the experiment covered the complete life-span of *M. borealis* from late juvenile instar to adult (the stages having the greatest potential impact on plants [Onsager 1983]). Termination of the experiment was also coincident with the onset of senescence of *Hieracium*, *Solidago*, *Phleum*, and *Fragaria*.

The responses of the plant species under different treatments were measured by clipping all aboveground live vegetation within each cage at the soil surface. The plant material was sorted to species, dried at 60°C for 48 h, and weighed.

#### Data analyses and results

Statistical analyses of all data were performed using SYSTAT for Windows version 5 (Wilkinson 1992). I conducted a factorial ANOVA on data for each plant species using the GLM module where the factors were blocks and year. There were no significant differences among blocks (all ANOVAs *P* > 0.10, df 7, 37) or years (all ANOVAs *P* > 0.10) so the data were pooled for both years in all subsequent analyses. Because there was a matched treatment and control in each experimental block, I conducted paired *t* tests to evaluate the effects of nitrogen and herbivore presses on each plant species.

The effect of a nitrogen press was evaluated by comparing the difference between plant species biomass in enclosures under a herbivore press only (control for the nitrogen press) with enclosures receiving both a nitrogen and herbivore press (treatment). For all four species, the sign of the mean difference was positive, indicating that N, on average, enhanced plant biomass (Table 5). This is consistent with predictions from the negative of the inverse matrix (Table 4). Except for *Hieracium*, all species exhibited significant responses

TABLE 5. Observed outcome of nitrogen- and herbivore-press experiments on plant species biomass in the Parry Sound, Canada, old-field study system. The values represent the net differences in steady-state plant biomass between control and press conditions. Data are means  $\pm$  1 SE.

Experiment	Species	Observed response ( $\bar{X} \pm 1$ SE)	<i>t</i>	df	<i>P</i>
Nitrogen press	<i>Hieracium</i>	0.03 $\pm$ 0.107	0.31	15	NS
	<i>Solidago</i>	1.11 $\pm$ 0.365	3.04	15	<0.01
	<i>Phleum</i>	0.95 $\pm$ 0.52	1.83	15	<0.05
	<i>Fragaria</i>	0.44 $\pm$ 0.16	2.75	15	<0.01
Herbivore press	<i>Hieracium</i>	-0.02 $\pm$ 0.39	0.05	15	NS
	<i>Solidago</i>	-0.90 $\pm$ 0.55	1.64	15	NS
	<i>Phleum</i>	-0.59 $\pm$ 0.57	1.04	15	NS
	<i>Fragaria</i>	0.20 $\pm$ 0.20	1.00	15	NS

to the nitrogen press (Table 5), again, completely consistent with predictions of the inverse community matrix (Table 4).

The effect of a herbivore press was evaluated by comparing the difference between plant species biomass in a nitrogen press only (control for the herbivore press) with enclosures receiving both a nitrogen and herbivore press (treatment). The signs of the mean difference were negative for *Hieracium*, *Solidago*, and *Phleum*, consistent with predictions (Table 5). Moreover, the experiment detected a sign mutualism between herbivores and *Fragaria*, consistent with predictions of the inverse community matrix (Table 4). None of the plant responses were significant, however (Table 5), again consistent with predicted outcomes based on the inverse community matrix (Table 4).

There was a good match between predictions of the inverse community matrix for the likelihood of a statistically significant experimental outcome and observed statistical outcome of the field experiments (cf. Tables 4 and 5). However, the inverse community matrix was less successful at predicting the exact magnitude of the net changes in plant species biomass. The model under-predicted the effects of N on plant species and over-predicted the effects of herbivores on plants (cf. Tables 4 and 5). It appears then that the best insight that the inverse community matrix can offer for this study is the likelihood of a statistically significant outcome of a field press experiment. Nevertheless, this result is extremely encouraging for community ecology given that the food-web model represented by Eq. 3 is, at best, a first-order approximation of community dynamics.

It is curious why the majority of plants showed significant responses to the nitrogen press and yet no significant response to the herbivore press. One reason for the difference between the press experiments may have been the errors associated with model predictions were two- to three-fold higher in the herbivore press than in the nitrogen press (Table 4). The implications of this is that a high proportion of replicates of an herbivore press are expected to respond opposite in direction to the mean (expected) response. To evaluate this in more

detail, I compared the frequency of all 16 experimental replicates that responded in the predicted direction with expected frequencies from the inverse community matrix. The means and standard errors of the inverse matrix, generated by the Monte Carlo simulation, could be used to calculate the expected proportion of times a plant species should respond opposite to the mean. However, these data yield a continuous distribution, whereas the data from the experiment are discrete. Consequently, differences between predicted and observed frequencies could arise simply as an artifact of comparing frequencies from a discrete and a continuous distribution.

I generated a discrete distribution of predictions using a modified version of the Monte Carlo simulation algorithm described above (see *Quantifying the community . . . : Inverse community matrix*). I ran a sequence of Monte Carlo simulations in which I obtained 16 separate inverses of the community matrix to represent 16 independent replicates of an experiment. For each species, I calculated the proportion of the 16 replicates in which the sign was the same as the predicted mean response. This "experiment" was repeated 10 times to generate a mean and standard error in predicted frequency.

The predicted and observed frequencies are presented in Table 6. The predicted frequencies are presented as the 95% confidence interval in Table 6. In all cases, except *Solidago* and *Hieracium* in the nitrogen press, the range-of-frequency values generated from the Monte Carlo simulation approximated the observed frequencies (Table 6), lending further support to the interpretation that the weak, mean responses of plants to a herbivore press was due to the high degree of uncertainty about the directional outcome of the press.

In summary, the inverse matrix offered good qualitative insight into the outcome of the nitrogen and herbivore press experiments. I was able to anticipate correctly the directional (sign) changes and the lack of quantitatively significant responses by individual plant species to nitrogen and herbivore presses.

TABLE 6. Predicted and observed proportions of 16 replicates in which plant species responded in the expected direction following nitrogen- and herbivore-press experiments in the Parry Sound, Canada, old-field study system. The analysis offers insight into the degree of directional determinacy in the outcome of field press experiments.

Experiment	Species	Frequency	
		Predicted <sup>†</sup>	Observed
Nitrogen press	<i>Hieracium</i>	0.93–0.83	0.63
	<i>Solidago</i>	0.77–0.54	0.94
	<i>Phleum</i>	0.79–0.65	0.67
	<i>Fragaria</i>	0.92–0.69	0.63
Herbivore press	<i>Hieracium</i>	0.53–0.34	0.50
	<i>Solidago</i>	0.73–0.60	0.73
	<i>Phleum</i>	0.63–0.44	0.63
	<i>Fragaria</i>	0.64–0.53	0.63

<sup>†</sup> 95% confidence intervals.

### DISCUSSION

The inverse-community-matrix method offers quantitative estimates of the net effects of all species presses on all other species in the old-field food web via all direct and indirect interaction pathways. A qualitative representation of the strengths of those interactions is presented in Fig. 3b. A revised representation of the initial hypothesis for interactions, based on empirical measures of direct effects in the field system (Table 3), is presented for comparison (Fig. 3a). There are several patterns that can be derived from the comparison of the two food-web diagrams in Fig. 3 that have important implications for predicting the outcome of field press experiments. First, there is a greater variety of interactions predicted by the inverse community matrix than by the community matrix. These include indirect mutualism (+/+), positive feedback (+), and sign of consumer–resource interactions (+/–) among competitors in the same trophic level and between non-adjacent trophic levels. Second, the emerging net direct and indirect effects in the inverse community matrix both outnumber and outweigh in strength the direct effects quantified in the community matrix. Community ecological theory makes it clear that this kind of scenario could increase the uncertainty in the outcomes of press experiments (Yodzis 1988, 1989, Pimm 1993). The food-web diagram (Fig. 3a) also suggests that species that are not in adjacent trophic levels can have a strong indirect effect on each other as a consequence of interacting directly with species in adjacent trophic levels (e.g., note the comparatively strong indirect mutualistic interaction between herbivores and nitrogen supply). Again, theory suggests that it will be difficult to understand the influence of one species on another in a food web solely through experimentation when faced with this kind of scenario (Schoener 1993). Given this bewildering complexity in food-web interactions, can ecologists hope to predict the outcome of perturbations on natural systems?

I suggest, based on the promising results from field

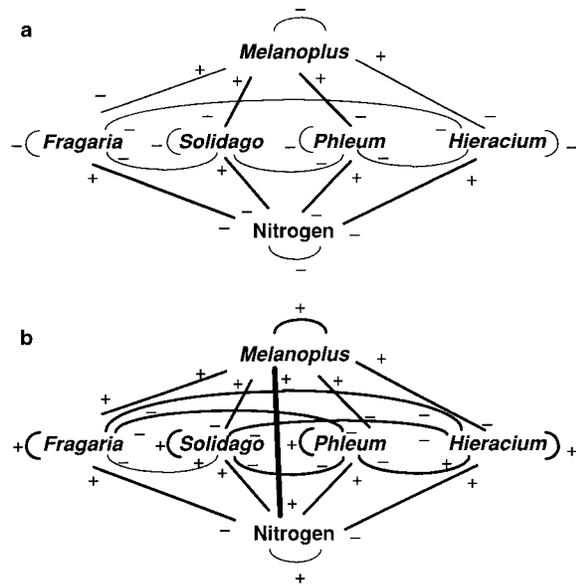


FIG. 3. Summary of (a) direct interactions among all species in the experimental food web, based on the measured community matrix, and (b) net direct and indirect interactions among all species as revealed through the negative inverse of the community matrix. Lines joining two species with + and – signs represent direct (adjacent trophic levels) consumer–resource interactions or the signs of within-trophic-level interactions; lines with two minus signs represent net direct and indirect interspecific competition; and lines with plus signs (one or two) represent indirect mutualisms. The magnitude of net direct and indirect interaction strength is indicated qualitatively by the thickness of lines joining any two species.

experiments in this study, that there may be considerable hope despite the high potential for indirect interactions swamping out main effects from direct interactions. However, this requires that one combine mathematical theory with field experimentation (sensu Kareiva 1989) in order to obtain the appropriate benchmark for evaluating the outcome of field experiments. This need is especially marked in cases where the predicted directional changes could not be derived from intuition or evaluations of direct interaction strengths alone because of the network of direct and indirect pathways through which the effect of one species can pass before it influences another species (Fig. 3).

For example, consider the interaction between grasshoppers and *Hieracium*. In a previous experiment (Schmitz 1994) I demonstrated that in unenriched conditions, grasshoppers mediated competitive interactions between edible plant species (*Solidago*, *Phleum*, and *Fragaria*) and *Hieracium*, which was resistant to herbivores because it possessed an antiherbivore defense. The grasshoppers, through preferential feeding on edible plants, acted as an indirect mutualist to *Hieracium* because they decreased the interspecific competitive effect of the other plants on *Hieracium*. This pattern was not retained under enriched conditions. In-

deed, *Hieracium* was functionally more similar to edible *Solidago* and *Phleum*. The indirect mutualism now occurred between edible *Fragaria* and grasshoppers, a wholly counterintuitive result that was anticipated by the inverse matrix approach. Even more counterintuitive, the presence of trichomes on *Hieracium* did not benefit the plant at the community level in enriched conditions. It is often thought that a plant's ability to resist herbivory is an important way to mediate competition with other plants in the presence of herbivores (Louda et al. 1990, Huntly 1991). The inverse community matrix suggests that, in the field experiment, the ability of *Hieracium* to resist the direct effects of herbivory was offset by the magnitude of indirect plant-species interactions.

The inverse-matrix approach also offered a priori insight into why the herbivore press experiments did not produce statistically significant changes in plant biomass whereas the nitrogen press experiments did. The inverse matrix showed, by way of a quasi "risk analysis" (Monte Carlo simulation) that the outcome of a herbivore press was expected to be far more uncertain than a nitrogen press to the extent, even, that it could be equally likely that a plant species should increase or decrease in response to increased herbivore abundances (Table 6). Again, there was qualitative congruence between predicted and observed probabilities that any single experiment would yield such indeterminate results (Table 6).

This study has important implications for the statistical analysis of data from manipulative experiments. The conventional approach in ecology is to evaluate the statistical significance of the main (treatment) effects and perhaps interactions. Usually, ANOVA or MANOVA is used to test whether a particular treatment had a significant effect on the experimental community (Hairston 1990, Schoener 1993). In this study, such an analysis would result in the conclusion that the nitrogen press would have highly significant effects whereas the herbivore press would have no significant effect on the plant species. The implication of this conclusion for community ecology would be that the system is viewed as being entirely driven by "bottom-up" (McQueen et al. 1986, DeAngelis 1992, Power 1992) processes. However, the inverse matrix offers an alternative, more mechanistic perspective suggesting that the conclusion based on ANOVA would not be correct. Even though herbivores have weak direct effects on any single plant species they propagate very strong indirect interactions among all plant species. Accordingly, herbivores have an extremely strong hand in shaping plant community structure. This suggests that the system is largely "top-down" (DeAngelis 1992, Power 1992) driven but that the top-down effect is distributed indirectly among many pathways, i.e., the direct effects of herbivores are swamped out by the indirect effects (Fig. 3).

This point is illustrated further by mathematically removing the effect of herbivores from the community

matrix (Bender et al. 1984). Removing the influence of herbivores is accomplished by eliminating the row and column elements of the community matrix corresponding to the effects of plants on herbivores and herbivores on plants (i.e., the last row and column of Table 3). The modified matrix allows one to evaluate the effects of nitrogen on plant community structure in the absence of herbivores. The inverse of this modified community matrix predicts that a nitrogen press should have benign effects on the overall organizational structure of the study system. For example, only *Fragaria* was expected to show a strong response to nitrogen, and all plant species were expected to exhibit only weak exploitative (indirect) competition for nitrogen.

Further evidence for top-down control was revealed through a sensitivity analysis of model parameters using the intact community matrix. In the sensitivity analysis, I systematically changed individual community-matrix values by 10% and observed the outcome in the inverse matrix. These small changes in parameter values never caused sign changes in the inverse matrix. Moreover, changes in the magnitude of the off-diagonal elements (i.e., consumer-resource interactions) had little influence on the strength of net effects predicted by the inverse matrix. The strengths of net direct and indirect interactions were most sensitive to the strengths of the negative feedback in nitrogen supply and the herbivore population with the greatest sensitivity in the latter. These are precisely the two factors that modulate the degree of top-down and bottom-up control in the community. Again, this point illustrates that a formal mathematical model of species interactions parameterized with empirical data is a valuable way to augment the statistical interpretation of species interactions in food webs. This issue was also raised previously by Billick and Case (1994) and Wootton (1994b), although it was applied in a somewhat different context.

The analysis of food-web complexity via press experiments and the inverse-community-matrix approach assumes that the system reaches equilibrium before one evaluates the outcome of the experiment. The time required to reach an equilibrium and whether systems do so is a significant point of concern (Yodzis 1988, Pimm 1993, Schoener 1993). The possibility that natural systems do not reach equilibrium would limit the general applicability of the inverse-matrix approach. Although the results of press experiments can be examined when systems exhibit transient dynamics (Yodzis 1988, 1995), one appeal of examining the dynamics of old-field systems with insect herbivores and perennials such as the one used here is that these systems will indeed reach a new steady state within a short time period following a perturbation (Ritchie and Tilman 1992, Belovsky and Slade 1993, 1995, Schmitz 1993, 1994). Consequently, such systems hold much promise to explore the inverse-matrix approach under much greater degrees of species complexity.

There is some pessimism about predicting dynamics

and structure of complex field systems, shared by both Yodzis (1988) and Pimm (1993). They feel that interpreting the outcome of field experiments may be very difficult if not impossible when there is a high degree of variation in parameter estimates and when the strength of indirect effects are larger than direct effects. These are empirical realities that field ecologists are likely to confront when dealing with complex communities, and they are precisely the conditions found in this study system. Despite the high degree of uncertainty in the directional outcome of a particular press, the experimental outcome, in terms of statistical significance, was still predictable. Moreover the location of the significant effect within the community could be identified. If this is true in general, it may require that we consider framing our hypotheses about experimental outcomes not as fixed directional changes but rather as probabilities of change. It would then require a redirection in focus; effort should be directed toward making sense of the variation in outcome of field experiments in addition to understanding only the mean directional outcome (see also Schoener 1993).

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