ELSEVIER

Ecological Modelling 161 (2003) 79–93

ECOLOGICAL MODELLING

www.elsevier.com/locate/ecolmodel

Qualitative predictions in model ecosystems

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Received 4 February 2002; received in revised form 5 August 2002; accepted 19 August 2002

Abstract

We compare qualitative predictions of press perturbation response from community matrix models with those of a range of numerical simulations on the same models. A technique of weighting the proportion of countervailing feedback cycles in qualitative response predictions (weighted predictions) was tested against quantitative predictions from the inverse community matrix. Specifically, in nine each of 5- and 10- variable models (of varying complexity) we randomly assigned quantitative values of interaction strength and measured correspondence with qualitative predictions in terms of response strength and sign. Based on the techniques and analyses presented herein, we report an expanded scope of inference for qualitative models of any size and complexity and conclude that system structure is of overriding importance.

Keywords: Community matrix; Community structure; Indirect effects; Inverse matrix; Press perturbation; Qualitative models

1. Introduction

Despite a long held appreciation for complex webs of interactions between species (Darwin, 1859; Elton, 1927), ecologists “typically study only a handful of species and a single pairwise interaction at any one time” (Kareiva, 1994). Particularly lacking has been an ability to pose critical hypotheses of complex biological systems that are consequential to an expanding environmental crisis (Peters, 1991). This lack undoubtedly can be attributed to a difficulty in quantifying each of the n^2 number of interactions for even a small-sized community matrix model. And while techniques for quantifying species interactions are available (Levins, 1968; Bender et al., 1984; Paine, 1992; Laska and Wootton, 1998), the means to do so are tedious and time consuming. Yet even supposing sufficient time and resources for quantification, analyses would still remain incomplete given the global challenge currently posed by

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PII: S0304-3800(02)00295-8

human dominated ecosystems, which requires consideration of such immeasurable variables as “the social, economic, cultural, and other drivers of human actions” (Vitousek et al., 1997).

One might suppose this dilemma a matter of precision, or lack thereof (Peters, 1991). Precision, however, is neither necessary nor essential to mathematical rigor; its overemphasis in ecological research appears as a manifestation of bias towards classical parametric statistics. This dilemma can be more deeply considered as a syndrome of reductionism, whereby qualitative understanding of the whole system is sacrificed in a quest for precise measurement of component parts (Levins, 1966). And while qualitative approaches can be used to complement, inform, and heuristically guide quantitative approaches in biological systems—as in island biogeography theory—their use in community ecology has remained somewhat limited. We maintain that the current situation is akin to looking for lost keys under a lamppost while suspecting they reside elsewhere in the night. While reductionist techniques are indeed illuminating, what is ultimately needed is a qualitative understanding of the behavior of the whole system to guide one’s research. Underlying our study is the premise that ecological understanding will advance more rapidly by incorporation of qualitative models. We concede, however, that broader acceptance of qualitative models will likely require an appreciation of their validity relative to quantitative models. This study develops criteria to determine a degree of confidence in accepting qualitative predictions from the community matrix.

Here we contrast quantitative and qualitative analyses of community matrix models, and examine the role that system feedback has in system response to perturbations. Examples of particular models will be used to define general concepts and specific measures of qualitative and quantitative response. These concepts and measures will then be applied, with numerical calculations, to an array of 5- and 10-variable models to assess confidence in qualitative predictions, first in terms of response strength or magnitude, and then in terms of response sign. System structure will be seen as a key factor.

2. Quantitative and qualitative analysis of the community matrix

As a descriptor of interactions among species in a community near equilibrium, the community matrix **A**, developed by Levins (1968), is first and foremost a predictive tool. It has been used to predict species richness (Levins, 1968; Vandermeer, 1972), population abundance (Cody, 1974; Yeaton, 1974), response of a community to a change in birth or death rates due to experimental or natural perturbations (Levins, 1979; Bender et al., 1984; Yodzis, 1988; Schmitz, 1997; Bodini, 1998, 2000; Dambacher et al., 1999; Hulot et al., 2000; Loiselle et al., 2000), or natural selection (Levins, 1975), and finally, to determine system stability (May, 1974; Li and Moyle, 1981; Puccia and Levins, 1985; Levitan, 1987; Roxburgh and Wilson, 2000).

The community matrix is potentially a powerful theoretical tool when specified with quantitative interaction terms, whether actually measured or given as plausible estimates. In particular, the inverse of the negative community matrix ($-\mathbf{A}^{-1}$) predicts the equilibrium response of community members following a sustained perturbation (Nakajima, 1992), such as a natural disturbance or experimental manipulation. Quantitative predictions from the inverse, however, have lacked generality and appear to be highly sensitive to the specific values of the a_{ij} interaction coefficients. As a result, inverse matrix predictions have suffered from a high degree of indeterminacy in ecological systems (Yodzis, 1988; Schmitz, 1997). Moreover, properly specifying a community matrix requires an extensive series of n press experiments, each with n measured responses (Bender et al., 1984), which is at best a laborious and time consuming task, and at worst impossible when important variables cannot be measured. The record is slim; we find only two published examples that have applied Bender et al.’s method in natural systems (Schmitz, 1997; Roxburgh and Wilson, 2000), and both of these dealt with relatively simple communities—an old-field food web and university lawn, respectively.

To address generality and circumvent the difficulty of quantitative specification of interaction terms, Levins (1974, 1975), developed a qualitative analysis technique that specifies the community matrix by only the sign (+, −, 0) of the interactions between species. ‘Loop analysis’ interprets signed digraphs of community matrix models to make qualitative predictions of system stability and perturbation response based on the balance of system feedback. Where system feedback is uniformly of the same sign, then the generality of predictions is maintained. Where there is a countervailing balance of feedback cycles, then model predictions are ‘conditional’ and can be expressed in relative terms: e.g. an increase in species x, due to an increase in the production of its prey y, is dependent upon the self-regulation of species z being strong. Interpreting conditional statements can lead to practical insights and identify reasons behind counterintuitive behavior in the system (Lane and Levins, 1977). Such insights are less easily gained from the numerical results of quantitative analyses, where one is left with a single number, the sign of which may or may not be generally consistent (Yodzis, 1988).

A number of approaches have been posed to predict the behavior of ecosystems by collapsing food webs into straight trophic chains. They differ primarily in the degree and placement of self-regulation (Oksanen et al., 1981; Mittlebach et al., 1988; Gleeson 1994), and linearity of interactions (Arditi and Ginzburg, 1989). While useful for framing general ecosystem theory, as in Hairston et al. (1960), straight-chain models have been found to be poor predictors of individual systems. Hulot et al. (2000) falsified these models using Levins’ loop analysis in models explicitly incorporating a diversity of variables at each trophic level.

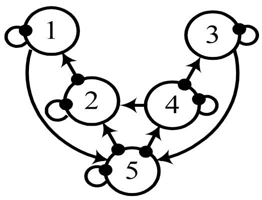
This approach exemplifies qualitative modeling’s strength of accounting for dynamic feedbacks common to biological systems. Moreover, qualitative modeling allows one to incorporate nonbiological variables (e.g. management interventions, economic parameters, etc.) that interact with the natural system. Qualitative modeling thus provides a practical means to rigorously confront complexity in biological systems, and is especially useful where component species and natural history are well known but not quantified. For instance, knowing only simple trophic interactions, Li and Moyle (1981) used qualitative modeling to assess the impact of an introduced zooplankton species in a deep lake system. Loiselle et al. (2000) used qualitative models to develop management and monitoring programs for a large wetland reserve. Incorporating local knowledge and natural history information, they were able to develop scenarios that balanced tradeoffs between tourism and conservation of key species. Dambacher et al. (1999) use qualitative modeling to explain an extensive record of published results pertaining to snowshoe hare, vegetation, and predator interactions in boreal forests, and suggest a critical experiment to falsify alternate models. Bodini et al. (2000) blended human societal variables, such as local tourism and recreation, with parameters of environmental quality in perifluvial wetlands to address long-term sustainability of local economies.

Although qualitative analysis can be a useful technique, in our estimation it has been underutilized. One difficulty with qualitative modeling is the all-or-none aspect of its predictions. Another difficulty is applying Levins’ loop algorithm, which relies upon a graphical interpretation of signed digraph models. For large (>5 variables) or complex systems (i.e. high connectance), signed digraph analysis grows not just exponentially, but factorially. Moreover, the multiple contingencies that arise in conditional statements from large complex models can defy practical interpretation, leading to overwhelming ambiguity. We have recently addressed these difficulties by reformulating Levins’ loop algorithm with equivalent matrix algebra equations (Dambacher et al., 2002). Our aim in surmounting these difficulties has been to extend qualitative analysis of the community matrix to large complex ecological systems.

3. Complementary feedback cycles

The computations required in the qualitative assessment of system response to perturbation are based upon feedback ‘loops’ or cycles. Levins (1974, 1975) originally coined the term ‘loop’ but now favors the term ‘cycle’ for its original and broader usage in graph theory (Levins and Puccia, 1988). In Levins’ graphical algorithm, a feedback cycle is $n-1$ in length and composed of the path of direct links between variables in a system and the indirect influence of complementary subsystems. In this work, we have extended the use of the word ‘complementary’ to mean more than just the influence of a subsystem, but to also describe an entire feedback cycle. Complementary feedback cycles are the vehicle by which the direct interactions detailed in the community matrix are translated, through matrix inversion, into the equilibrium response of community members. They constitute both the direct and indirect effects transmitted between variables in a system due to a sustained change in a growth parameter of a system variable, and are determined solely by the network properties of a system—*system structure*. The countervailing balance of these cycles determines the direction of change (+, −, 0) in the abundance of variables when the system is at or near equilibrium.

Examples of complementary feedback cycles are provided here by a plankton community model from Stone (1990) depicted by a signed digraph and a symbolically specified community matrix:



$$\mathbf{A}=\begin{bmatrix} -a_{1,1} & a_{1,2} & 0 & 0 & 0 \\ -a_{2,1} & -a_{2,2} & 0 & a_{2,4} & a_{2,5} \\ 0 & 0 & -a_{3,3} & a_{3,4} & 0 \\ 0 & 0 & -a_{4,3} & -a_{4,4} & a_{4,5} \\ a_{5,1} & -a_{5,2} & a_{5,3} & -a_{5,4} & -a_{5,5} \end{bmatrix}$$

Signed digraphs portray the network properties of a community matrix by linking system variables with arrows (→) where there is a positive effect of one variable upon another and filled circles (⊸) where the effect is negative. Self-effects are shown by links originating and ending in the same variable and are typically negative (↻), as in self-regulated variables or those with density dependence, but can also be positive (↻) where variables are self-enhancing.

For the plankton model in Eq. (1), a positive input to variable 4 elicits a change in the abundance of variable 2 composed of three complementary feedback cycles, each with link lengths equaling four: $+\boldsymbol{a_{2,4}}\; a_{1,1}\; a_{3,3}\; a_{5,5} - \boldsymbol{a_{2,5}}\; \boldsymbol{a_{5,4}}\; a_{1,1}\; a_{3,3} + \boldsymbol{a_{2,5}}\; \boldsymbol{a_{5,3}}\; \boldsymbol{a_{3,4}}\; a_{1,1}$—here and elsewhere links along the path from the input to response variable are in bold type, and links of the complementary subsystem are in regular type. The sign of this response is ambiguous and dependent upon the countervailing balance of one negative cycle against two positive cycles. Knowing the relative strength of the $\boldsymbol{a_{5,4}}$ term, which is unique to the negative cycle, one could make a conditional statement about the sign of the overall response—i.e. the standing crop of variable 2 increases if $\boldsymbol{a_{5,4}} < (\boldsymbol{a_{2,4}}\; a_{5,5})/\boldsymbol{a_{2,5}} + (\boldsymbol{a_{5,3}}\; \boldsymbol{a_{3,4}})/a_{3,3}$.

Qualitative modeling (or loop analysis) has previously relied upon interpretation of such symbolic inequalities to determine the likely sign of ambiguous responses. Where this is possible, it can lead to penetrating insights into system behavior, as all symbolic arguments are essentially Malthusian in nature, and counterintuitive behavior can be understood through the biology of system variables. Often, however, our knowledge of the relative strength of interactions is insufficient, or in large systems, symbolic arguments may contain too many terms—perhaps hundreds—to reasonably interpret. In these instances, qualitative modeling has been unsuccessful at addressing ambiguous or conditional results. Qualitative modeling has thus remained limited to relatively small systems, or systems of limited complexity. We approach this problem by ignoring the details of symbolic arguments and instead rely upon the relative degree of ambiguity of the response, as defined by the countervailing number of complementary feedback cycles. For example, in the plankton community the response of variable one due to a positive input to itself is governed by seven cycles, all of which are feedbacks composed entirely of complementary subsystems: $-a_{2,2}\ a_{3,4}\ a_{4,5}\ a_{5,3}+a_{2,2}\ a_{3,3}\ a_{4,4}\ a_{5,5}+a_{2,2}\ a_{3,3}\ a_{4,5}\ a_{5,4}+a_{2,2}\ a_{3,4}\ a_{4,3}\ a_{5,5}+a_{2,4}\ a_{4,5}\ a_{5,2}\ a_{3,3}+a_{2,5}\ a_{5,2}\ a_{3,3}\ a_{4,4}+a_{2,5}\ a_{5,2}\ a_{3,4}\ a_{4,3}$. The relative ambiguity of the sign of this response can be seen to be less severe than the previously discussed response, given that there is only one negative cycle that is weighed against six positive cycles, as opposed to one against two.

4. Weighted predictions

We provide a relative scale for ambiguity of response predictions through a ratio of the net and absolute number of complementary feedback cycles. In this way, feedback cycles are considered as whole units, and a net response results from cancellation between positive and negative cycles. Accounting for the net and absolute number of complementary feedback cycles is accomplished though a community matrix qualitatively specified with $+1$, -1, or 0 entries (denoted here as ${}^{\circ}\mathbf{A}$). The adjoint of $-{}^{\circ}\mathbf{A}$ details the net number of complementary feedback cycles contributing to response in system variables. It is equivalent to Levins' loop analysis algorithm and related to the inverse matrix by

$$-\mathbf{A}^{-1} = \mathrm{adjoint}(-\mathbf{A})/\mathrm{determinant}(-\mathbf{A}) \tag{2}$$

Here the inverse and adjoint matrices are both calculated with the negative of the community matrix. This maintains a sign convention in both even- and odd-sized systems such that positive input is read down the columns and responses along rows. When input to a variable is negative, the signs of the inverse and adjoint matrices are simply reversed.

The absolute number of complementary feedback cycles in a response, both positive and negative in value, can be calculated as

$$\mathbf{T}_{ij} = \mathrm{permanent}(\mathrm{minor}\ {}^{\bullet}\mathbf{A}_{ij})^{\mathrm{T}} \tag{3}$$

which yields the 'absolute-feedback' matrix $\mathbf{T}$, where ${}^{\bullet}\mathbf{A}$ denotes an adjacency matrix, which is specified by only 0's or 1's (i.e. absolute values of ${}^{\circ}\mathbf{A}$) and where T is the transpose of a matrix. The permanent of a matrix is computed in a manner similar to the determinant, but by addition only in computation of matrix minors, and without alternating sign during column and row expansion—i.e. while the determinant of $\begin{bmatrix} a & b \\ c & d \end{bmatrix}$ is $ad-bc$, its permanent is $ad+bc$ (Marcus and Minc, 1964; Minc, 1978; Eves, 1980).

Dividing the absolute value (| |) of each element of the adjoint matrix by each corresponding $\mathbf{T}_{ij}$ element yields the 'weighted-predictions' matrix ($\mathbf{W}$)

$$\mathrm{W} = \frac{\overrightarrow{|\mathrm{adj}\ {}^{\circ}\mathrm{A}|}}{\mathrm{T}} \tag{4}$$

where '→' is a vectorized matrix operator that denotes element-by-element division—note that $\mathbf{W}_{ij}=1$ when absolute feedback $\mathbf{T}_{ij}=0$. Each element of $\mathbf{W}$ scales the probability for sign determinacy of response predictions in the adjoint. When all complementary feedback cycles are of the same sign (e.g. adjoint $-{}^{\circ}\mathbf{A}_{ij} = +, +, +, +$), then sign determinacy is completely ensured and the weighted prediction ($\mathbf{W}_{ij}$) is equal to 1.0. A complete absence of complementary feedback cycles equates to a neutral response prediction in the adjoint with a perfect prediction weight of 1.0. When there is an equal number of positive and negative feedback cycles (e.g. adjoint $-{}^{\circ}\mathbf{A}_{ij} = +, +, -, -$) then $\mathbf{W}_{ij}=0$, and sign determinacy is completely ambiguous. A prediction weight of 0.5 is based upon cancellation of half of the cycles (e.g. adjoint $-{}^{\circ}\mathbf{A}_{ij} = +, +, +, -$; and $\mathbf{W}_{ij}=2/4$), and as we will show, a ratio of 0.5 is a general threshold for sign determinacy in models of any size.

Continuing our example of Stone's (1990) plankton community model (Eq. (1)), we have the following qualitatively specified community, adjoint, absolute-feedback, and weighted-predictions matrices

$$^{\circ}\mathbf{A} = \begin{bmatrix} -1 & 1 & 0 & 0 & 0 \\ -1 & -1 & 0 & 1 & 1 \\ 0 & 0 & -1 & 1 & 0 \\ 0 & 0 & -1 & -1 & 1 \\ 1 & -1 & 1 & -1 & -1 \end{bmatrix}$$

$$\text{adjoint}\,(-^{\circ}\mathbf{A}) = \begin{bmatrix} 5 & 2 & 2 & 1 & 3 \\ 1 & 2 & 2 & 1 & 3 \\ 2 & 0 & 4 & 2 & 2 \\ 2 & 0 & 0 & 2 & 2 \\ 4 & 0 & 4 & 0 & 4 \end{bmatrix}$$

$$\mathbf{T} = \begin{bmatrix} 7 & 4 & 4 & 3 & 3 \\ 7 & 4 & 4 & 3 & 3 \\ 2 & 2 & 8 & 4 & 2 \\ 2 & 2 & 6 & 4 & 2 \\ 4 & 4 & 6 & 6 & 4 \end{bmatrix} \tag{5}$$

$$\mathbf{W} = \begin{bmatrix} 0.71 & 0.50 & 0.50 & 0.33 & 1.0 \\ 0.14 & 0.50 & 0.50 & 0.33 & 1.0 \\ 1.0 & 0 & 0.50 & 0.50 & 1.0 \\ 1.0 & 0 & 0 & 0.50 & 1.0 \\ 1.0 & 0 & 0.67 & 0 & 1.0 \end{bmatrix}$$

Eight of the 25 adjoint predictions have complete sign determinacy ($\mathbf{W}_{ij} = 1.0$), and 5 are completely ambiguous ($\mathbf{W}_{ij} = 0$). What is of general interest here is not only the reliability of the other 13 predictions, but also the relative magnitude of the response as detailed by the net number of complementary feedback cycles in the adjoint matrix.

In what follows, the reliability of adjoint matrix predictions from qualitatively specified systems will be tested in terms of both response sign and relative response strength. This will be accomplished through numerical simulation using a randomly assigned parameter space for interaction terms in the community matrix. In doing so, we seek to determine the relative contribution of system structure versus interaction strength.

5. Analysis methods

Our analysis is patterned after that of Pimm and Lawton (1977, 1978) and Yodzis (1981) and Yodzis (1988). We chose from the literature, or constructed ourselves, 18 signed digraph models (Fig. 1) that, as will be shown, exhibited a full spectrum of predictability (i.e. relative level of ambiguity in qualitative response predictions). Models were constructed by successively adding interactions involving omnivory, competition, or mutualism. The qualitative stability of each model was assessed by the Routh-Hurwitz criteria for Lyapunov stability (May, 1974; Puccia and Levins, 1985; Logofet, 1992). Models **a** and **b** are unconditionally stable, and models **c**–**r** are conditionally stable. Qualitative predictions of system response were compared to those of quantitative analyses in which interaction terms of community matrices were randomly varied over two orders of magnitude. Self-regulation terms, in separate numerical simulations, were either varied randomly or fixed at a value of maximum strength. All matrix calculations were symbolically detailed and entered into relative cell references in a computer spreadsheet program (Microsoft© Excel 2000). The spreadsheet program had 5000 rows and approximately 250 columns. A pseudo-random number generator was used that assigned interaction strengths from an even distribution. A set of 5000 matrices could be quantitatively specified and evaluated within 10 s.

6. Correspondence between quantitative and qualitative predictions

Within any response prediction of the inverse or adjoint matrix there are, in mathematical terms, two processes involved: summation of feedback cycles, and multiplication within feedback cycles. The first is determined purely through the qualitative aspects of community structure, while the second comes from the intensity of interactions between community members. Since both qualitative and quantitative predictions involve the process of summation, it follows that there should be some positive relationship between the net number of complementary feedback cycles contributing to a response and the total numerical response. The difference between the two resulting only from multiplication effects (amplification or diminution) occurring within quantitative calculations.

In Fig. 2, we compare qualitative to quantitative predictions of response sign and strength for two

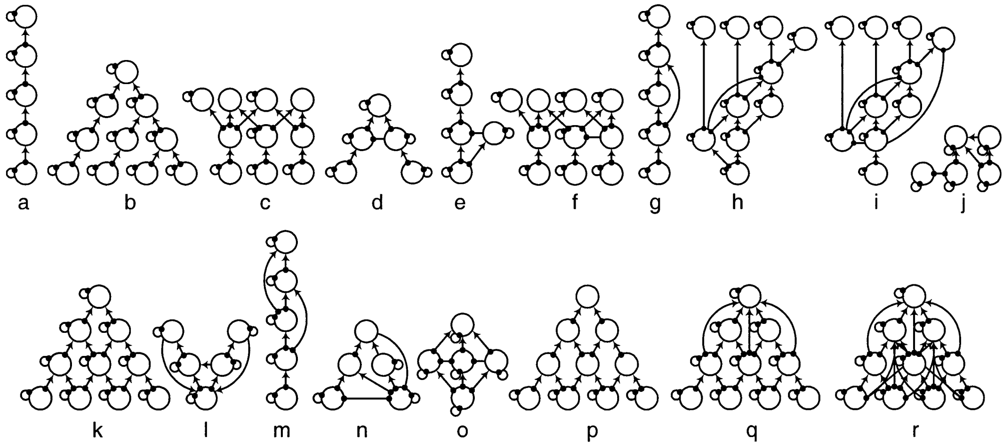


Fig. 1. Signed digraphs of 5- and 10-variable models analyzed in computer simulations. Model **f** is an avian, fish and benthic stream community adapted from Wright (1997). Models **h** and **i**, respectively, are of mesotrophic and eutrophic Danish shallow lakes studied by Jeppesen (1998), and model **l** is a plankton community from Stone (1990). Model **j** is patterned after a New England tide-pool community from Puccia and Pederson (1983), and model **o** after an old-field food web from Schmitz (1997). Remaining models constructed by adding or removing competitive (interference or resource), omnivorous, or mutualistic links to models **a**, **b**, **d** and **f**.

models. It is essentially a comparison of the effects of summation, based only on community structure, and multiplication, based on specific quantitative relationships. The models were specified with a single set of interaction terms. All qualitative predictions in model **a** matched the sign of corresponding numerical predictions—all points were within quadrants I and III. In this model there is no possibility for sign indeterminacy in the adjoint matrix, as all of its weighted predictions are equal to 1.0, which is a property of nearly all unconditionally stable models (Quirk and Ruppert, 1965; see their Theorem 6 for indecomposable sign stable matrices). In model **l**, which is Stone's (1990) plankton community model (Eq. (1)), 8 qualitative predictions did not match the sign of the quantitative response—as in dashed-line area of adjoint and inverse matrices in Fig. 2. Sign indeterminacy occurred where weighted predictions were less than 0.5—see **W** in Eq. (5).

For both models in Fig. 2, there was moderate correspondence ($r^2 > 0.5$) between qualitative and quantitative predictions of response strength. Model **a** had a r^2 higher than model **l**, even though it was quantitatively specified with terms that were weaker and more varied, as measured by the minimum and standard deviation (S.D.) of absolute values of non-zero terms.

7. Predictions of response strength

In the following analysis, we examine the relative degree to which correspondence between quantitative and qualitative predictions of response strength is affected by model structure, as well as by quantitative aspects of interaction strength. Using the concepts and measures derived from the particular examples presented in Fig. 2, we consider—through an extensive number of simulations—a full range of possible values and combinations of interaction strengths in four widely different models. A quantitatively specified community matrix is denoted here as $^{\#}\mathbf{A}$ and quantitative response predictions were calculated by $-^{\#}\mathbf{A}^{-1}$. Interaction terms were randomly assigned to all off-diagonal $^{\#}\mathbf{A}_{ij}$ elements of the community matrix. These elements were varied over a range of two orders of magnitude (0.01–1.0), while holding constant the sign of each interaction. For each model, two separate numerical assignments were run; either all $^{\#}\mathbf{A}_{ii}$ self-regulation terms were fixed at a maximal strength of -1.0, or all $^{\#}\mathbf{A}_{ii}$ terms were randomly varied along with off-diagonal elements. In these and all subsequent simulations Lyapunov stability of each quantitatively specified matrix was assessed by the

a. Qualitative analysis

Model a

$$\begin{bmatrix} -1 & 1 & 0 & 0 & 0 \\ -1 & -1 & 1 & 0 & 0 \\ 0 & -1 & -1 & 1 & 0 \\ 0 & 0 & -1 & -1 & 1 \\ 0 & 0 & 0 & -1 & -1 \end{bmatrix}$$

$\overset{\circ}{\mathbf{A}}$

qualitatively specified community matrix

Model l

$$\begin{bmatrix} -1 & 1 & 0 & 0 & 0 \\ -1 & -1 & 0 & 1 & 1 \\ 0 & 0 & -1 & 1 & 0 \\ 0 & 0 & -1 & -1 & 1 \\ 1 & -1 & 1 & -1 & -1 \end{bmatrix}$$

$$\begin{bmatrix} 5 & 3 & 2 & 1 & 1 \\ -3 & 3 & 2 & 1 & 1 \\ 2 & -2 & 4 & 2 & 2 \\ -1 & 1 & -2 & 3 & 3 \\ 1 & -1 & 2 & -3 & 5 \end{bmatrix}$$

adj $-\overset{\circ}{\mathbf{A}}$

qualitative response: net number and sign of complementary feedback cycles

$$\begin{bmatrix} 5 & 2 & 2 & \boxed{1} & 3 \\ \boxed{1} & 2 & 2 & \boxed{1} & 3 \\ 2 & \boxed{0} & 4 & 2 & 2 \\ 2 & \boxed{0} & \boxed{0} & 2 & 2 \\ 4 & \boxed{0} & 4 & \boxed{0} & 4 \end{bmatrix}$$

b. Quantitative analysis

Model a

MIN $(|{}^{\#}\mathbf{A}_{ij}| > 0) = 0.05$

SD $(|{}^{\#}\mathbf{A}_{ij}| > 0) = 0.39$

$$\begin{bmatrix} -1.0 & 0.05 & 0 & 0 & 0 \\ -0.5 & -1.0 & 0.05 & 0 & 0 \\ 0 & -0.5 & -1.0 & 0.05 & 0 \\ 0 & 0 & -0.5 & -1.0 & 0.05 \\ 0 & 0 & 0 & -0.5 & -1.0 \end{bmatrix}$$

${}^{\#}\mathbf{A}$

quantitatively specified community matrix

Model l

MIN $(|{}^{\#}\mathbf{A}_{ij}| > 0) = 0.1$

SD $(|{}^{\#}\mathbf{A}_{ij}| > 0) = 0.31$

$$\begin{bmatrix} -1.0 & 0.6 & 0 & 0 & 0 \\ -0.6 & -1.0 & 0 & 0.1 & 0.6 \\ 0 & 0 & -1.0 & 0.2 & 0 \\ 0 & 0 & -0.2 & -1.0 & 0.5 \\ 0.6 & -0.6 & 0.2 & -0.5 & -1.0 \end{bmatrix}$$

$-{}^{\#}\mathbf{A}^{-1}$

quantitative response

$$\begin{bmatrix} 0.98 & 0.048 & 0.0023 & 0.00011 & 0.0000057 \\ -0.48 & 0.95 & 0.047 & 0.0023 & 0.00011 \\ 0.23 & -0.47 & 0.95 & 0.047 & 0.0023 \\ -0.11 & 0.23 & -0.47 & 0.95 & 0.048 \\ 0.057 & -0.11 & 0.23 & -0.48 & 0.98 \end{bmatrix}$$

$$\begin{bmatrix} 0.9 & 0.4 & 0.05 & \boxed{-0.06} & 0.2 \\ \boxed{-0.2} & 0.7 & 0.09 & \boxed{-0.09} & 0.3 \\ 0.05 & \boxed{-0.01} & 1.0 & 0.1 & 0.07 \\ 0.2 & \boxed{-0.06} & \boxed{-0.09} & 0.8 & 0.4 \\ 0.5 & \boxed{-0.1} & 0.2 & \boxed{-0.3} & 0.7 \end{bmatrix}$$

c. Correspondence

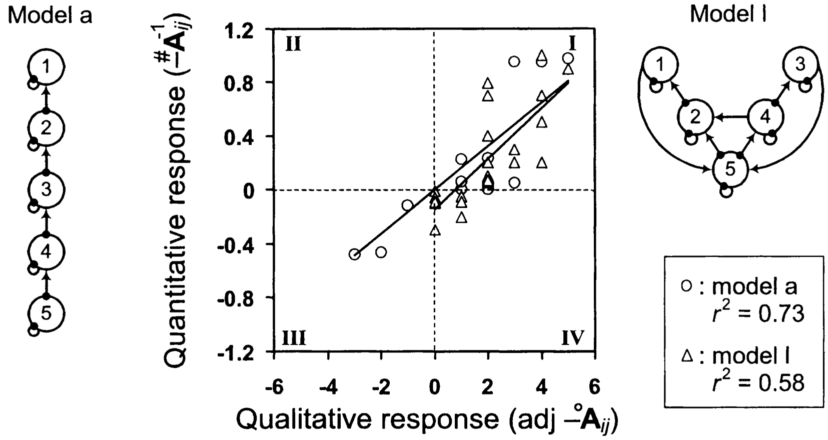


Fig. 2.

Routh-Hurwitz criteria, and only stable matrices were analyzed.

The correspondence (r^2) between qualitative and quantitative responses (Fig. 3) was compared to both the weakest link (minimum $|{}^{\#}\mathbf{A}_{ij}| > 0$) and spread of interactions (S.D. $|{}^{\#}\mathbf{A}_{ij}| > 0$). To gain a full spread of points along the horizontal axes of Fig. 3, interaction terms were sequentially varied in lots of 5000 matrices over a successively constricted range. Matrices in the first lot were assigned values between 0.01 and 1.0; subsequent lots were varied over a range of 0.10–1.0, 0.20–1.0, and so on to 0.90–1.0. Our results show the weakest values in each lot were clumped to the lower limit of each successive range, which created a saw-toothed pattern to the spread of data points in Fig. 3. The use of a successively constricted range was necessary because random numbers were assigned from a uniform distribution, and in any one assignation it was likely that at least one interaction term would be near the lower limit of a given range. Thus to obtain matrices with a full range of 'weakest' values, the lower limit had to be successively moved from 0.01 to 0.90. For each model in Fig. 3, we generated 50 000 separate assignations of interaction strength. We found that two orders of magnitude provided sufficient variation of interaction strength. Increasing the range to three orders of magnitude (i.e. 0.001–1.0) or more did not appreciably affect the results.

The spread of data points in Fig. 3 is an exhaustive exploration of a random and uniformly distributed parameter space. Each graph in Fig. 3 can be considered as originating from a singular point in which there is complete correspondence between the quantitative and qualitative response—i.e. $r^2 = 1.0$. This point, then, is a reference for an equivalent specification of quantitative and qualitative matrices, where all non-zero elements of ${}^{\#}\mathbf{A}$ are of equal absolute value. Outward from this point, differences between the quantitative and qualitative matrices can be described by a general erosion of correspondence. Within each model, correspondence (r^2) was diminished by both weak interactions and variation within the community matrix; especially where self-regulation was varied randomly. The degree to which correspondence was eroded by these factors differed greatly between models, and in Fig. 3, models are arrayed in ascending order of relative correspondence. We also examined the influence of the variance of eigenvalues of the community matrix (Jorgensen et al., 2000), but found that it did not account for any variation in correspondence within or between models. In this stage of the analysis, we are not concerned with the central tendency of the simulation results, which depends on the randomized spread of interaction strengths. Rather, it is the edges of the clouds of points in Fig. 3 that are important, which essentially define the limits of qualitative predictions.

8. Weighted predictions and sign determinacy of response

The next stage of our analysis develops confidence levels for qualitative model predictions. Here we seek to know what range of 'real' or numerical outcomes from 5000 matrices with randomly assigned interaction terms will correspond with the sign of qualitative predictions 80%—or 50, 75, or 95%—of the time. Numerical matrices for models **a** through **r** (Fig. 1) were analyzed under two scenarios with 5000 matrices each. In the first scenario, non-zero a_{ii} self-regulation terms were varied along with a_{ij} interactions, and interaction strengths were allowed, without restriction, any value between 0.01 and 1.0. In the second scenario, self-regulation for all

Fig. 2. Comparison of quantitative versus qualitative predictions of response for models **a** and **l** (Fig. 1). (a) Qualitative response, in terms of the net number and sign of complementary feedback cycles, is calculated as adjoint (adj) of qualitatively specified system $(\mathrm{adj}-{}^{\circ}\mathbf{A}_{ij})$. (b) Quantitative community matrices $({}^{\#}\mathbf{A})$ are specified with plausible interaction terms (model **l**'s are from Stone, 1990), and quantitative response calculated by matrix inverse $(-{}^{\#}\mathbf{A}^{-1})$. (c) Variation in quantitative responses that is explained by qualitative responses measured by regression r^2. Responses in quadrants II or IV, or on abscissae, indicate sign error of qualitative predictions and corresponding matrix elements are enclosed by dashed-lines. Measures of S.D. and minimum (MIN) pertain to non-zero elements of the community matrix ($|{}^{\#}\mathbf{A}_{ij}| > 0$), and are used as descriptors of system behavior and correspondence in Fig. 3.

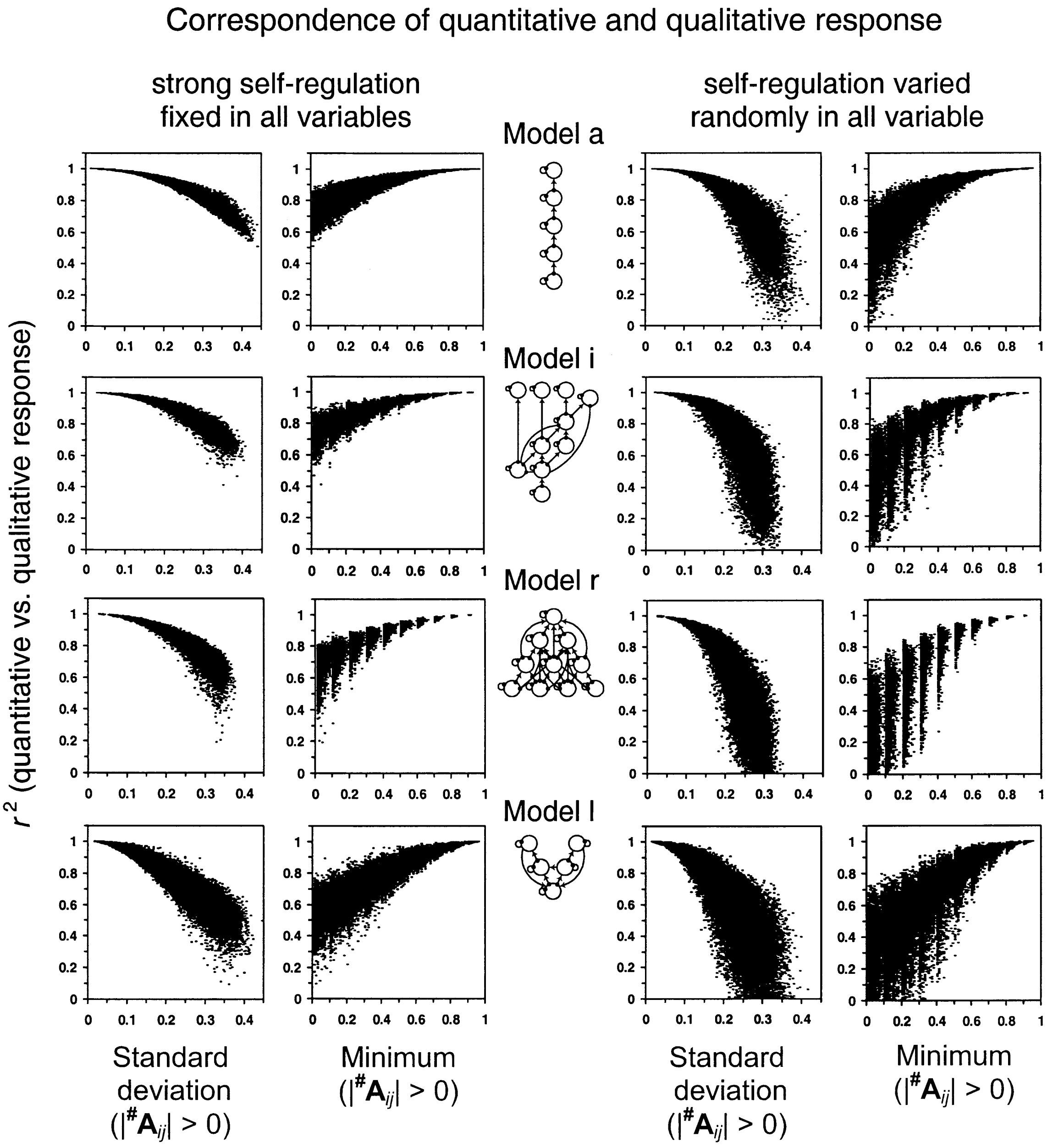


Fig. 3. Correspondence (r^2) between quantitative and qualitative response in four models, as affected by the minimum and S.D. of non-zero values in the community matrix. Community matrix elements were randomly assigned numeric values 50 000 times. Off-diagonal elements were varied by two orders of magnitude (0.01–1), and self-regulation was either fixed at strong value of −1 or, in a separate analysis, randomly varied along with off-diagonal elements.

variables was fixed at a maximal value of −1.0, and all else remained as in the first scenario. In both scenarios, weak interactions were likely to be included within each quantitatively specified matrix. The 0.01–1.0 range of values imposed a conservative, or most pessimistic, condition for sign determinacy, because $\mathbf{A}_{ij}$ values in this range produced the least agreement between quantitative

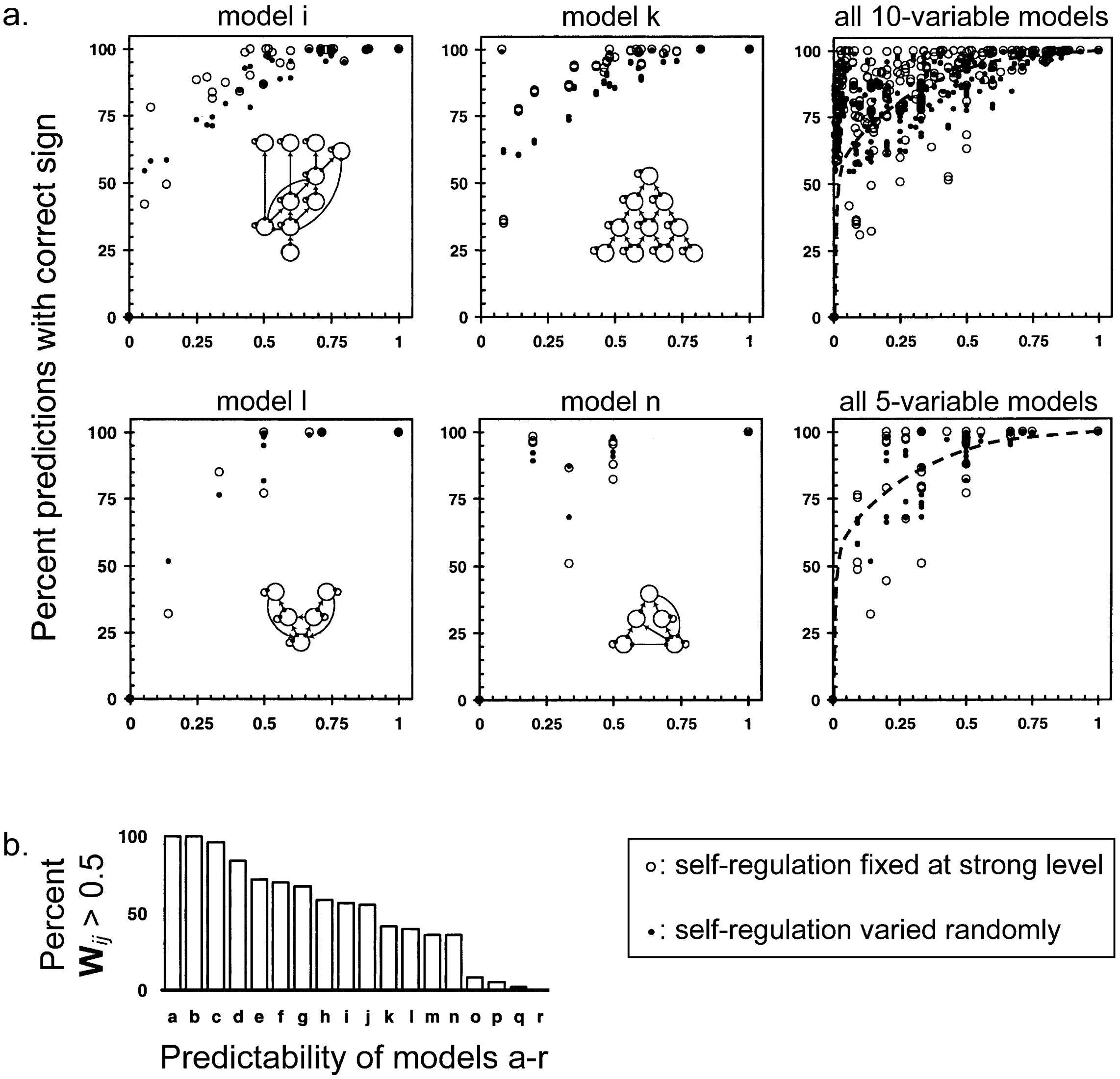


Fig. 4. (a) Sign determinacy of 5- and 10-variable models (Fig. 1). Data are from 5000 matrices in which interaction strength in elements of the community matrix were randomly varied between 0.01 and 1 in two separate scenarios, in which self-regulation was either fixed at a strong value of −1.0, or was varied randomly along with off-diagonal elements. Many points within graphs overlap and are not apparent. Dashed-line is drawn by hand through local means of combined results. Weighted predictions ($\mathbf{W}_{ij}$) greater than 0.5 generally have a high degree (> 90%) of sign determinacy. (b) Predictability of models **a**–**r** (Fig. 1) as defined by the percent of weighted predictions greater than 0.5.

and qualitative results in Fig. 3. In stable matrices, each ijth quantitative prediction ($-{}^{\#}\mathbf{A}_{ij}^{-1}$) was compared with the sign of the corresponding qualitative prediction (adjoint $-{}^{\circ}\mathbf{A}_{ij}$). The percent correct sign of the adjoint prediction was plotted against the corresponding prediction weight ($\mathbf{W}_{ij}$) in Fig. 4a. Repeated trials of 5000 simulations altered results by less than 2%, as did increasing the range of non-zero ${}^{\#}\mathbf{A}_{ij}$ values to three or more orders of magnitude.

Sign determinacy was high in all 5- and 10-variable models where weighted predictions ($\mathbf{W}_{ij}$)

were greater than 0.5 (Fig. 4a). Above $\mathbf{W}_{ij} = 0.5$ the proportion of predictions with correct sign was generally greater than 90%; below this, sign determinacy rapidly declined to zero. Strong self-regulation generally increased sign determinacy by as much as 10%, but it also decreased sign determinacy in some instances.

Extremes of the graphs in Fig. 4a represent fixed endpoints of the analysis. Weighted predictions equal to 1.0 contain no countervailing feedback cycles, and the sign of the qualitative predictions is always maintained. At $\mathbf{W}_{ij} = 0$, there is an equal number of positive and negative cycles creating, in qualitative terms, a neutral (or zero) response. In our numerical simulations, however, an exact zero response can never occur, thus giving a y-axis intercept of zero correct predictions in Fig. 4a. In practical application, consideration of sign determinacy must also include the relative strength of a response. A response that is deemed highly predictable (i.e. $\mathbf{W}_{ij} > 0.5$) may nevertheless be too weak to detect. Likewise, a neutral response with a perfect prediction for sign determinacy, where $\mathbf{W}_{ij} = 1$ and $\mathbf{T}_{ij} = 0$ results from a complete absence of complementary feedback cycles, must be judged against a statistical context of measurement or sample error.

Weighted predictions are calculated entirely from the sign-structure of a system, and their ability to scale sign determinacy of adjoint predictions is independent of system size. The 18 models examined in this study (Fig. 1) exhibited a full range of model predictability, as defined by the proportion of $\mathbf{W}_{ij}$'s > 0.5 in each model (Fig. 4b). The weighted prediction measure thus provides a means to compare the relative potential for sign determinacy within or between models of any size and complexity. For instance, **a**–**c**, **e**–**g**, **h**–**j**, **k**–**n**, and **o**–**p**, are all groupings of models dissimilar in size and structure (Fig. 1), but of similar predictability (Fig. 4b).

9. Discussion

We have set 'semi-quantitative' confidence levels on qualitative models by attributing a weight to the countervailing balance of complementary feedback cycles, and by analysis of thousands of randomly assigned numeric matrices in both 5- and 10-variable models. Elements of a qualitatively specified adjoint matrix can, in a limited capacity, serve as a predictor of relative response strength. The probability for sign determinacy of adjoint predictions was consistently gauged by elements of the weighted predictions matrix, and tests of these qualitative techniques were consistent between models of different size. The applicability of these results depends only upon the processes of summation among feedback cycles, and multiplication within feedback cycles, which pose no theoretical limit on system size.

While qualitative predictions of response strength from the adjoint matrix exhibited, in some instances, a high degree of correspondence with numerical responses, we consider this correspondence unreliable as it is easily eroded by weak interactions and variation of interaction strength. We therefore caution that qualitative predictions of response strength should be used only as a relative benchmark of expected system behavior.

Our demonstration that correlation between qualitative and quantitative predictions of response strength is reduced by the variation of interaction strengths and by the weakest interaction within the community has important implications for the process of model building. A species known to be only weakly connected to a system should perhaps be included with similar species in a trophic or functional guild. Bender et al. (1984) present a quantitative argument to exclude altogether weakly connected species from community matrix models. Through model simplification, predictability is increased, but at a trade-off with resolution. Thus, an intermediate level of resolution will likely optimize understanding of community dynamics (as in Hulot et al., 2000), the level of which is likely to differ from one system to the next.

We purposefully chose a conservative or 'most pessimistic' appraisal of the weighted predictions matrix by specifying our quantitative matrices with random numbers evenly distributed across two orders of magnitude, thus ensuring a high likelihood that most matrices had relatively weak interactions. Normal or skewed distributions of interaction strength—as in Berlow et al. (1999) for example—would decrease the variability of the elements of ${}^{\#}\mathbf{A}$. Our results show correspondence between qualitative and quantitative predictions to increase when ${}^{\#}\mathbf{A}_{ij}$ values are less variable.

High sign determinacy of weighted predictions greater than a general threshold value of 0.5 creates an expanded scope of inference for community matrix theory. Employing techniques of qualitative analysis, it is possible to attribute a structural context to each response prediction, thereby gaining an important investigative tool to complement press-type experiments (Bender et al., 1984), or studies of natural disturbances (Diamond, 1986). Whereas qualitative analysis has in some respects been previously limited to all-or-none predictions of response sign, predictions can now be judged across a spectrum of expected reliability. Previous findings of high indeterminacy of quantitative predictions have resulted, in part, from treating the inverse matrix essentially as a black box, with no context provided for which predictions should or should not be reliable. For instance, reliable response predictions were severely limited in the Narragansett Bay food web model studied by Yodzis (1988)—there all prediction weights were less than 0.31, and the average was 0.10. In an old-field food web studied by Schmitz (1997), we find only 4 of 36 responses to have non-zero prediction weights, and all of these were equal to 0.10. Encountering a high level of indeterminacy is an expected feature of these two systems, but we stress, not for all systems. In Dambacher et al. (2002) we demonstrate practical applications of these techniques in natural systems drawn from the literature.

Symbolic analysis of the community matrix forms the basis of this work, nearly all of which is reducible to the simple concept of a countervailing balance of complementary feedback cycles. At a fundamental level nothing more is at work here than the processes of summation and multiplication. The question ‘what is the difference between the qualitative and quantitative behavior of a system?’ is reduced to ‘what is the difference between the addition and subtraction among feedback cycles, and amplification and diminution within feedback cycles?’ The approach of weighting feedback, however, requires one to forfeit the symbolic content of feedback cycles, which constitutes an enormous loss of information. Where possible, as in small or sparsely connected systems, understanding of system behavior will be more advantageously approached through the biological implications of symbolic inequalities.

Our results emphasize the overriding importance of system structure. In ecological systems, it is exceedingly rare that actual values of interaction terms are defined for all community members or variables, or for that matter, that they are even measurable. Nevertheless, the composition and structure of the community is often well known, or it can be sufficiently encompassed by a manageable number of alternative models. These results offer hope that if we know the structure of a community, we can, to a discernable degree, also know its theoretical potential for predictability. Qualitative models of ecological communities can thus be used to rigorously evaluate results of quantitative models and manipulation experiments, allowing one to separate the structural influences of countervailing feedback cycles from parameter noise and measurement error.

Acknowledgements

We thank A. Bodini, J.M. Emlen, J.D. Hall, C.J. Puccia and two anonymous reviewers for comments that improved the clarity of this work. We also thank G.C. Castillo, S.S. Heppell, J. Jorgensen, J.L. Li, H.-K. Luh, and G.C. Montaño-Moctezuma of the OSU Loop Group for critiques and captivating discussions. This work was partially supported by the Biological Resource Division’s Cooperative Fish and Wildlife Research Unit (*USGS*).

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