RELEVANCE OF COMMUNITY STRUCTURE IN ASSESSING INDETERMINACY OF ECOLOGICAL PREDICTIONS

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Abstract. The community matrix is potentially a powerful tool for community ecology. While it details direct interactions between community members, it can also be used to quantify all indirect effects that occur in a community, and thereby to make predictions regarding population response to experimental treatments or natural disturbances. These predictions are essentially hypotheses of system behavior that can be rigorously evaluated. Use of the community matrix, however, has been hindered by indeterminacy and ambiguity in response predictions. In this study, we reveal a theoretical source of the problem that arises as a consequence of community structure.

Using a qualitative analysis of the community matrix, we detail the complementary feedback cycles that contribute to the response of a population following a sustained or press perturbation. Complementary feedback is the sum of all direct and indirect effects that can contribute to a response. We develop a ''weighted-predictions matrix'' that assigns a probability scale to sign determinacy of predicted responses. This matrix is formed by the quotient of the net sum of complementary feedback cycles and the absolute number of complementary feedback cycles.

A qualitative analysis of system structure provides a theoretical benchmark for understanding a spectrum of behavior in biological systems, and for framing and prioritizing management interventions for whole communities. This advance clarifies much of the uncertainty and ambiguity found in predicting the behavior of large and complex systems. We validate these tools by analyzing published studies of community response.

Key words: adjoint matrix; community matrix; food web; indeterminacy; indirect effects; inverse matrix; press perturbation; qualitative modeling; signed digraph; weighted-predictions matrix.

INTRODUCTION

An important approach for understanding and analyzing natural communities is analysis of perturbations, whether through planned experiments, or experiments capitalizing on natural disturbances (Diamond 1986, Walters and Holling 1990). Perturbations alter community equilibrium through input to one or more populations, ultimately changing rates of birth or death. The direct relationships between populations define community structure, and consequently determine how the effects of a perturbation are propagated through both direct and indirect paths of interaction.

For a Lotka-Volterra dynamical system of *n* interacting species or resource variables (N_i), change in the equilibrium population (N_i^*) of species *i*,

$$dN_i^*/dt = f_i(N_1, N_2, \ldots, N_n; C_1, C_2, \ldots, C_h) \quad (1)$$

is a function (f_i) of other species or variables in the system, and their associated growth rate parameters (C_h, where $h = 1 \ldots n$). At or near equilibrium $f_1 = f_2 = \ldots f_n = 0$. Direct relationships between commu-

nity members, formally organized in the Jacobian, or community matrix **A,** determine the interplay between population abundance **N,** and carrying capacity **K** (both column vectors), by the equation $\mathbf{AN} = \mathbf{K}$ (Levins 1968).

The inverse of the community matrix provides an estimate of the change in equilibrium abundance of each community member resulting from sustained input to the birth or death rates (C_h) of an *h*th species (where *h*th = *j*th species), such that its carrying capacity is altered:

$$\frac{dN_i^*}{dC_h} = -\mathbf{A}_{ij}^{-1}. \quad (2)$$

In derivation of the effects of sustained positive input to a variable (i.e., increase in birth rate or decrease in death rate), the inverse of the negative community matrix ($-\mathbf{A}^{-1}$) is obtained (Nakajima 1992). Taking the inverse of the negative community matrix maintains a sign convention for both even- and odd-sized systems, whereby positive input at species *j* is read down the columns of the inverse, and response of species *i* along the rows. When input is negative (decreased birth rate or increased death rate), the response signs are re-

versed. Nakajima (1992) presents a thorough derivation of the inverse, but see also those of Yodzis (1978, 1988), Bender et al. (1984), and Stone (1990).

Bender et al. (1984) formalized the use of the inverse matrix for conducting "press" experiments in ecology, whereby change in the equilibrium level of community members is measured following a sustained alteration in the abundance or density of a species or variable within the community. A positive input can be affected through an enhanced birth rate or depressed death rate, which can be achieved through various means, such as nutritional supplementation or a lessening of predation pressure, respectively. The goal of the experiment is to apply as large an input as is practical, such that equilibrium responses are relatively large and measurable, but not so dramatic as to cause the extinction of a community member. Reciprocally, it is possible to estimate each element of the community matrix through n press experiments, measuring each of n responses in abundance, and then "inverting" the inverse matrix itself. Press experiments assess the long-term consequence of direct and indirect effects at a new equilibrium. Conversely, a "pulse" perturbation experiment provokes an instantaneous alteration of a species' abundance, and examines the return of the community to a previous equilibrium state. This experiment addresses only the immediate effects from direct interactions detailed in the community matrix. Both pulse and press experiments depend upon a fixed set of community members and interactions, and cannot be equated to species addition or deletion experiments (as in Wootton 1994), which alter both community membership and structure.

The inverse community matrix is potentially a powerful tool for community analysis because it predicts the ultimate effect of an input on all community members. Each prediction, or element of the inverse matrix, is essentially a testable hypothesis of expected system behavior that can be rigorously evaluated by the parameters of birth rate, death rate, population size, and mean generation time. Experimentalists have commented, however, that predictions based on the inverse community matrix can be highly indeterminate, and appear to be overly sensitive to the values of the interaction coefficients. Response predictions that incur a high proportion of sign reversals are considered to have high "sign indeterminacy". Yodzis (1988) portrayed the problem of sign indeterminacy via computer simulations that randomly assigned the strength of interactions in elements of community matrices. Relatively small changes in interaction values were often found to reverse the direction (or sign) of a response, causing, for example, a population increase instead of a decrease. As an example, the following two community matrices demonstrate sign reversal in an inverse matrix prediction (bold font) that arises from small changes (± 0.1) in interaction strength:

$$\mathbf{A'} = \begin{bmatrix} -0.8 & -0.2 & -0.4 \\ 0.7 & 0 & -0.5 \\ 0.6 & 0.3 & 0 \end{bmatrix}$$

$$-\mathbf{A'}^{-1} = \begin{bmatrix} 1.0 & -0.8 & 0.7 \\ -2.1 & 1.7 & -4.7 \\ 1.4 & \mathbf{0.8} & 1.0 \end{bmatrix} \quad (3)$$

and

$$\mathbf{A''} = \begin{bmatrix} -0.8 & -0.3 & -0.5 \\ 0.6 & 0 & -0.4 \\ 0.7 & 0.2 & 0 \end{bmatrix}$$

$$-\mathbf{A''}^{-1} = \begin{bmatrix} 2.0 & -2.5 & 3.0 \\ -7.0 & 8.7 & -15.5 \\ 3.0 & \mathbf{-1.2} & 4.5 \end{bmatrix}. \quad (4)$$

In $-\mathbf{A'}^{-1}_{3,2}$ a positive input to species 2 causes an increase in the abundance of species 3, while in $-\mathbf{A''}^{-1}_{3,2}$, the abundance of species 3 decreases.

Thus predictions from the inverse matrix have been obscured, to an unknown degree, by a cloud of indeterminacy, the source of which has been attributed to natural variation in the values of interaction coefficients and to measurement error (Bender et al. 1984, Yodzis 1988, Schmitz 1997, Laska and Wootton 1998). This conclusion has been reached more or less by default, since the inverse matrix has been treated essentially as a black box, and a theory of indeterminacy, in and of itself, has not been formally addressed.

We submit that beyond variation in interaction strength, community structure can itself be an important, and at times overriding source of indeterminacy. We provide an analysis of this source of indeterminacy to shed further insight into the theory and practice of press perturbations and the interpretation of community responses. Three theoretical advances to the problem are presented herein. First, we use the so-called classical adjoint matrix to identify the relative strength of complementary feedback (as defined in *Analysis of the classical adjoint matrix*), with the conclusion that a source of indeterminacy arises from the value and number of complementary feedback cycles. Second, we derive an absolute feedback matrix that details the total number of complementary feedback cycles involved in each community response. Finally, we derive a weighted-predictions matrix that scales the responses of the adjoint, and allows for assessing the reliability of each prediction. We apply these tools to a number of published studies of biological communities, reinterpret conclusions, and illustrate practical management applications.

ANALYSIS OF THE CLASSICAL ADJOINT MATRIX

Community response to input for Lotka-Volterra systems was first addressed in the ecological literature by

Riebesell (1974) and Levins (1974, 1975). Riebesell presents an analytic solution, while Levins gives an equivalent matrix formulation based on Cramer's Rule

$$\frac{dN_j^*}{dC_h} = \frac{\det \begin{bmatrix} a_{1,1} & a_{1,2} & \cdot & a_{1,j-1} & \dfrac{-df_1}{dC_h} & a_{1,j+1} & \cdot & a_{1,n} \\ a_{2,1} & a_{2,2} & \cdot & a_{2,j-1} & \dfrac{-df_2}{dC_h} & a_{2,j+1} & \cdot & a_{2,n} \\ \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\ a_{n,1} & a_{n,2} & \cdot & a_{n,j-1} & \dfrac{-df_n}{dC_h} & a_{n,j+1} & \cdot & a_{n,n} \end{bmatrix}}{\det \mathbf{A}}$$

(5)

where the vector $[-df_i/dC_h]$ is substituted for the jth column in the determinant (det) of the community matrix (Appendices A and B). The $[-df_i/dC_h]$ terms represent a sustained change in the carrying capacity of a species or resource variable. A change in carrying capacity can be due to change in a parameter affecting rates of birth or death, and in biological systems can be considered in various contexts, such as (1) press disturbances or experiments, as in nutrient addition to a system, or (2) Mendelian selection, as in predator gaining increase food through sharper claws. In chemical systems or variables, carrying capacity is analogous to chemical solubility, and a press disturbance could be anything that causes change in reaction rates, such as a change in temperature or an input of reagents. Since quantification of all the terms in Eq. 5 is rarely possible, Levins developed an algorithm for hand computation that interprets signed digraph structure for a qualitative assessment of community response:

$$\frac{dN_j^*}{dC_h} = \frac{\overset{0}{\underset{i,k}{\sum}} \left[\frac{df_i}{dC_h}\right] [\text{Path}_{ji}^{(k)}][\text{Feedback}_{n-k}^{(\text{complementary})}]}{\text{Feedback}^{(\text{overall})}}.$$

(6)

We will discuss signed digraphs and the terms of this algorithm later; but note first that Eqs. 5 and 6 both include analogous formulations for a cofactor ($\mathbf{C}_{ji}$) of the community matrix, which, following the notation of Eq. 2, can generally be expressed as

$$\frac{dN_i^*}{dC_h} = \frac{\mathbf{C}_{ji}}{\det \mathbf{A}}.$$

(7)

Each community matrix cofactor, when transposed and divided by the system determinant, is the same as corresponding $\mathbf{A}_{ij}^{-1}$ inverse matrix elements (note that Eqs. 5 and 6 apply to the jth species, and results are transposed when related to Eqs. 2 and 7). Eqs. 5 and 6 give to the system of coupled differential equations in Eq. 1 a solution for the equilibrium abundance of any species or resource variable due to a change of a growth rate parameter C_h affecting carrying capacities in the system. Considering the matrix of all cofactors $\mathbf{C}$, we have the following algebraic equalities:

$$\mathbf{A}^{-1} = \frac{\mathbf{C}^{\text{trans}}}{\det \mathbf{A}} = \frac{\text{adj } \mathbf{A}}{\det \mathbf{A}}$$

(8)

where the transposed (trans) matrix of cofactors is, by definition, the same as the classical adjoint (adj) or adjugate matrix (Searle 1966). When taking the inverse of the negative community matrix, to predict the effects of press disturbance, we can also apply the adjoint of the negative community matrix through the equality

$$-\mathbf{A}^{-1} = \frac{\text{adj } -\mathbf{A}}{\det -\mathbf{A}}.$$

(9)

The denominator (det $-\mathbf{A}$) will be positive in stable systems of both even and odd size, and therefore it will not affect the sign of the adj $-\mathbf{A}_{ij}$ elements. Thus, the sign of $-\mathbf{A}_{ij}^{-1}$ elements will be the same as adj $-\mathbf{A}_{ij}$ elements in any stable system. We emphasize these equalities for their ease of computation by symbolic processors in computer software that are now widely available; see Supplement A for Maple V computer program and Appendices A and B for matrix methods used in this work.

Following Levins's terminology from Eq. 6, and the equalities in Eqs. 8 and 9, each response in the inverse matrix can be considered as a quotient of the feedback that is affecting a variable, divided by the feedback of the overall system. Overall feedback is the highest level of feedback of the entire system, and is calculated as the determinant of the community matrix. The determinant is a measure of a system's resistance to perturbation, and it scales the magnitude of each response. When disturbed, the stability of a system depends on its ability to exhibit self-damping or negative overall feedback (see sign convention for determinants in Appendix A). Thus, a necessary condition for stability is negative overall feedback. The numerator of Eq. 6 is a sum of the products of the sign of three terms: (1) all inputs to the jth variable $[-df_i/dC_h]$, (2) the different paths (of variable length k) of links connecting variable j to i [Path$_{ij}^{(k)}$], and (3) the linkages of complementary subsystems of $n - k$ variables not on a j-to-i path [Feedback$_{n-k}^{(\text{complementary})}$]. Together these terms constitute a feedback cycle (or loop) $n - 1$ in variable length, that contributes to change in the size of a population, or to the amount of a resource variable (see Levins 1974, 1975, and Puccia and Levins 1985, 1991 for a more detailed derivation and explanation of Eqs. 5 and 6). Levins (1974) coined the term ''loop,'' but now prefers the term ''cycle'' for its original and broader usage in graph theory (Levins and Puccia 1988).

Calculation of the entire set of n by n predictions from Eq. 6 makes up Levins's ''table of predictions,'' which, when transposed, is equivalent in sign to the inverse and adjoint matrices in Eq. 9. In this work, rather than coin a new term, we extend the use of the term ''complementary'' to mean more than a subsystem of variables not on a j-to-i path, but also to describe the entire feedback cycle constructed from the terms

in Eq. 6 (Appendix B). Complementary feedback cycles then, comprise the ultimate effects of a sustained perturbation to a system, and propagate through both direct and indirect paths.

The inverse of a matrix is equal to its classical adjoint matrix (referred to hereinafter as the adjoint matrix) divided by the determinant (Eq. 9). By extension, the adjoint of the negative community matrix is equivalent to Levins's table of predictions (but transposed), and therefore represents the complementary feedback contributing to each response in a system. Since the denominator, or determinant, is constant for all elements of the inverse matrix, the numerator, or adjoint, therefore contains all variation of responses within the system.

The above calculations presume that a system exhibits Lyapunov, or neighborhood stability (Lyapunov 1892), whereby a system is attracted to a local point of equilibrium, such that the abundance of all community members remain greater than zero. Unstable systems are extinction prone, while stable systems are not. From Eqs. 8 and 9 we see that matrix inversion requires a nonzero system determinant. A system with a negative determinant can have a local attractor and be stable (but not necessarily), while one with a positive determinant can never be stable (note sign convention of determinants in Appendix A). A system with a determinant equal to zero has no local attractor, and is termed "neutrally stable." A system at or close to neutral stability is prone to be controlled by exogenous input, with little or no self-determined response, or familiar states of equilibrium. The stability properties of a system are based on its eigenvalues, which can be analyzed through both quantitative (such as in O'Neil 1995) and qualitative means (May 1973, 1974, Puccia and Levins 1985).

ABSOLUTE FEEDBACK AND THE WEIGHTED-PREDICTIONS MATRIX

Each element of the adjoint matrix represents a sum of positive and negative cycles. To illustrate, we consider a community matrix specified by only the signed unity (-1, $+1$, 0) of its interaction terms (denoted as $°\mathbf{A}$). Qualitatively specified as such, calculations of system feedback, either complementary (adjoint) or overall (determinant), are rendered in the whole units of feedback cycles. Sign indeterminacy of a response prediction arises as follows. Any particular value, $+4$ for example, of an adjoint matrix element is difficult to interpret because it is derived from the sum of both positive and negative cycles. Three specific scenarios for the $+4$ value may be either 44 positive minus 40 negative cycles, or 6 positive minus 2 negative cycles, or only 4 positive cycles. If cycles contributing to a negative response were 15% stronger than the positive, then a negative response would occur in the first scenario, a positive response in the second, but only a positive response could occur in the third. This varying potential for sign indeterminacy illustrates that these are not equivalent predictions. The adjoint matrix, however, cannot be used to distinguish among them without a complete accounting of all the complementary feedback cycles.

Each element of the adjoint matrix can be weighted by the total number of cycles contributing to it (both positive and negative). This result is obtained from the following formula that yields the "absolute feedback" matrix ($\mathbf{T}$)

$$\mathbf{T}_{ij} = \text{per}(\text{min } {}^{\bullet}\mathbf{A}_{ij})^{\text{trans}} \qquad (10)$$

where the matrix permanent (per) is applied to each matrix minor of a community matrix that is specified by absolute qualitative values (i.e., by either 1 for all $a_{ij} \neq 0$, or by 0; denoted as ${}^{\bullet}\mathbf{A}$). The matrix permanent is computed as the determinant, but expansion is without alternating sign, or subtraction (Minc 1978; Appendix A); it is also referred to as a "plus determinant" (Marcus and Minc 1964, Eves 1980). Eq. 10 is similar to a cofactor calculation but without any negative elements in $\mathbf{A}$, or sign alternation in the expansion of minors. Each element of $\mathbf{T}$ is merely a count of the total number of both positive and negative feedback cycles in a response. Dividing the absolute value (ll) of each element of the adjoint matrix by each corresponding $\mathbf{T}_{ij}$ element, yields a matrix of ratios, or the "weighted-predictions" matrix ($\mathbf{W}$)

$$\mathbf{W} = \frac{\overrightarrow{\mathit{l}\text{adj }°\mathbf{A}\mathit{l}}}{\mathbf{T}} \qquad (11)$$

with $\mathbf{W}_{ij} = 1$ when absolute feedback $\mathbf{T}_{ij} = 0$, and where "$\rightarrow$" is a vectorized matrix operator that denotes element-by-element division.
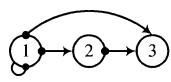
Possible values of $\mathbf{W}_{ij}$ range between 0 and 1. Values of $\mathbf{W}_{ij}$ near zero yield predictions that would be highly indeterminate. Reliability would increase with the value of $\mathbf{W}_{ij}$, such that predictions of $\mathbf{W}_{ij} = 1$ would be expected to be completely reliable in terms of their response sign or direction. In the three previous scenarios—two paragraphs above—the weighted predictions are 0.05, 0.5, and 1, respectively, ranging from high indeterminacy to absolute certainty. Where there is zero absolute complementary feedback (i.e., $\mathbf{T}_{ij} = 0$), there is a neutral response in the adjoint, and the weighted prediction is constrained to 1. Zero absolute complementary feedback often occurs in small ($n < 5$) or weakly connected systems, and is likely to be absent in large or highly connected systems.

SIGNED DIGRAPHS AND SYMBOLIC AND QUALITATIVE ANALYSIS

To illustrate the above techniques, we present symbolic (analytic) and qualitative analyses of the general model that corresponds to the quantitative analyses of the community matrices in Eqs. 3 and 4. Symbolically and qualitatively specified systems can be depicted in

signed digraph (sign directed graph) and matrix form. Signed digraphs depict relationships of system variables based on sign of interactions, with positive effects denoted by links terminating in an arrow ($\rightarrow$), and negative effects terminating in a filled circle ($\rightarrow\bullet$). In ecological systems, they represent community structure, and have direct correspondence with community matrices. Subscripts of a_{ij} matrix elements are interpreted as the direct effect of species j upon species i. Off-diagonal, or a_{ij}, terms of the community matrix can include predator–prey ($\bullet\rightarrow$), competitive ($\bullet-\bullet$), mutualistic ($\leftrightarrow$), commensal ($\rightarrow$), amensal ($-\bullet$), or neutral interactions. Self-effects, or a_{ii} diagonal terms, pertain to intraspecific interactions, such as density-dependent or self-regulation feedback (negative), or self-enhancing feedback (positive), and are depicted by links that connect a variable to itself.

A general model for the systems in Eqs. 3 and 4 is depicted below in signed digraph and symbolic matrix form; it has three sets of predator–prey interactions, one of which is omnivorous.

$$\mathbf{A} = \begin{bmatrix} -a_{1,1} & -a_{1,2} & -a_{1,3} \\ a_{2,1} & 0 & -a_{2,3} \\ a_{3,1} & a_{3,2} & 0 \end{bmatrix}. \quad (12)$$

Stability is ensured when the overall feedback, or determinant, of this system ($-a_{1,1}a_{2,3}a_{3,2} + a_{3,1}a_{1,2}a_{2,3} - a_{3,2}a_{2,1}a_{1,3}$) is negative. This result requires that the strength of a single positive feedback cycle be less than that of the two negative cycles combined. From Eq. 9, we obtain, in symbolic form, a set of predictions corresponding to the inverse matrix, and to Levins's transposed table of predictions.

adj $-\mathbf{A}$

$$= \begin{bmatrix} a_{2,3}a_{3,2} & -a_{1,3}a_{3,2} & a_{1,2}a_{2,3} \\ -a_{2,3}a_{3,1} & a_{3,1}a_{1,3} & -a_{1,1}a_{2,3} - a_{1,3}a_{2,1} \\ a_{2,1}a_{3,2} & a_{1,1}a_{3,2} - a_{1,2}a_{3,1} & a_{2,1}a_{1,2} \end{bmatrix}. \quad (13)$$

If one wanted to symbolically portray the absolute feedback matrix ($\mathbf{T}$) for this system, it would simply be the absolute value of the above matrix elements. In this example positive input to species 2 results in a decrease in its prey, species 1, by way of the complementary feedback cycle $-a_{1,3}a_{3,2}$. The response prediction of species 3 from input to 2, however, is ambiguous, and contingent upon the countervailing balance of complementary feedback cycles $a_{1,1}a_{3,2} - a_{1,2}a_{3,1}$. The $a_{1,2}a_{3,1}$ cycle, which here is negative, is also included in the system determinant, in conjunction with $a_{2,3}$, as a positive feedback cycle that must be weak for the system to be stable. Thus, one could draw inferences about expected system behavior based on these contingencies. Correct prediction of the sign of the response of

species 3 from input to species 2 requires quantitative knowledge of the relative strengths of the interaction terms involved. Where certain predictions are critical in the understanding or management of a system, development of key research questions can be based on this kind of analysis and knowledge of system structure.

Equivalent analysis of this system's qualitatively specified matrix

$$^{\circ}\mathbf{A} = \begin{bmatrix} -1 & -1 & -1 \\ 1 & 0 & -1 \\ 1 & 1 & 0 \end{bmatrix} \quad (14)$$

from Eqs. 9–11, gives the following results:

$$\text{adj} -^{\circ}\mathbf{A} = \begin{bmatrix} 1 & -1 & 1 \\ -1 & 1 & -2 \\ 1 & 0 & 1 \end{bmatrix} \qquad \mathbf{T} = \begin{bmatrix} 1 & 1 & 1 \\ 1 & 1 & 2 \\ 1 & 2 & 1 \end{bmatrix}$$

$$\mathbf{W} = \frac{\overrightarrow{|\text{adj} \,^{\circ}\mathbf{A}|}}{\mathbf{T}} = \begin{bmatrix} 1 & 1 & 1 \\ 1 & 1 & 1 \\ 1 & 0 & 1 \end{bmatrix} \quad (15)$$

which can be seen to correspond with the above symbolic analysis and the quantitative matrices in Eqs. 3 and 4.

Interpretation of the symbolically rendered adjoint matrix is an equivalent formulation of Levins's loop analysis technique, which can provide rich insight into the behavior of complex systems. In ecological systems, it is exceedingly rare that we have sufficient knowledge for a quantitative analysis; indeed, techniques for field measurement of interaction strengths have only recently been available (Paine 1992, Laska and Wootton 1998). Often available, however, is much descriptive information on community structure that can be incorporated into a symbolic or qualitative analysis. In small or sparsely connected systems, analysis of a qualitatively specified community matrix ($^{\circ}\mathbf{A}$) with the adjoint, absolute, and weighted-predictions matrices is of less value than a symbolic analysis, as loss of the symbolic contingencies represents an enormous sacrifice of information. In large or highly connected systems, however, symbolic output is difficult, if not impossible to interpret, for the number of complementary feedback cycles, and hence logical contingencies, multiply factorially with system size and connectivity. In these circumstances, use of the qualitatively specified adjoint and weighted-predictions matrices can distinguish between the relative contribution of community structure and interaction strength, and help interpret community response to input. To illustrate this point, we analyze four published studies in which indeterminacy plays an important role in the interpretation of presses.

Plankton–bacteria–protozoa community

1) R = protozoa
2) B = bacteria
3) Z = zooplankton
4) P = phytoplankton
5) N = nutrients

Symbolically specified
community matrix

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

Quantitatively specified
community matrix

$$\mathbf{A} = \begin{bmatrix} -1 & 0.6 & 0 & 0 & 0 \\ -0.6 & -1 & 0 & 0.1 & 0.6 \\ 0 & 0 & -1 & 0.2 & 0 \\ 0 & 0 & -0.2 & -1 & 0.5 \\ 0.6 & -0.6 & 0.2 & -0.5 & -1 \end{bmatrix}$$

Inverse community matrix

$$-\mathbf{A}^{-1} = \begin{bmatrix} 0.9 & 0.4 & 0.05 & -0.06 & 0.2 \\ -0.2 & 0.7 & 0.09 & -0.09 & 0.3 \\ 0.05 & -0.01 & 1 & 0.1 & 0.07 \\ 0.2 & -0.06 & -0.09 & 0.8 & 0.4 \\ 0.5 & -0.1 & 0.2 & -0.3 & 0.7 \end{bmatrix}$$
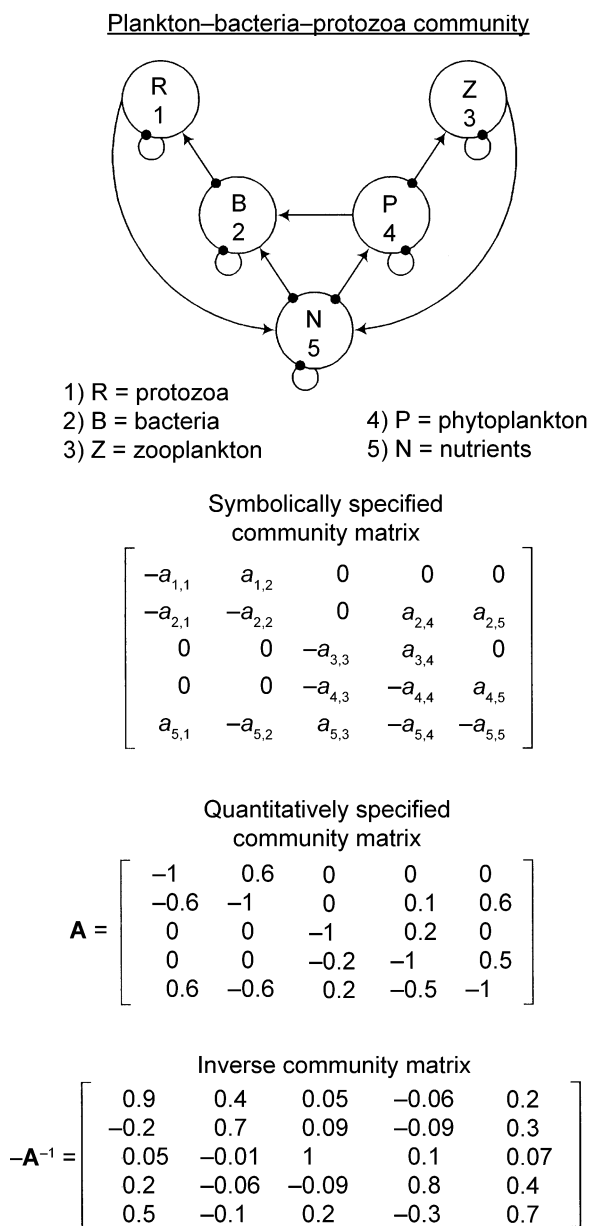
FIG. 1. Signed digraph, community matrix, and inverse matrix for the plankton community model; interaction terms are quantitatively specified with plausible numeric values (from Stone 1990).

APPLICATIONS

A paradox from plankton.—Stone (1990) presented a plankton community model (Fig. 1) with a community matrix specified by plausible interaction terms. He analyzed both quantitative inverse matrix predictions and symbolically rendered predictions to explain the paradoxical benefit to phytoplankton that is possible from its commensal contribution of organic carbon to a resource competitor. We use Stone's system as a point of departure to compare qualitative and quantitative predictions of response sign and magnitude.

Comparing Stone's quantitative results with a qualitative analysis of the adjoint matrix, we found that a third of the predictions did not match in terms of response direction or sign (Fig. 2). We calculated the weighted-predictions matrix for this system (Fig. 2) and found that all inconsistencies had low weighted-prediction values. Examining the first column of the inverse of Stone's matrix (which are responses caused by positive input to protozoa; Fig. 1), we noticed that the second $(-\mathbf{A}_{2,1}^{-1})$ and fourth $(-\mathbf{A}_{4,1}^{-1})$ elements have the same absolute strength but are opposite in sign. The second element, however, does not match the sign of the qualitative prediction. The cause for this inconsistency is identified in the qualitative and symbolic rendering of the adjoint matrix (Fig. 2). The second term of the first adjoint matrix column consists of seven countervailing cycles (four positive and three negative) that yield a sum of +1 complementary feedback cycle. When divided by the absolute number of cycles, as done in the weighted-predictions matrix, a low value of 0.14 is observed, meaning that only 14% of cycles— one in this case—contribute to the net direction of the response. Thus, a minor quantitative change can easily reverse the direction of this prediction. In the fourth term (of first column), only two cycles contribute to the response, but both are positive; it therefore receives a value of one in the weighted-predictions matrix.

Because the adjoint of a qualitatively specified system details the net number of complementary feedback cycles contributing to a given response, it follows that there should be some positive relationship between it and the inverse matrix of a quantitatively specified system. A test of this assertion in the plankton community model found that complementary feedback accounted for 58% of the variation in quantitative responses (Fig. 3). However, this system was specified with antisymmetric interaction terms (i.e., all predator–prey interactions were of equal magnitude but opposite sign), which are not typical of other biological systems (Yodzis 1988, de Ruiter et al. 1995). We repeated this test of Stone's system, but scaled the positive effects of prey to predators ($a_{1,2}$, $a_{2,5}$, $a_{3,4}$, $a_{4,5}$) to 1/10, and 1/100 of their original values, with proportional reductions in terms ($a_{5,1}$, $a_{5,3}$, $a_{2,4}$) for nutrient flux. Results of both tests were similar to our first assessment; the same predictions remained incorrect in sign. Complementary feedback explained 46% and 41%, respectively, of the variation in quantitative response. While a substantial proportion of the variation in quantitative response is still explained by system structure, we emphasize the equally high degree of variation due to system quantification. We thus consider the net number of complementary feedback cycles only as a theoretical benchmark for the expected relative magnitude of system responses. In Dambacher (2001), we define the limits of qualitative predictions of response strength and sign with computer simulations, across an array of system

Quantitative and symbolic analysis of plankton community model

qualitatively specified
community matrix   adjoint   absolute feedback   weighted predictions

$$
{}^{\circ}\mathbf{A} = \begin{bmatrix} -1 & 1 & 0 & 0 & 0 \\ -1 & -1 & 0 & 1 & 1 \\ 0 & 0 & -1 & 1 & 0 \\ 0 & 0 & -1 & -1 & 1 \\ 1 & -1 & 1 & -1 & -1 \end{bmatrix}
\quad
\text{adj} - {}^{\circ}\mathbf{A} = \begin{bmatrix} 5 & 2 & 2 & \mathbf{1} & 3 \\ \mathbf{1} & 2 & 2 & \mathbf{1} & 3 \\ 2 & 0 & 4 & 2 & 2 \\ 2 & 0 & 0 & 2 & 2 \\ 4 & 0 & 4 & 0 & 4 \end{bmatrix}
\quad
\mathbf{T} = \begin{bmatrix} 7 & 4 & 4 & 3 & 3 \\ 7 & 4 & 4 & 3 & 3 \\ 2 & 2 & 8 & 4 & 2 \\ 2 & 2 & 6 & 4 & 2 \\ 4 & 4 & 6 & 6 & 4 \end{bmatrix}
\quad
\mathbf{W} = \begin{bmatrix} 0.7 & 0.5 & 0.5 & \mathbf{0.3} & 1 \\ \mathbf{0.1} & 0.5 & 0.5 & \mathbf{0.3} & 1 \\ 1 & \mathbf{0} & 0.5 & 0.5 & 1 \\ 1 & \mathbf{0} & \mathbf{0} & 0.5 & 1 \\ 1 & \mathbf{0} & 0.7 & \mathbf{0} & 1 \end{bmatrix}
$$

first column of
symbolically rendered adjoint

$$
\text{adj} - \mathbf{A}_{i,1} = \begin{bmatrix}
a_{2,2}a_{3,3}a_{4,4}a_{5,5} + a_{2,2}a_{3,3}a_{4,5}a_{5,4} + a_{2,2}a_{4,3}a_{3,4}a_{5,5} + a_{5,2}a_{3,3}a_{2,4}a_{4,5} + a_{5,2}a_{3,3}a_{2,5}a_{4,4} + a_{5,2}a_{4,3}a_{2,5}a_{3,4} - a_{2,2}a_{5,3}a_{3,4}a_{4,5} \\
a_{2,1}a_{5,3}a_{3,4}a_{4,5} + a_{5,1}a_{3,3}a_{2,4}a_{4,5} + a_{5,1}a_{3,3}a_{2,5}a_{4,4} + a_{5,1}a_{4,3}a_{2,5}a_{3,4} - a_{2,1}a_{3,3}a_{4,4}a_{5,5} - a_{2,1}a_{3,3}a_{4,5}a_{5,4} - a_{2,1}a_{4,3}a_{3,4}a_{5,5} \\
a_{2,1}a_{5,2}a_{3,4}a_{4,5} + a_{5,1}a_{2,2}a_{3,4}a_{4,5} \\
a_{2,1}a_{5,2}a_{3,3}a_{4,5} + a_{5,1}a_{2,2}a_{3,4}a_{4,5} \\
a_{2,1}a_{5,2}a_{3,3}a_{4,4} + a_{2,1}a_{5,2}a_{4,3}a_{3,4} + a_{5,1}a_{2,2}a_{3,3}a_{4,4} + a_{5,1}a_{2,2}a_{4,3}a_{3,4}
\end{bmatrix}
$$

Fig. 2. Qualitatively specified community matrix ($^{\circ}\mathbf{A}$) for the plankton community model (as in Fig. 1), with adjoint (adj $-^{\circ}\mathbf{A}$), absolute feedback ($\mathbf{T}$), and weighted-predictions matrices ($\mathbf{W}$). Adjoint matrix elements that differ in sign from the inverse matrix of quantitatively specified system (Fig. 1) are in bold type, as are corresponding elements of $\mathbf{T}$ and $\mathbf{W}$. The eight qualitative predictions that do not agree with the quantitative response predictions have low prediction weights, all being ≤ 0.3. Column 1 of adjoint matrix is rendered symbolically to illustrate the net and absolute number of complementary feedback cycles. The ratio adj $^{\circ}\mathbf{A}_{ij}/\mathbf{T}_{ij}$, defines the elements of the weighted-predictions matrix $\mathbf{W}$.

structure. We find weighted-prediction values >0.5 to exhibit high (near 95%) sign determinacy.

Old-field food web.—Schmitz (1997) encountered indeterminacy in a field experiment. This study is remarkable and noteworthy because it is one of the few completely specified community matrices published that applies the experimentally derived inverse method championed by Bender et al. (1984). He performed *n* press experiments upon each species in an old-field food web (Fig. 4) to estimate all interaction terms of the community matrix, with an associated variance. He then pressed the system in two separate ways (top-down and bottom-up), and compared the reliability of

observed results to predicted ones, in terms of response magnitude. He concluded that the system had high indeterminacy, and attributed it to variation of interaction strength.

We calculated the weighted-predictions matrix of this system and found that the vast majority of responses (32 of 36) were zero (Fig. 4). Our results indicate that complementary feedback cycles in this system have an inherent tendency to cancel each other, or to put it differently, most predictions are a coin flip if positive and negative complementary feedback cycles are of similar strength. While variation in interaction strength is undeniably a source of indeterminacy in this system, the large absolute number of countervailing complementary feedback cycles (from 26 to 64) within each response clearly amplifies this phenomenon. Furthermore, the overall feedback of the quantified system was relatively small (det $\mathbf{A} = -0.47$), and the qualitative model was neutrally stable and had zero overall feedback (det $^{\circ}\mathbf{A} = 0$). The tendency towards cancellation of complementary feedback, and zero overall feedback, arises from the webby structure of this system. We conclude that, from a theoretical perspective, this particular system will exhibit little, if any, reliability in predicting press experiments. Here we find community structure in and of itself to be an overriding source of indeterminacy.

Danish shallow lakes.—The adjoint and weighted matrices can each be used to propose and prioritize alternative management options. Jeppesen (1998) thoroughly documented changes in the level of guild community members in shallow lakes of Denmark, resulting from decades-long nutrient press (anthropogenic
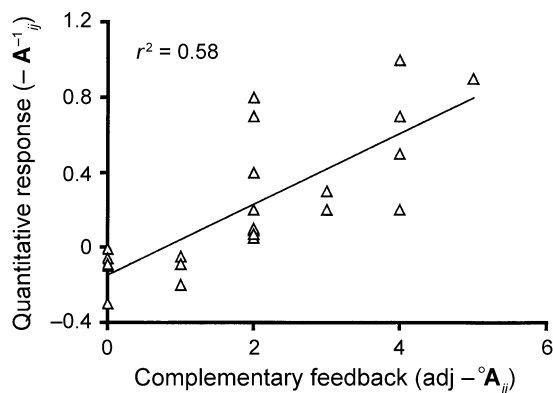
Fig. 3. Relationship between the quantitative and qualitative response for the plankton community model. Each element of the adjoint matrix from the qualitatively specified matrix (adj $-^{\circ}\mathbf{A}$, Fig. 2) is compared to the corresponding element of the inverse matrix of the quantitatively specified system ($-\mathbf{A}^{-1}$, Fig. 1).

Old-field food web

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

$$\begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 3 & -3 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & -3 & 3 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \end{bmatrix}$$

$$\mathbf{T}$$

$$\begin{bmatrix} 30 & 26 & 26 & 60 & 42 & 26 \\ 36 & 31 & 31 & 50 & 50 & 36 \\ 50 & 42 & 42 & 64 & 50 & 50 \\ 32 & 28 & 28 & 64 & 36 & 32 \\ 36 & 31 & 31 & 50 & 50 & 36 \\ 26 & 26 & 26 & 60 & 42 & 30 \end{bmatrix}$$

1) M = *Melanoplus borealis*
2) F = *Fragaria canadensis*
3) P = *Phleum pratense*
4) S = *Solidago altissima*
5) H = *Hieracium aurantiacum*
6) N = soil nitrogen

$$\mathbf{W}$$

$$\begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.1 & 0.1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.1 & 0.1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \end{bmatrix}$$
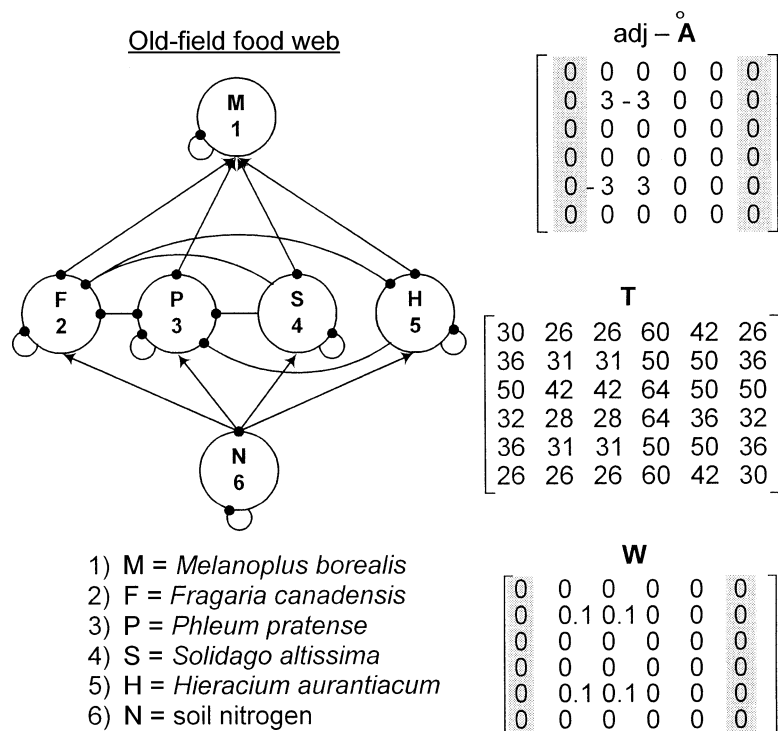
FIG. 4. Signed digraph of the community matrix specified by Schmitz (1997; adapted from his Table 3), for interactions among a grasshopper (*Melanoplus borealis*), four perennial plants, and soil nitrogen in an old-field food web, with corresponding adjoint of the qualitatively specified community matrix (adj $-\overset{\circ}{}\mathbf{A}$), absolute feedback matrix ($\mathbf{T}$), and weighted-predictions matrix ($\mathbf{W}$). Schmitz evaluated shaded responses in nitrogen and herbivore press experiments and found them to be highly indeterminate in terms of response magnitude.

phosphorous addition) that resulted in eutrophication. Based on the results of numerous (25) studies compiled and synthesized in the above citation, we constructed signed digraphs of the mesotrophic (Fig. 5) and eutrophic (Fig. 6) states. For a bottom-up nutrient press (positive input to variable 10), adjoint matrices and weighted-predictions matrices of both of these models match the reported responses, except for one element in the eutrophic model (Fig. 6), of low predictive weight. Top-down management interventions in eutrophic systems to reduce phytoplankton populations were studied through experiments that added macrophytes, reduced cyprinids, and increased juvenile piscivorous fish. Model predictions for these inputs matched six of eight observed responses in the eutrophic system (Fig. 6).

While we expected piscivorous fish to decrease when cyprinids were being harvested in eutrophic systems (Fig. 6; adjoint $-\overset{\circ}{}\mathbf{A}_{6,7} = 9$, for a negative input to variable 7 the sign is reversed in the effect to 6), no change in abundance was observed. This discrepancy can be rationalized by the low predictive weight of the response ($\mathbf{W}_{6,7} = 0.4$). No explanation can account for the one wrong prediction in the top-down effect on nutrients (adjoint $-\overset{\circ}{}\mathbf{A}_{10,7} = -7$), which comes with a, theoretically speaking, perfectly weighted prediction ($\mathbf{W}_{10,7} = 1$). This deviation indicates model error and

implies that important links or variables are missing. Indeed, nutrient cycling linkages, fluxes between sediment stores, denitrification losses, and bacterial communities have been proposed as essential, but undescribed, features of these lakes (Jeppesen et al. 1998). If predictions that are more accurate are required for top-down effects on nutrient stores, a more detailed submodel of nutrient cycling must be described. Other than that, the model of the system appears highly predictive.

Despite this limited and identifiable shortcoming, we conclude that the signed digraph models and consequent qualitative community matrices that arise from Jeppesen's description of the community are robust. Thus, it has high heuristic value. For instance, inspection of the entire adjoint matrix can suggest additional experiments and management options. Reducing algal blooms in the eutrophic system can occur most effectively in two ways: reduce nutrient inputs or increase zooplankton biomass. These predictions have high weighted values, and the greatest potential response magnitude (i.e., greatest number of complementary feedback cycles in ninth row of adjoint matrix, Fig. 6). We would predict input to the other members of the community (first seven predictions in the ninth row of adjoint, Fig. 6) to elicit a response in phytoplankton of a more or less similar magnitude. All of these predic-
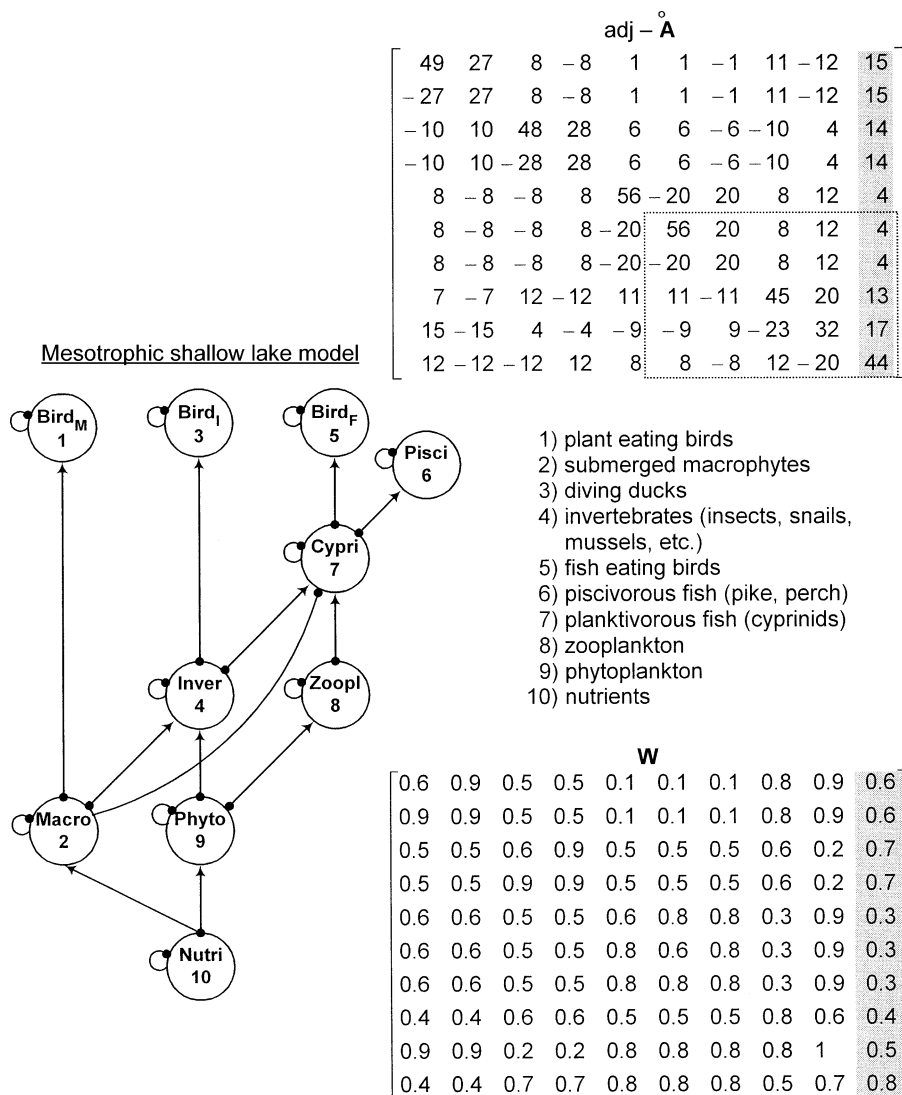
FIG. 5. Signed digraph of Danish shallow lakes in mesotrophic state, as described in studies compiled in Jeppesen (1998), with corresponding adjoint of qualitatively specified community matrix (adj $-°\mathbf{A}$), and weighted-predictions matrix ($\mathbf{W}$). Shaded regions of matrices refer to responses observed over a range of nutrient enrichment; the boxed-in region (dotted line) of the adjoint matrix is compared to a deep-lake model (Fig. 7) in *Discussion*.

tions have high weighted values indicating a high potential for sign determinacy. Response strengths of phytoplankton in the mesotrophic model (Fig. 5) are similar to the eutrophic model, input to macrophytes and their avian grazers, however, takes on a greater importance in the mesotrophic model.

Lake Saint George deep pelagia.—The adjoint matrix can also be used to interpret results of "natural" press-like perturbations to assess the structure of the community. Puccia and Levins (1985) demonstrate how qualitative responses can be used to reconstruct the structure of a community through the process of "inverting the inverse." Bodini (1998) used published results to reconstruct, through qualitative analysis, a community that experienced top-down and bottom-up inputs through fish kills and nutrient loading.

Two alternative models were constructed that both yielded qualitative predictions matching field observations (models A and B, Fig. 7). These models display a degree of uncoupling and support assertions by McQueen et al. (1986, 1989) that community members had some one-way links between prey and predator guilds. We tested whether or not a more plausible model, that is, of a system with complete predator–prey links (model C, Fig. 7) was not as consistent. Comparing the adjoint matrix from model C with the prediction tables from models A and B, mismatches occur where feedback strength is weakest in terms of the number of cycles contributing to the response.

Results from model C suggest that the more plausible coupled model of a chain of predator–prey interactions is acceptable. We submit that the lack of a measured

adj – °$\overset{\circ}{\mathbf{A}}$

$$\begin{bmatrix} 30 & 24 & 7 & -7 & 1 & 1 & -1 & 10 & -11 & -11 \\ -24 & 24 & 7 & -7 & 1 & 1 & -1 & 10 & -11 & -11 \\ -12 & 12 & 35 & 19 & 5 & 5 & -5 & -4 & -1 & -1 \\ -12 & 12 & -19 & 19 & 5 & 5 & -5 & -4 & -1 & -1 \\ 6 & -6 & -4 & 4 & 38 & -16 & 16 & 2 & 14 & 14 \\ 0 & 0 & -9 & 9 & -9 & 45 & 9 & 18 & -9 & -9 \\ 6 & -6 & -4 & 4 & -16 & -16 & 16 & 2 & 14 & 14 \\ 0 & 0 & 9 & -9 & 9 & 9 & -9 & 36 & 9 & 9 \\ 6 & -6 & 5 & -5 & -7 & -7 & 7 & -16 & 23 & 23 \\ -6 & 6 & -5 & 5 & 7 & 7 & -7 & 16 & -23 & 31 \end{bmatrix}$$

Eutrophic shallow lake model

1) plant eating birds
2) submerged macrophytes
3) diving ducks
4) invertebrates (insects, snails, mussels, etc.)
5) fish eating birds
6) piscivorous fish (pike, perch)
7) planktivorous fish (cyprinids)
8) zooplankton
9) phytoplankton
10) nutrients

W

$$\begin{bmatrix} 0.5 & 0.7 & 0.4 & 0.4 & 0.1 & 0.1 & 0.1 & 0.7 & 0.7 & 0.7 \\ 0.7 & 0.7 & 0.4 & 0.4 & 0.1 & 0.1 & 0.1 & 0.7 & 0.7 & 0.7 \\ 0.8 & 0.8 & 0.5 & 0.8 & 0.6 & 0.6 & 0.6 & 0.3 & 0.06 & 0.06 \\ 0.8 & 0.8 & 0.8 & 0.8 & 0.6 & 0.6 & 0.6 & 0.3 & 0.06 & 0.06 \\ 0.5 & 0.5 & 0.3 & 0.3 & 0.5 & 0.9 & 0.9 & 0.08 & 0.9 & 0.9 \\ 0 & 0 & 0.4 & 0.4 & 0.4 & 0.7 & 0.4 & 0.5 & 0.3 & 0.3 \\ 0.5 & 0.5 & 0.3 & 0.3 & 0.9 & 0.9 & 0.9 & 0.08 & 0.9 & 0.9 \\ 0 & 0 & 0.6 & 0.6 & 0.6 & 0.6 & 0.6 & 0.8 & 0.3 & 0.3 \\ 0.8 & 0.8 & 0.5 & 0.5 & 1 & 1 & 1 & 0.8 & 1 & 1 \\ 0.8 & 0.8 & 0.5 & 0.5 & 1 & 1 & 1 & 0.8 & 1 & 0.4 \end{bmatrix}$$
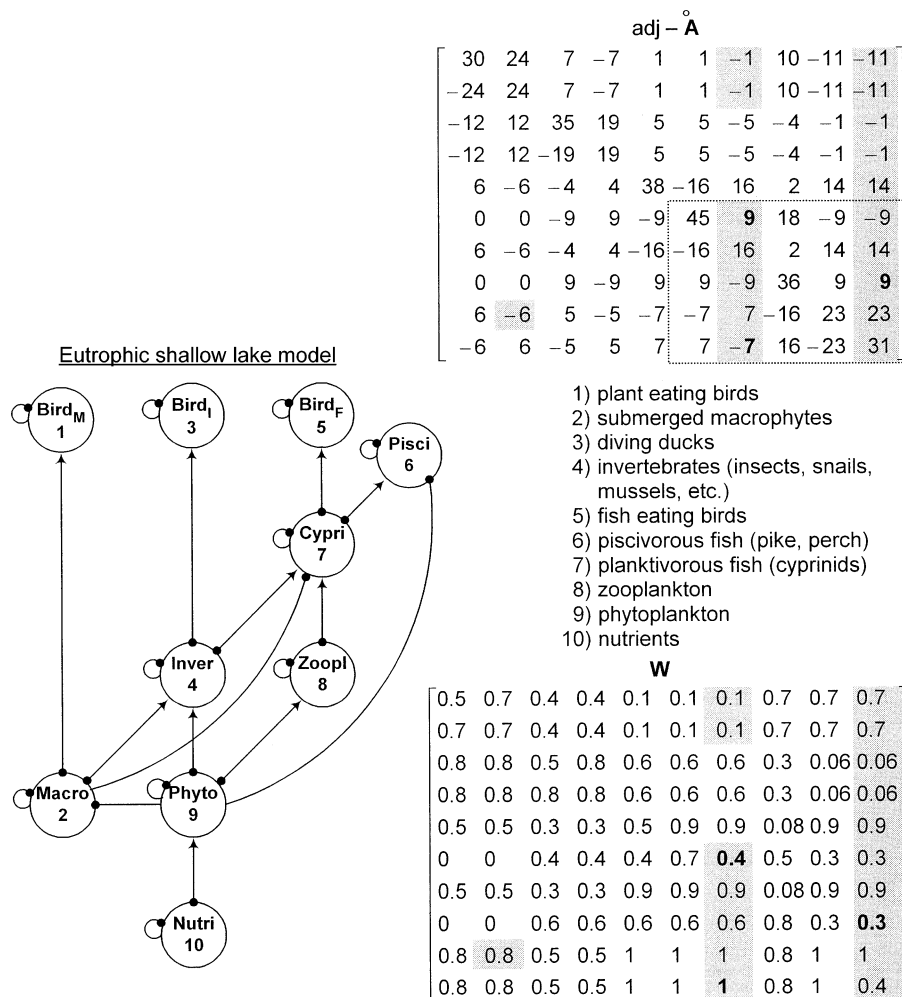
FIG. 6. Signed digraph representation of Danish shallow lakes in eutrophic state, as described in studies compiled in Jeppesen (1998), with corresponding adjoint of qualitatively specified community matrix (adj $-°\mathbf{A}$), and weighted-predictions matrix (**W**). Shaded regions of matrices refer to responses observed over a range of nutrient enrichment, and in manipulations of macrophytes (addition and protection), cyprinids (experimental removals and winter fish kills), and piscivorous fish (experimental additions of juveniles in spring). Additions of juvenile piscivorous fish were interpreted as a negative input to their cyprinid prey, as stocked juveniles did not survive beyond summer. Adjoint predictions not supported by field observation are in bold type. Boxed-in region (dotted line) of adjoint matrix is compared to a deep-lake model (Fig. 7) in *Discussion*.

response was more likely due to the weakness of response, rather than to an actual decoupling between trophic levels. All responses in model C are predicted to be completely reliable in terms of their sign (i.e., all $\mathbf{W}_{ij} = 1$), a feature of all straight chain systems. Input to planktivorous fish would resolve the choice of models.

An additional application of the adjoint and absolute feedback matrices is that complementary feedback can be added across columns to assess multiple inputs to the system. This is by extension of a superposition rule for the inverse matrix (Nakajima 1992). Simultaneous negative top-down (winter fish kill) and positive bottom-up (nutrient loading) presses on model C are assessed in Fig. 7b. We observe a phenomenon of cancellation and addition of complementary feedback cycles that creates a generally positive increase in three of the four lower trophic levels, with a neutral response in the middle of the food chain. Predictability of the response for the middle variable (zooplankton) is completely lost. This neutral response prediction is not the result of decoupling, as complementary feedback cycles are transferred to the far ends of the food chain.

DISCUSSION

The inverse of the community matrix offers an estimate of community response resulting from press experiments or natural disturbance. Its practical use in ecology, however, has been hampered by ambiguous
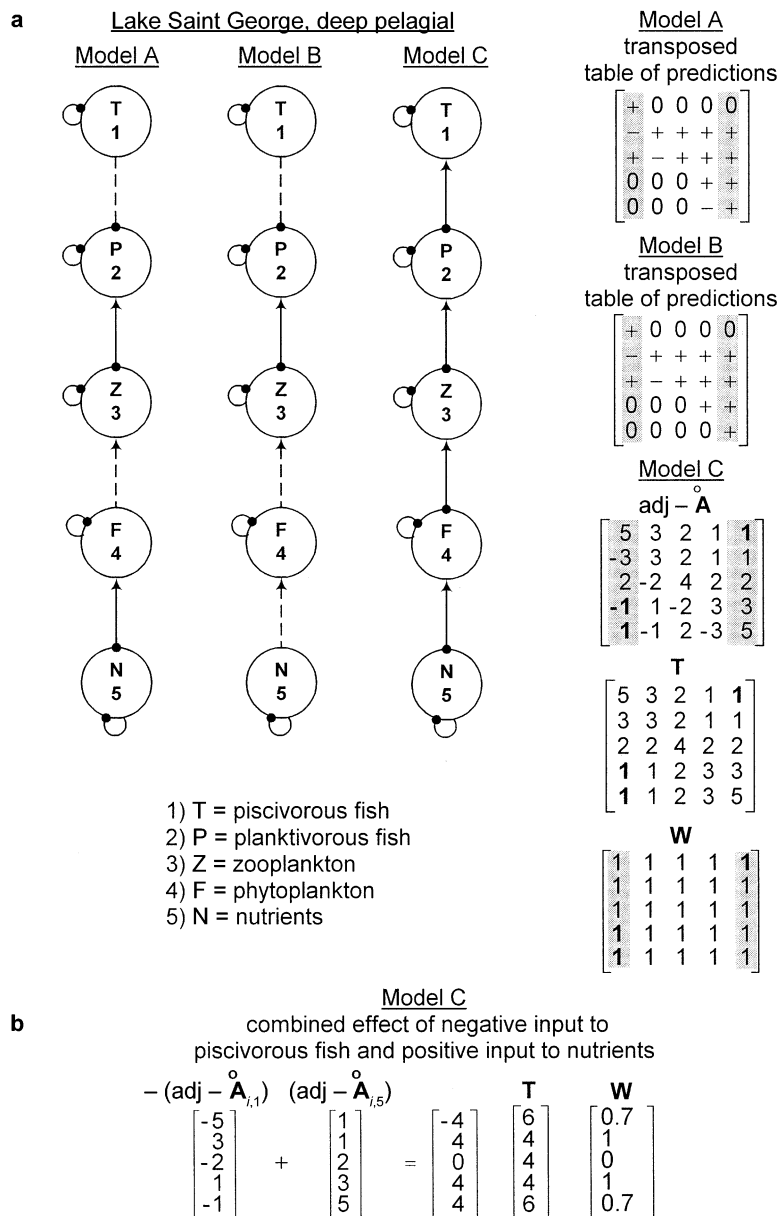
a　Lake Saint George, deep pelagial

Model A　　Model B　　Model C

Model A
transposed
table of predictions

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

Model B
transposed
table of predictions

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

Model C

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

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

T

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

W

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

1) T = piscivorous fish
2) P = planktivorous fish
3) Z = zooplankton
4) F = phytoplankton
5) N = nutrients

b　Model C
combined effect of negative input to
piscivorous fish and positive input to nutrients

$$-(\mathrm{adj} - \overset{\circ}{\mathbf{A}}_{i,1})\quad (\mathrm{adj} - \overset{\circ}{\mathbf{A}}_{i,5})$$

$$\begin{bmatrix} -5 \\ 3 \\ -2 \\ 1 \\ -1 \end{bmatrix} + \begin{bmatrix} 1 \\ 1 \\ 2 \\ 3 \\ 5 \end{bmatrix} = \begin{bmatrix} -4 \\ 4 \\ 0 \\ 4 \\ 4 \end{bmatrix} \quad \begin{matrix} \mathbf{T} \\ \begin{bmatrix} 6 \\ 4 \\ 4 \\ 4 \\ 6 \end{bmatrix} \end{matrix} \quad \begin{matrix} \mathbf{W} \\ \begin{bmatrix} 0.7 \\ 1 \\ 0 \\ 1 \\ 0.7 \end{bmatrix} \end{matrix}$$

FIG. 7. (a) Alternative signed digraph models for trophic interactions in the pelagia of Lake Saint George. Models A and B, constructed by Bodini (1998) using loop analysis, invoke incomplete predator–prey interactions to explain apparent decoupling between trophic levels, as suggested by McQueen et al. (1986, 1989). Shaded regions of prediction tables correspond to the observation by McQueen et al. (1989) of responses to nutrient enrichment (positive bottom-up input) and winter fish kill (negative top-down input). Model C, with complete predator–prey interactions, agrees with predictions from models A and B, except where complementary feedback (adj $-\overset{\circ}{}$A) is weakest, as denoted in bold type. (b) Predicted response of simultaneous top-down and bottom-up input calculated by adding columns 1 and 5, in the adjoint (adj $-\overset{\circ}{}$A) and absolute feedback matrices (**T**). Negative top-down input was calculated by reversing the response sign in column 1 of the adjoint matrix.

or sign-indeterminate predictions. Equilibrium responses of communities are composed of both direct and indirect effects, and it is expected that these can produce counterintuitive long-term outcomes (Yodzis 1995). Previous theoretical and experimental treatments (Bender et al. 1984, Yodzis 1988, Schmitz 1997), however, have taken the inverse matrix at face value.

While these works identify the contribution of quantitative sources of indeterminacy, there has not been an appreciation of the potential impact of system structure in the use of the inverse matrix. Though qualitative techniques advanced by Levins have long encompassed this issue, these techniques have been severely hampered by ambiguity in large or complex systems. We

recommend a qualitative analysis of the adjoint of the community matrix because it explicitly accounts for the feedback cycles that ultimately determine perturbation response. Two additional mathematical tools augment the utility of the adjoint. The first is the absolute feedback matrix, which details the absolute number of cycles in a response. The second is the weighted-predictions matrix, which gives the proportion of cycles contributing to a response, and, therefore, its potential for sign determinacy. We stress that quantitative considerations are still important, as Yodzis (1988) so clearly demonstrated. Our study, however, complements these results with a qualitative approach based only on system structure, providing practical insights when quantification is unlikely or difficult.

The problem of indeterminacy was insightfully treated by Yodzis (1988) through computer simulations that randomly varied interaction strengths. He introduced the concepts of directional (sign) and topological indeterminacy. Directional indeterminacy is a statistical criterion, wherein an indeterminate prediction is one that is <95% consistent in the direction or sign of a response. Topological indeterminacy addresses, in relative terms, which responses are consistently the largest in each column or row of the inverse matrix. The technique, however, does not consider the absolute value of a response in itself, but only in comparison to others. A ''major'' effect could be very weak as long as it is the largest. Yodzis' topological indeterminacy is an original and valid approach, but difficult to generalize to practical applications. The adjoint and weighted matrix can yield a similar insight. With the adjoint and weighted-predictions matrix, one can predict which community members are likely to exhibit the greatest response to a disturbance or experimental treatment. Although large values of the adjoint matrix need not be matched by high prediction weights, when they are, then quantitative responses should be consistently large. The old-field food web model (Fig. 4) can be seen to have no potential for topological determinacy, or any degree of sign determinacy for that matter, while in the deep-lake model C (Fig. 7), all of the diagonal elements would be expected to consistently predict the largest responses of the system.

Nakajima (1992) notes that diagonal elements of the inverse, and by extension the adjoint, will always be the largest column element when the matrix is nonnegative (i.e., all elements ≥0). The qualitative adjoint of the plankton community model (Fig. 2) is an example of a non-negative matrix. Examination of the adjoint matrix columns of the straight chain model C in Fig. 7 illustrates further generalities. Top-down responses are seen to exhibit the well-known pattern of sign alternation between adjacent variables, and of uniform sign for bottom-up responses. Overlying this pattern, we find that complementary feedback cycles attenuate in number away from the source (jth) variable of input, along direct paths of system linkages. In Dam-

bacher (2001) we show this pattern of attenuation to follow the Fibonacci number series, where $F_n = F_{n-1} + F_{n-2}$ (i.e., 1, 1, 2, 3, 5,. . . ; as in model C Fig. 7). Models with more complex structural linkages exhibit variations on these basic patterns.

The hierarchical structure of model subsystems provides important insights into the behavior of the entire community. Tansky (1978) describes a rationale for assessing whole-system stability, based on the branching pattern of interconnected subsystems. By way of the adjoint matrix, similar subsystems from models of different ecosystems can be delineated for comparison. For instance, variables 6–10 of the shallow-lake models form a subsystem that is trophically equivalent to variables 1–5, respectively, in the Lake Saint George deep pelagia model. Inspection of the adjoint matrices reveals identical system behavior for the mesotrophic subsystem (Fig. 5, see boxed area of adjoint) and the deep-lake model C (Fig. 7). The interference that phytoplankton imposes on piscivorous fish in the eutrophic shallow-lake model (Fig. 6) creates different bottom-up predictions for piscivorous fish arising from input to variables 9 or 10. Imposing this same interference link in the deep-lake model creates predictions matching those of the eutrophic shallow-lake model, thus offering a working hypothesis for expected system behavior in the event of an extreme nutrient press to the deep-lake system.

While community matrix theory is a powerful tool for applied ecology, there are important limitations to bear in mind. The underlying premise, or requirement, that a system is near a local attractor can be challenged by long lasting transient behavior, chaotic behavior from nonlinearity in system parameters, or inequities of multiple attractors (Hastings 1995). Furthermore, gradual change in the environment can produce sudden and discontinuous shifts in the boundaries of basin attractors, resulting in extinction (Vandermeer and Yodzis 1999). These difficulties add yet another layer of complexity and ambiguity to management and research programs. While these difficulties cannot be explicitly addressed by qualitative techniques, neither can they be addressed by quantitative means and greater precision. And while managers will always want to know precisely ''how many more y will come from the money we put into x,'' often the more critical question is knowing the suite of possible options or the most important variables to measure within a limited budget. Attempts to incorporate community-level models into decision-making processes have been criticized (Hilborn 1992) for their burdensome demands on collection and analysis of multiscale data sets, and for their failure to keep pace with decision-making schedules. Walters and Holling (1990) stress that while testable hypotheses are trivial to define, strategies for adaptive management must proceed from critical hypotheses relevant to the internal structure of ecosystems.

The strength of qualitative techniques is in their gen-

erality (Levins 1966). Alternative models can be rapidly generated. We view them as a heuristic tool to augment statistical and mechanistic approaches, and caution that making inferences about the behavior of natural communities purely from statistical or quantitative descriptions can be potentially misleading. Thus correlations between adjacent trophic levels could lead to the conclusion that observed system behavior was due to decoupling, or some inherent primacy of bottom-up influences, when in fact both bottom-up and top-down influences can be operating together in fully connected systems. In a review of top-down vs. bottom-up control in food chains, Power (1992) called for "... testable theory that can address dynamic feedbacks between adjacent and nonadjacent trophic levels. These feedbacks may create indeterminacies that will impede the test of mechanistic food web models, but they are too pervasive to ignore." Qualitative analysis of the community matrix, made possible through use of the adjoint, absolute feedback, and weighted-predictions matrices provides, we submit, this much-needed theoretical perspective.

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APPENDIX A

An appendix outlining matrix methods for qualitative analysis of the community matrix is available in ESA's Electronic Data Archive: *Ecological Archives* E083-022-A1.

APPENDIX B

An explanation of Cramer's Rule and complementary feedback is available in ESA's Electronic Data Archive: *Ecological Archives* E083-022-A2.

SUPPLEMENTARY MATERIAL

Maple V program commands for qualitative and symbolic analysis of the community matrix, version 1.0, is available in ESA's Electronic Data Archive: *Ecological Archives* E083-022-S1.

Ecological Archives **E083-022-A1**

Jeffrey M. Dambacher, Hiram W. Li, and Philippe A. Rossignol. 2002. Relevance of community structure in assessing indeterminacy of ecological predictions. *Ecology* **83:1372-1385.**

Appendix A. Matrix methods for qualitative analysis of the community matrix.

The determinant (det) of a second order system is: $\det\begin{bmatrix} a_{1,1} & a_{1,2} \\ a_{2,1} & a_{2,2} \end{bmatrix} = a_{1,1}a_{2,2} - a_{1,2}a_{2,1}.$

Calculation of the determinant of larger systems is by expansion of its matrix minors (min) along either its columns or its rows. For a third order system, the $\mathbf{A}_{1,1}$ minor is formed by deletion of the first row and column, giving

$$\begin{bmatrix} a_{1,1} & a_{1,2} & a_{1,3} \\ a_{2,1} & a_{2,2} & a_{2,3} \\ a_{3,1} & a_{3,2} & a_{3,3} \end{bmatrix} \implies \quad \min \mathbf{A}_{1,1} = \begin{bmatrix} a_{2,2} & a_{2,3} \\ a_{3,2} & a_{3,3} \end{bmatrix}$$

.

Calculation of the determinant for the entire matrix thus becomes:

$$a_{1,1} \cdot \det\begin{bmatrix} a_{2,2} & a_{2,3} \\ a_{3,2} & a_{3,3} \end{bmatrix} - a_{1,2} \cdot \det\begin{bmatrix} a_{2,1} & a_{2,3} \\ a_{3,1} & a_{3,3} \end{bmatrix} + a_{1,3} \cdot \det\begin{bmatrix} a_{2,1} & a_{2,2} \\ a_{3,1} & a_{3,2} \end{bmatrix}.$$

.

Expansion of the determinant can proceed along any row or column, provided the correct sign is applied in the terms of the minors, according to the formula: -1^{i+j}. Determinants of matrices greater than third order are calculated by expansion with the minor method, but calculations become tedious.

Stability is equated with self-damping or negative overall feedback in a system (Levins 1975). Overall feedback is defined as the determinant of a system. The concept of self-damping being synonymous with negative overall feedback, however, is confounded by determinants of stable even-sized systems always being positive. A sign convention is therefore employed of (-1^{n+1}) det $\mathbf{A}$, which ensures that stability can be equated with negative overall feedback in both even- and odd-sized systems.

Another source of potential confusion is associated with the denominator of Eq. 9, where $-\mathbf{A}^{-1}$ = adjoint $-\mathbf{A}$ / det $-\mathbf{A}$. In stable systems with negative overall feedback (following the convention of the -1^{n+1} multiplier), the sign of the det $-\mathbf{A}$ term in the denominator will always be positive in both even- and odd-sized systems (the -1^{n+1} multiplier is <u>not</u> applied to the det $-\mathbf{A}$ term in Eq. 9). Thus the det $-\mathbf{A}$ term will not alter the equality of the signs of corresponding elements of the inverse and adjoint matrices. In unstable systems with positive overall feedback, however, the det $-\mathbf{A}$ term will be negative in both even- and odd-sized systems. Thus the sign of the adjoint $-\mathbf{A}_{ij}$ elements will be opposite to those of corresponding $-\mathbf{A}^{-1}_{ij}$ elements. Confusion notwithstanding, this inconsistency leaves us with a useful condition for unstable systems, for the adjoint $-\mathbf{A}_{ij}$ elements will always have response signs *as if* a system were stable. As a consequence, systems that are conditionally or neutrally stable can be assessed in terms of an expected or possible equilibrium behavior—a result not possible through use of the inverse matrix, which depends on a nonzero determinant for matrix inversion.

Calculation of a matrix permanent (per) is similar to the determinant, but without subtraction within matrix minors, and with an all positive sign convention for expansion terms: $(+1)^{i+j}$ (Marcus and Minc 1964, Minc 1978, Eves 1980). Thus the permanent of a second order matrix becomes

$$\text{per}\begin{bmatrix} a_{1,1} & a_{1,2} \\ a_{2,1} & a_{2,2} \end{bmatrix} = a_{1,1}a_{2,2} + a_{1,2}a_{2,1}$$

and that of a third order

$$a_{1,1} \cdot \text{per}\begin{bmatrix} a_{2,2} & a_{2,3} \\ a_{3,2} & a_{3,3} \end{bmatrix} + a_{1,2} \cdot \text{per}\begin{bmatrix} a_{2,1} & a_{2,3} \\ a_{3,1} & a_{3,3} \end{bmatrix} + a_{1,3} \cdot \text{per}\begin{bmatrix} a_{2,1} & a_{2,2} \\ a_{3,1} & a_{3,2} \end{bmatrix}.$$

.

Cofactors of a matrix ($\mathbf{C}_{ij}$) are determinants of each matrix minor, with the same $(-1)^{i+j}$ sign convention applied in the expansion, such that the matrix of all cofactors ($\mathbf{C}$) becomes

$$C_{1,1} = + \det\begin{bmatrix} a_{2,2} & a_{2,3} \\ a_{3,2} & a_{3,3} \end{bmatrix} \quad C_{1,2} = - \det\begin{bmatrix} a_{2,1} & a_{2,3} \\ a_{3,1} & a_{3,3} \end{bmatrix} \quad C_{1,3} = + \det\begin{bmatrix} a_{2,1} & a_{2,2} \\ a_{3,1} & a_{3,2} \end{bmatrix}$$

$$C_{2,1} = - \det\begin{bmatrix} a_{1,2} & a_{1,3} \\ a_{3,2} & a_{3,3} \end{bmatrix} \quad C_{2,2} = + \det\begin{bmatrix} a_{1,1} & a_{1,3} \\ a_{3,1} & a_{3,3} \end{bmatrix} \quad C_{2,3} = - \det\begin{bmatrix} a_{1,1} & a_{1,2} \\ a_{3,1} & a_{3,2} \end{bmatrix}.$$

$$C_{3,1} = + \det\begin{bmatrix} a_{1,2} & a_{1,3} \\ a_{2,2} & a_{2,3} \end{bmatrix} \quad C_{3,2} = - \det\begin{bmatrix} a_{1,1} & a_{1,3} \\ a_{2,1} & a_{2,3} \end{bmatrix} \quad C_{3,3} = + \det\begin{bmatrix} a_{1,1} & a_{1,2} \\ a_{2,1} & a_{2,2} \end{bmatrix}$$

.

The adjoint matrix is simply a transposed matrix of cofactors, such that adjoint $A_{ij} = C_{ji}$. Calculation of the *absolute feedback matrix* (**T**) from Eq. 10 is similar to the above cofactor calculations (transposed), but it uses the matrix permanent instead of the determinant, and all expansion terms are positive.
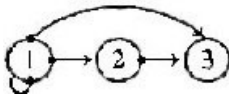
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<p style="text-align:center">*Ecological Archives* **E083-022-A2**</p>

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Appendix B. Cramer's Rule and complementary feedback.

Considering the omnivory system (as in Eq. 12),

$$\mathbf{A} = \begin{bmatrix} -a_{1,1} & -a_{1,2} & -a_{1,3} \\ a_{2,1} & 0 & -a_{2,3} \\ a_{3,1} & a_{3,2} & 0 \end{bmatrix} \tag{B.1}$$

we assess the effects to the entire community that results from positive input to a single species through Cramer's Rule (as in Eq. 5). This is accomplished by systematically inserting the column vector $[-df_i/dC_h]$ into the jth column of $\mathbf{A}$ and calculating each cofactor of the community matrix. Specifically, we calculate a single cofactor $\mathbf{C}_{3,3}$ to determine the change (d) in equilibrium abundance of species 3 due to some change in a function (f_3) of its growth rate, as controlled by some parameter C_3. This is within the context of a positive input to variable 3 through a press disturbance or experiment that creates a sustained change to the growth parameter C_3. This sustained change can be, for example, from Mendelian selection that enhances prey capture (e.g., sharper claws), or perhaps experimental supplementation (e.g., food addition to top predator); either of these changes can increase the birth rate of species 3, and thus alter its carrying capacity. The vector $[0, 0, -df_3/dC_3]$ is transposed and inserted into the third column of $\mathbf{A}$ in Eq. B.1 to obtain

$$\frac{dN_3^*}{dC_3} = \frac{\det\left(-\begin{bmatrix} -a_{1,1} & -a_{1,2} & 0 \\ a_{2,1} & 0 & 0 \\ a_{3,1} & a_{3,2} & -df_3/dC_3 \end{bmatrix}\right)}{\det -\mathbf{A}} = \frac{df_3(a_{1,2}a_{2,1})}{dC_3(-a_{3,1}a_{1,2}a_{2,3} + a_{1,1}a_{2,3}a_{3,2} + a_{2,1}a_{1,3}a_{3,2})} \tag{B.2}$$

The first two elements of the inserted column vector are zero since input here is only through species 3. Inputs through other species can be considered simultaneously by a superposition rule (Nakajima 1992), whereby multiple effects are additive within the inverse matrix, and by extension, the cofactor, adjoint, and absolute feedback matrices (as demonstrated in Fig. 7b). The answer in Eq. B.2 is composed of the $\mathbf{C}_{3,3}$ cofactor ($a_{1,2}a_{2,1}$), multiplied by the magnitude of the input $[df_3/dC_3]$, and divided by the system determinant (note sign convention of determinant in Appendix A). The result is equal to the corresponding element of the inverse ($-\mathbf{A}^{-1}_{3,3}$), and adjoint (adj $-\mathbf{A}_{3,3}$) matrices. Off-diagonal (i,j) elements of the inverse and adjoint matrices correspond to transposed cofactors ($\mathbf{C}_{ji}$). The negative community matrix is used in both the numerator and denominator of the left side of Eq. B.2, which maintains a sign convention in both even- and odd-sized systems (as in Eq. 9 and Appendix A).

The insertion of the $[-df_i/dC_h]$ column vector in Eq. B.2 is equivalent to deleting the ith row and the jth column in a cofactor expansion (Appendix A). In terms of the system's linkages, the effect of input is calculated by eliminating all linkages originating in the response variable i, and all linkages terminating in the input variable j. This has the effect of breaking all closed cycles (or loops) having the a_{ij} linkage, which creates an isolated subsystem. Here the response of variable 3 to input to itself leaves a subsystem that can be depicted either as a matrix minor or signed digraph subsystem

$$\begin{bmatrix} -a_{1,1} & -a_{1,2} & -a_{1,3} \\ a_{2,1} & 0 & -a_{2,3} \\ a_{3,1} & a_{3,2} & 0 \end{bmatrix} \Rightarrow \min \mathbf{A}_{3,3} = \begin{bmatrix} -a_{1,1} & -a_{1,2} \\ a_{2,1} & 0 \end{bmatrix} \Rightarrow \tag{B.3}$$

Taking the determinant of the $\mathbf{A}_{3,3}$ minor matrix defines a complementary subsystem that includes variables 1 and 2, the linkages between which comprise the complementary feedback cycle $a_{2,1}a_{1,2}$. This cycle, multiplied by the magnitude of the input $[df_3/dC_h]$, and scaled by the system determinant, defines the equilibrium response of the system (as in the result of Eq. B.2). According to Levins' (1974, 1975) terminology the $a_{2,1}$ and $a_{1,2}$ linkages graphically define the subsystem that is complementary to the path connecting the input variable j to the response variable i, which in this example is the path from variable 3 to 3. In determinants of off-diagonal minors, however, disjunct cycles are formed that are not entirely composed of complementary subsystems, but include also linkages along the path from variable j to i. In this work however, to avoid new terminology, we have extended the definition of complementary feedback to include all feedback cycles derived from determinants of matrix minors.

Acknowledgments

We thank J. M. Emlen and J. D. Hall for their thoughtful reviews.

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