AN ABSTRACT OF THE DISSERTATION OF

Jeffrey M. Dambacher for the degree of Doctor of Philosophy in Fisheries Science presented on April 13, 2001. Title: Qualitative Analysis of the Community Matrix

Abstract approved: Hiram W. Li
Hiram W. Li

This work sets forth a reformulation of Levins' loop analysis for the qualitative modeling of complex dynamical systems. Relationships between members of ecological communities can be analyzed through a qualitatively specified community matrix, whereby +1, -1, or 0 represent effects of one species upon another. A contribution is made to the analysis of ambiguity in predictions of system response to disturbance and system stability. The equilibrium response of a perturbed model system is determined by the countervailing balance of complementary feedback cycles, which are composed of all direct and indirect effects. The degree to which the correct sign or direction of a response can be predicted is determined by the proportion of countervailing feedback, as detailed in a 'weighted predictions' matrix. Similarly, the potential for qualitative stability is determined by a countervailing balance of overall system feedback, through the measure of 'weighted stability'. These measures are determined by system structure, are independent of system size, and are derived through the use of the matrix permanent, and classical adjoint matrix.

These qualitative techniques are tested against an array of ecological systems selected from the published literature, and are used to pose falsifiable hypotheses for previously unexplained results, and provide novel insights into system behavior. Further validation is accomplished through simulations that suggest the weighted measures of prediction and stability are a robust means to assess system ambiguity. A discovery was made of the occurrence of the Fibonacci number series embedded within the prediction matrices. The reciprocal relationship between community members can be described, in a dynamical sense, by a convergent value of *Phi*. This work supports Levins' original theme that a qualitative understanding of community structure can provide critical insights into biological complexity.

QUALITATIVE ANALYSIS OF THE COMMUNITY MATRIX

by

Jeffrey M. Dambacher

A Dissertation
submitted to
Oregon State University

in partial fulfillment of
the requirements for the
degree of

Doctor of Philosophy

Presented April 13, 2001
Commencement June 2001

Doctor of Philosophy dissertation of Jeffrey M. Dambacher presented on April 13, 2001

APPROVED:

Hiram W. Li

Major Professor, representing Fisheries Science

W. Daniel Edge

Head of Department of Fisheries and Wildlife

Sally Francis

Dean of Graduate School

I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Jeffrey Dambacher

Jeffrey M. Dambacher, Author

ACKNOWLEDGEMENTS

I thank Drs. John Emlen, Hiram Li, Philippe Rossignol, David Sampson, and Anthony Vella for service as my graduate committee; their advice and guidance in this work has been valuable; working with them has been fun and challenging. I thank Dr. Gordon Reeves for initial support at the beginning of my doctoral work, and I also thank Dr. Gretchen Oosterhout for early advice as an invited member of my graduate committee. I especially thank Hiram Li and Philippe Rossignol for enthusiastic explorations of community ecology, which continues to be immensely rewarding and enjoyable. This work is based on and inspired by theoretical foundations laid down by Richard Levins and Charles Puccia of the Harvard School of Public Health; I thank the latter for a first-rate review of Chapter 4. Further inspirations have come from weekly meetings (since fall 1997) of the OSU Loop Group, for which I thank Gonzalo Castillo, Selina Heppell, Jane Jorgensen, Hiram Li, Gabriela Montaño-Moctezuma, and Philippe Rossignol.

David Finch, Ronald Guenther and Bent Petersen of the OSU Department of Mathematics, kindly provided advice and helpful suggestions that led to some key improvements to mathematical formulations in this work. This work was greatly clarified and improved by the many helpful comments of reviewers, and I thank Sebastian Diehl, John Emlen, Selina Heppell, Tim Work, and three anonymous reviewers. I am especially indebted to James Hall for yet another careful job of editing.

I am continually grateful for the kindness and patience of Kim Jones, Oregon Department of Fish and Wildlife, who allowed me the opportunity to pursue this work. I am appreciative for the enthusiasm and support given by Paul Utz. I am particularly thankful for my parents, Aleck and Walda Dambacher, for their continued inspiration and support of my education. Above all, I am grateful for the nurturing presence of Clare Raffety; this work would not have been possible without her support and encouragement.

CONTRIBUTION OF AUTHORS

Drs. Hiram Li and Philippe Rossignol were involved in the design of the research, and in the writing of manuscripts. Dr. Jerry Wolff contributed to the literature base and development of Chapter 2.

TABLE OF CONTENTS

Page

TABLE OF CONTENTS (CONTINUED) Page

LIST OF FIGURES

LIST OF FIGURES (CONTINUED)

LIST OF TABLES

LIST OF APPENDICES

QUALITATIVE ANALYSIS OF THE COMMUNITY MATRIX

CHAPTER 1
INTRODUCTION

While the need to research and manage whole ecosystems rather than just single species has been recognized, working notions of how to accomplish this daunting task have been vague. Part of this challenge comes from the recognition that ecosystems are complex, response times are long, and the self-determined nature of biological systems can produce counterintuitive outcomes. These features present complexities and dynamics beyond the limits of our immediate cognition, and thus require simplification and abstraction in the form of models. The task of community ecology is to integrate the biological community in context with the physical environment. This can be accomplished through the community matrix (Levins 1968), which details the interaction of all populations in a biological community.

Levins (1966) ascribes three properties to all models: *generality*, *realism*, and *precision*. For a model to be practical only two of these can be emphasized in a given application. Maximizing all three would essentially require a duplication of nature, which, besides being unwieldy, would be impossible. The critical decision then, is to decide which property to sacrifice for the other two. Models that sacrifice generality for realism and precision can be described as *mechanistic models*; they are commonly applied by natural resource managers, especially in fisheries (e.g. stock–recruitment and yield models, bioenergetic models). Intensive data collection and comprehensive equations yield precise and testable predictions, but these are restricted to a narrow range of initial conditions. *Statistical models* sacrifice realism, and emphasize generality and precision. While these models are useful for describing general patterns with measured confidence, one is left with little understanding of the real world, as correlation is not synonymous with causation. *Qualitative models* sacrifice precision for the sake of generality and realism. They are free from the constraints of extensive and expensive data collection, and while predictions are imprecise, they are nonetheless rigorous in their derivation, and are testable. This approach was used extensively in the development of island biogeography theory.

Levins (1974, 1975) developed a qualitative analysis of the community matrix, termed 'loop analysis', but more generally referred to herein as qualitative modeling, which is ideally suited to the study of complex biological systems. Qualitative community matrix models are ideally suited to meet the requirement of ecosystem or community-level problems. They accommodate large temporal and spatial scales, are generally applicable, mathematically rigorous, and have high correspondence between model parameters and the biology of the system. Community matrix models are centered in the population–community approach to ecosystems (O'Neill et al. 1986), and operate under the assumption that systems are at or near equilibrium. System variables are based upon, but not limited to, interacting populations within a community. Through qualitative modeling, complex physical and social/human variables can also be incorporated into community matrix models, and the effects of environmental and human impacts can be assessed through the method. Qualitative modeling is a powerful technique that has basic data requirements (essentially food web structure, but also nontrophic variables and interactions), and it can be used to quickly and rigorously evaluate community stability, predict ecological change due to disturbance or experimental input, and focus research efforts on critical interactions and hypotheses.

In Chapter 2, qualitative modeling is applied to a meta-analysis of the experimental record of the snowshoe hare in boreal forests, with the result of a novel and testable hypothesis of system structure. While the use of qualitative models for the study of complex systems has proven insightful, it nonetheless is difficult to apply to large or highly connected systems. This has been due, in part, to difficulty in the hand calculation of symbolic algorithms, but also to the interpretation of ambiguous results that arise in large complex systems. Recent computer software advances in symbolic processors, however, have eliminated the tedium of hand calculations. The present work takes advantage of these advances, and sets forth, in Chapter 3 a reformulation of Levins' loop analysis technique. More importantly, this work presents a theoretical advance in the treatment of model ambiguity, which is validated herein through published studies of biological communities in Chapter 3, and through computer simulations in Chapter 4. Arising from this treatment, a novel insight is gained in Chapter 5 that shows that reciprocal relations between community members adhere to an underlying dynamical pattern related to the Fibonacci number series, and the golden mean, *Phi*. This work demonstrates an increased scope of inference for the qualitative analysis of large complex systems, and highlights Levins' original theme of the importance of system structure in advancing useful theory for the discipline of community ecology.

CHAPTER 2

PARSIMONIOUS INTERPRETATION OF THE IMPACT OF VEGETATION, FOOD, AND PREDATION ON SNOWSHOE HARE

Jeffrey M. Dambacher, Hiram W. Li,
Jerry O. Wolff and Philippe A. Rossignol

Published March 1999 in Oikos 84(3):530–532

The cyclical fluctuation of snowshoe hares (*Lepus americanus*) and their predators is a prominent feature in the boreal forests of North America that has been intensively studied by biologists for over 50 years. Controversy exists as to the causative mechanism, and research has focused on what factors initiate the decline phase of the cycle. Opinions are split between bottom-up, or top-down control. Keith proposed that food becomes limiting for hares during peak densities, and their decline is intensified by increased predation and decreased reproduction (Keith 1963, 1990, Keith and Windberg 1978, Keith et al. 1984). Others have come to favor predation pressure as sufficient to initiate and complete the decline of hares (Krebs et al. 1986, Sinclair et al. 1988). Hypotheses have been based on observations of hare and predator demographics throughout the cycle, and on experimental manipulation of vegetation, hare, and predator populations.

Krebs et al. (1995) summarized an 8-year experiment that measured the response of hare density to feeding, predator reduction, and plant fertilization, and concluded that the system has three interacting trophic levels. Food addition and predator reduction treatments each had positive effects, and together were multiplicative. These results were consistent with working assumptions of the importance of food and predation to the hare cycle, but the authors were puzzled by results of fertilization. They reported that all elements of the flora in the boreal forest responded dramatically to fertilization, but in spite of this, no response in hares was measured. Fertilization, it was concluded, was an ineffective method of food addition.

This paradox could be resolved if it were understood how the three elements of this natural system interact, and whether or not they are sufficient to account for experimental observations. Therefore we constructed a parsimonious three-trophic-level model to account for the experimental results of Krebs et al. (1995), and to gain further insight into the interaction among vegetation, hares, and predators.

Application of Qualitative Modeling

Using qualitative analysis (Levins 1974, Riebesell 1974, Puccia and Levins 1985) and based upon the literature available in published journals, we compared model behavior with experimental results. In qualitative analysis, herbivory-vegetation and predator-prey interactions are depicted in terms of system feedback to populations, with consumers receiving a positive link, and the consumed receiving a negative link. Negative feedback connecting a population to itself is termed a self-effect. In plants this is commonly manifested as a density-dependent effect through nutrient limitations, and is called 'self-regulation'. A predator that obtains food from outside the model system, through alternate prey, allows the predator population to not depend solely on prey from within the model. From the context of the model, this equates to a self-effect, and the predator is termed 'regulated'. A population that receives all predation losses and food from variables within a model system has no self-effect, and its growth rate is determined solely by variables from within the model.

Experimental manipulations are interpreted as input to the population elements of a system in terms of increases or decreases to birth and death rates. An exclusionary reduction of predators is equated as a decrease in the death rate of prey, but not as an increase in the death rate of predators; addition of hare food pellets is an increase in hare birth rate (a basic Lotka–Volterra assumption) and is mathematically equivalent to reduction in predation pressure. Similarly, the fertilization of vegetation is viewed as input to vegetative growth, but not a direct input to hares. Procedures for carrying out these calculations on a PC-based symbolic processor such as *Mathcad* (Mathsoft, Cambridge, MA) are available in Li et al. (1999).

Model Linkages and Predictions

Interactions among vegetation, hares, and predators are most simply portrayed by model A (Figure 2.1). Predators in the model represent a guild of mammalian and avian predators that are regulated, whereby hares are a dominant, but not exclusive source of

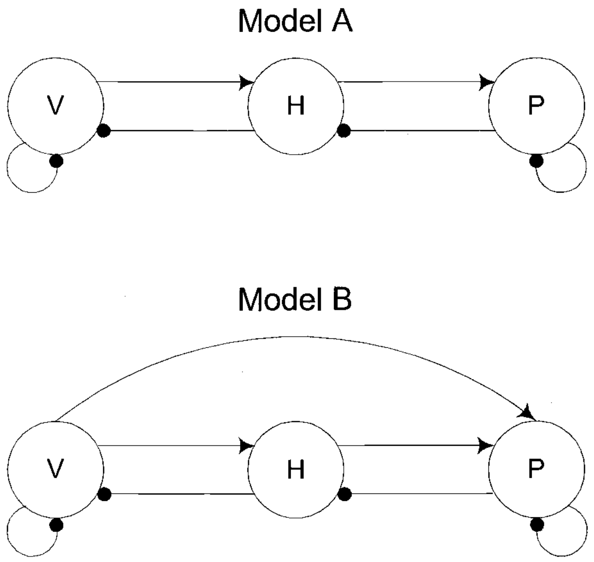


Figure 2.1. Models of possible interactions between vegetation (V), snowshoe hares (H), and predators (P). Lines with arrows indicate positive links, those with filled circles denote negative links. The self-effect to vegetation represents self-regulation and to predators, another prey source.

food (Nellis et al. 1972, Rusch et al. 1972). Vegetation is also depicted as being self-regulated, which connotes density-dependent effects common to this trophic level, but is also indicated by nitrogen limitation in boreal forests (Bonan and Shugart 1989, Nams et al. 1993).

Using techniques for deriving the effects of input (Levins 1974, Riebesell 1974, Puccia and Levins 1985), model A's predictions (Table 2.1) of a positive response of vegetation to fertilization, and a positive response of hares to feeding and predator reduction is consistent with results of all published field experiments (Windberg and Keith 1976, Krebs et al. 1986, 1995, John and Turkington 1995). But the Krebs et al. (1995) observation of no response of hares to plant fertilization is in contradiction to a positive response predicted by model A. The parsimonious model with predictions consistent with this result, and with results in all other reports, was attained from model B (Figure 2.1, Table 2.1), by the addition of a positive link from vegetation to predators.

Table 2.1. Calculated response to input for alternative models depicted in Figure 2.1; effects of positive input to vegetation, snowshoe hare, or predators, are portrayed as changes that are positive (+), negative (–), or neutral (0). The boxed-in areas (dashed-lines) represent the extent of measured responses in Krebs et al. (1995).

Model	Positive input to	Direction of response of vegetation	hare	predator
A	vegetation	+	+	+
	hare	–	+	+
	predator	+	–	+
B	vegetation	+	0	+
	hare	–	+	0
	predator	+	–	+

The predictions for models A and B (Table 2.1) differ only in the response of hares to input in vegetation, and of predators to input to hares, both of which are positive in model A, and neutral in model B. Neutral responses in the context of experimental results arise as treatment effects that are not discernable from control values (Puccia and Levins 1985). They occur where countervailing positive and negative system feedback upon a variable cancel out, either completely or to an extent that measured responses are weak and statistically insignificant. Two additional models, variations of A and B with no self-effect to predators, were considered in our analysis, but were discounted, as their prediction of a neutral response from hares to feeding, or to an exclusionary reduction of predators was inconsistent with a positive response in reported experiments (Windberg and Keith 1976, Krebs et al. 1986, 1995).

Predicted responses for model B imply an important link between vegetation and predators that in effect neutralizes any net benefit from fertilization being passed on to snowshoe hare. In model B, fertilization could translate to an increased birth rate of hares, but it would also effect an increased death rate in hares through predation, with no net change in the population size of hares. In this context fertilization of vegetation is not equivalent to food addition to hares, which is apparently the source of the puzzlement in Krebs et al.'s (1995) interpretation of their data.

The exact nature of the vegetation-predator link is as of yet undefined, but is presumably nontrophic, and we submit, may be associated with increased predator efficiency through vegetative cover. This link is admittedly counterintuitive and, by our examination, does not appear in the literature on snowshoe hares; this should not be surprising, as nontrophic interactions are difficult to substantiate, and most likely to be revealed through unexpected experimental results. We speculate that vegetative growth might confer a tactical advantage to lynx (*Lynx canadensis*). O'Donoghue et al. (1998) report that lynx use hunting beds to ambush both hare and red squirrels (*Tamiasciurus hudsonius*), and use of hunting beds increased during the decline and low phases of the hare cycle. The vegetation-predator link that we are suggesting here need not occur for all species in the predator guild; model B only requires that an overall positive link, possibly quite weak, be present.

Verification and Properties of Model B

Experimental studies of this natural system have focused on responses of vegetation and hares. Our analysis suggests a critical test would also include measurement of the experimental response of predators, either density or predation pressure, to an input to hares. A neutral response (Table 2.1) would favor model B over model A.

An important difference between models A and B, is that A can be globally stable, and B can only achieve conditional stability (Levins 1974, Puccia and Levins 1985). A stable system is difficult to disturb and not likely to oscillate, which is inconsistent with the well known fluctuations exhibited by hares and their predators. Oscillatory response to input inherently arises in model B from the large positive loop through a vegetation-to-predator-to-hare-to-vegetation linkage. Cyclical fluctuations in abundance could be a natural feature of the positive feedback running through all elements of this biological system, and the effects of a perturbation to any one element of the system would likely be carried on through time to all elements of the system. System oscillations could be manifested and maintained both by external input to the system and internal system dynamics. Top-down or bottom-up influences may vary temporally and spatially (Ranta et al. 1997) and need to be considered in the context of the overall effects of the system's linkages.

CHAPTER 3

RELEVANCE OF COMMUNITY STRUCTURE IN ASSESSING INDETERMINACY OF ECOLOGICAL PREDICTIONS

Jeffrey M. Dambacher, Hiram W. Li and Philippe A. Rossignol

Abstract

The community matrix is potentially a powerful tool for community ecology. While it details the direct interactions between community members, it can also be used to quantify all of the indirect effects that occur in a community, and thereby 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.

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 $\mathbf{N}$, change in the equilibrium population $\mathbf{N}^*$ of species i

$$d\mathbf{N}_\mathrm{i}^* / dt = f_i(N_1, N_2, \ldots, N_n; p_1, p_2, \ldots, p_c) \tag{3.1}$$

is a function (f_i) of other species or variables in the system, and their associated growth parameters (p_c). At or near equilibrium $f_1 = f_2 = \ldots f_n = 0$. Direct relationships between community members, formally organized in the Jacobian, or community matrix $\mathbf{A}$, determine the interplay between population abundance $\mathbf{N}$, and carrying capacity $\mathbf{K}$ (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 of a j^{th} species, such that its carrying capacity is altered.

$$\frac{d\mathbf{N}_\mathrm{i}^*}{d\mathbf{K}_\mathrm{j}} = \mathbf{A}_\mathrm{ij}^{-1} \tag{3.2}$$

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 (increased death rate or decreased birth rate), the response signs are reversed. 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. The goal of the experiment is to apply as large an input as is practical, so 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.

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 in essence a testable hypothesis of expected system behavior that can be rigorously evaluated by the Malthusian 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.

$$\mathbf{A}' = \begin{bmatrix} -0.8 & -0.2 & -0.4 \\ 0.7 & 0 & -0.5 \\ 0.6 & 0.3 & 0 \end{bmatrix} \qquad -\mathbf{A}'^{-1} = \begin{bmatrix} 1.0 & -0.8 & 0.7 \\ -2.1 & 1.7 & -4.7 \\ 1.4 & \mathbf{0.8} & 1.0 \end{bmatrix}$$

$$\mathbf{A}'' = \begin{bmatrix} -0.8 & -0.3 & -0.5 \\ 0.6 & 0 & -0.4 \\ 0.7 & 0.2 & 0 \end{bmatrix} \qquad -\mathbf{A}''^{-1} = \begin{bmatrix} 2.0 & -2.5 & 3.0 \\ -7.0 & 8.7 & -15.5 \\ 3.0 & \mathbf{-1.2} & 4.5 \end{bmatrix}$$

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 below), 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 for Lotka–Volterra systems was first addressed in the ecological literature by Riebesell (1974) and Levins (1974, 1975). Riebesell presented a general derivation, leading to (adapted from his equation 19),

$$\mathbf{N}_\mathrm{i}^* = \frac{1}{det\,\mathbf{A}} \sum_{j=1}^{n} \left[(-1)^{i+j}\, det(min\, \hat{\mathbf{A}}_{\mathrm{ij}}) \mathbf{K}_\mathrm{j} \right] \tag{3.3}$$

where $\hat{\mathbf{A}}_{\mathrm{ij}}$ is the matrix formed by replacing the j^{th} column of the community matrix **A** with the column vector **K** of carrying capacities, *det* is the matrix determinant, and *min* denotes the n–1 by n–1 minor matrix formed by deleting the i^{th} row and j^{th} column in a matrix. Input is assessed here through change in the inserted column vector **K**. This is an application of Cramer's Rule to determine how the general solution of **AN** = **K** is affected by change in **K** (such as in O'Neil 1995). Levins presents an equivalent matrix formulation,

$$\frac{d\mathbf{N}_{\mathbf{i}}^{*}}{dp_c} = \frac{det\begin{bmatrix} a_{1,1} & a_{1,2} & \cdot & a_{1,j-1} & \frac{-df_1}{dp_c} & a_{1,j+1} & \cdot & a_{1,n} \\ a_{2,1} & a_{2,2} & \cdot & a_{2,j-1} & \frac{-df_2}{dp_c} & a_{2,j+1} & \cdot & a_{2,n} \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ a_{n,1} & a_{n,2} & \cdot & a_{n,j-1} & \frac{-df_n}{dp_c} & a_{n,j+1} & \cdot & a_{n,n} \end{bmatrix}}{det\,\mathbf{A}} \tag{3.4}$$

where the vector $[-df_i/dp_c]$ is substituted in the j^{th} column of the determinant of the community matrix. Via Cramer's Rule, the cofactor expansion in Equation 3.4 gives, to the system of differential equations in Equation 3.1, a solution for the change in equilibrium abundance of an i^{th} species or resource variable, due to a change of parameter p_c for a j^{th} variable. Since quantification of terms in Equations 3.3 and 3.4 is rarely possible, Levins developed an algorithm for hand computation, which interprets signed digraph structure for a qualitative assessment of community response.

$$\frac{d\mathbf{N}_{\mathbf{i}}^{*}}{dp_c} = \frac{\sum_{j,k}\left[\frac{df_j}{dp_c}\right]\left[Path_{ij}^{(k)}\right]\left[Feedback_{n-k}^{(complementary)}\right]}{Feedback_{n}^{(overall)}} \tag{3.5}$$

We discuss the terms of this algorithm below; but note first that Equations 3.3–3.5 all include analogous formulations of a cofactor expansion of the community matrix. These can generally be expressed as

$$\mathbf{N}_{\mathbf{i}}^{*} = \frac{1}{det\mathbf{A}}\mathbf{C}_{\mathbf{ji}}\mathbf{K}_{\mathbf{j}} \tag{3.6}$$

where $\mathbf{C}_{\mathbf{ji}}$ is a cofactor of **A** (i.e. $\mathbf{C}_{\mathbf{ji}} = (-1)^{i+j}\, det(min\mathbf{A}_{\mathbf{ij}})$, Appendix 1). Each matrix cofactor, when transposed (*trans*) and divided by the system determinant, is the same as corresponding elements of an inverse matrix. Considering the matrix of all cofactors **C**, we have the following algebraic equalities,

$$\mathbf{A}^{-1} = \frac{\mathbf{C}^{trans}}{det\,\mathbf{A}} = \frac{adj\,\mathbf{A}}{det\,\mathbf{A}} \tag{3.7}$$

where the transposed 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

$$-\mathbf{A}^{-1} = \frac{adj \text{ - } \mathbf{A}}{det \text{ - } \mathbf{A}} \tag{3.8}$$

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 $-\mathbf{A}^{-1}{}_{ij}$ elements will be the same as $adj\ -\mathbf{A}_{ij}$ elements in any stable system (Appendix 1). We emphasize these equalities for their ease of computation by symbolic processors in computer software that are now widely available. Appendix 1 briefly explains these and subsequent matrix methods used in this work.

Following Levins' terminology from Equation 3.5, and the equalities in Equation 3.8, 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 (Appendix 1). 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. Thus a necessary condition for stability is negative overall feedback. The numerator of Equation 3.5 is a sum of the products of the sign of three terms: 1) all inputs to the j^{th} variable [df_j/dp_c], 2) the different paths (length k, where $k \leq n$) of linkages 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 [$Feedback_{n-k}^{(complementary)}$]. Together these terms constitute a feedback cycle (or loop), n–1 in length that contributes to change in the size of a population, or to the amount of a resource variable (see Levins 1974, 1975, or Puccia and Levins 1985, 1991 for a more detailed derivation and explanation of Equations 3.4 and 3.5). 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 Equation 3.5 makes up Levins' 'table of predictions', which, when transposed, is equivalent in sign to the inverse and adjoint matrices in Equation 3.8. 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 Equation 3.5. 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 (Equation 3.8). By extension, the adjoint of the negative community matrix is equivalent to Levins' 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 > 0. Unstable systems are extinction prone, while stable systems are not. From Equations 3.7 and 3.8 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 1). 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 $\overset{\circ}{\mathbf{A}}$). 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 percent 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 (**T**)

$$\mathbf{T}_{ij} = per\left(min\, \overset{\bullet}{\mathbf{A}}_{ij} \right)^{trans} \tag{3.9}$$

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 $\overset{\bullet}{\mathbf{A}}$). The matrix permanent is computed as the determinant, but expansion is without alternating sign, or subtraction (Minc 1978, Appendix 1); it is also referred to as a 'plus determinant' (Eves 1980, Marcus and Minc 1964). Equation 3.9 is similar to a cofactor calculation, as in Equation 3.3, but without any negative elements in **A**, or sign alternation in the expansion of minors (Appendix 1). Each element of **T** is merely a count of the total number of both positive and negative feedback cycles in a response.

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

$$\mathbf{W} = \overset{\overset{\longrightarrow}{\circ}}{\frac{|adj\ \ \mathbf{A}\,|}{\mathbf{T}}} \tag{3.10}$$

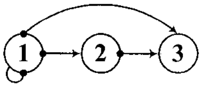
with $\mathbf{W}_{ij} = 1$ when absolute feedback $\mathbf{T}_{ij} = 0$, and where '$\longrightarrow$' is a vectorized matrix operator that denotes element-by-element division.

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 (2 paragraphs above), these ratios 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 Example

To illustrate the above techniques, we present an example system in signed digraph (*sign di*-rected *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 (→), and negative effects terminating in a filled circle (–•). In ecological systems, they represent community structure, and have direct correspondence with community matrices. Subscripts of $a_{i,j}$ 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 (•→), competitive (•–•), mutualistic (↔), commensal (→), amensal (–•), 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.

The following system, depicted in signed digraph and community matrix form, corresponds to the quantitatively specified matrices on page 14; it has three sets of predator-prey interactions, one of which is omnivorous.



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

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 (Appendix 1). This result requires that the strength of a single positive feedback cycle be less than that of the two negative cycles combined. From Equation 3.8 we obtain, in symbolic form, a set of predictions corresponding to the inverse matrix, and to Levins' transposed table of predictions.

$$adj\text{ - }\mathbf{A} = \begin{bmatrix} a_{2,3}a_{3,2} & -a_{1,3}a_{3,2} & a_{1,2}a_{2,3} \\ -a_{2,3}a_{3,1} & a_{3,1}a_{1,3} & -a_{1,1}a_{2,3}\text{-}a_{1,3}a_{2,1} \\ a_{2,1}a_{3,2} & a_{1,1}a_{3,2}\text{-}a_{1,2}a_{3,1} & a_{2,1}a_{1,2} \end{bmatrix}$$

If one wanted to symbolically portray the absolute feedback matrix (**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,

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

from Equations 3.8–3.10, gives the following results,

$$adj\text{-}\overset{\circ}{\mathbf{A}} = \begin{bmatrix} 1 & -1 & 1 \\ -1 & 1 & -2 \\ 1 & 0 & 1 \end{bmatrix} \quad \mathbf{T} = \begin{bmatrix} 1 & 1 & 1 \\ 1 & 1 & 2 \\ 1 & 2 & 1 \end{bmatrix} \quad \mathbf{W} = \frac{\overrightarrow{|adj\ \overset{\circ}{\mathbf{A}}\,|}}{\mathbf{T}} = \begin{bmatrix} 1 & 1 & 1 \\ 1 & 1 & 1 \\ 1 & 0 & 1 \end{bmatrix}$$

which can be seen to correspond with the above symbolic analysis and the quantitative matrices on page 14.

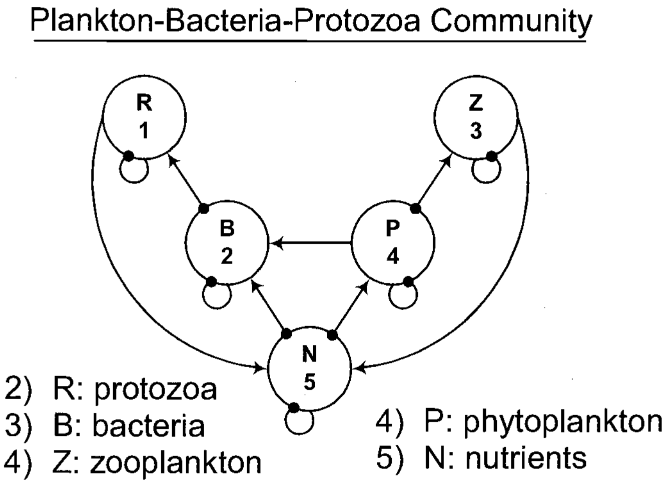
Interpretation of the symbolically rendered adjoint matrix is an equivalent formulation of Levins' loop analysis technique, which can provide rich insight into the behavior of complex systems. In ecological systems it is exceedingly rare that we have sufficient knowledge for a quantitative analysis; 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 ($\overset{\circ}{\mathbf{A}}$) 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 as will be shown, 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. Except for a noted exception, the systems below are qualitatively or quantitatively stable.

Applications

A Paradox From Plankton: Stone (1990) presented a plankton community model (Figure 3.1) 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 (Figure 3.2). We calculated the weighted predictions matrix for this system (Figure 3.2) and found that all inconsistencies had low weighted prediction values. Examining the first column of the inverse of Stone's matrix (representing the indirect effects to community members from positive input to protozoa, Figure 3.1), we noticed that the second ($-\mathbf{A}^{-1}{}_{2,1}$) and fourth ($-\mathbf{A}^{-1}{}_{4,1}$) 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 (Figure 3.2). The second term of the first adjoint matrix column consists of 7 countervailing cycles (4 positive and 3 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% (1 cycle in this case) of cycles 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 2 cycles contribute to the response, but both are positive; it therefore receives a value of 1 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



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

$$-\mathbf{A}^{-1} = \begin{bmatrix} 0.9 & 0.4 & 0.05 & -0.06 & 0.2 \\ -0.2 & 0.7 & 0.09 & -0.09 & 0.3 \\ 0.05 & -0.01 & 1 & 0.1 & 0.07 \\ 0.2 & -0.06 & -0.09 & 0.8 & 0.4 \\ 0.5 & -0.1 & 0.2 & -0.3 & 0.7 \end{bmatrix}$$

Figure 3.1. Signed digraph, community matrix, and inverse matrix for plankton community model; interaction terms quantitatively specified with plausible numeric values (from Stone 1990).

Qualitative and Symbolic Analysis of Plankton Community Model

qualitatively specified community matrix

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

adjoint

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

absolute feedback

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

weighted predictions

$$\mathbf{W} = \begin{bmatrix} 0.7 & 0.5 & 0.5 & \mathbf{0.3} & 1 \\ \mathbf{0.1} & 0.5 & 0.5 & \mathbf{0.3} & 1 \\ 1 & \mathbf{0} & 0.5 & 0.5 & 1 \\ 1 & \mathbf{0} & \mathbf{0} & 0.5 & 1 \\ 1 & \mathbf{0} & 0.7 & \mathbf{0} & 1 \end{bmatrix}$$

first column of symbolically rendered adjoint

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

Figure 3.2. Qualitatively specified community matrix ($\mathring{\mathbf{A}}$) for plankton community model (as in Figure 3.1), with adjoint (*adj* –$\mathring{\mathbf{A}}$), absolute feedback (**T**) , and weighted predictions matrices (**W**). Adjoint matrix elements that differ in sign from inverse matrix of quantitatively specified system (Figure 3.1) in bold type, as are corresponding elements of **T** and **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* –$\mathring{\mathbf{A}}_{ij}$ / $\mathbf{T}_{ij}$, defines the elements of the weighted predictions matrix **W**.

complementary feedback accounted for 58% of the variation in quantitative responses (Figure 3.3). 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 1/10th, and 1/100th 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 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 Chapter 4 we define the limits of qualitative predictions of response strength and sign with computer simulations, across an array of system 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 (Figure 3.4) 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 a total of 36) were zero (Figure 3.4). Our results indicate that complementary feedback cycles contributing to indirect effects 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.

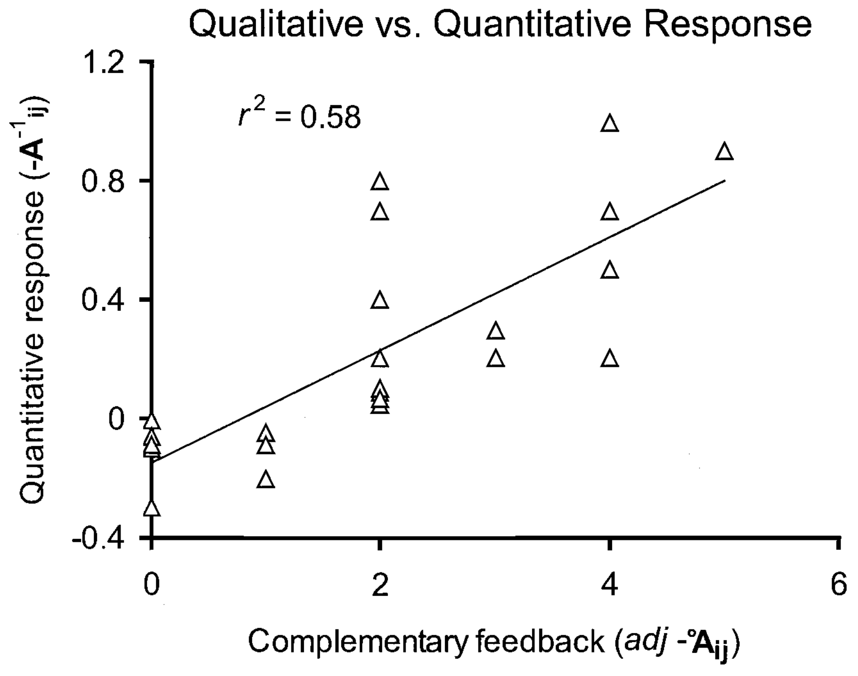
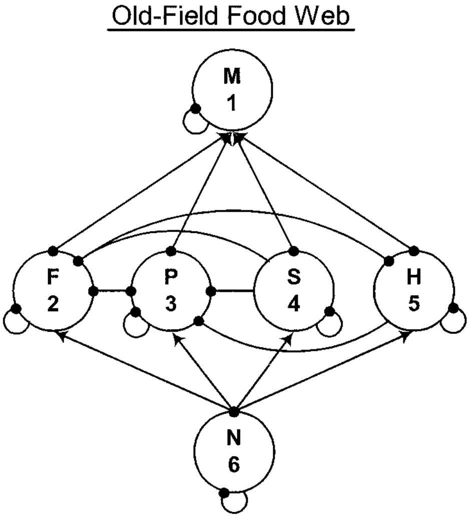


Figure 3.3. Relationship between the quantitative and qualitative response for plankton community model. Each element of adjoint matrix from qualitatively specified matrix (*adj* $-\overset{\circ}{\mathbf{A}}$, Figure 3.2) is compared to corresponding element of inverse matrix of quantitatively specified system ($-\mathbf{A}^{-1}$, Figure 3.1).



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

$$adj\,-\overset{o}{\mathbf{A}}$$
$$\begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 3 & -3 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & -3 & 3 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \end{bmatrix}$$

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

$$\mathbf{W}$$
$$\begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.1 & 0.1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.1 & 0.1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \end{bmatrix}$$

Figure 3.4. Signed digraph of community matrix specified by Schmitz (1997, adapted from his Table 3), for interactions between a grasshopper (*Melanoplus borealis*), four perennial plants, and soil nitrogen in an old-field food web, with corresponding adjoint of qualitatively specified community matrix ($adj\,-\overset{o}{\mathbf{A}}$), absolute feedback matrix (**T**), and weighted predictions matrix (**W**). Schmitz evaluated shaded responses in nitrogen and herbivore press experiments, and found them to be highly indeterminate in terms of response magnitude.

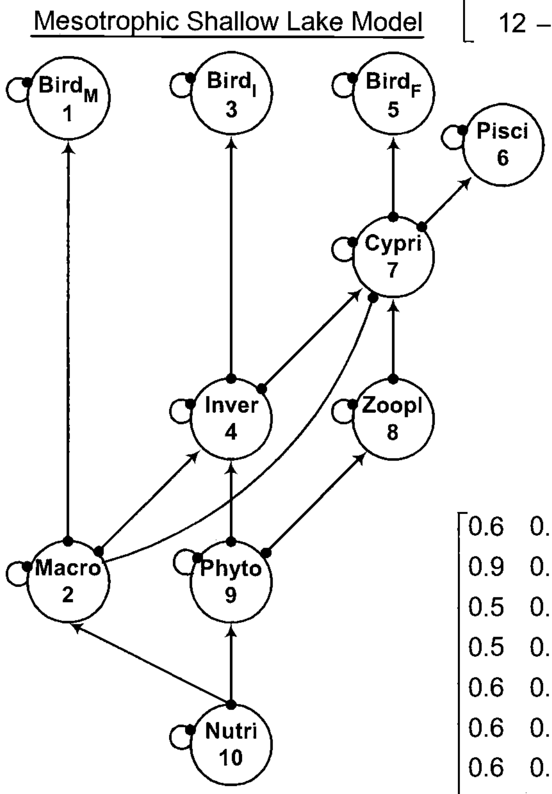
While variation in interaction strength is undeniably a source of indeterminacy in this system, the large absolute number of countervailing complementary feedback cycles (from 26 to 64) within each response clearly amplifies this phenomenon. Furthermore, the overall feedback of the quantified system was relatively small (*det* $\mathbf{A} = -0.47$), and the qualitative model was neutrally stable and had zero overall feedback (*det* $\overset{o}{\mathbf{A}} = 0$). 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 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 (Figure 3.5) and eutrophic (Figure 3.6) 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 (Figure 3.6), 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 6 of 8 observed responses in the eutrophic system (Figure 3.6).

While we expected piscivorous fish to decrease when cyprinids were being harvested in eutrophic systems (Figure 3.6; *adjoint* $-\overset{o}{\mathbf{A}}_{6,7} = 9$, 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* $-\overset{o}{\mathbf{A}}_{10,7}$), which comes with a, theoretically speaking, perfectly

$$adj - \mathring{\mathbf{A}}$$

$$\begin{bmatrix}
49 & 27 & 8 & -8 & 1 & 1 & -1 & 11 & -12 & 15 \\
-27 & 27 & 8 & -8 & 1 & 1 & -1 & 11 & -12 & 15 \\
-10 & 10 & 48 & 28 & 6 & 6 & -6 & -10 & 4 & 14 \\
-10 & 10 & -28 & 28 & 6 & 6 & -6 & -10 & 4 & 14 \\
8 & -8 & -8 & 8 & 56 & -20 & 20 & 8 & 12 & 4 \\
8 & -8 & -8 & 8 & -20 & 56 & 20 & 8 & 12 & 4 \\
8 & -8 & -8 & 8 & -20 & -20 & 20 & 8 & 12 & 4 \\
7 & -7 & 12 & -12 & 11 & 11 & -11 & 45 & 20 & 13 \\
15 & -15 & 4 & -4 & -9 & -9 & 9 & -23 & 32 & 17 \\
12 & -12 & -12 & 12 & 8 & 8 & -8 & 12 & -20 & 44
\end{bmatrix}$$



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

$$\mathbf{W}$$

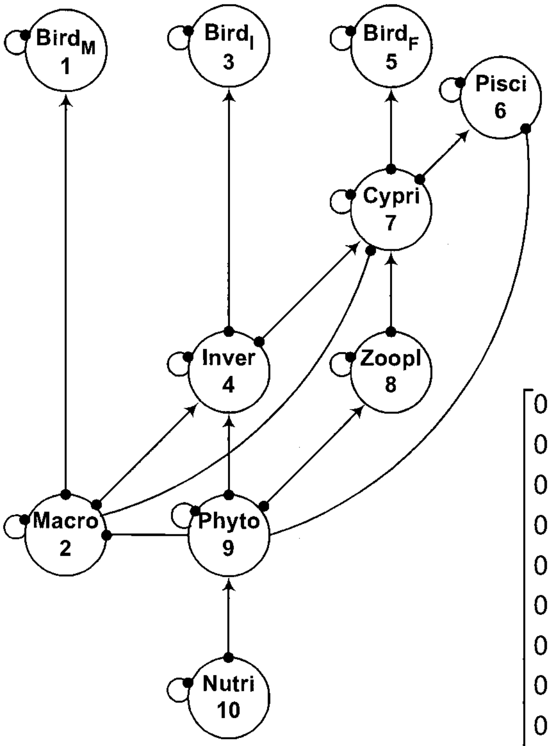
$$\begin{bmatrix}
0.6 & 0.9 & 0.5 & 0.5 & 0.1 & 0.1 & 0.1 & 0.8 & 0.9 & 0.6 \\
0.9 & 0.9 & 0.5 & 0.5 & 0.1 & 0.1 & 0.1 & 0.8 & 0.9 & 0.6 \\
0.5 & 0.5 & 0.6 & 0.9 & 0.5 & 0.5 & 0.5 & 0.6 & 0.2 & 0.7 \\
0.5 & 0.5 & 0.9 & 0.9 & 0.5 & 0.5 & 0.5 & 0.6 & 0.2 & 0.7 \\
0.6 & 0.6 & 0.5 & 0.5 & 0.6 & 0.8 & 0.8 & 0.3 & 0.9 & 0.3 \\
0.6 & 0.6 & 0.5 & 0.5 & 0.8 & 0.6 & 0.8 & 0.3 & 0.9 & 0.3 \\
0.6 & 0.6 & 0.5 & 0.5 & 0.8 & 0.8 & 0.8 & 0.3 & 0.9 & 0.3 \\
0.4 & 0.4 & 0.6 & 0.6 & 0.5 & 0.5 & 0.5 & 0.8 & 0.6 & 0.4 \\
0.9 & 0.9 & 0.2 & 0.2 & 0.8 & 0.8 & 0.8 & 0.8 & 1 & 0.5 \\
0.4 & 0.4 & 0.7 & 0.7 & 0.8 & 0.8 & 0.8 & 0.5 & 0.7 & 0.8
\end{bmatrix}$$

Figure 3.5. 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* $-\mathring{\mathbf{A}}$), and weighted predictions matrix (**W**). Shaded regions of matrices refer to responses observed over a range of nutrient enrichment; boxed-in region (dashed-line) of the adjoint matrix is compared to a deep lake model (Figure 3.7) in discussion.

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

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

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

$$\mathbf{W}$$

$$\begin{bmatrix} 0.5 & 0.7 & 0.4 & 0.4 & 0.1 & 0.1 & 0.1 & 0.7 & 0.7 & 0.7 \\ 0.7 & 0.7 & 0.4 & 0.4 & 0.1 & 0.1 & 0.1 & 0.7 & 0.7 & 0.7 \\ 0.8 & 0.8 & 0.5 & 0.8 & 0.6 & 0.6 & 0.6 & 0.3 & 0.06 & 0.06 \\ 0.8 & 0.8 & 0.8 & 0.8 & 0.6 & 0.6 & 0.6 & 0.3 & 0.06 & 0.06 \\ 0.5 & 0.5 & 0.3 & 0.3 & 0.5 & 0.9 & 0.9 & 0.08 & 0.9 & 0.9 \\ 0 & 0 & 0.4 & 0.4 & 0.4 & 0.7 & \mathbf{0.4} & 0.5 & 0.3 & 0.3 \\ 0.5 & 0.5 & 0.3 & 0.3 & 0.9 & 0.9 & 0.9 & 0.08 & 0.9 & 0.9 \\ 0 & 0 & 0.6 & 0.6 & 0.6 & 0.6 & 0.6 & 0.8 & 0.3 & \mathbf{0.3} \\ 0.8 & 0.8 & 0.5 & 0.5 & 1 & 1 & 1 & 0.8 & 1 & 1 \\ 0.8 & 0.8 & 0.5 & 0.5 & 1 & 1 & \mathbf{1} & 0.8 & 1 & 0.4 \end{bmatrix}$$

Figure 3.6. 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 ($adj\,-\overset{\circ}{\mathbf{A}}$), 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 (dashed-line) of adjoint matrix is compared to a deep lake model (Figure 3.7) in discussion.

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 more accurate predictions 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.

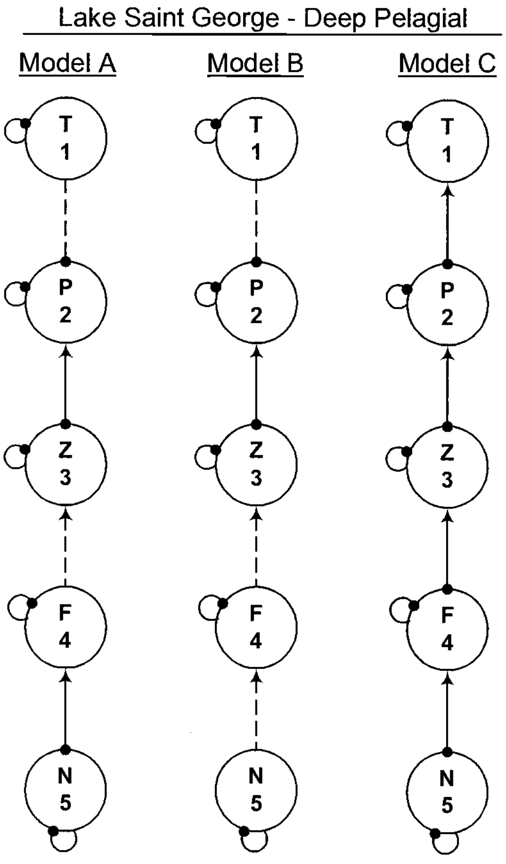
Despite this limited and identifiable shortcoming, we conclude that the signed digraph models and consequent qualitative community matrices that arise from Jeppesen's description of the community are robust. Thus it has high heuristic value. For instance, inspection of the entire adjoint matrix can suggest 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 9th row of adjoint matrix, Figure 3.6). We would predict input to the other members of the community (first seven predictions in the 9th row of adjoint, Figure 3.6) to elicit a response in phytoplankton of a more or less similar magnitude. All of these predictions have high weighted values indicating a high potential for determinacy. Response strengths of phytoplankton in the mesotrophic model (Figure 3.5) 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, Figure 3.7). These models display a

Figure 3.7. (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 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 ($adj\ -\overset{o}{\mathbf{A}}$) 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 ($adj\ -\overset{o}{\mathbf{A}}$) and absolute feedback matrices (**T**). Negative top-down input calculated by reversing the response sign in column 1 of adjoint.

a)



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

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

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

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

T

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

W

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

b)

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

$$\begin{array}{ccccccc} -(adj-\overset{o}{\mathbf{A}}_{i,1}) & & (adj-\overset{o}{\mathbf{A}}_{i,5}) & & & \mathbf{T} & \mathbf{W} \\ \begin{bmatrix} -5 \\ 3 \\ -2 \\ 1 \\ -1 \end{bmatrix} & + & \begin{bmatrix} 1 \\ 1 \\ 2 \\ 3 \\ 5 \end{bmatrix} & = & \begin{bmatrix} -4 \\ 4 \\ 0 \\ 4 \\ 4 \end{bmatrix} & \begin{bmatrix} 6 \\ 4 \\ 4 \\ 4 \\ 6 \end{bmatrix} & \begin{bmatrix} 0.7 \\ 1 \\ 0 \\ 1 \\ 0.7 \end{bmatrix} \end{array}$$

Figure 3.7.

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 linkages (model C, Figure 3.7) 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 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. Simultaneous negative top-down (winter fish kill) and positive bottom-up (nutrient loading) presses on model C are assessed in Figure 3.7b. We observe a phenomenon of cancellation and amplification 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 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 less than 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 and 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 impact from 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 (Figure 3.4) 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 (Figure 3.7), 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 non-negative (i.e. all elements ≥ 0). The qualitative adjoint of the plankton community model (Figure 3.2) is an example of a non-negative matrix. Examination of the adjoint matrix columns of the straight chain model C in Figure 3.7 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 (j^{th}) variable of input, along direct paths of system linkages. 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 through 10 of the shallow lake models form a subsystem that is trophically equivalent to variables 1 through 5, respectively, in the Lake Saint George deep pelagia model. Inspection of the adjoint matrices reveals identical system behavior for the mesotrophic subsystem (Figure 3.5, see boxed area of adjoint) and the deep lake model C (Figure 3.7). The interference that phytoplankton imposes on piscivorous fish in the eutrophic shallow lake model (Figure 3.6) 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 shallow eutrophic 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 cannot be explicitly addressed by qualitative techniques, neither can they be addressed by greater degrees of precision and quantification. 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 multi-scale 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 generality (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.

CHAPTER 4
PREDICTION LIMITS OF QUALITATIVE MODELS IN COMMUNITY ECOLOGY

Jeffrey M. Dambacher, Hiram W. Li and Philippe A. Rossignol

Abstract

We compare the outcome of qualitative predictions of 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 simulations. Specifically, we randomly assigned quantitative values of interaction strength and measured correspondence with qualitative predictions in terms of response strength and sign determinacy. This technique, applied to the weighting of countervailing cycles at each level of total system feedback, was used to develop an overall measure of stability (weighted stability). This measure was tested in quantitative simulations against criteria for Lyapunov stability: 1) all negative polynomial coefficients, and 2) all positive Hurwitz determinants. Except in a limited and identifiable class of models, weighted stability accounted for over 98% of model failures in quantitatively specified systems. The Hurwitz determinants were insensitive to quantitative simulation, accounting for less than 2 percent of model failures. The overall potential for model predictability and stability was closely related, and consistently described by the single measure of weighted stability. We report an expanded scope of inference for qualitative modeling based on the techniques presented, and conclude that system structure is of overriding importance.

Introduction

A formidable obstacle to the practice of community ecology is the gulf between theory and observation, the latter rarely supporting assertions of the former (Peters 1991). A corollary also holds, namely, that the use of quantitative observations to verify simulations still does not lead to widely accepted results. The conflict has also been expressed in terms of qualitative versus quantitative modeling approaches (Levins 1966, 1974). Qualitative analysis addresses issues of generality or efficacy (does it work or not?), whereas quantitative analysis addresses precision or efficiency (how well does it work?). The latter assumes the former issue or question has been assessed, which is often not the case.

Community theory has developed potentially powerful tools such as the inverse of the community matrix, which predicts response in all variables in a system following input to a specific variable (Bender et al. 1984). Both in simulation studies (Yodzis 1988) and field trials (Schmitz 1997) reliable response predictions have proven elusive. Correspondence between theory and actual systems appears obscured by a fog of indeterminacy.

Quantitative models can incorporate a large number of variables, while qualitative analyses have been restricted to small- or moderate-sized systems. It seems that insight into complex systems thus tends to rely on specific simulations with poor generalization, or from generalizations arising from theoretical analyses of far simpler systems (May 1973, Pimm and Lawton 1978).

Underlying our study is the premise that the future of ecological modeling, if not ecological research itself, will rest, in large part, with qualitative models. Acceptance of qualitative models requires a semi-quantitative appreciation of their predictions. This paper develops criteria to determine the degree of confidence to accept these predictions. Paradoxically, the support for qualitative models stems from comparison with quantitative numerical models, similar to May's approach (1974) in using model ecosystems to study the relation between complexity and stability in real ecosystems.

We suggest that a major obstacle to the application of community matrix theory has been the all-or-none results that arise from current tools of analysis. In applying the inverse of the community matrix, there has been an emphasis on precision and parameterization of community matrix models, with less attention paid to the influence of community structure, in and of itself, as being of central importance, each perspective corresponding to the conflict between practice and theory, respectively. A dissection of the predicted theoretical response leading to a more flexible analysis has been lacking. We propose that when system feedback is detailed in qualitative terms and is used as a benchmark for the analysis of ecological communities, the gulf between theory and practice will be narrowed.

Here we contrast quantitative and qualitative analyses of community matrix models, and examine the relative role that system feedback has in system response and stability. Examples of particular model systems will be used to define general concepts and specific measures of qualitative and quantitative responses. These concepts and measures will then be applied, with numerical calculations, to an array of 5-variable models to assess confidence in qualitative model predictions, first in terms of response strength or magnitude, and then in terms of response sign. Applying these same concepts to numerical analyses, we derive and test a new qualitative measure of system stability. Finally, the interrelation between predictability and stability will be demonstrated, as will the generality of our results to randomly constructed systems and to larger systems. System structure will be seen as a key factor.

Qualitative and Quantitative Analyses of the Community Matrix- As a descriptor of interactions among species in a community near equilibrium, the community matrix, 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 (Yeaton 1972, Cody 1974), response of a community to a change in birth or death rates due to disturbance, experimental manipulation (Levins 1979, Bender et al. 1984, Yodzis 1988, Schmitz 1997, Bodini 1998, Dambacher et al. 1999a), or natural selection (Levins 1975), and finally, determination of system stability (May 1974, Li and Moyle 1981, Puccia and Levins 1985, Levitan 1987, Roxburgh and Wilson 2000).

As a theoretical tool, the community matrix lends itself to direct applications when it is specified in quantitative interactions terms, whether actually measured or given as plausible estimates. These results, however, have lacked generality, and appear to be highly sensitive to the specific values of the interactions. Response predictions have suffered from a high degree of indeterminacy (Yodzis 1988, Schmitz 1997), and stability analyses have, at times, been inconclusive (Roxburgh and Wilson 2000, but see Levitan 1987). Furthermore, properly specifying a community matrix requires an extensive series of *n* press experiments (Bender et al. 1984), which at best is a laborious and time consuming task (Laska and Wootton 1998), and at worst, is 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 (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. Levins' 'loop analysis' interprets signed digraphs of community models to predict system response and stability. 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 predictions of response and stability are 'conditional', and can be expressed in relative terms: e.g. an increase in species x, due to an increase in 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.

While qualitative analysis can be a useful technique, it has, in our estimation, been underutilized. One difficulty with qualitative modeling is the all-or-none aspect of its predictions. There is no theoretical basis to address response strength or magnitude. Another difficulty is applying Levins' loop algorithm, which relies upon a graphical interpretation of signed digraph models. For large (> 5 variable) 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 of response and stability of large systems, can defy practical interpretation, leading to overwhelming ambiguity. We have recently addressed these difficulties by reformulating Levins' loop algorithm with equivalent matrix algebra equations. Our aim in surmounting these difficulties has been to extend qualitative analysis of the community matrix to large complex ecological systems.

Analysis Methods

Our analysis is patterned after that of Pimm and Lawton (1977, 1978) and Yodzis (1981, 1988). We chose from the literature, or constructed ourselves, 12 signed digraph model systems (Figure 4.1) that, as will be shown, exhibited a full spectrum of system stability and predictability (i.e. relative level of ambiguity in qualitative response predictions). Models were constructed by successively adding interactions involving omnivory, competition, and mutualism. Qualitative predictions of system response and stability were compared to those of quantitative analysis, in which community matrix interaction terms were randomly varied over two orders of magnitude. Self-regulation terms, in alternate numerical matrix simulations, were either varied randomly or fixed at a value of maximum strength.

A quantitatively specified system is denoted here as $^{\#}\mathbf{A}$, and quantitative response predictions are calculated by $-^{\#}\mathbf{A}^{-1}$, the inverse of the negative community matrix (Bender et al. 1984). A qualitatively specified community matrix, where only the signs of the interaction terms are entered as +1, –1, or 0, is denoted here as $\mathring{\mathbf{A}}$. The *adjoint* $-\mathring{\mathbf{A}}$ details the net response from input to a system in the qualitative terms of complementary feedback cycles. It is directly analogous to Levins' loop analysis algorithm (Equation 3.5), and related to the inverse matrix by: $-\mathbf{A}^{-1}$ = *adjoint* ($-\mathbf{A}$) / *determinant* ($-\mathbf{A}$) (Equation 3.8). The inverse and adjoint matrices are calculated with the negative of the community matrix, which maintains a sign convention in both even and odd numbered systems (see Appendices 1–4 for examples of these and all subsequent matrix calculations and for corresponding computer commands).

Lyapunov stability (Lyapunov 1892) was assessed for both qualitatively and quantitatively specified models using the Routh–Hurwitz criteria of 1) all negative polynomial coefficients, given the convention of the base coefficient $a_0 = -1$, and 2) all positive Hurwitz determinants (Hurwitz 1895, Appendix 3). Both of these conditions guarantee the existence of a local equilibrium neighborhood (Lewontin 1969) to which a system will return following a disturbance. Polynomial coefficients (a_n) are calculated for both qualitatively and quantitatively specified systems as: *determinant* ($\mathbf{A}-\lambda\mathbf{I}$) = 0,

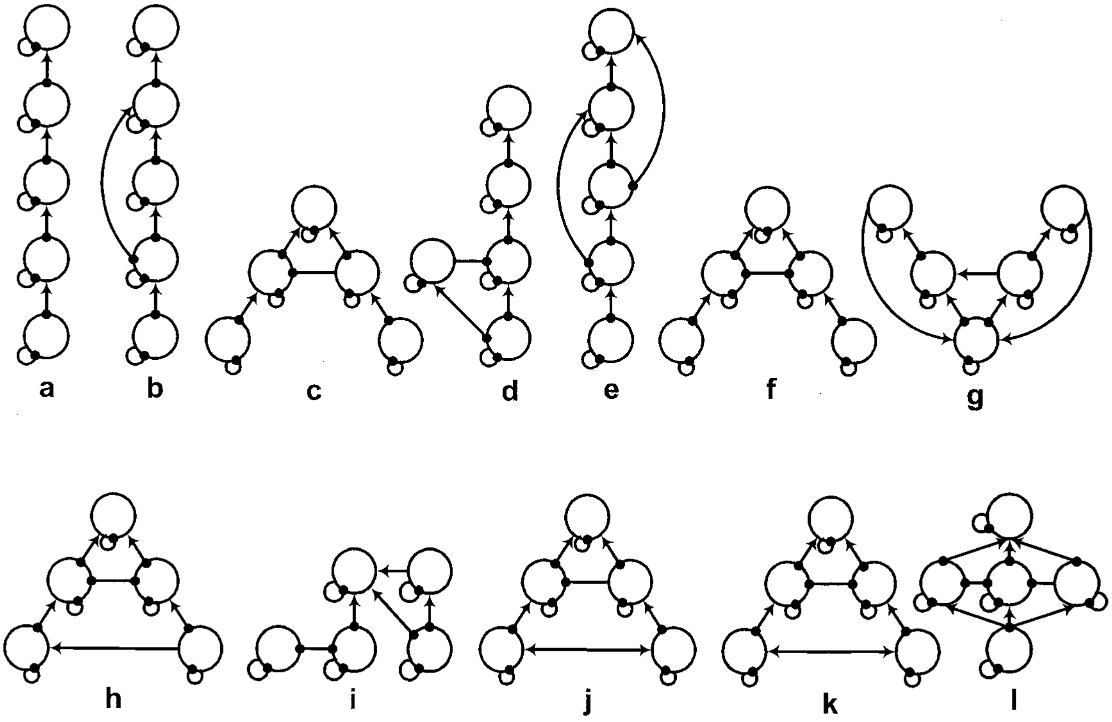


Figure 4.1. Signed digraphs of 12 model systems analyzed in computer simulations. Model **g** is from Stone (1990); **i** is patterned after Puccia and Pederson (1983), and **l** after Schmitz (1997); remaining models constructed by adding linkages to **a** and **c**.

using $\mathring{\mathbf{A}}$ or $^{\#}\mathbf{A}$ respectively, where **I** is the identity matrix. Each polynomial coefficient corresponds to a successive level of system feedback (Appendices 2 and 3).

All matrix calculations were symbolically detailed and entered into relative cell references in a computer spreadsheet program (Microsoft© Excel 2000). The spreadsheet program had 5,000 rows and approximately 250 columns. A pseudo-random number generator was used, that assigned interaction strengths from an even distribution. A set of 5,000 matrices could be quantitatively specified and evaluated within 35 seconds.

Complementary Feedback

The mathematical computations required in the assessment of system response and stability are based upon feedback cycles (Puccia and Levins 1985, Levins and Puccia 1988). A feedback cycle is a path between variables in a dynamical system, along which effects are transmitted from one variable to the next; their countervailing balance determines system behavior. We present below a discussion of complementary feedback and system response, and in a later section, similar ideas relating to system stability.

Complementary feedback cycles are the vehicle by which the direct interactions detailed in the community matrix are translated, through matrix inversion, into the ultimate effects that form the equilibrium response of a community. Within any response prediction of the inverse matrix, there are, in mathematical terms, two processes involved: 1) cancellation or summation of feedback cycles, and 2) a diminution or multiplication of 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. For example, a particular response might be composed of 3 complementary feedback cycles: $-a_{1,1}\,a_{2,2}\,a_{4,3}-a_{1,2}\,a_{2,1}\,a_{4,3}+a_{1,1}\,a_{2,3}\,a_{4,2}$. In qualitative terms, a cancellation of one positive and negative cycle leaves 1 negative cycle. However, when the system is quantitatively specified by setting $a_{4,3}$ equal to 0.4, and all other interactions equal to 1.0, there is a diminution of the two negative cycles, and the overall response becomes positive.

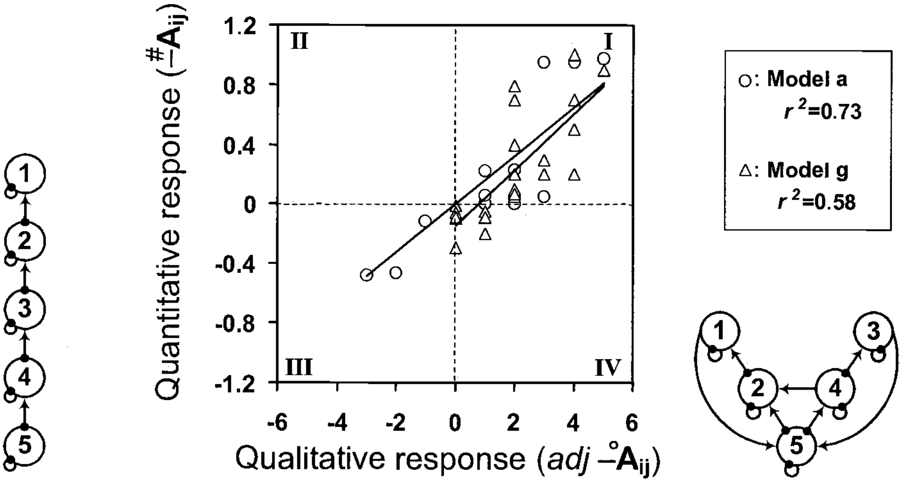
Concepts and Measures of Correspondence

Since both qualitative and quantitative predictions involve the process of cancellation, 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 from diminution effects occurring only in quantitative calculations.

Figure 4.2 compares qualitative to quantitative predictions of response strength for two model systems; it is essentially a comparison of summation effects, based only on community structure, and multiplication effects, based on specific biological relationships. The models were specified with a single set of interaction terms that varied by one or two orders of magnitude (0.05 to 1.0). In model **a**, the sign of all qualitative predictions matched their corresponding numerical prediction; all points were within quadrants I and III. In model **g**, 7 qualitative predictions had sign indeterminacy, or points that occurred in quadrants II or IV (i.e. did not match the sign of the quantitative response, see dashed-line boxed area of adjoint and inverse matrices in Figure 4.2). For both models in Figure 4.2 there was a moderate correspondence ($r^2 > 0.5$) between qualitative and quantitative predictions of response strength.

Predictions of Response Strength

Using the concepts and measures derived from the particular examples presented in Figure 4.2, we next simulated a full range of possible values and combinations of interaction strengths, for the purpose of defining the limits of qualitative predictions of response strength. 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



Model a

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

$\mathring{\mathbf{A}}$
qualitatively specified
community matrix

Model g

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

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

$adj\,-\mathring{\mathbf{A}}$
complementary feedback

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

$min(|{}^{\#}\mathbf{A}_{ij}| > 0) = 0.05$
$stdev(|{}^{\#}\mathbf{A}_{ij}| > 0) = 0.39$

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

${}^{\#}\mathbf{A}$
quantitatively specified
community matrix

$min(|{}^{\#}\mathbf{A}_{ij}| > 0) = 0.1$
$stdev(|{}^{\#}\mathbf{A}_{ij}| > 0) = 0.31$

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

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

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

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

Figure 4.2. Comparison of quantitative versus qualitative response for two model systems. Quantitative community matrices (${}^{\#}\mathbf{A}$) are specified with plausible interaction terms, and quantitative responses calculated by inverse ($-{}^{\#}\mathbf{A}^{-1}$). Qualitative response are calculated as adjoint (*adj*) of qualitatively specified system ($adj\,-\mathring{\mathbf{A}}_{ij}$). Predictions in quadrants II and IV indicate qualitative predictions with sign error, and their associated matrix elements are enclosed by dashed-lines. Variation in quantitative response explained by qualitative response measured by regression r^2, and measures of the *standard deviation* (*stdev*) $\mathbf{A}_{ij}$, and *minimum* (*min*) $\mathbf{A}_{ij}$ pertain to only nonzero elements of the community matrix ($|\,{}^{\#}\mathbf{A}_{ij}\,| > 0$), which are used as descriptors of system behavior and correspondence in Figure 4.3.

orders of magnitude (0.01 to 1.0), while holding constant the sign of each interaction. For each model, two separate numerical assignments were run; either 1) all $\mathbf{A}_{ii}$ self-regulation terms were fixed at a maximal strength of –1.0, or 2) all $\mathbf{A}_{ii}$ were randomly varied (along with the off-diagonal elements).

The correspondence (r^2) between qualitative and quantitative responses (Figure 4.3) was compared to both the weakest link, and spread of interactions (called here the 'standard deviation' of the quantitatively specified matrix elements). To gain a full spread of points along the horizontal axis in Figure 4.3, interactions terms were sequentially varied in lots of 5,000 matrices, over a successively constricted range. Matrices in the first lot were assigned values between 0.01 and 1; subsequent lots were varied from 0.10 to 1, 0.20 to 1, and so on, to 0.90 to 1. 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 Figure 4.3. The use of a successively constricted range was necessary, because random numbers were assigned from a uniform distribution, and in any one assignation, there was a high probability that at least one interaction term would be near the lower limit of the possible range. Thus to obtain models 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 Figure 4.3, we generated 50,000 separate assignations of interaction strength.

Differences between predictions of qualitative models versus numerically specified models stemmed from four components of the community matrix: 1) the weakest interaction in the system, 2) the overall variation of the interaction strengths, 3) limited self-regulation, and 4) system structure. 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 model agreement. Qualitative and quantitative models showed the best agreement in a straight chain system (model **a**) with strong self-regulation. Increasing the range of variation in the interaction strengths by three orders of magnitude (i.e. 0.001 to 1.0) did not affect the results.

In this stage of the analysis we are not concerned with the central tendency of the model results, which depend on the randomized spread of interaction strengths. Rather,

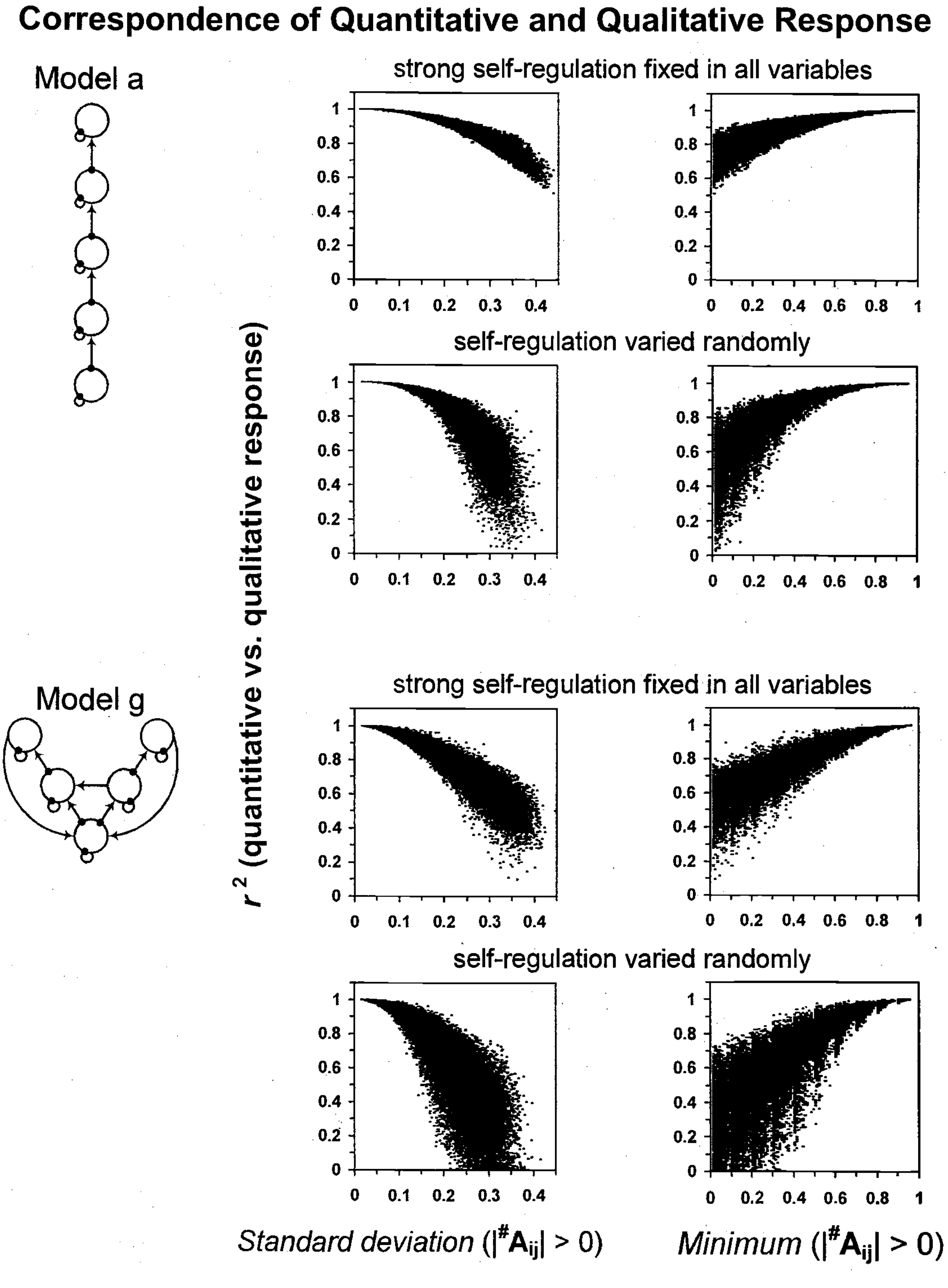


Figure 4.3. Correspondence (r^2) between quantitative and qualitative response for two model systems, as affected by the *minimum* and *standard deviation* of nonzero values in the community matrix. Community matrix elements were randomly assigned numeric values 50,000 times. Off-diagonal elements were varied by two orders of magnitude (0.01 to 1.0), and self-regulation was either fixed at strong value of –1.0, or in a separate analysis, randomly varied along with off-diagonal elements.

it is the borders of the clouds of points in Figure 4.3 that are important, which essentially define the limits of qualitative predictions.

Weighted Predictions and Sign Determinacy of Response

This next stage of our analysis develops confidence levels for qualitative model predictions. Here we seek to know what range of 'real' outcomes from 5,000 matrices with randomly assigned interaction terms will correspond with qualitative model predictions 80 percent (or 50, 75, or 95 percent) of the time. Qualitative ecological models predict impacts on the components of the community matrix with a sign (+, –, 0) rather than a number. For example, a population's abundance may increase (+) due to a drop in the abundance of its competitor (–), though the standing crop of their shared resource may remain unchanged (0). In small systems (< 5 variables), most predictions of population change can be unambiguous, but as model size increases, so does the potential for complexity and ambiguity of response predictions.

Resolution of model ambiguities to determine the likely sign of a response requires 'weighting' model predictions by a ratio of the net number to the total number of complementary feedback cycles. The total number of complementary feedback cycles in a response, both positive and negative in value, can be calculated as $\mathbf{T}_{ij}$ = *permanent (minor* $\dot{\mathbf{A}}_{ij}$*)* ^{transpose}, where $\dot{\mathbf{A}}$ denotes a community matrix specified by only 0's or 1's (i.e. absolute values of $\mathring{\mathbf{A}}$). 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 signs during column and row expansion (Marcus and Minc 1964, Minc 1978 Eves 1980). Dividing the absolute value of each element of the *adjoint* $-\mathring{\mathbf{A}}_{ij}$ by each $\mathbf{T}_{ij}$ element yields the weighted predictions matrix, **W**. Each element of **W** scales the potential for sign determinacy of response predictions in the adjoint. Note that when $\mathbf{T}_{ij} = 0$, $\mathbf{W}_{ij}$ is taken to equal 1.0.

When all complementary feedback cycles are of the same sign (e.g. *adjoint* $-\mathring{\mathbf{A}}_{ij}$ = +,+,+,+), then sign determinacy is completely ensured and the weighted prediction ($\mathbf{W}_{ij}$) is equal to 1.0. A complete absence of complementary feedback equates to a neutral response prediction in the adjoint, which also has a perfect prediction weight of 1.0. When there is an equal number of positive and negative feedback cycles (e.g. *adjoint* $-\mathring{\mathbf{A}}_{\mathbf{ij}} = +,+,-,-$) then $\mathbf{W}_{\mathbf{ij}} = 0$, and there is no potential for sign determinacy. A prediction weight of 0.5 is based upon cancellation of half of the cycles (e.g. *adjoint* $-\mathring{\mathbf{A}}_{\mathbf{ij}} = +,+,+,-$; and $\mathbf{W}_{\mathbf{ij}} = 2/4$), and as we will show, a ratio of 0.5 is a critical threshold for sign determinacy of all qualitative predictions.

Numerical matrices for model systems **a** through **g** (Figure 4.1) were analyzed under two scenarios, with 5,000 matrices each. In the first scenario, a_{ii} self-regulation terms were varied along with a_{ij} interactions, and interaction strengths were allowed any value between 0.01–1.0, without restriction. These values imposed a conservative condition for sign determinacy, because A_{ij} values less than 0.2 had the least agreement between qualitative model and simulation predictions (Figure 4.3), especially where self-regulation was not fixed at a strong level. In the second scenario, self-regulation was set to a maximum of -1.0 for all variables, and all else remained as in the first scenario. The stability of each scenario was assessed 5,000 times, and only stable systems were analyzed for sign determinacy. In stable systems, each ij^{th} quantitative prediction ($-{}^{\#}\mathbf{A}^{-1}_{\mathbf{ij}}$) was compared with the sign of the corresponding qualitative prediction (*adjoint* $-\mathring{\mathbf{A}}_{\mathbf{ij}}$), and the percent correct sign plotted against the corresponding prediction weight ($\mathbf{W}_{\mathbf{ij}}$) (Figure 4.4). Repeated trials altered results by less than 2%.

Sign determinacy was consistently high for weighted predictions ($\mathbf{W}_{\mathbf{ij}}$) greater than 0.5 (Figure 4.4); above this, the proportion of predictions with correct sign was generally greater than 95%. Below $\mathbf{W}_{\mathbf{ij}} = 0.5$, sign determinacy rapidly declined (Figure 4.4). Sign determinacy generally increased with strong self-regulation, by as much as 10 percent in some instances, but was also seen to sometimes decrease where prediction weights were less than 0.20 (i.e. see model **g**, Figure 4.4).

The extremes of the graphs in Figure 4.4 represent the fixed endpoints of this analysis. Weighted predictions equal to 1.0 contain no countervailing feedback cycles, and the sign of the qualitative predictions is always maintained. At $\mathbf{W}_{\mathbf{ij}} = 0$, there is an equal number of positive and negative cycles creating, in qualitative terms, a neutral (or zero) response. In quantitative terms, however, an exactly zero response rarely if ever occurs, thereby forcing a y-intercept of zero correct predictions.

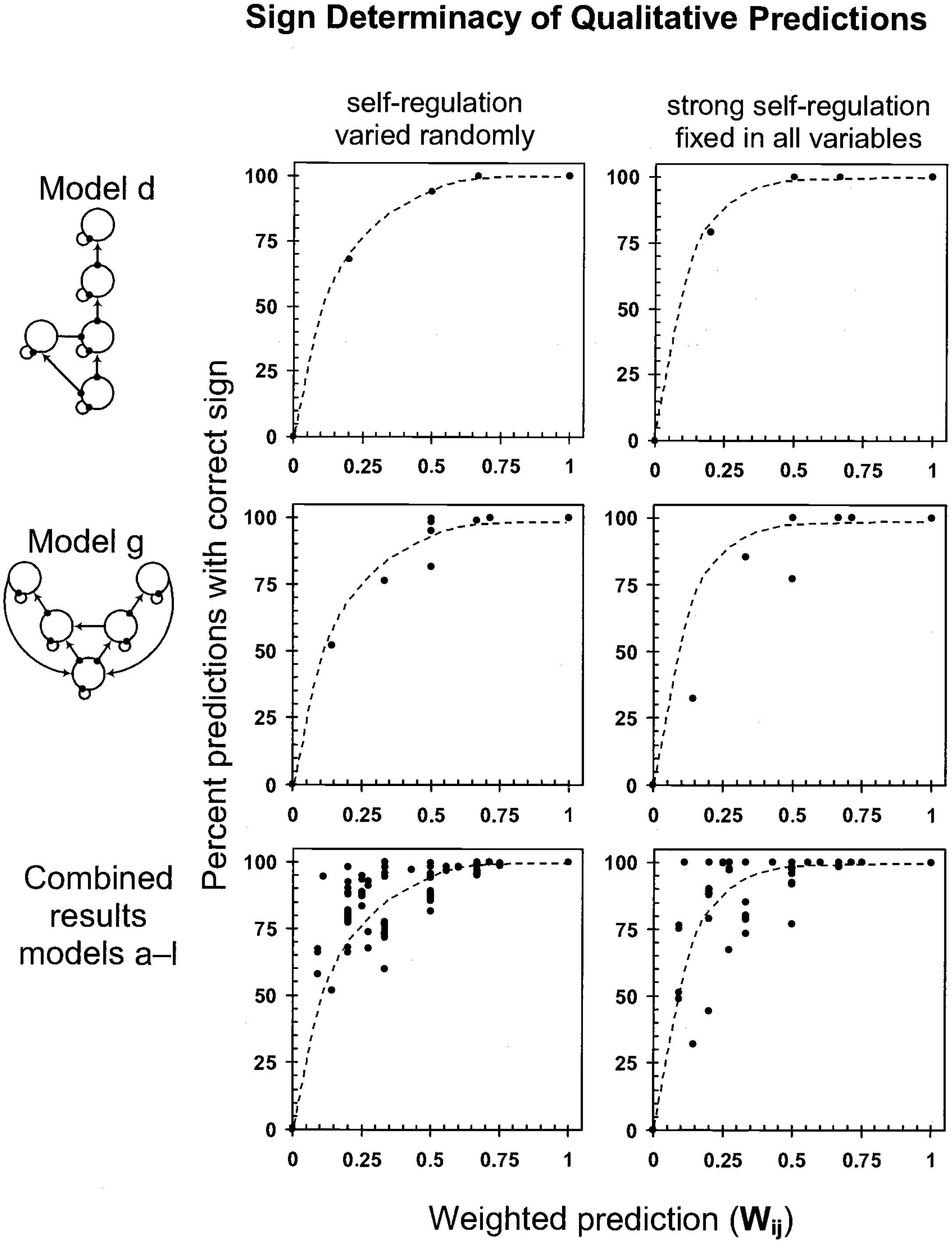


Figure 4.4. Sign determinacy of qualitative predictions for two model systems, and combined results of all 12 models in Figure 4.1. Data are from 5,000 matrices in which interaction strengths in elements of the community matrix were randomly varied between 0.01 and 1.0 through two separate scenarios, in which 1) self-regulation was either fixed at a strong value of –1.0, or 2) randomly varied along with off-diagonal elements. Dashed-line drawn by hand as a visual aid.

Consideration of sign determinacy must also include the relative response strength. A response that is highly predictable (i.e. $\mathbf{W}_{ij} > 0.5$) may still be too weak to detect. Conversely, a neutral response with perfect prediction of sign determinacy ($\mathbf{W}_{ij} = 1$), which results from a complete absence of complementary feedback ($\mathbf{T}_{ij} = 0$), must be judged against a context of measurement or statistical error.

Weighted Stability: Derivation and Testing

We now determine whether a system that is qualitatively stable remains so when its interaction terms are quantitatively specified. This is nearly the same question as that addressed for sign determinacy. The coefficients associated with the roots of the characteristic equation can themselves be the result of a summation of both positive and negative feedback cycles (Appendix 2 and 3). We derived the total number of positive and negative cycles for each level of feedback by: *permanent* $(\dot{\mathbf{A}}+\lambda\mathbf{I}) = 0$. We name this resulting type of characteristic equation the 'absolute polynomial', and denote its coefficients as *absolute* F_n.

At each n^{th} feedback level (Appendices 2), we divide the net number of feedback cycles by the total number of cycles to create a measure of weighted feedback: $wF_n = |F_n|$ / *absolute* F_n, (wF_n is without sign, and we use the absolute value (i.e.: '| |') of the net feedback in the numerator, which can be different in value from the 'absolute number' of feedback cycles, in the denominator). This calculation yields n number of weighted feedback values. We chose the smallest as the indicator of overall system stability, and so define *minimum* wF_n as the 'weighted stability' of the system. Most often, the *minimum* wF_n is at the highest level of feedback in the system, but as will be seen, this is not always the case. Weighted stability addresses only the first Routh–Hurwitz criterion for Lyapunov stability.

We tested weighted stability as an indicator of overall system stability by numerically assigning values to matrix elements in the 12 models (Figure 4.1), which together presented the full range of possible *minimum* wF_n values, from 1.0 to 0. Eleven of the models were qualitatively stable; model **l**, however, passed the second criterion in qualitative terms (all positive Hurwitz determinants, Appendix 3) but failed the first (all negative polynomial coefficients). With a *minimum* $wF_n = 0$, model **l**'s highest level of feedback (and determinant) is zero, and in qualitative terms, is neutrally stable.

A total of 5,000 matrices were numerically specified for each model, for both scenarios as above, by either fixing or varying the self-regulation terms. Under the strong self-regulation scenario, over 98% of the matrices were stable for each model (Figure 4.5). For the scenario of varied self-regulation, separate tabulations were made of the sign of each Hurwitz determinant, and each polynomial coefficient (Table 4.1). The proportion of stable systems generated from each model increased with its weighted stability (Figure 4.5, Table 4.1). Model stability was high for *minimum* $wF_n \geq 0.5$, while below 0.5, system stability sharply decreased. Most model failures were accounted for by positive polynomial coefficients from the same feedback level associated with the *minimum* wF_n (Table 4.1). Up to 10% additional model failures occurred at other feedback levels, and usually at the next lowest level.

A surprising and practical result was that if the qualitative models met the second criterion for stability, then nearly all of the numerical matrices also met the second stability criterion, failing in less than 2% of the time. Moreover, it was exceeding rare (< 1%) for quantitatively specified matrices to fail the second stability criterion after passing the first (Table 4.1, section D). We conclude therefore, that it is practical to dispense with consideration of the Hurwitz determinants after they have first been assessed qualitatively. One can then rely upon weighted stability as an indicator of overall potential for system stability. Below, however, we place a caveat on this assertion that excludes an identifiable class of models from the predictive scope of the weighted stability measure.

Tests of Randomly Constructed Models

We were concerned that the generality of the above results might be limited to the class of models we tested in Figure 4.1. Specifically, we had observed a high degree of model failure from the second stability criterion in a variant of model **l**, in which wF_4

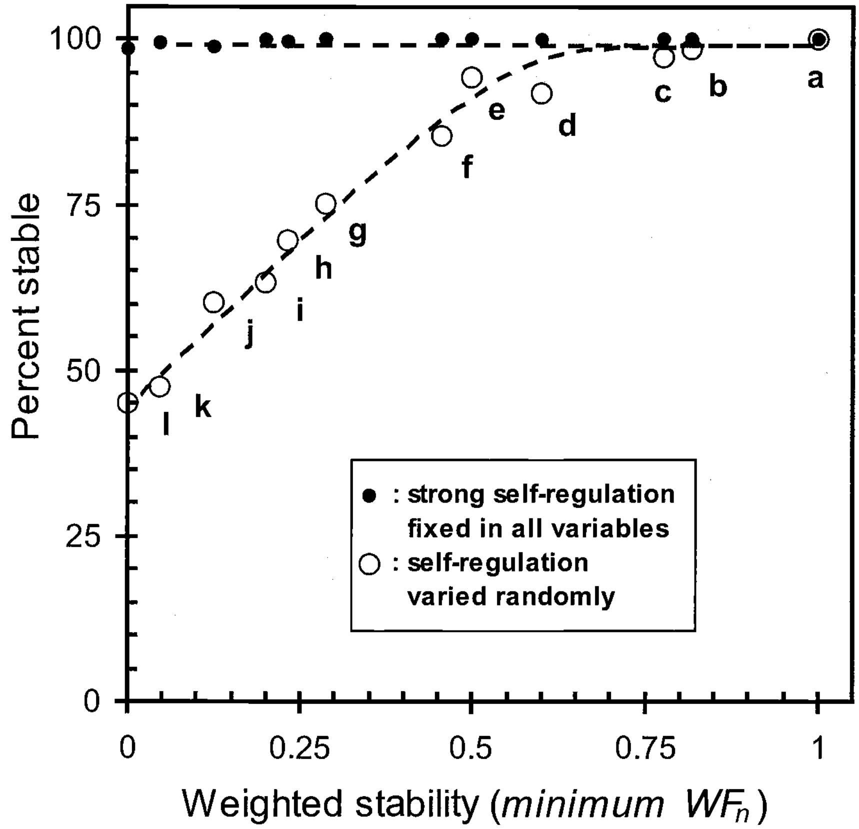


Figure 4.5. Percent stability versus weighted stability for 12 models (Figure 4.1) in which interaction strengths of community matrix elements were randomly varied by two orders of magnitude and assigned to 5,000 separate matrices. Self-regulation was either fixed at a strong value of –1.0, or varied randomly along with off-diagonal elements. Stability of the quantitatively specified systems was judged by the criteria of all negative polynomial coefficients, and all positive Hurwitz determinants.

Table 4.1. Summary of stability analysis for 5,000 matrices specified with randomly assigned numeric values to each of 12 models (**a**–**l**, Figure 4.1). Stability was assessed by the criteria of 1) all negative polynomial coefficients for each F_n level of system feedback, and 2) all positive Hurwitz determinants (det.). All models were stable, in qualitative terms, except for model **l**, which failed the first criterion at its highest ($n = 5$) level of feedback. All a_{ii} and a_{ij} interaction terms were randomly assigned values that were varied by 2 orders of magnitude, except as indicated in F below. A) Qualitative measure of weighted feedback (wF_n) for each n level of system feedback. Percent model failure of respective stability criterion for B) negative polynomial coefficients, and C) positive Hurwitz determinants. D) Percent potential error for relying only upon the first criterion, and E) the overall percentage of models failing either criteria 1 or 2. Weighted stability measure derived from *minimum* wF_n values, in bold font, which in all of these models occurs at the highest, n = 5, level of feedback. F) Overall percentage of model failure in separate assignments to matrices where a_{ii} terms were fixed at a strong value.

Model system:	a	b	c	d	e	f	g	h	i	j	k	l
A. Weighted feedback	Qualitative Measures of System Feedback											
wF_5	**1.0**	**0.82**	**0.78**	**0.60**	**0.50**	**0.45**	**0.29**	**0.23**	**0.20**	**0.13**	**0.048**	**0**
wF_4	1.0	0.85	0.82	0.82	0.68	0.48	0.63	0.43	0.55	0.43	0.20	0.15
wF_3	1.0	0.93	0.91	0.91	0.88	0.63	0.84	0.63	0.74	0.69	0.47	0.51
wF_2	1.0	1.0	1.0	1.0	1.0	0.87	1.0	0.87	0.86	0.87	0.75	0.88
wF_1	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
Weighted stability	1.0	0.82	0.78	0.60	0.50	0.45	0.29	0.23	0.20	0.13	0.048	0
B. Percent polynomial coefficients ≥ 0	Results of Quantitative Matrix Analysis											
F_5	0	1.1	2.3	8.0	5.4	11	25	29	36	38	43	51
F_4	0	0.46	0.84	0.86	0.78	8.8	3.2	11	12	15	31	31
F_3	0	0	0.080	0.060	0.020	2.2	0.080	2.3	1.5	1.5	7.6	4.0
F_2	0	0	0	0	0	0.020	0	0.020	0.060	0.040	0.16	0
F_1	0	0	0	0	0	0	0	0	0	0	0	0
Percent failure 1st stability criterion	0	1.2	2.5	8.1	5.5	14	25	30	36	40	53	55

Table 4.1 (continued).

Model system:	a	b	c	d	e	f	g	h	i	j	k	l
C. Percent Hurwitz determinants ≥ 0												
1st Hurwitz det.	0	0	0	0	0	0	0	0	0	0	0	0
2nd Hurwitz det.	0	0.020	0	0	0.020	0	0	0	0.18	0.020	0.020	0
3rd Hurwitz det.	0	0.16	0.080	0.14	0.12	1.7	0.22	1.1	1.7	0.12	1.6	1.4
Percent failure 2nd stability criterion	0	0.16	0.080	0.14	0.12	1.7	0.22	1.1	1.7	0.14	1.7	1.4
D. Percent error of using only 1st criterion†	0	0.16	0.021	0	0.13	0.90	0.11	0.29	0.72	0.033	0.17	0.18
E. Percent failing 1st or 2nd criteria if a_{ii} varied	0	1.3	2.5	8.1	5.6	14	25	30	37	40	53	55
F. Percent failing 1st or 2nd criteria if a_{ii} fixed	0	0	0	0	0	0	0	0.12	0	1.0	0.44	1.4

†: Potential error of relying only on 1st Routh–Hurwitz stability criterion, calculated as: [100*(number of matrices passing 1st criterion, and failing 2nd) divided by number passing 1st].

and wF_5 were both equal to 0 (an extreme case of neutral stability). This led us to consider models in which feedback was more severely compromised at intermediate feedback levels, such that wF_3 or wF_4 was less than wF_5. Unable to devise our own, we sorted through over 20,000 randomly constructed 5-variable models. We chose 6 that were qualitatively stable, and in which wF_3 or wF_4 was less than wF_5, and greater than 0, thus avoiding neutrally stable models. The resulting models (Figure 4.6) had a high degree of connectance via omnivorous, competitive, and mutualistic linkages. While these randomly constructed models violate general notions of what is biologically plausible (Lawlor 1978, DeAngelis 1975), we do not exclude them from being so, as systems similar to models **m–r** appear to be common in vertically compressed environments, such as benthic estuarine communities (Castillo et al. 2000).

We constructed numerical matrices corresponding to the models, as before, by either randomly assigning self-regulation terms, or fixing them at a strong level (Table 4.2). Where self-regulation was varied, the models failed the first stability criterion by a proportion similar to models **g–j**, (i.e. models **g–j**, and **m–r** exhibit a comparable degree of failure due to the first criterion (16% to 47%), over a similar range of weighted stability (0.12 to 0.31; Tables 4.1 and 4.2). In the randomly constructed models, however, a substantial proportion of failures (7% to 49%) resulted from violations of the second criterion. Moreover, there was a large potential error (8% to 43%), in relying only upon weighted stability as an indicator of overall potential stability. Model failure from the second criterion was greatest in model **q**, where the *minimum* wF_n occurred at a level lower (3rd level) than in any other model system.

The randomly constructed models exhibited a high level of stability (≥ 94%) where self-regulation was fixed at a strong level (Table 4.2). We also tested, but do not show here, the reliability of weighted predictions from 2,000 randomly constructed 5-variable models, and found results identical to those for models **a–l**.

While weighted stability (*minimum* wF_n) does not directly address the status of the Hurwitz determinants, the relative value of weighted feedback (wF_n) at each level of a system does, however, identify the potential for nonpositive Hurwitz determinants. Models with positive second (H_2) or third (H_3) Hurwitz determinants suggest that

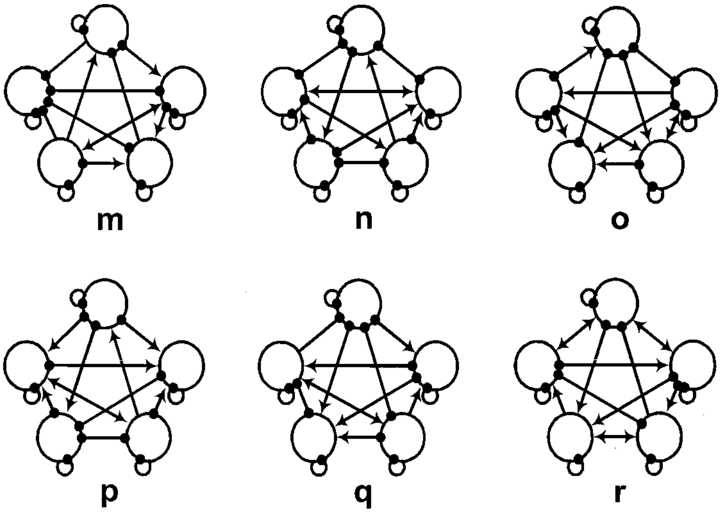


Figure 4.6. Signed digraphs of 6 randomly constructed model systems. Large open circles represent model variables, or species, with links ending in an arrow signifying a positive effect, and links ending in a small filled circle indicating a negative effect. Negative self-effects (self-regulation) are denoted by links starting and ending in the same variable.

Table 4.2. Summary of 5,000 numerical matrices in which system stability was assessed in 6 randomly constructed models (**m–r**, Figure 4.6) by criteria of 1) all negative polynomial coefficients for each F_n level of system feedback, and 2) all positive Hurwitz determinants (det.). All models were qualitatively stable, and all a_{ii} and a_{ij} interaction terms were randomly assigned values that were varied by 2 orders of magnitude, except as indicated in F below. A) Qualitative measure of weighted feedback (wF_n) for each n level of system feedback. Percent model failure of respective stability criterion for B) negative polynomial coefficients, and C) positive Hurwitz determinants. D) Percent potential error for relying only upon the first criterion, and E) the overall percentage of models failing either criterion 1 or 2. Weighted stability measure derived from *minimum* wF_n values, in bold font, which in these models occurs at the 3rd or 4th level of feedback. F) Overall percentage of unstable matrices where a_{ii} terms were fixed at a strong value (-1), and a_{ij} elements were assigned random values.

Model system:	m	n	o	p	q	r
A. Weighted feedback	Qualitative Measures of System Feedback					
wF_5	0.38	0.25	0.26	0.25	0.28	0.21
wF_4	**0.31**	**0.24**	**0.23**	**0.20**	0.19	**0.12**
wF_3	0.37	0.30	0.39	0.41	**0.16**	0.13
wF_2	0.63	0.58	0.67	0.68	0.53	0.44
wF_1	1.0	1.0	1.0	1.0	1.0	1.0
Weighted stability	0.31	0.24	0.23	0.20	0.16	0.12
B. Percent polynomial coefficients ≥ 0	Results of Quantitative Matrix Analysis					
F_5	6.8	9.5	12	11	9.5	16
F_4	10	11	14	17	19	27
F_3	7.9	9.9	4.3	2.6	28	30
F_2	1.6	1.3	0.50	0.15	2.7	5.7
F_1	0	0	0	0	0	0
Percent failure 1st criterion	16	19	19	21	36	47
C. Percent Hurwitz determinants ≤ 0						
1st Hurwitz det.	0	0	0	0	0	0
2nd Hurwitz det.	3.2	2.4	1.9	1.7	1.7	3.9
3rd Hurwitz det.	31	34	12	6.5	49	41
Percent failure 2nd criterion	31	34	13	7.0	49	41
D. Percent error of using only 1st criterion†	31	34	14	7.8	43	38
E. Percent failing 1st or 2nd criteria if a_{ii} varied	42	47	30	27	64	67

Table 4.2. (continued)

Model system:	m	n	o	p	q	r
F. Percent failing 1st or 2nd criteria if a_{ii} fixed at strong level	1.1	2.2	1.8	1.8	5.1	6.2

†: Potential error of relying only on 1st Routh–Hurwitz stability criterion, calculated as: [100*(number of matrices passing 1st criterion, and failing 2nd) divided by number passing 1st].

feedback at lower levels is greater than feedback at higher levels (i.e. $H_2 > 0$ when $F_1F_2 > -F_3$, and $H_3 > 0$ when $F_1[F_1F_4+F_5] > F_3[F_1F_2+F_3]$; remembering that F_n terms are, by convention here, negative). Where feedback at intermediate levels is compromised by a countervailing balance of cycles, as indicated by relatively low values of weighted feedback, then there arises a significant potential for negative Hurwitz determinants, and failure of the second Routh–Hurwitz criterion (Tables 4.1 and 4.2).

System Predictability and Stability

A comparison of Figures 4.4 and 4.5 demonstrates that the processes of cancellation and diminution of feedback cycles are similarly involved in system response and stability, when self-regulation is not fixed at a strong level. The shape and threshold points in the graphs of both figures are roughly the same except for their y-intercepts. In Figure 4.5, a *minimum* wF_n value of 0 indicates approximately an equal chance for feedback to be either positive or negative, while in Figure 4.4 the intercept is forced to zero, as there are no exactly neutral responses. Beyond this difference, Figures 4.4 and 4.5, under the varied self-regulation scenario, show numerical simulations to have an equal effect upon the countervailing balance of feedback cycles, whether from complementary feedback or total system feedback. In fact, the relationship between the potential stability and overall predictability of response signs for a system is linear (Figure 4.7). A system that has a high potential for stability will also have a high

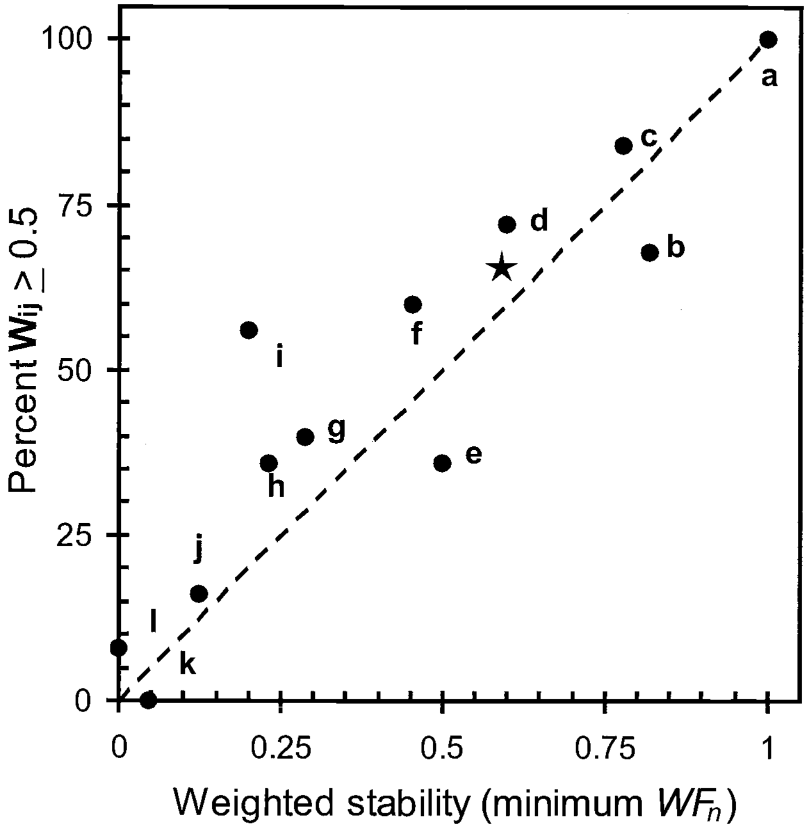


Figure 4.7. Predictability (proportion of weighted predictions ≥ 0.5) versus weighted stability for 12 5-variable model systems (models **a**–**l**, Figure 4.1), and one 10-variable model system (Figure 4.8) denoted by ★.

potential for sign determinacy in its responses; one of low stability will tend towards low sign determinacy. A single measure of weighted stability can thus be employed as an overall descriptor of a system's potential for stability and predictability.

Differing Effect of Self-Regulation

Why does strong self-regulation stabilize each model in nearly all quantitative matrices (>98% models **a–l**, and >94% models **m–r**), whereas sign determinacy is only marginally (roughly 10%) improved? The answer is to be found in the symbolic descriptions of system feedback, where we see an unequal distribution of self-regulation terms among cycles of different sign. Within any given response, there was a general tendency for a_{ii} terms to be associated with feedback cycles that were of the same sign as the net response of the adjoint. This caused a small increase in sign determinacy when the a_{ii} terms were strengthened (Figure 4.4), though in some instances the opposite occurred, and there self-regulation terms were more closely allied to cycles opposing the net response of the adjoint.

In overall system feedback, a_{ii} terms were found to be associated with negative cycles in two ways that practically guaranteed a stable balance of cycles when self-regulation was fixed at a strong level: 1) a_{ii} terms are more numerous within negative cycles, and 2) a_{ii} terms were more frequently arranged as multipliers of each other in negative cycles than in positive ones. This arrangement produces a dramatic effect in the quantitative value of feedback. For example, consider two sets of feedback cycles, each with three cycles of equal length: set 1) [0.2*0.2*1] + [0.2*0.2*1] + [0.2*0.2*1] and set 2) [0.2*0.2*0.2] + [0.2*0.2*0.2] + [1*1*1]. While both sets of cycles are composed of the same number and strength of interactions, in the second set the stronger terms are combined together, and this arrangement causes the value of overall feedback (1.02) to be 8.5 times greater than that of the first (0.12).

In model **l** there is, at the highest level of feedback, an equal number of positive and negative cycles, which affords the least potential for stability of the 12 models considered in this study (Figure 4.4). Yet at this highest level of feedback, there were 31

a_{ii} terms within negative cycles, and 23 within positive cycles (Table 4.3). In negative cycles, the a_{ii} terms were more frequently combined together in groups of 3 or more. This general pattern of the amount and arrangement of the a_{ii} terms occurs at all other levels of feedback in model **I** (Table 4.3); it is in fact a feature general to all community matrix models, and the mechanism by which strong self-regulation can exert an overwhelming influence on system stability.

Table 4.3. Arrangement of self-regulation (a_{ii}) terms in positive (+) and negative (–) feedback cycles, at each n^{th} level of system feedback in model **I** (Figure 4.1). Self-regulation terms in negative feedback cycles are more numerous, and more frequently at higher degrees of combination†, than in positive feedback cycles.

	Frequency of combination for each n^{th} level of system feedback in positive (+) and negative (–) cycles									
a_{ii} degree of combination†	$n = 5$		$n = 4$		$n = 3$		$n = 2$		$n = 1$	
	+	–	+	–	+	–	+	–	+	–
5th	0	1	*	*	*	*	*	*	*	*
4th	**	**	0	5	*	*	*	*	*	*
3rd	1	6	**	**	0	10	*	*	*	*
2nd	6	0	3	18	**	**	0	10	*	*
1st	8	8	12	0	3	10	**	**	0	5
Total number of a_{ii} terms	23	31	18	56	3	40	0	20	0	5
Number of cycles with a_{ii} terms	15	15	15	23	3	20	0	10	0	5
Total number of cycles	21	21	23	31	9	28	1	16	0	5

†: Defined here as number of a_{ii} terms per cycle, e.g. $-a_{1,1}\,a_{2,2}\,a_{3,3}\,a_{4,5}\,a_{5,4}$ is a negative cycle of length $n = 5$, and 3rd degree of combination.

*: Feedback at level n is composed of cycles of length n; and a degree of combination can exist only within a cycle of equal or greater length.

**: Self-regulation terms comprise 'disjunct loops' (as in $a_{1,1}\,a_{2,2}\,a_{3,3}$ above†), which are joined with 'conjunct loops' (as in $a_{4,5}\,a_{5,4}$ above†) in formation of feedback cycles (Puccia and Levins 1985); n–1 degrees of combination are therefore precluded from cycles of length n.

Large Systems

While we have shown the utility of 'weighting' feedback cycles for 5-variable model systems, we question the generality of these results for larger systems. Though larger systems have feedback cycles that are longer and usually more numerous, the processes of cancellation and diminution act uniformly upon cycles of any length and number. To demonstrate this, we assigned values to 5,000 matrices from a 10-variable system, and analyzed response strength and sign determinacy. This 10-variable model is a representation of eutrophic Danish lakes (Jeppesen 1998) and is discussed in Chapter 2 of this work. Results (Figure 4.8) were identical to those from 5-variable models (Figures 4.3 and 4.4).

Limitations of computer spreadsheet software prevented us from evaluating the Hurwitz determinants for matrices with 10 variables. We were, however, able to calculate the determinant of each numerically specified matrix, which is also the polynomial coefficient at the highest ($n = 10$) level of system feedback. The weighted stability for this system, equal to 0.59, was also derived from the highest feedback level. In this 10-variable system, the determinant of each of the 5,000 matrices was negative 95% of the time, which is similar to results for the 5-variable model **d** (Table 4.1), which had a weighted stability of 0.60, and was stable in 92% of its numeric matrices. The relationship between system stability and predictability for the 10-variable system (Figure 4.8), was in agreement with that of the smaller systems (note '★' in Figure 4.7).

Discussion

We have set 'semi-quantitative' confidence levels on qualitative models by attributing a weight to the countervailing balance of feedback, and by analysis of thousands of randomly assigned numeric matrices. Elements of a qualitatively specified adjoint matrix can serve in a limited capacity as a benchmark of expected quantitative response strength. The potential sign determinacy of adjoint predictions was

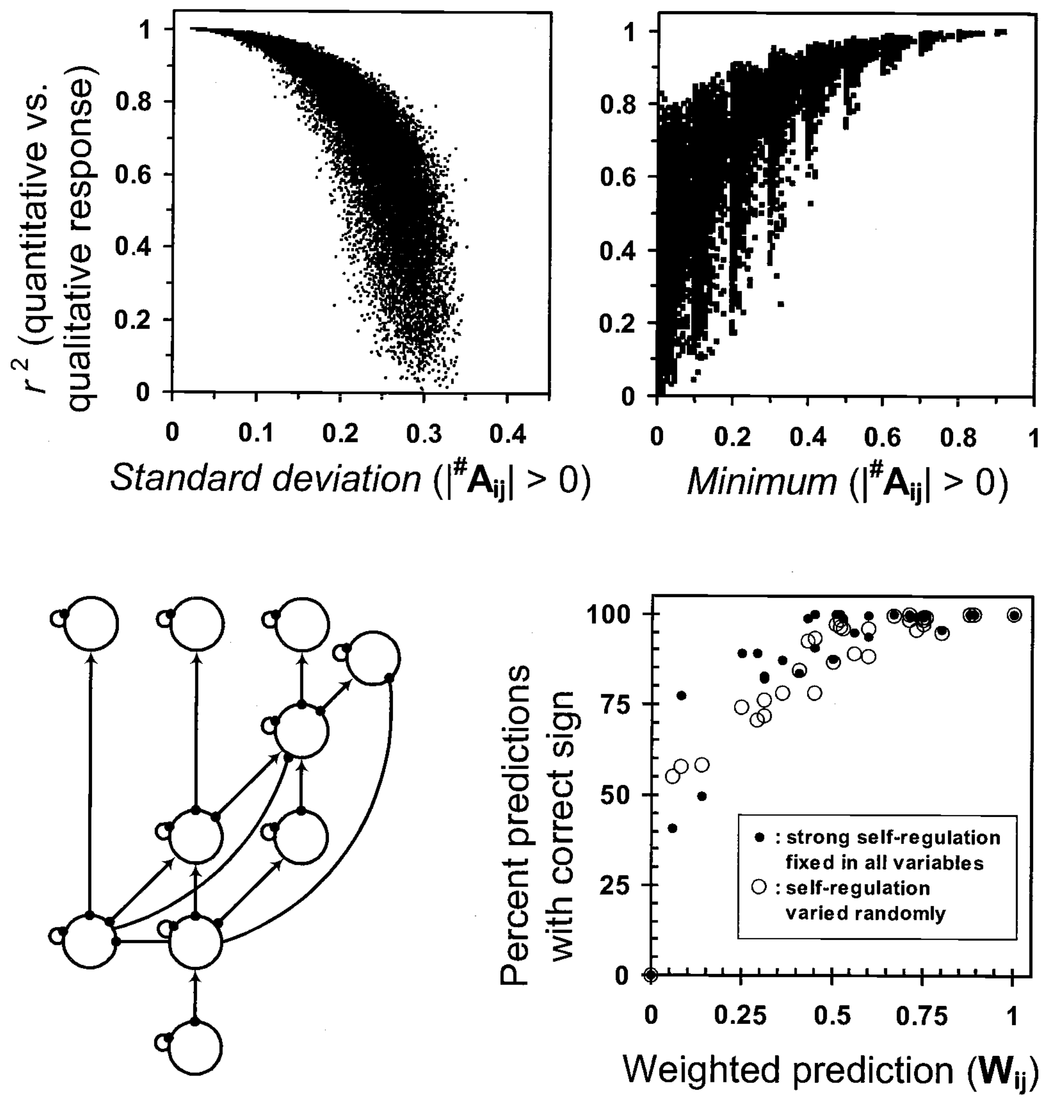


Figure 4.8. Sign determinacy and correspondence between quantitative and qualitative response predictions for a 10-variable model system; from 5,000 matrices with randomly assigned elements, as in Figures 4.2 and 4.3. Model system derived from a study of shallow eutrophic Danish lakes (Jeppesen 1998).

consistently gauged by elements of the weighted predictions matrix. The corollary measure of weighted stability exhibited a similar degree of reliability except in an easily identifiable class of models. System predictability was shown to be closely related to stability, and consistently described by the single measure of weighted stability. We explain a differential effect of strong self-regulation on system stability and predictability, by variation in both the amount and arrangement of a_{ii} terms within complementary and total system feedback cycles. Tests of these qualitative techniques were mainly on 12 5-variable models, but also a single 10-variable model. The applicability of these results, however, depends only upon the processes of cancellation and diminution of feedback cycles, which pose no theoretical limit on system size.

While predictions of response strength from the adjoint matrix exhibit in some instances a high degree of correspondence with numerical responses, we consider this correspondence to be unreliable, as it is easily eroded by a single weak interaction in the system. Qualitative predictions of response strength can be used, however, as a heuristic tool in structuring hypotheses of expected system behavior.

Our demonstration that correlation between qualitative and quantitative predictions of response 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 altogether exclude weakly connected species from community 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 (Levins 1966), the level of which is likely to differ from one system to the next.

High sign determinacy of weighted predictions greater than or equal to 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 previously been 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 response 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 the potential for reliable response predictions was severely limited in the Narragansett Bay food web studied by Yodzis (1988), which we find to have prediction weights no greater than 0.31. In an old-field food web studied by Schmitz (1997), we find only 4 of 36 responses to have nonzero 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.

The weighted stability measure provides a novel means to assess the potential stability of large complex systems, and also serves as an indicator of a system's overall potential for sign determinacy. Systems of various sizes and complexity can now be compared by a single unifying measure based on system structure. Our results suggest that Hurwitz determinants primarily address the structural aspects of a system, and depend only to a negligible degree upon the relative value of the interaction terms. While the measure of weighted stability is unreliable in models where total system feedback is compromised at an intermediate level, these models are easily identified by their relative wF_n values. Such models will have an inherently low potential for stability, and therefore little predictive scope is forfeited by this caveat.

Symbolic analysis of the community matrix forms the basis of this work, nearly all of which is reducible to the simple concept of countervailing balances in feedback cycles. At a fundamental level, nothing more is at work here than the processes of addition, subtraction, and multiplication. Processes of cancellation and diminution of feedback cycles work similarly in the formulation of system response and stability. The question 'what is the difference between the qualitative and quantitative behavior of a system?', is reducible to 'what is the difference between the effects of addition and subtraction among feedback cycles, and the effects of multiplication within feedback cycles?'

We purposefully chose 12 biologically plausible models (**a**–**l**) that exhibited a full spectrum of potential system stability and predictability. Sequential additions of links for competition, mutualism, and omnivory resulted in a general diminishment of system stability, which supports May's (1973, 1974) conclusion that system stability is ultimately at odds with system complexity. However, we found stability to diminish significantly only beyond a threshold value of *minimum* $wF_n = 0.5$. One sees in Figure 4.5 that models with a substantial degree of complexity were highly stable in numerical analyses.

This work has led us to consider that neutral stability is not a "razor's-edge" division (May 1974). Rather we consider the possibility that neutral stability can exist practically over a much broader dynamical space. Communities can be driven toward neutral stability through species invasions (Dambacher et al. 1999b) and still persist (Castillo et al. 2000). In the overall feedback of model **k**, there are 11 negative cycles balanced against 10 positive cycles. In qualitative terms this system is near neutral stability (i.e. *minimum* $wF_n = 0.048$). It exhibited positive overall feedback in 43% of the numeric matrices where both inter- (a_{ij}) and intraspecific (a_{ii}) interactions were varied, but was completely self-damped (100% stable) when a_{ii} terms were fixed at a strong level. In some ecosystems, the relative intensities of inter- and intraspecific interactions can be expected to wax and wane over time, with successional cycles (Holling 1992) or evolutionary change. Variation in interaction intensity could cause a system like model **k** to librate in negative and positive feedback, and be held in check by a large balance of countervailing feedback. Indeed, Goh (1977) proves that sufficient conditions exist for global stability in Lotka–Volterra systems where self-regulation is strong relative to interspecific interactions. He postulates a differential effect of self-regulation on system stability as communities cycle through high and low population densities. Our findings of nearly complete stability in numeric models where self-regulation was fixed at a strong value agree both with Goh's theoretical analysis and Yodzis' (1981) computer simulation. Our symbolic analysis of system feedback (Table 4.3) attributes the underlying cause to the unique affinity and arrangement of a_{ii} terms within self-damped or negative feedback cycles.

The above results emphasize the overriding importance of system structure. In ecological systems it is exceedingly rare that the actual values of the interaction terms are defined for all community members or variables, or for that matter, that they are even measurable. But often the composition and structure of the community is 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 system predictability and stability. 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. We submit that these techniques, and the insights they provide, should increase agreement between the theory and practice in community ecology.

CHAPTER 5
THE GOLDEN RULE OF COMPLEMENTARY FEEDBACK

Jeffrey M. Dambacher and Philippe A. Rossignol

Abstract

This work demonstrates the occurrence of the Fibonacci number series in the complementary feedback of Lotka–Volterra dynamical systems; herein we show a convergent value of *Phi* to govern reciprocal effects between neighboring variables. The impact to the entire community from input to a population variable can be predicted from the adjoint of the community (Jacobian) matrix, which we render in qualitative terms of complementary feedback cycles. Sequences of complementary feedback cycles follow the Fibonacci number series, and are also configured as multiples and overlapping harmonics thereof. We derive an absolute feedback matrix that clarifies the series. Patterns of complementary feedback are determined by community structure, which can also be portrayed and understood in terms of signed digraph structure.

Introduction

In the 13th century, Fibonacci (Leonardo Pisano) pondered the rate of reproduction in rabbits. This seemingly benign question brought forth a most enduring and powerful mathematical paradigm, namely, series. Fibonacci's solution to the rate of reproduction in rabbits also gave birth, so to speak, to the discipline of population dynamics. Fibonacci's rabbits, history tells us, were immortal. Benefiting from the protection of an enclosing wall, they reproduced unchecked by the forces of predation, disease, and starvation. While modern analyses otherwise make more realistic assumptions, Fibonacci's basic principle of exponential population growth nevertheless endured, to be taken up much later, and more apocalyptically, by Thomas Malthus. Fibonacci's recursive relation $n_{t+2} = n_t + n_{t+1}$, where t is generation class, can be expressed in Leslie matrix form as:

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

which projects, through time, mating pairs of rabbits and offspring over t generations. First row elements represent births of two offspring to each mating pair in generation t, and subdiagonal elements represent survival of each year class (here 100%). The final diagonal element confers immortality to the population. The largest positive real eigenvalue of this matrix (λ_1) is the exponentiated growth rate of the population (i.e. $\lambda_1 = e^r$). For successive generations of Fibonacci's rabbits, λ_1 converges to the golden ratio *Phi* (1.618…), and the next largest eigenvalue (λ_2) converges to a negative value of *phi* (0.618…, where *phi* = 1 / *Phi*). Left to themselves in the 799 yr since their discovery, Fibonacci's rabbits would today have a 'global' population of nearly $5.3*10^{2003}$; given that the number of electrons in the visible universe has been estimated at 10^{79}, some biological control is clearly in order!

We are concerned therefore with the limits to growth for an entire ecological community, which for n interacting species, is described by the Lotka–Volterra equations in the general form of:

$$\frac{d\mathbf{N_i}}{dt} = \frac{r_i}{\mathbf{K_i}} \mathbf{N_i} \left(\mathbf{K_i} - \sum_{j=1}^{n} \alpha'_{ij} \mathbf{N_j} \right) \qquad (5.1)$$

where $\mathbf{N}$ is the column vector of population size or density of species i, $\mathbf{K}$ is the column vector of carrying capacities, and α'_{ij} is the interaction coefficient that represents the direct per capita effect of species j on i. At equilibrium, with growth rates equal to zero, the carrying capacity for each population in the community becomes:

$$\mathbf{K_i} = \sum_{i=1}^{n} \alpha'_{ij} \mathbf{N_j^*} \qquad (5.2)$$

where $\mathbf{N}^*$ represents the equilibrium abundance of a population. Substituting this equilibrium into Equation 5.1 gives, for each species, the nonlinear function:

$$\frac{d\mathbf{N}_\mathbf{i}^*}{dt} = \frac{r_i}{\mathbf{K}_\mathbf{i}}\mathbf{N}_\mathbf{i} \sum_{j=1}^{n} \alpha'_{ij}\left(\mathbf{N}_\mathbf{j}^* - \mathbf{N}_\mathbf{j}\right) \tag{5.3}$$

Equation 5.3 can be linearized through a Taylor series expansion, with *m* variables, around the equilibrium values of $\mathbf{N}^*_\mathbf{i}$, to give:

$$\frac{d\mathbf{N}_\mathbf{i}^*}{dt} = f_i\left(N_1, N_2, N_3, \ldots, N_n; c_1, c_2, c_3, \ldots, c_m, t\right) \tag{5.4}$$

where $c_i = r_i/\mathbf{K}_\mathbf{i}$. In this derivation, c_i represents a general parameter related to growth and carry capacity of a population.

Other forms of the Lotka–Volterra equation can subsume additional parameters within c_i, such as the capture efficiency for predators, etc. The first order partial differential of Equation 5.4 is

$$\frac{d\mathbf{N}_\mathbf{i}^*}{dt} = \sum_{j=1}^{n} \frac{\partial f_i}{\partial \mathbf{N}_\mathbf{j}}\left(\mathbf{N}_\mathbf{j}{}^* - \mathbf{N}_\mathbf{j}\right) \tag{5.5}$$

where f_i is the function for the growth rate of $\mathbf{N}_\mathbf{i}$. The Jacobian matrix **J** is composed of the first partials of each $i^{th}j^{th}$ term in Equation 5.5:

$$\mathbf{J} = \begin{bmatrix} \frac{\partial f_1}{\partial N_1} & \frac{\partial f_1}{\partial N_2} & \frac{\partial f_1}{\partial N_3} & \cdots & \frac{\partial f_1}{\partial N_n} \\ \frac{\partial f_2}{\partial N_1} & \frac{\partial f_2}{\partial N_2} & \frac{\partial f_2}{\partial N_3} & \cdots & \frac{\partial f_2}{\partial N_n} \\ \frac{\partial f_3}{\partial N_1} & \frac{\partial f_3}{\partial N_2} & \frac{\partial f_3}{\partial N_3} & \cdots & \frac{\partial f_3}{\partial N_n} \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ \frac{\partial f_n}{\partial N_1} & \frac{\partial f_n}{\partial N_2} & \frac{\partial f_n}{\partial N_3} & \cdots & \frac{\partial f_n}{\partial N_n} \end{bmatrix} \tag{5.6}$$

Each $\partial f_i / \partial \mathbf{N}_\mathbf{i}^*$ term of the Jacobian matrix is equivalent to the interaction coefficients α_{ij} that comprise the community matrix **A**, where

$$\mathbf{A} = \begin{bmatrix} \alpha_{11} & \alpha_{12} & \alpha_{13} & \cdots & \alpha_{1n} \\ \alpha_{21} & \alpha_{22} & \alpha_{23} & \cdots & \alpha_{2n} \\ \alpha_{31} & \alpha_{32} & \alpha_{33} & \cdots & \alpha_{3n} \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ \alpha_{n1} & \alpha_{n2} & \alpha_{n3} & \cdots & \alpha_{nn} \end{bmatrix} \tag{5.7}$$

In matrix form Equation 5.6 is expressed as

$$\frac{d\mathbf{N}}{dt} = \mathbf{AN}^* \tag{5.8}$$

Perturbations to the equilibrium of the community, through alterations in the rates of population birth or death, can be assessed as a change in the parameter $\partial f_i / \partial c_h$ in Equation 5.5, at or near equilibrium. Employing the rules of partial derivatives, with c_h as an independent variable

$$\frac{\partial}{\partial c_h}\left(\frac{d\mathbf{N}_\mathbf{i}^*}{dt}\right) = \frac{\partial}{\partial c_h} f_i(x_1, x_2, x_3, \ldots, x_n; c_1, c_2, c_3, \ldots, c_m, t) = 0 \tag{5.9}$$

and

$$\frac{\partial f_i}{\partial c_h} + \frac{\partial f_i}{\partial \mathbf{N}_\mathbf{j}} \frac{\partial \mathbf{N}_\mathbf{j}^*}{\partial c_h} = 0 \tag{5.10}$$

Knowing $\partial f_i / \partial c_h$, the parameters through which disturbance is acting upon the system, a solution for $\partial \mathbf{N}_\mathbf{j} / \partial c_h$ is obtained through Cramer's Rule which, by cofactor expansion (Appendix 1), calculates the total direct and indirect effects on species *i* through a change in parameter c_h. We obtain this solution by replacing the i^{th} column of the system determinant with the column vector $-\partial f_i / \partial c_h$:

$$\frac{\partial \mathbf{N}_\mathbf{i}^*}{\partial c_h} = \frac{\begin{vmatrix} \alpha_{11} & \alpha_{12} & \alpha_{13} & \cdots & \alpha_{1,j-1} & -\frac{\partial f_1}{\partial c_h} & \alpha_{1,j+1} & \cdots & \alpha_{1n} \\ \alpha_{21} & \alpha_{22} & \alpha_{23} & \cdots & \alpha_{2,j-1} & -\frac{\partial f_2}{\partial c_h} & \alpha_{2,j+1} & \cdots & \alpha_{2n} \\ \alpha_{31} & \alpha_{32} & \alpha_{33} & \cdots & \alpha_{3,j-1} & -\frac{\partial f_3}{\partial c_h} & \alpha_{3,j+1} & \cdots & \alpha_{3n} \\ \cdot & \cdot & \cdot & \cdots & \cdot & \cdot & \cdot & \cdots & \cdot \\ \cdot & \cdot & \cdot & \cdots & \cdot & \cdot & \cdot & \cdots & \cdot \\ \cdot & \cdot & \cdot & \cdots & \cdot & \cdot & \cdot & \cdots & \cdot \\ \alpha_{n1} & \alpha_{n2} & \alpha_{n3} & \cdots & \alpha_{n,j-1} & -\frac{\partial f_n}{\partial c_h} & \alpha_{n,j+1} & \cdots & \alpha_{nn} \end{vmatrix}}{\begin{vmatrix} \alpha_{11} & \alpha_{12} & \alpha_{13} & \cdots & \alpha_{1n} \\ \alpha_{21} & \alpha_{22} & \alpha_{23} & \cdots & \alpha_{2n} \\ \alpha_{31} & \alpha_{32} & \alpha_{33} & \cdots & \alpha_{3n} \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ \alpha_{n1} & \alpha_{n2} & \alpha_{n3} & \cdots & \alpha_{nn} \end{vmatrix}} \tag{5.11}$$

The denominator of the right side of Equation 5.11 is the determinant ('| |') of the community matrix **A**, and the numerator is the cofactor $\mathbf{C}_{ji}$, which details the effect of subsystems complementary to species *i* and *j*. Complementary feedback is formed by subsystems of populations that are not on the direct path between species *i* and *j*, and is the product of disjunct loops. A solution for the entire community system is obtained through a matrix of all cofactors, the signs of which correspond to Levins' table of predictions (Puccia and Levins 1985):

$$\mathbf{N}_i^* = \frac{\mathbf{C}_{ji}}{det\ \mathbf{A}} \mathbf{K}_j \tag{5.12}$$

where *det* is the determinant. Elements of the classical adjoint, or adjoint matrix are equivalent to transposed cofactors (i.e. *adjoint* $\mathbf{A}_{ij} = \mathbf{C}_{ji}$), thus a solution for the entire equilibrium system can reached by:

$$\mathbf{N}^* = \frac{adjoint\ \mathbf{A}}{det\ \mathbf{A}} \mathbf{K} \tag{5.13}$$

and by definition of an inverse matrix:

$$\mathbf{N}^* = \mathbf{A}^{-1}\mathbf{K} \tag{5.14}$$

In Equations 5.12–5.14 we can anticipate the fate of equilibrium population levels due to input to the system. The carrying capacity, **K**, is constant in these equations, as is the denominator, *det* **A**, which represents overall system feedback. The full numerical response of a population is mediated or scaled by a system's overall feedback, which provides resistance to perturbations. It is useful to distinguish the adjoint from the inverse of the community matrix, as the adjoint contains all of the variation of response within a system, and is an expression of complementary feedback. In dynamical systems, complementary feedback propagates as cycles (or loops) through direct and indirect paths, and these cycles convey the impact of system input to all community members.

In derivation of the effects of input to a system variable (Nakajima 1992), we obtain the inverse of the negative community matrix ($-\mathbf{A}^{-1}$), and by extension the adjoint of the negative community matrix (*adjoint* $-\mathbf{A}$). This maintains a sign convention for both even- and odd-sized systems. Input in the inverse and adjoint matrices is, by convention, interpreted as positive, through either an increase in birth rates or a decrease in death rates. Input to the inverse and adjoint matrices is read down column, and responses along rows. If input is negative, then the signs of the inverse and adjoint matrix elements are reversed.

Signed Digraphs and Qualitative Analysis

Signed digraphs (*di*-rected *graphs*) portray relationships between populations in an ecological community (Figure 5.1), all of which can be qualitatively rendered with positive, negative, or neutral links (edges) between system variables (vertices). Qualitative specification of a system's linkages is often the best that ecologists can do, since it is difficult, or often impossible, to actually measure all elements of the community matrix. Yet simply knowing the signs of the interactions can provide important insights into behavior of complex systems. Counterintuitive behavior in a system often results from complex interactions, and this behavior can often be revealed through qualitative analysis (Puccia and Levins 1991). When community matrix elements are qualitatively specified with +1, –1, or 0, calculating the adjoint matrix yields the net number of complementary feedback cycles in a response.

As an example, we present a model (Figure 5.2) of the dynamics of snowshoe hare (North American relatives of Fibonacci's rabbits) interactions with vegetation, and a guild of predators, including lynx and great horned owls (Dambacher et al. 1999a, Chapter 2). In this system we reveal the counterintuitive response that fertilization of vegetation (a positive input observed down the first column of the adjoint), can result in an increase of plant biomass, and hence forage, but can also lead to a neutral response in hares (read along the second row, i.e. *adjoint* $-\mathbf{A}_{2,1}$). One might expect that more forage would equal more hares, but a null response occurs due to a countervailing balance of complementary feedback cycles ($a_{2,1}\, a_{3,3} - a_{2,3}\, a_{3,1}$) exerting opposing effects. This results from the positive effect that vegetative cover ($a_{3,1}$) confers upon predators, which are known to use cover from which to ambush their prey.

The adjoint matrix reveals the net number of complementary feedback cycles in a response. We are, however, also interested in the absolute number of cycles, which we

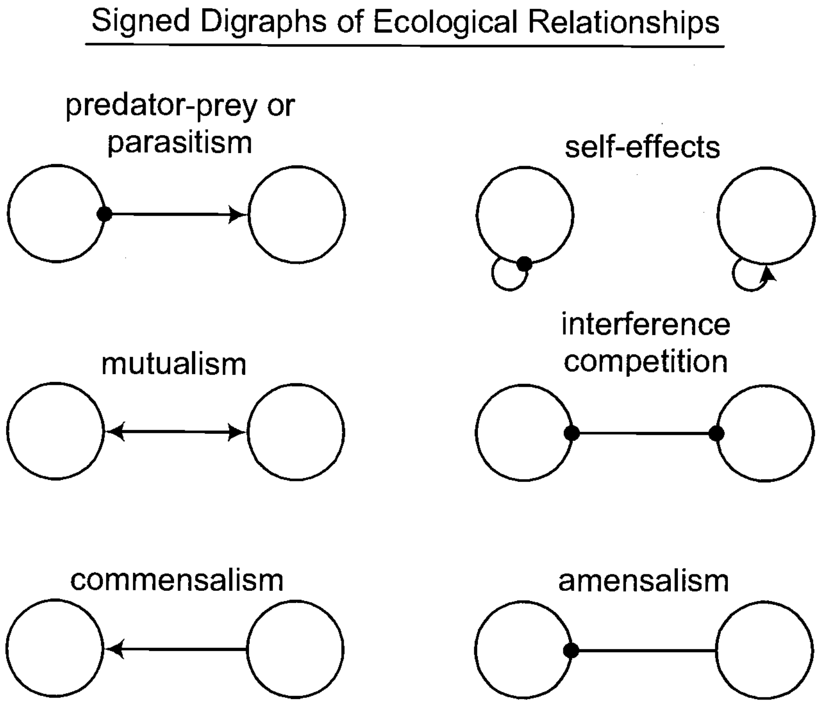
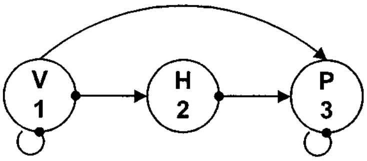


Figure 5.1. Signed digraphs of possible pair-wise ecological relationships and self-effects, graph links (edges) can include either one-way or two-way interactions; arrows denote positive effects, filled circles negative effects.



Symbolically specified community matrix **A**

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

Qualitatively specified community matrix **A**

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

adjoint –**A**

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

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

Figure 5.2. Signed digraph model of interactions between boreal forest vegetation (V), snowshoe hare (H), and predator guild (P), with symbolically and qualitatively specified community matrices, and adjoint matrix predictions of system response.

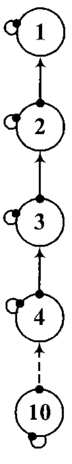
calculate through use of the permanent in minors of a community matrix specified only by the absolute values of its linkages (${}^{\bullet}\mathrm{A}$; i.e. by 1's or 0's only, essentially an adjacency matrix that includes self-loops). This gives us the absolute feedback matrix **T**:

$$\mathbf{T}_{\mathbf{ij}} = \mathit{permanent}\left(\mathit{minor}\ {}^{\bullet}\mathbf{A}_{\mathbf{ij}}\right)^{\mathit{transpose}} \qquad (5.15)$$

Taking the ratio of each element of the adjoint to the absolute feedback matrix, we can obtain a potential for ambiguity in system response, a sort of signal-to-noise ratio (Appendices 1 and 2).

Fibonacci's Series

Having defined the terms of our argument, we turn to special properties of the adjoint and absolute feedback matrices, where we find complementary feedback cycles that follow Fibonacci's series. To reveal clearly the occurrence of this series, we consider a system much larger than our snowshoe hare example. From a 10-variable straight-chain system, we obtain the following adjoint matrix:

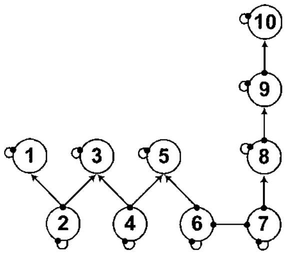


$$\begin{bmatrix}
55 & 34 & 21 & 13 & 8 & 5 & 3 & 2 & 1 & 1 \\
-34 & 34 & 21 & 13 & 8 & 5 & 3 & 2 & 1 & 1 \\
21 & -21 & 42 & 26 & 16 & 10 & 6 & 4 & 2 & 2 \\
-13 & 13 & -26 & 39 & 24 & 15 & 9 & 6 & 3 & 3 \\
8 & -8 & 16 & -24 & 40 & 25 & 15 & 10 & 5 & 5 \\
-5 & 5 & -10 & 15 & -25 & 40 & 24 & 16 & 8 & 8 \\
3 & -3 & 6 & -9 & 15 & -24 & 39 & 26 & 13 & 13 \\
-2 & 2 & -4 & 6 & -10 & 16 & -26 & 42 & 21 & 21 \\
1 & -1 & 2 & -3 & 5 & -8 & 13 & -21 & 34 & 34 \\
-1 & 1 & -2 & 3 & -5 & 8 & -13 & 21 & -34 & 55
\end{bmatrix}$$

In this matrix, ignoring the signs, one sees the Fibonacci number series along the first and last columns and rows. The left and right off-diagonal elements of the other columns are multiples of the first or last column, respectively, and the multipliers themselves are of the Fibonacci series. Considering the signs, where positive input propagates down the trophic chain (read down the columns), impacts alternate between positive and negative values, corresponding to a reversed Fibonacci series (i.e. $n_{t-2} = n_t - n_{t-1}$, giving: … , 13, –8, 5, –3, 2, –1, 1, 0, 1, 1). One also sees negative starting values for the series embedded within the matrix columns (i.e. … , –13, 8, –5, 3, –2, 1, –1, 0, –1, –1). As positive input propagates up the trophic chain, impacts are uniformly positive. The matrix is trans-diagonally symmetrical. Since there is no countervailing feedback in this particular system, elements of the absolute feedback matrix **T** are equivalent to the absolute value of the adjoint matrix elements.

While a straight-chain system is a simple portrayal of interactions between trophic levels in an ecosystem, a 10-tiered system is highly improbable due to limitations in transfer efficiencies between trophic levels. In Figure 5.3 we portray a more complex and plausible 10-variable system, where there is direct (interference) competition between variables 6 and 7, and indirect (scramble or resource) competition for shared food resources between variables 1, 3, and 5. While the signs of the adjoint matrix elements in this system do not always correspond to a Fibonacci series, the values do. Here we find a break in the regular Fibonacci series in variables adjacent to 6 or 7. Comparison of the adjoint and absolute feedback matrices reveals this break to be from separate harmonic sequences that underlie an absolute number of cycles following a regular Fibonacci series (or multiple thereof). The absolute feedback matrix **T** for the model in Figure 5.3 is identical to that for the 10-variable straight-chain system discussed above (there **T** is not shown, but is the same as the absolute value of the adjoint). In this respect, the model in Figure 5.3 behaves as a straight-chain system. Although opposing cycles of complementary feedback create overlying harmonics, and thus different net responses in the adjoint, the regular Fibonacci series becomes clear in the system's absolute feedback matrix **T**.

We consider next, in Figure 5.4, the behavior of an asymmetrical model with a branched structure incorporating interference competition and mutualism between basal species. Here competitive and mutualistic interactions impart positive feedback to subsystems of the model, causing counterintuitive responses. We also see the curious result that increasing the birth rate of variables 5 and 10 can result in a decrease in their equilibrium populations. In this system the Fibonacci series splits at the nodal 4th



adjoint −**A**

$$\begin{bmatrix}
\textcircled{25} & 16 & -9 & -7 & 2 & 5 & -3 & 2 & -1 & 1 \\
-16 & 16 & -9 & -7 & 2 & 5 & -3 & 2 & -1 & 1 \\
-9 & 9 & 18 & 14 & -4 & -10 & 6 & -4 & 2 & -2 \\
7 & -7 & -14 & 21 & -6 & -15 & 9 & -6 & 3 & -3 \\
2 & -2 & -4 & 6 & \textcircled{10} & 25 & -15 & 10 & -5 & 5 \\
-5 & 5 & 10 & -15 & -25 & 40 & -24 & 16 & -8 & 8 \\
3 & -3 & -6 & 9 & 15 & -24 & 39 & -26 & 13 & -13 \\
2 & -2 & -4 & 6 & 10 & -16 & 26 & \textcircled{10} & -5 & 5 \\
1 & -1 & -2 & 3 & 5 & -8 & 13 & 5 & 18 & -18 \\
1 & -1 & -2 & 3 & 5 & -8 & 13 & 5 & 18 & 23
\end{bmatrix}$$

absolute feedback **T**

$$\begin{bmatrix}
\textcircled{55} & 34 & 21 & 13 & 8 & 5 & 3 & 2 & 1 & 1 \\
34 & 34 & 21 & 13 & 8 & 5 & 3 & 2 & 1 & 1 \\
21 & 21 & 42 & 26 & 16 & 10 & 6 & 4 & 2 & 2 \\
13 & 13 & 26 & 39 & 24 & 15 & 9 & 6 & 3 & 3 \\
8 & 8 & 16 & 24 & \textcircled{40} & 25 & 15 & 10 & 5 & 5 \\
5 & 5 & 10 & 15 & 25 & 40 & 24 & 16 & 8 & 8 \\
3 & 3 & 6 & 9 & 15 & 24 & 39 & 26 & 13 & 13 \\
2 & 2 & 4 & 6 & 10 & 16 & 26 & \textcircled{42} & 21 & 21 \\
1 & 1 & 2 & 3 & 5 & 8 & 13 & 21 & 34 & 34 \\
1 & 1 & 2 & 3 & 5 & 8 & 13 & 21 & 34 & 55
\end{bmatrix}$$

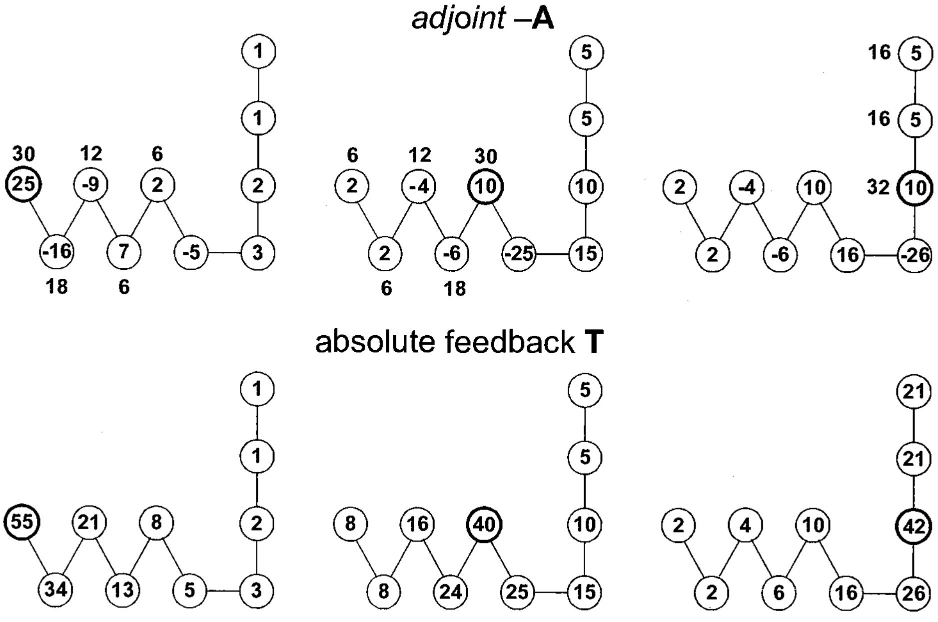
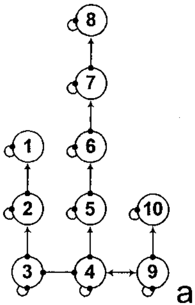


Figure 5.3. Ten-variable model system with direct and indirect competition. Three selected columns of the adjoint and absolute feedback matrices are portrayed in system response graphs, which detail the number of complementary feedback cycles generated from a given input; variables receiving input are denoted by thick-lined circles. Numbers next to adjoint response graphs are total number of countervailing feedback cycles canceled in calculation of the net response. These canceled cycles constitute an overlaying harmonic that sums with the adjoint to equal the absolute amount of feedback in the system, all of which follow the Fibonacci series, or multiples thereof.



adjoint **–A**

$$\begin{bmatrix} \enclose{circle}{12} & 1 & 11 & -10 & 6 & -4 & 2 & -2 & -5 & 5 \\ -1 & 1 & 11 & -10 & 6 & -4 & 2 & -2 & -5 & 5 \\ 11 & -11 & 22 & -20 & 12 & -8 & 4 & -4 & -10 & 10 \\ -10 & 10 & -20 & 30 & -18 & 12 & -6 & 6 & 15 & -15 \\ -6 & 6 & -12 & 18 & \enclose{circle}{-3} & 2 & -1 & 1 & 9 & -9 \\ -4 & 4 & -8 & 12 & -2 & 10 & -5 & 5 & 6 & -6 \\ -2 & 2 & -4 & 6 & -1 & 5 & 4 & -4 & 3 & -3 \\ -2 & 2 & -4 & 6 & -1 & 5 & 4 & 9 & 3 & -3 \\ -5 & 5 & -10 & 15 & -9 & 6 & -3 & 3 & 14 & -14 \\ -5 & 5 & -10 & 15 & -9 & 6 & -3 & 3 & 14 & \enclose{circle}{-1} \end{bmatrix}$$

absolute feedback **T**

$$\begin{bmatrix} \enclose{circle}{52} & 31 & 21 & 10 & 6 & 4 & 2 & 2 & 5 & 5 \\ 31 & 31 & 21 & 10 & 6 & 4 & 2 & 2 & 5 & 5 \\ 21 & 21 & 42 & 20 & 12 & 8 & 4 & 4 & 10 & 10 \\ 10 & 10 & 20 & 30 & 18 & 12 & 6 & 6 & 15 & 15 \\ 6 & 6 & 12 & 18 & \enclose{circle}{39} & 26 & 13 & 13 & 9 & 9 \\ 4 & 4 & 8 & 12 & 26 & 38 & 19 & 19 & 6 & 6 \\ 2 & 2 & 4 & 6 & 13 & 19 & 32 & 32 & 3 & 3 \\ 2 & 2 & 4 & 6 & 13 & 19 & 32 & 51 & 3 & 3 \\ 5 & 5 & 10 & 15 & 9 & 6 & 3 & 3 & 34 & 34 \\ 5 & 5 & 10 & 15 & 9 & 6 & 3 & 3 & 34 & \enclose{circle}{49} \end{bmatrix}$$

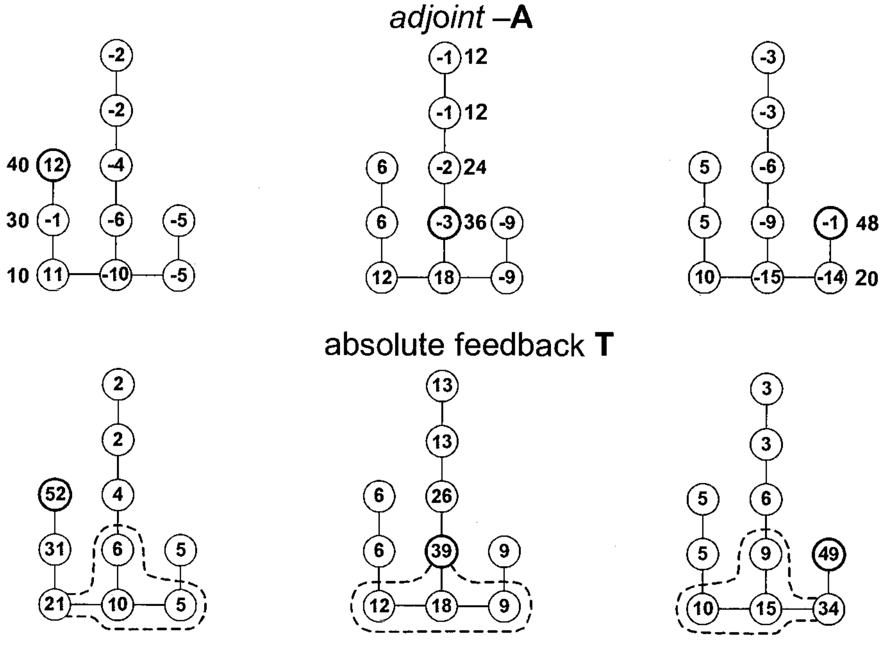


Figure 5.4. Asymmetrical and branched model system with mutualism and interference competition linkages specifically associated with nodal variable 4 (format follows Figure 5.3). Complementary feedback passing through variable 4 is split into separate series, but maintains an overall Fibonacci series in terms of absolute feedback. Complementary feedback to variables that are immediately posterior to both variable 4 and the input variable (encompassed by dashed-line) sum to the absolute number of cycles in the variable that is either medial to the nodal and input variables, or the input variable itself (where either are denoted by terminus of dashed-line).

variable into separate sequences of unequal magnitude (or into Fibonacci series with different starting values). Harmonic sequences are isolated within branch segments containing the variable of input, and do not pass through variable 4. As in the previous example (Figure 5.3), countervailing complementary feedback cycles sum to a greater Fibonacci series in the absolute feedback matrix **T**, however, the absolute feedback matrix **T** from this system differs from those of straight-chain systems.

We have observed, but do not show here, that in systems with long interaction loops (as might be caused by an omnivorous relationship between variables 6 and 10 in the above models), aperiodic sequences of complementary feedback cycles become folded back upon themselves, and the Fibonacci series become less interpretable. With increased structural connectivity the pattern becomes lost altogether, and the sequences appear as so much noise, although the number and sign of the responses remain biologically interpretable.

Discussion

In biological terms, impacts from perturbations propagate through ecosystems via complementary feedback cycles that diminish in number away from the source of input, according to a Fibonacci number series. While we have seen that Fibonacci's celebrated description of reproduction leads us to a convergent value of *Phi* for a population's growth rate, so too does a convergent value of *Phi* (or *phi*) denote the proportion of complementary feedback cycles passed between adjacent members of an ecological community, as in the golden rule (doing unto others . . .), and thus determines the reciprocal effect of neighbor upon neighbor.

We report the discovery of the Fibonacci number series in the adjoint of the community (Jacobian) matrices, arising from simple food web models. The presence of this series seems to have been unnoticed, or unreported, in matrix or graph theory literature. Given that complementary feedback cycles can be positive or negative under different conditions and therefore cancel each other, we present the derivation of the novel 'absolute feedback' matrix, the elements of which represent the absolute number of cycles in each response. This derivation makes use of the permanent rather than the determinant of matrix minors. Both the adjoint and permanent are recursive functions, which give rise to the observed Fibonacci series in our qualitatively specified systems. Our aim at this point has been to describe a previously unobserved pattern and its underlying cause. It is also our hope that the general observations presented in the above examples may lead to a more formal analysis by matrix and graph theoreticians.

CHAPTER 6
CONCLUSIONS

Nothing is more practical than theory.
—Richard Levins

In the quarter-plus century that has ensued since Levins (1966, 1974) introduced qualitative modeling to ecologists, there has been inadequate attention paid to the theory and technique. This can most surely be attributed, in part, to the reductionistic slant of western science. While generality and realism are dearly sought attributes of even the most ardent reductionist, to sacrifice precision is surely a heretical act. Inroads, however, are being made. Bayesian inference is a thin wedge that is exerting greater influence in both applied and theoretical ecology. Qualitative predictions of system behavior provide an obvious source of Bayesian priors. Furthermore, ecological research and management efforts are increasingly more inclined to address indirect effects, which are best understood in terms of complementary feedback.

A qualitative analysis of the community matrix provides a theoretical basis from which to judge the relevance of community structure to the behavior of ecological systems. This work demonstrates practical application to the research and management of real systems drawn from the published literature. It also provides simulations that define the limits to predictions of qualitative models.

Although this work makes it possible to analyze larger and more complex systems than previously possible, it is important to keep in mind a number of limitations inherent in any treatment of Lotka–Volterra systems. 1) The assumption of being at or near equilibrium can be easily violated where a system is frequently impacted by disturbance. Here a statistical model of the system is likely to be more useful than one assuming deterministic behavior. 2) There is an assumption of instantaneous, or at least time invariant, responses. Time lags produced by distinctive biological features of community members can produce staggered transitions to equilibrium, and interpretation of system response needs to be judged accordingly. 3) Elements of the community matrix are formed by linearizable relationships. Nonlinear interactions, such as functional responses, can produce community (Jacobian) matrix terms that vary in their sign, depending on the relative abundance of community neighbors. Although nonlinearities can present critical limitations to qualitative analyses, opting for a more quantitative approach is no guarantee of success, as knowing the exact form of the equations involved is still a theoretical exercise. Moreover, obtaining precise measurement of all model parameters is a nearly futile exercise.

In Chapter 2, qualitative modeling is used to explain an extensive record of published results pertaining to snowshoe hare, vegetation, and predator interactions in the boreal forest. A strength of qualitative modeling is here demonstrated by the hypothesis of a system linkage that is likely beyond quantification or immediate perception. In Chapter 3 further comparisons are made with various examples from the published literature, thus demonstrating the applicability of the technique to a broad class of ecological systems.

This work sets forth in Chapter 3 an algebraic reformulation of Levins' original loop analysis technique. It takes advantage of recent advances in software to remove the tedium of hand calculation, which previously posed a serious limitation to large and complex systems. The concept of weighting feedback cycles is a fundamental advance, which now enables one to address model ambiguity, both in terms of response predictions and stability analysis. Qualitative predictions were previously limited to an either-or assessment, primarily in small and simple systems; the weighting of feedback cycles now provides for such assessments by potential degree for large and complex models of any size, based solely on system structure.

Arising from the literature comparisons in Chapter 3, we find a general reliability of weighted predictions ≥ 0.5. This is more rigorously supported by simulation studies in Chapter 4. The concept of weighted stability evolved out of these simulation studies, and it provides a novel metric that rates both the potential predictability and stability of a model system. The concept of weighted stability now offers a means of judging the degree of potential stability, except in an identifiable class of models (i.e. where the *minimum* wF_n does not occurs at the highest level of feedback). Model systems that are compromised at lower feedback levels appear prone to failure by the second Routh–Hurwitz criterion. This result falls in line with the general intuitive understanding that feedback at lower levels must be greater than that at higher levels, to achieve positive Hurwitz determinants and overall system stability.

Complementary feedback cycles are emphasized in this work as the basis for understanding the perturbed response of dynamical systems. The concept of feedback cycles (or loops) arises from elementary graph theory, and was applied to Lotka–Volterra dynamical systems by Levins in his hand-calculated algorithm. The present work demonstrates that community structure provides a template upon which the reciprocal relationships between community members are organized and resolved, through the countervailing balance of complementary feedback cycles. In Chapter 5 we have the novel discovery that complementary feedback cycles propagate according to the Fibonacci number series, which means that in a dynamical sense, the reciprocal relationships between community neighbors are determined by a convergent value of *Phi*.

It has been demonstrated that a qualitative understanding of community structure can provide critical insights into the behavior of complex biological systems. This work furthers Levins' original theme that a theoretical perspective is by far the most practical means to approach biological complexity. While many research and management efforts have shown that 'everything is connected' and 'life is complex', these phrases are often provided as closing apologies for indeterminate results or unexpected outcomes. A qualitative analysis of the community matrix allows one to rigorously confront these difficulties and to proceed with, and celebrate, the notion that life is indeed interconnected and complex.

BIBLIOGRAPHY

Bender, E.A., T.J. Case, and M.E. Gilpin. 1984. Perturbation experiments in community ecology: theory and practice. Ecology **65**:1–13.

Bodini, A. 1998. Representing ecosystem structure through signed digraphs; Model reconstruction, qualitative predictions and management: the case of a freshwater ecosystem. Oikos **83**:93–106.

Bonan, G. B. and H.H. Shugart. 1989. Environmental factors and ecological processes in boreal forests. Annual Review of Ecology and Systematics **20**:1–28.

Castillo, G.C., H.W. Li, and P.A. Rossignol. 2000. Absence of overall feedback in a benthic estuarine community: a system potentially buffered from impacts of biological invasions. Estuaries **23**:275–291.

Cody, M.L. 1974. Competition and the Structure of Bird Communities. Princeton University Press, Princeton.

Dambacher, J.M., H.W. Li, J.O. Wolff, and P.A. Rossignol. 1999a. Parsimonious interpretation of the impact of vegetation, food, and predation on snowshoe hare. Oikos **84**:530–532.

Dambacher, J.M., H.W. Li, and P.A. Rossignol. 1999b. Historical reconstruction, through qualitative modeling, of the effects of exotic fish introductions in Tenmile Lakes Oregon. Pages 219–233. *In* Proceedings of the ODFW and NMFS Workshop. Management Implications of Co-occurring Native and Introduced Fishes, National Marine Fisheries Service, Portland.

DeAngelis, D.L. 1975. Stability and connectance in food web models. Ecology **56**:238–243.

de Ruiter, P.C., A.-M. Neutel, and J.C. Moore. 1995. Energetics, patterns of interaction strengths, and stability in real ecosystems. Science **269**:1257–1259.

Diamond, J. 1986. Overview: laboratory experiments, field experiments, and natural experiments. Pages 3–22. *In* J. Diamond and T.J. Case, *editors*. Community Ecology. Harper and Row, New York.

Eves, H. 1980. Elementary Matrix Theory. Dover Publications, Inc., New York.

Gantmacher, F.R. 1960. The Theory of Matrices, Volume 2. Chelsea Publishing Company, New York.

Goh, B.S. 1977. Global stability in many-species systems. American Naturalist **111**:135–143.

Hastings, A. 1995. What equilibrium behavior of Lotka–Volterra models does not tell us about food webs. Pages 211–217. *In* G.A. Polis and K.O. Winemiller, *editors*. Food Webs: Integration of Patterns and Process. Chapman and Hall, New York.

Hilborn, R. 1992. Current and future trends in fisheries stock assessment and management. South African Journal of Marine Science **12**:975–988.

Holling, C.S. 1992. Cross-scale morphology, geometry, and dynamics of ecosystems. Ecological Monographs **62**:447–502.

Hurwitz, A. 1895. On the conditions under which an equation has only roots with negative real parts. *Translated from the German by* H.G. Bergman. 1964. Pages 72–82. *In* R.E. Bellman and R. Kalaba, *editors*. Selected Papers on Mathematical Trends in Control Theory. Dover Publications, Inc., New York.

Jeppesen, E. 1998. The Ecology of Shallow Lakes – Trophic Interactions in the Pelagial. DSc. Dissertation; NERI Technical Report Number 247, National Environmental Research Institute, Silkeborg, Denmark.

Jeppesen, E., J.P. Jensen, M. Søndergaard, T. Lauridsen, P.H. Møller, and K. Sandby. 1998. Changes in nitrogen retention in shallow eutrophic lakes following a decline in density of cyprinids. Archiv für Hydrobiologie. **142**:129–152.

John, E. and R. Turkington. 1995. Herbaceous vegetation in the understory of the boreal forest: does nutrient supply or snowshoe hare herbivory regulate species composition and abundance? Journal of Ecology **83**: 581–590.

Jorgensen, J., A.M. Rossignol, C.J. Puccia, R. Levins, and P.A. Rossignol. 2000. On the variance of eigenvalues of the community matrix: derivation and appraisal. Ecology **81**:2928–2931.

Keith, L. B. 1963. Wildlife's Ten Year Cycle. University of Wisconsin Press, Madison.

Keith, L. B. 1990. Dynamics of snowshoe hare populations. Pages 119–195. *In* H.H. Genoways, *editor*. Current Mammalogy. Plenum Press, New York.

Keith, L.B., J.R. Carey, O.J. Rongstad, and M.C. Brittingham. 1984. Demography and ecology of a declining snowshoe hare population. Wildlife Monographs **90**:1–43.

Keith, L.B. and L.A. Windberg. 1978. A demographic analysis of the snowshoe hare cycle. Wildlife Monographs **58**:1–59.

Krebs, C. J., B.S. Gilbert, S. Boutin, A.R.E. Sinclair, and J.N.M. Smith. 1986. Population biology of snowshoe hares. I. Demography of food-supplemented populations in the southern Yukon, 1976–84. Journal of Animal Ecology **55**:963–982.

Krebs, C.J., S. Boutin, R. Boonstra, A.R.E. Sinclair, J.N.M. Smith, M.R.T. Dale, K. Martin, and R. Turkington. 1995. Impact of food and predation on the snowshoe hare cycle. Science **269**:1112–1115.

Lane, P. and R. Levins. 1977. The dynamics of aquatic systems. 2. The effects of nutrient enrichment on model plankton communities. Limnology and Oceanography **22**:454–471.

Laska, M.S. and J.T. Wootton. 1998. Theoretical concepts and empirical approaches to measuring interaction strength. Ecology **79**:461–476.

Lawlor, L.R. 1978. A comment on randomly constructed model ecosystems. American Naturalist **112**:445–447.

Levins, R. 1966. The strategy of model building in population biology. American Scientist **54**:421–431.

Levins, R. 1968. Evolution in Changing Environments: Some Theoretical Explorations. Princeton University Press, Princeton.

Levins, R. 1974. The qualitative analysis of partially specified systems. Annals of the New York Academy of Sciences **231**:123–138.

Levins, R. 1975. Evolution in communities near equilibrium. Pages 16–50. *In* M. Cody and J.M. Diamond, *editors*. Ecology and Evolution of Communities. Harvard University Press, Cambridge, UK.

Levins, R. 1979. Asymmetric competition among distant taxa. American Zoologist **19**:1097–1104.

Levins, R. and C.J. Puccia. 1988. The controlling factor in biological communities. Coenoses **3**:149–154.

Levitan, C. 1987. Formal stability analysis of a planktonic freshwater community. Pages 71–100. *In* W.C. Kerfoot and A. Sih, *editors*. Predation: Direct and Indirect Impacts on Aquatic Communities. University Press of New England, Hanover.

Lewontin, R.C. 1969. The meaning of stability. Brookhaven Symposia in Biology **22**:13–24.

Li, H.W. and P.B. Moyle. 1981. Ecological analysis of species introductions into aquatic systems. Transactions of the American Fisheries Society **110**:772–782.

Li, H.W., P.A. Rossignol, and G. Castillo. 1999. Risk analysis of species introductions: insights from qualitative modeling. Pages 431–447. *In* R. Claudi and J.H. Leach, *editors*. Nonindigenous Fresh Water Organisms: Vectors, Biology, and Impacts. Lewis Publishers, Boca.

Lyapunov, A.M. 1892. The General Problem of the Stability of Motion. *Translated from the Russian to the French by* Édouard Davaux *in 1893, and translated from the French to the English and edited by* A.T. Fuller. 1992. Taylor and Francis, London, UK.

Marcus, M. and H. Minc. 1964. A Survey of Matrix Theory and Matrix Inequalities. Dover Publications, New York.

May, R.M. 1973. Qualitative stability in model ecosystems. Ecology **54**:638–641.

May, R.M. 1974. Stability and Complexity in Model Ecosystems, 2nd edition. Princeton University Press, Princeton.

McQueen, D.J., J.R. Post, and E.L. Mills. 1986. Trophic relationships in freshwater pelagic ecosystems. Canadian Journal of Fisheries and Aquatic Sciences **43**:1571–1581.

McQueen, D.J., M.R.S. Johannes, J.R. Post, T.J. Stewart, and D.R.S. Lean. 1989. Bottom-up and top-down impacts on freshwater pelagic community structure. Ecological Monographs **59**:289–309.

Minc, H. 1978. Permanents. Encyclopedia of Mathematics and its Applications, Volume 6. Addison–Wesley Publishing Company, Reading, UK.

Nakajima, H. 1992. Sensitivity and stability of flow networks. Ecological Modeling **62**:123–133.

Nams, V.O., N.F.G. Folkard, and J.M.N. Smith. 1993. Effects of nitrogen fertilizer on several woody and nonwoody boreal forest species. Canadian Journal of Botany **71**:93–97.

Nellis, C.H., S.P. Wetmore, and L.B. Keith. 1972. Lynx-prey interactions in central Alberta. Journal of Wildlife Management **36**:320–329.

O'Donoghue, M., S. Boutin, C.J. Krebs, D.L. Murray, and E.J. Hofer. 1998. Behavioral responses of coyote and lynx to the snowshoe hare cycle. Oikos **82**:169–183.

O'Neil, P.V. 1995. Advanced Engineering Mathematics, 4th edition. Brooks/Cole Publishing Co., Pacific Grove.

O'Neill, R.V., D.L. DeAngelis, J.B. Waide, and T.F.H. Allen. 1986. A Hierarchical Concept of Ecosystems. Princeton University Press, Princeton.

Paine, R.T. 1992. Food-web analysis through field measurement of per capita interaction strength. Nature **355**:73–75.

Peters, R.H. 1991. A Critique for Ecology. Cambridge University Press, Cambridge, UK.

Pimm, S.L. and J.H. Lawton. 1977. Number of trophic levels in ecological communities. Nature **268**:329–331.

Pimm, S.L. and J.H. Lawton. 1978. On feeding on more than one trophic level. Nature **275**:542–544.

Power, M.E. 1992. Top-down and bottom-up forces in food webs: do plants have primacy? Ecology **73**:733–746.

Puccia, C.J. and J. Pederson. 1983. Models and field data of New England tide pools. Pages 709–718. *In* W.K. Lauenroth, G.V. Skogerboe, and M. Flug, *editors*. Analysis of Ecological Systems: State-of-the-Art in Ecological Modeling. Elsevier, New York.

Puccia, C.J. and R. Levins. 1985. Qualitative Modeling of Complex Systems: An Introduction to Loop Analysis and Time Averaging. Harvard University Press, Cambridge, UK.

Puccia, C.J. and R. Levins. 1991. Qualitative Modeling in Ecology: Loop Analysis, Signed Digraphs, and Time Averaging. Pages 119–143. *In* P.A. Fishwick and P. A. Luker, *editors*. Qualitative Simulation Modeling and Analysis, Springer–Verlag, New York.

Ranta, E., V. Kaitala, and P. Lundberg. 1997. The spatial dimension in population fluctuations. Science **278**:1621–1623.

Riebesell, J.F. 1974. Paradox of enrichment in competitive systems. Ecology **55**:183–187.

Roxburgh, S.H. and J.B. Wilson. 2000. Stability and coexistence in a lawn community: mathematical prediction of stability using a community matrix with parameters derived from competition experiments. Oikos **88**:395–408.

Rusch, D.H., E.C. Meslow, P.D. Doerr, and L.B. Keith. 1972. Response of great horned owl populations to changing prey densities. Journal of Wildlife Management **36**:282–296.

Schmitz, O.J. 1997. Press perturbations and the predictability of ecological interactions in a food web. Ecology **78**:55–69.

Searle, S.R. 1966. Matrix Algebra for the Biological Sciences: Including Applications in Statistics. John Wiley and Sons, Inc., New York.

Sinclair, A.R.E., C.J. Krebs, J.N.M. Smith, and S. Boutin. 1988. Population biology of snowshoe hares. III. Nutrition, plant secondary compounds and food limitation. Journal of Animal Ecology **57**:787–806.

Stone, L. 1990. Phytoplankton-bacteria-protozoa interactions: a qualitative model portraying indirect effects. Marine Ecology Progress Series **64**:137–145.

Tansky, M. 1978. Stability of multispecies predator-prey systems. Memoirs of the College of Science, Imperial University of Kyoto, Series B **7**:87–**94**.

Vandermeer, J.H. 1972. On the covariance of the community matrix. Ecology **53**:187–189.

Vandermeer, J. and P. Yodzis. 1999. Basin boundary collision as a model of discontinuous change in ecosystems. Ecology **80**:1817–1827.

Walters, C.J. and C.S. Holling. 1990. Large-scale management experiments and learning by doing. Ecology **71**:2060–2068.

Windberg, L.A. and L.B. Keith. 1976. Snowshoe hare population response to artificial high densities. Journal of Mammalogy **57**:523–553.

Yeaton, R.I. 1972. An Ecological Analysis of Chaparral and Pine Forest Bird Communities on Santa Cruz Island and Mainland California. DSc. Dissertation, University of California, Los Angeles.

Yodzis, P. 1978. Competition for Space and the Structure of Ecological Communities. Lecture Notes in Biomathematics, Volume 25. Springer–Verlag, New York.

Yodzis, P. 1981. The stability of real ecosystems. Nature **289**:674–676.

Yodzis, P. 1988. The indeterminacy of ecological interactions as perceived through perturbation experiments. Ecology **69**:508–515.

Yodzis, P. 1995. Food webs and perturbation experiments: theory and practice. Pages 192–200. *In* G.A. Polis and K.O. Winemiller, *editors*. Food Webs: Integration of Patterns and Process. Chapman and Hall, New York.

APPENDICES

Appendix 1. Matrix Algebra Methods

The determinant (*det*) of a 2nd 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 3rd order system, the $\mathbf{A}_{1,1}$ minor is formed by deletion of the first row and column, giving

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

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 3rd 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 $(-1^{n+1})\cdot det\ \mathbf{A}$, 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 Equation 3.8, 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 be 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 Equation 3.8). 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: $(+1)^{i+j}$. Thus the permanent of a 2nd order matrix becomes

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

and that of a 3rd order

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

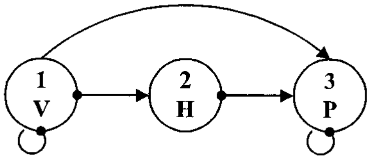
Cofactors of a matrix ($\mathbf{C}_{ij}$) are simply the determinants of each matrix minor, with the same $(-1)^{i+j}$ sign convention applied in the expansion, such that the matrix of all cofactors becomes

$$\begin{array}{lll}
\mathbf{C}_{1,1} = +\det\begin{bmatrix} a_{2,2} & a_{2,3} \\ a_{3,2} & a_{3,3} \end{bmatrix} & \mathbf{C}_{1,2} = -\det\begin{bmatrix} a_{2,1} & a_{2,3} \\ a_{3,1} & a_{3,3} \end{bmatrix} & \mathbf{C}_{1,3} = +\det\begin{bmatrix} a_{2,1} & a_{2,2} \\ a_{3,1} & a_{3,2} \end{bmatrix} \\
\mathbf{C}_{2,1} = -\det\begin{bmatrix} a_{1,2} & a_{1,3} \\ a_{3,2} & a_{3,3} \end{bmatrix} & \mathbf{C}_{2,2} = +\det\begin{bmatrix} a_{1,1} & a_{1,3} \\ a_{3,1} & a_{3,3} \end{bmatrix} & \mathbf{C}_{2,3} = -\det\begin{bmatrix} a_{1,1} & a_{1,2} \\ a_{3,1} & a_{3,2} \end{bmatrix} \\
\mathbf{C}_{3,1} = +\det\begin{bmatrix} a_{1,2} & a_{1,3} \\ a_{2,2} & a_{2,3} \end{bmatrix} & \mathbf{C}_{3,2} = -\det\begin{bmatrix} a_{1,1} & a_{1,3} \\ a_{2,1} & a_{2,3} \end{bmatrix} & \mathbf{C}_{3,3} = +\det\begin{bmatrix} a_{1,1} & a_{1,2} \\ a_{2,1} & a_{2,2} \end{bmatrix}
\end{array}$$

The *adjoint matrix* is simply a transposed matrix of cofactors, such that *adjoint* $\mathbf{A}_{ij} = \mathbf{C}_{ji}$. Calculation of the *absolute feedback matrix* (**T**) from Equation 3.9 is similar to the above cofactor calculations (transposed), but it uses the matrix permanent instead of the determinant, and all expansion terms are positive.

Appendix 2. Symbolic, Qualitative, and Quantitative Analyses of the Community Matrix

Example calculations of system response and stability for a 3-variable community matrix model using symbolic, qualitative, and quantitative analysis techniques. The signed digraph below describes possible interactions between boreal forest vegetation V, snowshoe hare H, and predator guild P, from model B (Figure 2.1). A positive effect from vegetation to predators is interpreted as a benefit of cover to predators, such as lynx (*Lynx canadensis*), which ambush their prey from hunting beds.



SYMBOLIC ANALYSIS

Community Matrix:

$$\mathbf{A}$$

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

Response Predictions:

adjoint –**A**

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

The symbolic adjoint details complementary feedback to each i^{th} variable in the system resulting from positive input to j^{th} variable. Complementary feedback is the product of conjunct and disjunct paths, which define the subsystem of all elements that are not directly in line with linkages connecting variables j to i. Two response predictions, *adjoint* –$\mathbf{A}_{1,2}$ and *adjoint* –$\mathbf{A}_{3,2}$, are conditional, and therefore ambiguous without knowledge of the relative strengths of interactions in the community matrix. Both of these responses have in common the $a_{3,1}$ linkage, and so depend on the relative strength of the vegetation–predator interaction.

Stability Analysis: System feedback (F_n) for each n^{th} level in the system is derived from the a_n coefficients of the characteristic polynomial (*determinant* $(\mathbf{A}-\lambda\mathbf{I}) = 0$):

$$\begin{array}{lcr}
F_3\text{:} & -a_{1,1}\,a_{2,3}\,a_{3,2} - a_{2,1}\,a_{1,2}\,a_{3,3} + a_{3,1}\,a_{1,2}\,a_{2,3} & = a_3 \\
F_2\text{:} & -a_{2,3}\,a_{3,2} - a_{1,1}\,a_{3,3} - a_{2,1}\,a_{1,2} & = a_2 \\
F_1\text{:} & -a_{3,3} - a_{1,1} & = a_1 \\
F_0\text{:} & -1 & = a_0
\end{array}$$

where **I** is the identity matrix. System stability depends on the criteria that 1) all $F_n < 0$ (given convention of $F_0 = -1$), and 2) all positive Hurwitz determinants. In this system, the first stability criterion is met only when the one positive feedback cycle in F_3 is relatively small; that is to say, the positive effect of vegetation on predators ($a_{3,1}$) must be weak compared to self-regulation and predator-prey (including vegetation-herbivore) interactions in the system. The first Hurwitz determinant ($H_1 = -F_1$), here is always positive, the second ($H_2 = F_1F_2+F_3$) is negative when feedback at the highest level (F_3) is weaker than the product of lower levels (remembering that F_n terms are, by convention here, negative), a condition that again depends on the relative weakness of the vegetation–predator ($a_{3,1}$) linkage (see Appendix 3 on Hurwitz determinants).

QUALITATIVE ANALYSIS

Qualitatively Specified Community Matrix: $\mathring{\mathbf{A}}$

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

Response Predictions: Based on number of complementary feedback cycles for a given response. For example, at $a_{2,1}$ (circled below) there is a net response of zero complementary feedback cycles (*adjoint* $-\mathring{\mathbf{A}}_{2,1}$), formed by the cancellation of a total of two cycles (absolute feedback $\mathbf{T}_{2,1}$), giving a weighted prediction ($\mathbf{W}_{2,1}$) of 0.

$$\begin{array}{ccc} \textit{adjoint}\ -\mathring{\mathbf{A}} & \text{absolute feedback } \mathbf{T} & \text{weighted predictions } \mathbf{W} \\ \begin{bmatrix} 1 & -1 & 1 \\ \textcircled{0} & 1 & -1 \\ 1 & 0 & 1 \end{bmatrix} & \begin{bmatrix} 1 & 1 & 1 \\ \textcircled{2} & 1 & 1 \\ 1 & 2 & 1 \end{bmatrix} & \begin{bmatrix} 1 & 1 & 1 \\ \textcircled{0} & 1 & 1 \\ 1 & 0 & 1 \end{bmatrix} \end{array}$$

We obtain the total number of complementary feedback cycles in a response, both positive and negative in value, by $\mathbf{T}_{ij} =$ *permanent (minor* ${}^{\bullet}\mathbf{A}_{ij}$*)* ^{transpose}, where ${}^{\bullet}\mathbf{A}$ denotes the community matrix specified by only 0's or 1's (i.e. absolute values of $\mathring{\mathbf{A}}$). The permanent of a matrix is computed in a similar way as a matrix determinant, but with no subtraction in computation of matrix minors, and no alternating signs during column and row expansion (Appendix 1; Marcus and Minc 1964, Minc 1978, Eves 1980). Dividing the absolute value of each element of the *adjoint* $-\mathring{\mathbf{A}}_{ij}$ by each $\mathbf{T}_{ij}$ element yields the weighted predictions matrix $\mathbf{W}$; when $\mathbf{T}_{ij} = 0$, $\mathbf{W}_{ij}$ is taken to equal 1.0. The adjoint is calculated with the negative of the community matrix, which maintains the correct sign convention in even and odd numbered systems.

Stability Analysis: System feedback (F_n) for each n^{th} level in the system derived from coefficients of the characteristic polynomial (*determinant* $(\mathring{\mathbf{A}}-\lambda\mathbf{I}) = 0$): $F_0 = -1$, $F_1 = -2$, $F_2 = -3$, $F_3 = -1$. In qualitative terms, all polynomial coefficients of the system are of the same sign, and both Hurwitz determinants are positive, i.e. $H_1 = -F_1 = 2$, and $H_2 = F_1F_2+F_3 = (-2)(-3)+(-1) = 5$ (see also Appendix 3 on Hurwitz determinants). The absolute feedback (*absolute* F_n) at each n^{th} level in the system, is derived from the coefficients of what we term the 'absolute polynomial', computed as *permanent* $({}^{\bullet}\mathbf{A}+\lambda\mathbf{I}) = 0$, where ${}^{\bullet}\mathbf{A}$ denotes a community matrix specified by only 0's or 1's (i.e. absolute values of $\mathring{\mathbf{A}}$). Dividing the net feedback by the absolute feedback, gives the weighted feedback (wF_n) for each n^{th} level of feedback in the system (i.e. $wF_n = |F_n|/$*absolute* F_n). Note that wF_n is without sign, we therefore use the 'absolute value' (| |) of the net feedback in the numerator, which is different in value from the 'absolute number' of feedback cycles in the denominator. At the highest level of feedback (F_3), there is a net number of one negative cycle, and an absolute number of three feedback cycles (two negative and one positive), giving a $wF_n = |-1|/3 = 0.33$. Since there is no countervailing feedback in lower levels in the system, this value is also the *minimum* wF_n, or weighted stability of the system.

QUANTITATIVE ANALYSIS

We present here a community matrix that is quantitatively specified with a single set of plausible interaction terms.

Community Matrix:

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

$$\begin{bmatrix} -1 & -.5 & 0 \\ .5 & 0 & -.5 \\ .2 & .1 & -.2 \end{bmatrix}$$

Response Predictions: The numerical response of all populations in a community is detailed by the inverse of negative of the community matrix.

Inverse Matrix:

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

$$\begin{bmatrix} 1.0 & -2.0 & 5.0 \\ 0 & 4.0 & -10 \\ 1.0 & 0 & 5.0 \end{bmatrix}$$

Stability Analysis: System feedback (F_n) for each n^{th} level in the system derived from coefficients of the characteristic polynomial (*determinant* ($^{\#}\mathbf{A} - \lambda\mathbf{I}) = 0$): $F_0 = -1$, $F_1 = -1.2$, $F_2 = -0.5$, $F_3 = -0.5$. In quantitative terms, the system meets both Routh–Hurwitz criteria: 1) all polynomial coefficients are of the same sign, and 2) both Hurwitz determinants (Appendix 3) are positive, i.e. $H_1 = -F_1 = 0.5$, and $H_2 = F_1F_2 + F_3 = (-1.2)(-0.5) + (-0.5) = 0.1$. This particular specification of the model thus achieves Lyapunov (neighborhood) stability.

Appendix 3. Hurwitz Determinants

The characteristic equation for any homogenous set of equations is derived from $|\mathbf{A}-\lambda\mathbf{I}| = 0$, where here and below, '| |' denotes the determinant (elsewhere it is taken to mean absolute value). The resulting polynomial is of the form $a_0\lambda^n + a_1\lambda^{n-1} + a_2\lambda^{n-2} + . . . + a_n = 0$. Here a_0 is taken as negative; if not, we multiply the polynomial by –1. This maintains a sign convention, whereby each polynomial coefficient is interpreted as the strength of feedback (F_n) at each n^{th} level of the system, and negative feedback is understood to be stabilizing to the system (Puccia and Levins 1985). Interpretation of actual characteristic polynomials requires deciphering, without the aid of subscript notation, which F_n corresponds to which a_n coefficient. This is done thru the power of the λ terms. The highest level of feedback to the system, F_n, corresponds to the a_n coefficient that lacks a companion λ term (i.e. it has a λ to the power of zero: λ^{n-n}). The lowest level of feedback in the system is with the term with the highest power (i.e. λ^{n-0}). We thus have the correspondence of F_0 with λ^{n-0}, F_1 with λ^{n-1}, F_2 with λ^{n-2}, . . . and F_n with λ^{n-n}.

In 1893 Adolf Hurwitz was presented with the problem of how to determine the conditions under which the characteristic equation has only roots (eigenvalues) with negative real parts, without knowing the complete solution to the differential equations involved. A system with all negative real roots meets the necessary and sufficient conditions for local neighborhood stability that had been recently proved by Alexander Lyapunov in 1892. The problem was given to Hurwitz by Aurel Stodola, who was interested in the stability of a 7th order regulatory system for a high-pressure water turbine at a spa in Davos, Switzerland. At that time, before the advent of computers and efficient algorithms, it was very difficult to even approximate solutions for characteristic equations above degree 5. Hurwitz's (1895) solution to the problem involves a sequence of determinants constructed from the polynomial coefficients of characteristic equations of a system of any order. An equivalent solution was discovered independently by Edward Routh; consequently we have the so-called 'Routh–Hurwitz' criteria for stability.

Calculation of the Hurwitz determinants is here adapted from Hurwitz (1895), but with the notational difference of F_n for the a_n polynomial coefficients, and the sign convention of $F_0 = -1$. In practical terms we are given two criteria. If 1) all F_n are the same sign (here negative), and none are zero, then the below conditions of 2) all positive Hurwitz determinants (H_n), ensure that all roots of the characteristic polynomial have negative real parts.

$$H_1 = -F_1 > 0,\ H_2 = \begin{vmatrix} -F_1 & -F_3 \\ -F_0 & -F_2 \end{vmatrix} > 0,\ H_3 = \begin{vmatrix} -F_1 & -F_3 & -F_5 \\ -F_0 & -F_2 & -F_4 \\ 0 & -F_1 & -F_3 \end{vmatrix} > 0, \ldots,$$

$$H_n = \begin{vmatrix} -F_1 & -F_3 & -F_5 & \cdots & -F_{2n-1} \\ -F_0 & -F_2 & -F_4 & \cdots & -F_{2n-2} \\ 0 & -F_1 & -F_3 & \cdots & -F_{2n-3} \\ 0 & -F_0 & -F_2 & \cdots & -F_{2n-4} \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & -F_n \end{vmatrix} > 0$$

Together, these two criteria guarantee the existence of a neighborhood of local stability to which a system will return after being disturbed (Lyapunov 1892). In terms of system feedback, positive Hurwitz determinants, and therefore system stability, generally depend on lower levels of feedback being stronger than higher levels. For instance, a positive H_2 requires that $F_1F_2 > -F_3$, a positive H_3 requires that $F_1[F_1F_4+F_5] > F_3[F_1F_2+F_3]$, remembering that F_n terms, by convention herein, are negative. Interpretation of inequalities from higher order Hurwitz determinants, however, are less straightforward. See also Gantmacher (1960, page 195), and Puccia and Levins (1985, page 167) for additional discussions of the Hurwitz determinants.

Appendix 4. Maple® V Program Commands for Qualitative and Symbolic Analysis of the Community Matrix

Commands are for Maple® V Release 5. Matrix input below includes example input for model **a** (Figure 4.1). Input n:=***x***, at second command line, for ***x*** number of species or system variables, and input $\mathbf{\mathring{A}}_{ij}$ community matrix elements as **0**, **1**, or **–1**.

Matrix Input

```
[>with(linalg):with(share):with(Hurwitz):
[>n:=5:A:=array(1..n,1..n,[[-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]]);
```

Qualitative Analysis

```
[>p:=charpoly(A,l):P:=permanent(abs(A)+band([1],n)):Pc:=[seq(-1*coeff
  (p,l,degree(p)-i),i=0..degree(p))]:polynomial_coefficients:=Pc;
  Hurwitz _criterion=Hurwitz(p,l);aPc:=[seq(coeff(P,l,degree(P)-i),
  i=0..degree (P))]:z:=proc(x,y)if y=0then 1; else x/y;fi;end:evalf
  (wFn=matrix(1, degree(p)+1,(i,j)->abs (z(Pc[j],aPc[j]))),2);
[>adjoint_A=adj(-A);T:=matrix(n,n,(i,j)->permanent(minor(abs(A),j,i)));
  evalf(weighted_predictions_W=matrix(n,n,(i,j)->abs(z(adjoint(A)[i,j],
  T[i,j]))),2);
```

Symbolic Analysis: input [***n***] in 2nd-to-last command line below to detail symbolic conditions of *n*th level of system feedback; input [***i,j***] in last command line to detail *ij*th adjoint element, use ‘`evalm(symbolic_adjoint);`’ to show entire matrix.

```
[>t:=proc(x,y)x*y:end:a=array(1..n,1..n):Symbolic_A:=matrix(n,n,(i,j)-
  >t((A)[i,j], (a)[i,j]));symbolic_feedback:=[seq(-1*coeff(charpoly
  (Symbolic_A,l),l,degree(p)-i-1),i=0..degree(p)-1)]:symbolic_adjoint:=
  adj(-Symbolic_A):
[>symbolic_feedback[n];
[>symbolic_adjoint[i,j];
```