



UNDERSTANDING AND PREDICTING EFFECTS OF MODIFIED INTERACTIONS THROUGH A QUALITATIVE ANALYSIS OF COMMUNITY STRUCTURE

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ABSTRACT

Models of ecological communities are traditionally based on relationships between pairs of species, where the strengths of per capita interactions are fixed and independent of population abundance. A growing body of literature, however, describes interactions whose strength is modified by the density of either a third species or by one of the species involved in a pairwise interaction. These modified interactions have been treated as indirect effects, and the terminology addressing them is diverse and overlapping. In this paper, we develop a general analytical framework based on a qualitative analysis of community structure to account for the consequence of modified interactions in complex ecological communities. Modified interactions are found to create both direct and indirect effects between species. The sign of a direct effect can change in some instances depending on the magnitude of a key variable or parameter, which leads to a threshold change in system structure and dynamics. By considering alternative structures of a community, we extend our ability to model perturbations that move the system far from a previous equilibrium. Using specific examples, we reinterpret existing results, develop hypotheses to guide experiments or management interventions, and explore the role of modified interactions and positive feedback in creating and maintaining alternative stable states. Through a qualitative analysis of community structure, system feedback is demonstrated as being key in understanding and predicting the dynamics of complex ecological communities.

INTRODUCTION

UNDERSTANDING the dynamics of an ecological community depends on a basic knowledge of the relationships of its member species. Collectively, these interactions define community structure and determine how effects are transmitted from one species to another. In complex systems, effects can propagate along direct and indirect paths, and it is not uncommon for indirect effects to oppose direct effects, causing, for instance, a population to increase despite a change in circumstance that favors its enemy or diminishes its food (Sih et al. 1985). Understanding how effects propagate through a system, therefore, requires an accounting of all ecological relationships in the community. Within a generalized Lotka–Volterra framework, this calls for determination of the α_{ij} interaction coefficients, and the product $\alpha_{ij}N_j$ determines the direct effect of species N_j on the per capita rate of growth of N_i . Here, N is the population density or biomass of a species, and interactions are defined on a pairwise basis, with the magnitude of the coefficients considered as fixed and independent of population density. In such systems, effects can propagate as a sequence of interactions (as in Figure 1a, where species 3 affects species 2, which then affects species 1). There is a growing body of ecological literature (Wootton 1994, 2002; Werner and Pecor 2003), however, which demonstrates that per capita effects shared between two species are not always fixed, but rather can vary as a function of a third species (as in Figure 1b, where species 3 modifies the intensity of 1 and 2's interaction). This literature has treated modified interactions as an indirect effect, which results from species 3 influencing a phenotypically plastic trait of species 1 or 2, or by species 3 invoking change in some factor, environmental agent, or context involved in the interaction.

The increase of documented examples of various modes of interaction has been matched by a profusion of terminology, and it is possible to find a variety of terms related to these concepts in the ecological literature. Synonyms for Figure 1a include trophic linkage indirect effect (Miller and Kerfoot 1987), interaction chain (Wootton 1993), numerical indirect interaction (Janssen et al. 1998), and

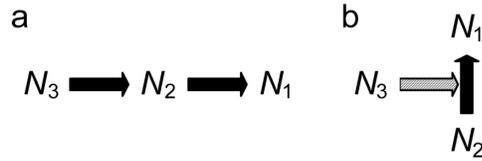


FIGURE 1. TWO MECHANISMS BY WHICH N_3 AFFECTS N_1

Species 3 affects species 1 by (a) affecting species 2, or (b) modifying the intensity of the interaction between species 1 and 2. Adapted from Figure 1 of Wootton (1993).

density-mediated indirect interaction (Werner and Pecor 2003). Synonyms for Figure 1b include higher-order interaction (Vandermeer 1969; Billick and Case 1994), interaction modification (Wootton 1993), functional indirect interaction (Janssen et al. 1998), trait-mediated indirect interaction (Werner and Pecor 2003), trait-initiated indirect effect (Abrams 2004), and a rheagogy (Arditi et al. 2005). Additionally, for Figure 1b, Miller and Kerfoot (1987) distinguish between behavioral indirect effect and chemical response indirect effect, and Wootton (2002) recognizes an environment-mediated interaction modification as being distinct from a trait-mediated indirect interaction. Miller and Kerfoot (1987) define species 1 in Figure 1 as the species of interest (calling it focal) and species 2 its associate. Conversely, Damiani (2005) refers to species 3 as the associate and species 2 as intermediate. Abrams (1996) defines species 1, 2, and 3 as receiver, transmitter, and initiator, respectively. These definitions, in a sense, are taken from the observer's point of view and applied within the context of a single species of interest or sequence of interactions. But even in relatively simple systems, multiple sequences of interaction can be operating simultaneously, blurring cause and consequence, and where more than one species is of interest, the meanings of focal, associate, and initiator become confused. Such complexity and shifting points of view can easily outstrip the capacity of terminology alone to advance our understanding or to predict the consequences of indirect effects (Wootton 2002). And like Allee et al. (1949), "[w]e have wished to avoid further implementation of the facetious definition of ecology as being that phase of biology primarily aban-

done to terminology” (p 9); instead, we seek to develop an analytical framework based on the structure of the whole system.

In this work, we develop the means to formally account for the effects of modified interactions in complex ecological communities. We begin with the basic definition of the community matrix and its derivation from a system’s growth equations. Typically, however, the exact form of an equation is unknown, and rarer are measurements of interaction strength, even for simple pairwise relationships. But by adopting an analytical framework that is qualitative, description of the essential relationships in a system is permitted, and we are freed of the need to define the exact form of a function or the precise measurement of its parameters. Trading off the benefits of precision for a general understanding of the dynamics of the whole system (Levins 1966) opens two avenues of approach. One is to work from natural history observation, and by first principles posit relationships that lead to equations and models of a general form. The other is to work backward from observations or experimental results and ask what model structure is consistent with these findings. It will be instructive to work from an array of alternative models and seek relevant differences in qualitative results, thereby developing hypotheses that guide experiments and management interventions and, within the context of the problems or questions involved, focus measurement effort on the critical interactions and parameters of the system.

DEFINING DIRECT EFFECTS FROM THE COMMUNITY MATRIX

Elements of the community matrix **A** (Levins 1968) define the direct effect of one species on another, and are derived from the first partials of a system’s per capita growth equations taken at equilibrium (Laska and Wootton 1998)

$$a_{ij} = \left. \frac{\partial \left(\frac{dN_i}{N_i dt} \right)}{\partial N_j} \right|_* \tag{1}$$

where the condition of equilibrium is denoted by an asterisk. An essential feature of Equation 1 is that it represents a linearized formulation of how species N_j affects the per capita growth rate of species N_i at or near equilibrium. For systems whose interactions are fixed and independent of population size (i.e., the per capita growth rate of N_i is a linear function of N_j), community matrix elements will simply equal the α_{ij} interaction coefficients of a generalized Lotka–Volterra system. But where one or more interactions are instead modified by a function f_{ij} of one or more populations or system variables, the growth equations will be nonlinear and of the general form

$$\frac{dN_i}{N_i dt} = \sum_j \alpha_{ij} N_j f_{ij}(N_1, N_2, \dots, N_n) + r_i \tag{2}$$

$(i = 1, \dots, n),$

where r_i is an intrinsic rate of growth describing density independent rates of birth, death, and migration, and n is the number of populations or variables in the system. The function f_{ij} is dimensionless and alters the strength, and possibly even the sign, of the interaction between species i and j according to the magnitude of a system variable. In this kind of system, elements of the community matrix will be defined as

$$a_{ij} = \alpha_{ij} f_{ij} + \sum_k \alpha_{ik} N_k \left. \frac{\partial f_{ik}}{\partial N_j} \right|_* \tag{3}$$

$(i = 1, \dots, n; j = 1, \dots, n).$

By this formulation, the community matrix incorporates the influence of one or more species on a pairwise interaction by generating terms that either modify the intensity of the pairwise interaction, via $\alpha_{ij} f_{ij}$, or establish what can be formally considered as direct effects emanating from N_j to species N_i and N_k involved in the pairwise interaction, via $\alpha_{ik} N_k (\partial f_{ik} / \partial N_j)$. As a first example, consider Figure 1b with species 1 as a consumer of species 2 and its rate of consumption a function of species 3, giving growth equations

$$\begin{aligned} \frac{dN_1}{N_1 dt} &= \alpha_{1,2} N_2 f_{1,2}(N_3) - r_1, \\ \frac{dN_2}{N_2 dt} &= -\alpha_{2,1} N_1 f_{2,1}(N_3) + r_2, \end{aligned} \tag{4}$$

and community matrix

$$\mathbf{A} = \begin{bmatrix} 0 & \alpha_{1,2} f_{1,2} & \alpha_{1,2} N_2^* \frac{\partial f_{1,2}}{\partial N_3} \\ \alpha_{2,1} f_{2,1} & 0 & -\alpha_{2,1} N_1^* \frac{\partial f_{2,1}}{\partial N_3} \\ 0 & 0 & 0 \end{bmatrix}. \tag{5}$$

In this system, species 3 has a direct effect on the other species, via interaction terms $a_{1,3}$ and $a_{2,3}$, which both are the product of $\alpha_{ik} N_k^*$ and $\partial f_{ik} / \partial N_3$. If species 3 suppresses the interaction of species 1 and 2, then $f_{1,2}$ and $f_{2,1}$ will both be decreasing functions of the abundance of species 3, and thus $\partial f_{ik} / \partial N_3$ will be negative. This gives a community matrix with a sign (sgn) structure of

$$\text{sgn } \mathbf{A} = \begin{bmatrix} 0 & + & - \\ - & 0 & + \\ 0 & 0 & 0 \end{bmatrix}. \tag{6}$$

The consequence of a modified interaction to system structure can also be considered and understood through the use of sign directed graphs, or signed digraphs, which are an equivalent representation of the sign structure of the community matrix (Levins 1975; Puccia and Levins 1985). A variable (node) receiving a positive direct effect from another variable will receive a link (arc) ending in an arrow. A link that ends in a filled circle denotes a negative direct effect, while a link connecting a variable to itself denotes a self-effect. Negative self-effects denote self-regulation in a variable and contribute to system stability, while positive self-effects denote variables with a self-enhancing growth function and contribute to system instability. In this paper, we portray direct effects between variables with solid-line links and the modifying influence of a variable on a pairwise interaction (i.e., $\partial f_{ik} / \partial N_j$) as a dashed-line link.

Figure 2 shows effects generated by a third species that modifies the interaction of two others, and it can be seen that the direct effect of species 3 on either species 1 or species 2 is merely a product of the sign of the dashed-line link and of the pairwise solid-line link that leads to the other species. Alternately, the sign of an indirect effect is the product of all links along a path greater than length one leading from one variable to another (e.g., for case of enhanced predator-prey interaction, $\text{sgn } N_3 \rightarrow N_2 \rightarrow N_1 < 0$) and, in some instances, it can oppose the sign of a direct effect (e.g., $\text{sgn } N_3 \rightarrow N_1 > 0$). Figure 2 illustrates that a species can have both a direct and indirect effect on another species as a consequence of it influencing a pairwise interaction in which the other species is involved.

For simplicity, we have treated the modifying functions in Figure 2 as being symmetrical with respect to the species pair involved, such that $\text{sgn } f_{ij} = \text{sgn } f_{ji}$. This is not a necessity, however, and the technique can easily be extended to address functions that are asymmetrical in the sign of their effect. To account for such functions, one merely has to draw each α_{ij} solid-line link and each $\partial f_{ik} / \partial N_j$ dashed-line link separately; the additional direct effects are then calculated from their sign products as before.

The preceding examples have addressed the consequences of one species modifying the interaction of two others, although the principles involved can be extended to situations involving a lesser or greater number of species, or where multiple interactions are involved. For a two species predator-prey system, we consider the case where prey respond, almost instantaneously, to a perceived increase in predator numbers by altering their behavior, say through hiding, so as to decrease their vulnerability to predation. The rate of prey consumption in this system is a decreasing function of the predator's density. Adapting Equation 4 to this example (by replacing N_3 with N_1), the corresponding community matrix would be

$$\mathbf{A} = \begin{bmatrix} \alpha_{1,2} N_2^* \frac{\partial f_{1,2}}{\partial N_1} & \alpha_{1,2} f_{1,2} \\ -\alpha_{2,1} f_{2,1} - \alpha_{2,1} N_1^* \frac{\partial f_{2,1}}{\partial N_1} & 0 \end{bmatrix}. \tag{7}$$

| Pairwise interaction of N_1 and N_2 : $\text{sgn}(a_{1,2}, a_{2,1})$ | Suppressed interaction of N_1 and N_2 | | Enhanced interaction of N_1 and N_2 | |
|--|---|----------------|---|----------------|
| | Modified interaction | Direct effects | Modified interaction | Direct effects |
| Predator-prey or parasitic: (+, -) | | | | |
| Competitive: (-, -) | | | | |
| Mutualistic: (+, +) | | | | |
| Commensal: (+, 0) | | | | |
| Amensal: (0, -) | | | | |

FIGURE 2. PAIRWISE INTERACTIONS MODIFIED BY ABUNDANCE OF THIRD SPECIES

Signed digraphs show the effects of population variables (open circles), with solid-line links denoting direct effects between species, and dashed-line links denoting the effect of species 3 on the interaction between species 1 and 2. Solid- (or dashed-) line links ending in a filled circle denote a negative effect (or suppressed interaction), and those ending in an arrow denote a positive effect (or enhanced interaction).

Since $\partial f_{ij} / \partial N_1$ is negative, so is $a_{1,1}$ always. The sign of $a_{2,1}$ is ambiguous, however, and the net effect of the predator on the prey population can be positive when predator numbers are relatively high and the diminishing effect of prey behavior on consumption is dramatic, such that $N_1^* > f_{2,1} |\partial f_{2,1} / \partial N_1|^{-1}$, where “ $||$ ” is an absolute value. This then leads to two al-

ternative model structures in Figure 3. Self-regulation in the predator emerges as a consequence of its effect on prey behavior. The strength of this self-regulation is proportional to the abundance of the prey N_2 , which gives a most simple example of a prey refugia—albeit behaviorally induced—and its potentially stabilizing effect on a predator-prey system.

Figure 3 illustrates the general case that where a species modifies its pairwise interaction with another species, it can gain a self-effect and impart ambiguity to the sign of its effect on the other species. Analysis of the specific conditions underlying this ambiguity reveals key variables and parameters that define system thresholds and alternative model structures. Representing a single ecological system through alternative qualitative models essentially creates separate approximations of how the system behaves when near a given equilibrium. By virtue of their structure, alternative models can display distinctively different dynamics, which can be analyzed qualitatively.

The effect of one species on another's behavior may not always be instantaneous. For example, in aquatic ecosystems where vision is limited for many organisms, natural enemies are commonly perceived through non-lethal cues that provide information about the risk of predation or competition (Ruther et al. 2002; Lass and Spaak 2003). These cues are often in the form of a chemical compound that, when sensed by another species, can induce a phenotypic change that is in direct proportion to the compound's concentration. Since these compounds can accumulate in the environment and are prone to breakdown or bacterial decomposition (Tollrian and Dodson 1999), they can act as a true state variable and increase the system's dimension. In Figure 4, the predator N_1 produces a chemical cue represented by the state variable N_3 , which suppresses predation of N_2 . Compared to the system in Figure 3, N_1 does not gain self-regulation due to the suppressed interaction, rather it is regulated through its interaction with N_3 . Moreover, the sign of $a_{2,1}$ is no longer ambiguous. But the ambiguity has been transferred to the larger system, and the sign of the path in Figure 4b from N_1 to N_3 to N_2 opposes that of the direct path from N_1 to N_2 . Modified interactions of this kind are increasingly being identified in all major taxa (Tollrian and Harvell 1999).

In Figure 5, we extend the example of Figure 3 to consider that prey avoiding predators can also suffer from a diminished capacity to consume their own resource. The consumption of basal resource N_3 by N_2 is a decreasing

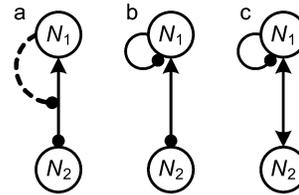


FIGURE 3. PREDATION RATE SUPPRESSED BY ABUNDANCE OF PREDATOR

Signed digraphs of a system where (a) the abundance of predator N_1 has a suppressing effect on its consumption of N_2 , which results in a community matrix (Equation 7) with ambiguity in the sign of $a_{2,1}$. This ambiguity leads to two alternative model structures when predator numbers and their effect on the rate of prey consumption are (b) relatively low and (c) relatively high.

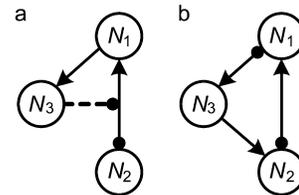


FIGURE 4. PREDATION RATE SUPPRESSED BY CHEMICAL CUE

Signed digraphs of a system where (a) production of a chemical cue N_3 by predator N_1 suppresses the predator's consumption of N_2 . In (b), this suppressed interaction results in N_3 directly affecting the predator N_1 and the prey N_2 .

function of N_1 , from which N_3 receives a direct positive effect from the top predator. As in Figure 3, N_1 gains self-regulation from suppressing its consumption of N_2 , and the sign of $a_{2,1}$ is ambiguous, leading to two alternative model structures in Figure 5. But now $a_{2,1}$ is more likely to be negative as a result of an additional term derived from the suppressed consumption of N_3 , thus $a_{2,1}$ is negative when

$$\alpha_{2,1}f_{2,1} + \alpha_{2,3}N_3^* \left| \frac{\partial f_{2,3}}{\partial N_1} \right| > \alpha_{2,1}N_1^* \left| \frac{\partial f_{2,1}}{\partial N_1} \right|. \quad (8)$$

While symbolic arguments such as Equation 8 may at times be difficult to interpret, a general assessment of alternative structures can easily be gained by inspection of a system's signed digraph. In Figure 5a, there are three ways in which N_1 directly influences

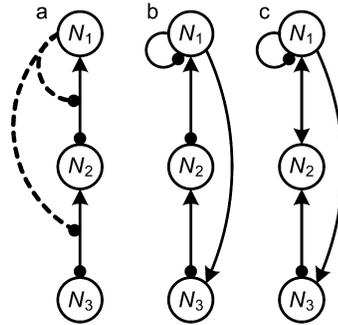


FIGURE 5. CONSUMPTION RATES SUPPRESSED ACROSS TWO TROPHIC LEVELS

Signed digraphs of a system where (a) the abundance of predator N_1 has a suppressing effect on its consumption of N_2 , as well as on N_2 's consumption of N_3 , which results in ambiguity in the sign of $a_{2,1}$ (Equation 8). This ambiguity leads to two alternative model structures when the number of top predators and their effect on the rate of consumption of N_2 is (b) relatively low and (c) relatively high.

N_2 . One is by the solid-line link with a negatively signed effect. The other two ways involve negatively signed dashed-line links joined with solid-line links. The sign products of their union form two additional effects that are opposite in sign, which imparts ambiguity to the sign of the net direct effect of N_1 on N_2 , and leads to the two alternative model structures in Figure 5. This accounting emphasizes that the net direct effect of one species on another can be complex and constituted by both pairwise and modified interactions.

The preceding examples are based only on general statements about species interactions where the form of f_{ij} in Equation 2 was not specified. However, different functional forms can lead to a variety of community dynamics and, to a large extent, these differences can be interpreted and understood on the basis of system structure. Besides behavioral or morphological changes driven by exposure to natural enemies, another mechanism by which interactions are modified is through change in resource density. Holling (1959, 1961) defines four types of responses that describe how a predator's rate of consumption can change with prey abundance (Figure 6a). Each response is a function of

prey density, the per capita rate at which prey are attacked (simply the standard interaction coefficient for predation mortality), and the handling time required to subdue, consume, and digest each unit of prey. The product of the latter two parameters defines h , which has dimension of mass^{-1} , and is essentially the proportion of time required to capture and consume a single unit of prey in relation to the total time available. The inverse of h , then, defines the prey density at which a predator becomes saturated, and in Figure 6a, it provides a relative scale by which the various functional responses can be interpreted.

From the form of the functional response curves in Figure 6a, thresholds in prey abundance are identified that correspond to shifts in system structure and dynamics. Of interest here is the sign (positive, negative, zero) of the slope of the predator's per capita rate ($\alpha_{2,1}f_{2,1}$) and standard rate of consumption ($\alpha_{2,1}N_2f_{2,1}$), as this determines the sign of the prey's self-effect and the effect of the prey on the predator. Specifically, the slope of the standard rate of consumption in Figure 6a determines the sign of the direct effect of prey on their predators in Figure 6b. The sign of the slope of per capita consumption rate corresponds with $\text{sgn } \partial f_{2,1} / \partial N_2$, the effect of prey density on the consumption rate of the predator. If negative, this rate is suppressed, and the prey gain a positive self-effect; if positive, then the self-effect is negative. There are nine conceivable combinations of model structure, five of which are realized through the Holling equations (see Appendix A for a more detailed treatment of these equations).

The ecological literature contains a large number of equations for functional responses that address specific biological and mathematical assumptions (e.g., Gutierrez 1996; Getz 1999; Jeschke et al. 2002; Ramos-Jiliberto 2005), and a predator could exhibit different functional responses for different prey. Nevertheless, this approach illustrates how the general shape of a function can be used to infer system structure. On the other hand, for practical purposes, it would be meaningless to distinguish between specific types of functional responses if the predator is effectively saturated, as in the asymptotic regions of the Type II and III curves (Figure 6a), in which

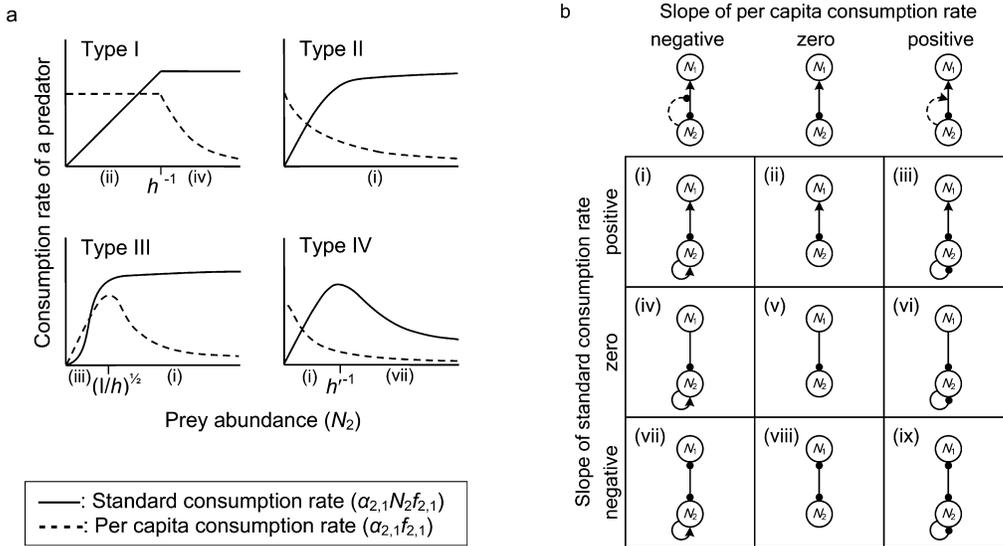


FIGURE 6. MODEL STRUCTURES WHERE PREDATION RATE IS MODIFIED BY ABUNDANCE OF PREY
 (a) Holling's (1959, 1961) Type I-IV functional responses that describe the ability of an individual predator (N_1) to consume prey (N_2) as a function of the prey's abundance. System thresholds h^{-1} , $(I/h)^{1/2}$ (where I is a mass constant here set equal to one), and h^{-1} correspond to sign changes in the slope of the functional response curves. (b) The slope of the per capita rate of consumption determines whether the prey suppresses, enhances, or has no effect on its pairwise interaction with the predator, and thus determines the sign of the prey's self-effects. The slope of the standard rate of consumption determines the sign of the direct effect of the prey on the predator. This leads to nine alternative model structures, of which i-iv and vii correspond to regions of the functional response curves in (a).
 See text for further explanation and Appendix A, specifically, for a discussion of the Holling equations and definitions of h and h' .

case it would suffice to consider the slope of the standard consumption rate in these regions as being essentially equal to zero. Moreover, while the ability of prey to suppress their mortality allows their population to grow without control by predators, their new equilibrium level will almost certainly be constrained by another limiting factor. In the examples presented thus far, we have omitted standard self-regulation effects to highlight effects arising from modified interactions. In nature, prey that have escaped control by predators may still be strongly regulated via resource limitation. Even when their predators are saturated, their overall self-effect can still be negative. Thus, where predators are effectively saturated and prey are known or presumed to be self-regulated, then model vi (Figure 6b) can serve as a practical representation of the system.

DEFINING NET EFFECTS FROM THE ADJOINT OF THE COMMUNITY MATRIX

Once direct effects in a system are defined in the community matrix, it is possible to address how a system will respond to a perturbation through summation of all direct and indirect effects that can be transmitted between nodes of the community network. This is accomplished through analysis of $-\mathbf{A}^{-1}$, the inverse of the negative community matrix (Bender et al. 1984; Nakajima 1992; Dambacher et al. 2002). At equilibrium, Equation 2 can be expressed more generally as

$$\frac{dN_i}{N_i dt} = g_i(N^*(p_h), p_h) (i = 1, \dots, n; h = 1, \dots, m), \quad (9)$$

where the growth function of a species (g_i) is determined by n number of population variables, and all of m growth parameters (p_h) in the system, which variously describe rates of

birth, death, and migration, or component factors such as metabolic efficiency or handling time. A sustained alteration to any one of the system’s parameters constitutes a “press” perturbation (Bender et al. 1984), which can alter both the equilibrium abundance of each population, as well as average life expectancy (Levins 1975; Dambacher et al. 2005). Differentiation of Equation 9 with respect to p_h gives the change in equilibrium abundance for each population as

$$\frac{\partial \mathbf{N}^*}{\partial p_h} = -\mathbf{A}^{-1} \frac{\partial \mathbf{g}}{\partial p_h}. \tag{10}$$

(See Dambacher et al. (2005) for a more detailed derivation.) From the matrix equality

$$-\mathbf{A}^{-1} = \frac{1}{\det(-\mathbf{A})} \text{adj}(-\mathbf{A}), \tag{11}$$

where “adj” is the adjoint of a matrix, and “det” is the matrix determinant, Equation 10 can be expressed as

$$d\mathbf{N}^* = \underbrace{\frac{1}{\det(-\mathbf{A})}}_{\text{overall feedback}} \times \underbrace{\text{adj}(-\mathbf{A})}_{\text{complementary feedback}} \times \underbrace{\frac{\partial \mathbf{g}}{\partial p_h} dp_h}_{\text{strength of input or press perturbation}}, \tag{12}$$

which gives the net effect of input in the form of system feedback, decomposed into the adjoint matrix and system determinant. This formulation is useful because elements of the adjoint matrix account for both the direct and indirect effects of a perturbation in terms of complementary feedback cycles (Dambacher et al. 2002), and the determinant represents the overall feedback of the system and scales the magnitude of each variable’s response. The sign of $\det(-\mathbf{A})$ will always be positive in stable systems of any size, so the adjoint matrix will give a correct accounting of the signs of the feedback cycles, allowing one to determine the implications of multiple paths of influence between variables. In a qualitative analysis of perturbations, we are only interested in knowing whether populations will increase, decrease, or stay the same as a result of parameter change, and thus, we

seek a general solution for $\text{sgn } d\mathbf{N}^*$ in Equation 12. Being interested only in the sign of the input, and not its magnitude, we omit quantification of $(\partial \mathbf{g} / \partial p_h) dp_h$, and only consider the sign structure of the system’s adjoint matrix.

Change in a system parameter can lead to change in one or more growth functions in the system, and can be a consequence of processes or forces that are either internal to the system (as in natural selection) or external to the system (as in environmental or experimental perturbations). We emphasize that all biological interactions are essentially trait-mediated, as every α_{ij} interaction coefficient has component factors representing properties of an organism that are phenotypically plastic or subject to natural selection. In analysis of press perturbations, inputs are read down the column of the variable(s) whose growth function contains the changed parameter, and responses are read along the rows. Positive inputs result from increasing a parameter affecting a rate of birth or immigration, or decreasing one that controls a rate of death or emigration—where input to the system is negative, the signs of the adjoint matrix elements are simply reversed.

The following example demonstrates an analysis of the adjoint matrix using the system depicted in Figure 5b, but with N_3 self-regulated:

$$\text{adj}(-\mathbf{A}) = \begin{bmatrix} a_{2,3}a_{3,2} & a_{1,2}a_{3,3} & a_{1,2}a_{2,3} \\ a_{2,3}a_{3,1} - a_{2,1}a_{3,3} & a_{1,1}a_{3,3} & a_{2,3}a_{1,1} \\ a_{3,2}a_{2,1} & a_{3,1}a_{1,2} - a_{3,2}a_{1,1} & a_{1,2}a_{2,1} \end{bmatrix}. \tag{13}$$

For this system, we consider a parameter change caused by natural selection, though analyses of perturbations from environmental or experimental sources will be along the same line. Natural selection will spread a trait or increase the proportion of a genotype in population i if it positively influences its growth equation, such that $\partial g_i / \partial p_h > 0$. If selection increased the metabolic efficiency of N_1 , then only its growth equation would be affected and $\text{sgn } \partial \mathbf{g} / \partial p_h = [+ , 0 , 0]^T$. Response predictions for a positive input to N_1

are read down the first column of the adjoint matrix, and the abundances of N_1 and N_3 in Equation 13 are both predicted to increase. The predicted response of N_2 is ambiguous, however, and is composed of both a positive and negative feedback cycle. Were selection to advantage the predator N_1 , say with sharper claws, then the magnitude of both $a_{1,2}$ and $a_{2,1}$ would increase and $\text{sgn } \partial \mathbf{g} / \partial p_h = [+ , - , 0]^T$. Thus, the spread of this genotype through the predator's population would constitute a positive input to N_1 and a negative input to N_2 . Responses to this multiple input are assessed through a summation of the first column with the negative of the second column of Equation 13. The predicted response of N_2 is ambiguous as before, but now the response of N_1 is ambiguous as well. If the feedback cycle $-a_{1,2}a_{3,3}$ dominates, then the spread of a trait that increased the individual fitness of a predator will, perhaps counterintuitively, lead to a decrease in the abundance of its population.

In this system, links $a_{1,1}$ and $a_{3,1}$ result solely from modified interactions. These links appear in five feedback cycles in the system's adjoint matrix, and are responsible for ambiguous or nonzero predictions in four of the nine possible responses. Their considerable influence in the system's dynamics highlights the importance of analyzing modified interactions within the context of the larger community in which they are embedded, as they affect community structure and contribute to the feedback properties of the whole system. In the following applications, we demonstrate how modified interactions influence or are implicated in the dynamics of relatively simple and complex communities.

EXAMPLE APPLICATIONS

Snowshoe Hare

Populations of snowshoe hare (*Lepus americanus*) in boreal forests exhibit a cyclical fluctuation in abundance and have received extensive attention in demographic studies, as well as in experiments that have manipulated their food, their predators, and vegetation. A summary of experimental results found hares to increase in density when supplemented with food, or when partially protected from

their predators, but, contrary to expectations, a dramatic increase in vegetation from fertilization did not result in more hares (Dambacher et al. 1999). These treatments can be interpreted as positive inputs to vegetation and hares, and a negative input to predators. Observed responses correspond to a partially specified inverse community matrix with a sign structure of

$$\text{sgn}(-\mathbf{A}^{-1}) = \begin{matrix} & \text{veg.} & \text{hare} & \text{pred.} \\ \text{veg.} & + & & \\ \text{hare} & 0 & + & - \\ \text{pred.} & & & \end{matrix} \quad (14)$$

Working backward from experimental results and "inverting the inverse matrix," one can ask what model structure(s) is consistent with these observed responses (Puccia and Levins 1985). Dambacher et al. (1999) sought to develop a most simple model that was consistent not only with the observed responses, but also the known biology of the system. Specifically, it is accepted that vegetation is self-regulated through nutrient limitation, hares consume vegetation, and predators of hare consume other prey as a substantial portion of their diet. These other prey constitute a resource external to the model that enters the system through the predator, which effectively imparts a negative self-effect to predators—that is, the benefit in growth that N derives from consuming a resource that is not specified as a variable within its model system is added to its growth equation (g) as a fixed rate (R), such that $dN/dt = Ng + R$. With no self-effects in g , this equation in per capita form $dN/Ndt = g + R/N$ yields a negative derivative with respect to N , such that $\partial(dN/Ndt)/\partial N = -R/N^2$. Thus, within the context of the model, the predator has gained self-regulation.

Model A in Figure 7 is based only on the known trophic interactions and self-effects and cannot account for the measured null response of hares in fertilization experiments, as its prediction for effect of fertilization on hares in $\text{adj}(-\mathbf{A})_{2,1}$ is unambiguously positive. Models B, C, D, and E (Figure 7) were generated by an algorithm developed by Montaña-Moctezuma et al. (2007) that considered all possible sign structures

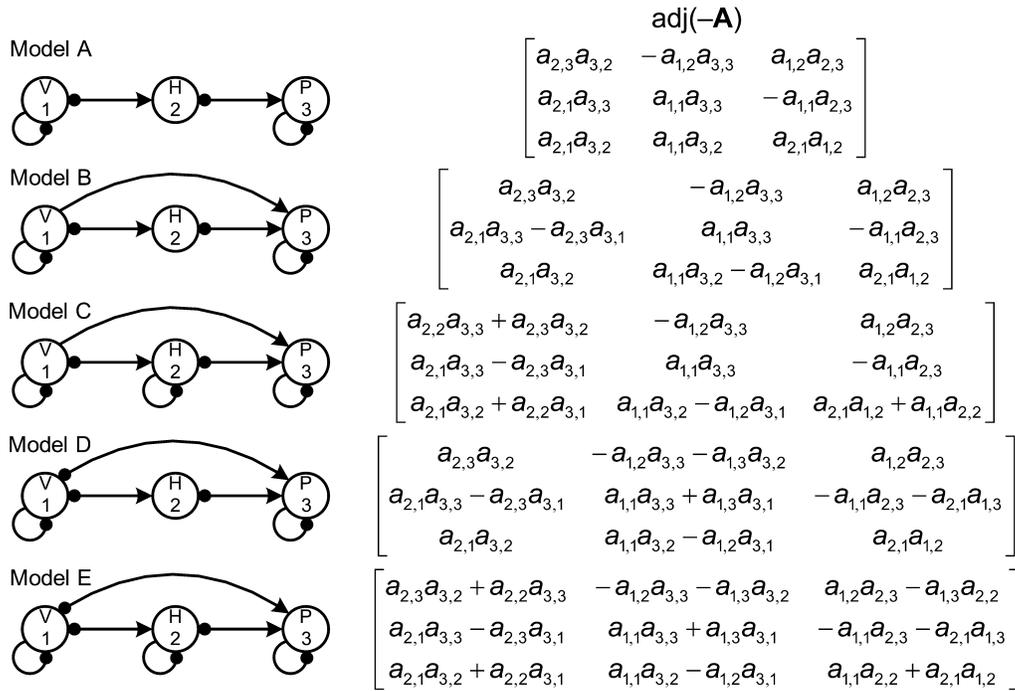


FIGURE 7. ALTERNATIVE MODELS OF SNOWSHOE HARE IN BOREAL FORESTS

Signed digraph models of vegetation (V), snowshoe hare (H), and predator (P) interactions, as well as corresponding adjoint matrices.

for a three variable community matrix and identified models with adjoint matrices that could be interpreted as being consistent with Equation 14. All of these models included a positive link between vegetation and predators, which creates an ambiguous prediction in $\text{adj}(-A)_{2,1}$ for the response of hares to input to vegetation. If the strength of the feedback cycle $a_{2,1}a_{3,3}$ is taken as being roughly equal to $a_{2,3}a_{3,1}$, then these four models can be considered as consistent with the nonsignificant differences reported between hare numbers measured in fertilized plots and those measured in control plots. Models D and E are implausible, however, as they both imply that predators consume vegetation. Models B and C give equivalent qualitative predictions and differ only in the number of feedback cycles for three of the response predictions. The positive vegetation-to-predator link in Models B and C (presumably nontrophic) does not appear in the literature. However, O'Donoghue et al. (1998) report that lynx (*Lynx canadensis*), a principal

predator of hare, use hunting beds when ambushing prey. Dambacher et al. (1999) speculated that increased vegetative growth in fertilized treatment plots might have conferred a tactical advantage to lynx when hunting hare. Moving beyond speculation, predictions from the adjoint matrix for Models B and C suggest measuring predator density or predation pressure after a positive input to hares as a critical experiment. A neutral or negative response in predators would add support for the vegetation-to-predator link, whereas a positive response would favor Model A, but would not be completely inconsistent with Models B and C.

We propose that the intensity of the predator-prey interaction could be modified by vegetation through a function of the form:

$$f_{ij} = 1 + \frac{v}{K_1} N_1; \text{ for } i, j = 2, 3 \text{ or } i, j = 3, 2. \quad (15)$$

Here, f_{ij} is patterned after logistic growth, with the difference that it is an increasing function

of vegetation N_1 , and the tactical advantage v afforded predators by vegetation has its greatest influence as vegetation approaches its carrying capacity K_1 . Applying this function to the interactions governing consumption of hare and presuming logistic growth for vegetation, no self-regulation in hares, and predators consuming an external resource R_3 , gives a community matrix matching that of Model B in Figure 7

$$\mathbf{A} = \begin{bmatrix} -\frac{r}{K_1} & -\alpha_{1,2} & 0 \\ \alpha_{2,1} - \alpha_{2,3} N_3^* \frac{v}{K_1} & 0 & -\alpha_{2,3} \left(1 + \frac{v}{K_1} N_1^*\right) \\ \alpha_{2,3} N_2^* \frac{v}{K_1} & \alpha_{3,2} \left(1 + \frac{v}{K_1} N_1^*\right) & -\frac{R_3}{N_3^{*2}} \end{bmatrix} \quad (16)$$

The sign of $a_{2,1}$ can be negative when the predator population is superabundant. However, $a_{2,1}$ can be reasonably constrained to positive values, as the term $-\alpha_{2,3} N_3^* (v/K_1)$ will be relatively weak as long as the equilibrium biomass of predators N_3^* is well below K_1 (the maximum possible biomass of vegetation).

Hydroid-Hermit Crab Symbiosis

Hydroids (*Hydractinia symbiolongicarpus*) colonize the surface of snail shells occupied by hermit crabs (*Pagurus longicarpus*). This relationship is considered facultative symbiotic (Williams and McDermott 2004); the hydroids receive the benefit of a mobile platform from which to filter feed on suspended organic particles, and hermit crabs gain a measure of protection from predators, which are repelled by the hydroid's stinging nematocysts and unpalatable secondary compounds. The nematocysts can also restrict the free range of movement of hermit crab limbs, however, thereby interfering with the crab's ability to forage and possibly even reproduce. Damiani (2003) measured considerable reductions in hermit crab fecundity (up to 29%) when they were hosts of hydroids. Damiani (2005) measured the effect of hydroids on the growth rate of experimental populations of hermit crabs

with and without the presence of two predators that differed in their sensitivity to the hydroid's nematocysts. Striped burrfish (*Chilomycterus schoepfi*) consume hermit crabs by crushing their shells in their mouths, but they are stung by hydroid-colonized shells, and thus quickly learn to recognize and avoid them. Blue crabs (*Callinectes sapidus*) break open snail shells with their claws, however, and are largely immune to the presence of hydroids. Using a population projection matrix approach, Damiani (2005) calculated population growth rates for hermit crabs in a series of short-term mesocosm experiments. The direct effect of hydroids on hermit crabs was defined as the difference in growth rate between hermit crabs with and without hydroid-colonized shells. Net effects were calculated by subjecting hermit crabs to predators and calculating their population growth rate with and without hydroids. Indirect effects were taken as net effects minus direct effects. In the presence of blue crabs, the net effect of hydroids on hermit crabs was negative, but the net effect was positive when burrfish were used as the system's predator.

Extending Damiani's (2003, 2005) results to consider the implications of this symbiotic relationship to the feedback properties of the whole system, we propose a set of equations that attempts to capture the essential features of the system's biology

$$\begin{aligned}
 \text{predators } \frac{dN_1}{dt} &= N_1 \left(\alpha_{1,2} N_2 \left[1 - \frac{\rho}{N_2} N_3 \right] - r_1 \right) + R_1, \\
 \text{hermit crabs } \frac{dN_2}{dt} &= N_2 \left(\alpha_{2,1} N_1 \left[1 - \frac{\rho}{N_2} N_3 \right] - r_2 \right) \\
 &\quad + R_2 \left(1 - \frac{\sigma}{N_2} N_3 \right), \\
 \text{hydroids } \frac{dN_3}{dt} &= N_3 (-r_3) + R_3 \left(1 - \frac{N_3}{N_2} \right).
 \end{aligned} \quad (17)$$

In Equation 17, hydroid abundance is taken as a hermit crab shell that has been effectively colonized by hydroids, that is, where more than 50% of the shell surface is covered by hydroids (Damiani 2003). Hydroids depend on planktonic drift for delivery of food resources and settlement of planula larvae. These delivery rates are combined and treated as a single external resource R_3 , and analogous to logistic growth, the unrealized

capacity for hydroids to settle and grow on uncolonized shells is a function of the richness of the planktonic drift and the proportion of uncolonized shells $(1 - N_3/N_2)$. This proportion also appears in the suppression of the predator-prey interaction, where $f_{ij} = (1 - \rho N_3/N_2)$, and ρ is the degree to which a predator's attack is suppressed by a colonized shell. Predators and hermit crabs both have population growth rates (R_1 and R_2) that depend on inflows of resources that are external to the model system. In hermit crabs, this rate is restricted by σ , which represents the limiting effect that a hydroid-colonized shell has on hermit crab fecundity.

The community matrix for this system of equations is

$$\mathbf{A} = \begin{bmatrix} \frac{-R_1}{N_1^{*2}} & \alpha_{1,2} & -\alpha_{1,2}\rho \\ -\alpha_{2,1}\left(1 - \frac{\rho N_3^*}{N_2^*}\right) - \alpha_{2,1}N_1^* \frac{\rho N_3^*}{N_2^{*2}} - R_2 \frac{N_2^* - 2\sigma N_3^*}{N_2^{*3}} & \alpha_{2,1}N_1^* \left(\frac{\rho}{N_2^*}\right) & \frac{R_2\sigma}{N_2^{*2}} \\ 0 & \frac{R_3}{N_2^*} & \frac{-R_3}{N_3^{*2}} \end{bmatrix} \quad (18)$$

Sign ambiguity in community matrix elements $a_{2,1}$, $a_{2,2}$, and $a_{2,3}$ leads to at least eight possible alternative models, that is, for three ambiguities with two sign values (positive, negative) there are 2^3 (or 8) possible alternative models. But if zero is considered as a possible sign value, then there are 3^3 (or 27) permutations. By interpreting the symbolic inequalities involved, however, it is possible to narrow our alternatives to a more practical number. The sign of $a_{2,1}$ can be constrained to negative values by the condition that the fraction of colonized shells (N_3^*/N_2^*) can never exceed one. Also, the sign of $a_{2,2}$ will be negative for the system considered here. As for vanishingly small values of either $\alpha_{2,1}$, N_1^* , or ρ , which enter only into the first negative term, the inequality ensuring a negative value of $a_{2,2}$ can be reduced to $\sigma N_3^*/N_2^* < 1/2$. In practice, this inequality can always be expected to hold, as σ is bound between zero and one, and in Damiani's (2005) mesocosm experiments, the fraction of shells colonized by hydroids was set at 1/2, and has been observed to average about 1/5 in natural populations (Damiani 2003). Finally, the sign of $a_{2,3}$ equals

$\text{sgn}(\alpha_{2,1}N_1^*N_2^*\rho - R_2\sigma)$, and can be either positive or negative depending on parameter strength and the relative abundance of predators and hermit crabs. This then leads to Models F and G (Figure 8).

When the predator's rate of attack is only weakly suppressed by hydroids (i.e., when blue crabs are predators), then ρ will be relatively small. If the suppressive effect of hydroids on hermit crab fecundity is great, then σ will be relatively large. Either condition maintains the inequality $\alpha_{2,1}N_1^*N_2^*\rho < R_2\sigma$ in $a_{2,3}$, which in Model F defines hydroids as having a net parasitic relationship with hermit crabs. Conversely, when ρ is relatively strong or σ is weak, then hydroids will be net mutualists of hermit crabs, as in Model G. These conditions correspond with Damiani's (2005) experimental results, in which the measures of indirect and direct effects are equivalent to $\alpha_{2,1}N_1^*(\rho/N_2^*)$ and $-R_2\sigma/N_2^{*2}$, respectively, in $a_{2,3}$ of Equation 18. Thus, within the context of the community matrix, Damiani's (2005) measure of indirect effects can be formally considered as an additive component of the direct effect of hydroids on hermit crabs.

The differences in system structure of Models F and G (Figure 8) lead to differences in adjoint matrix predictions

$$\begin{aligned} \text{adj}(-\mathbf{A}_{\text{model F}}) &= \begin{bmatrix} a_{2,2}a_{3,3} + a_{2,3}a_{3,2} & a_{1,2}a_{3,3} - a_{1,3}a_{3,2} & -a_{1,2}a_{2,3} - a_{1,3}a_{2,2} \\ -a_{2,1}a_{3,3} & a_{1,1}a_{3,3} & -a_{2,3}a_{1,1} + a_{2,1}a_{1,3} \\ -a_{3,2}a_{2,1} & a_{3,2}a_{1,1} & a_{1,2}a_{2,1} + a_{1,1}a_{2,2} \end{bmatrix}, \\ \text{adj}(-\mathbf{A}_{\text{model G}}) &= \begin{bmatrix} a_{2,2}a_{3,3} + a_{2,3}a_{3,2} & a_{1,2}a_{3,3} - a_{1,3}a_{3,2} & a_{1,2}a_{2,3} - a_{1,3}a_{2,2} \\ -a_{2,1}a_{3,3} & a_{1,1}a_{3,3} & a_{2,3}a_{1,1} + a_{2,1}a_{1,3} \\ -a_{3,2}a_{2,1} & a_{3,2}a_{1,1} & a_{1,2}a_{2,1} + a_{1,1}a_{2,2} \end{bmatrix}, \end{aligned} \quad (19)$$

which can be used to guide field studies and mesocosm experiments. The differences in the third column of these matrices suggest measuring the response of predators and hermit crabs with an input to hydroids as a set of experiments to discern the relative importance of direct versus indirect effects under different intensities of the modified interaction.

Danish Shallow Lakes

In this final example, we examine models of Danish shallow lakes that are either above

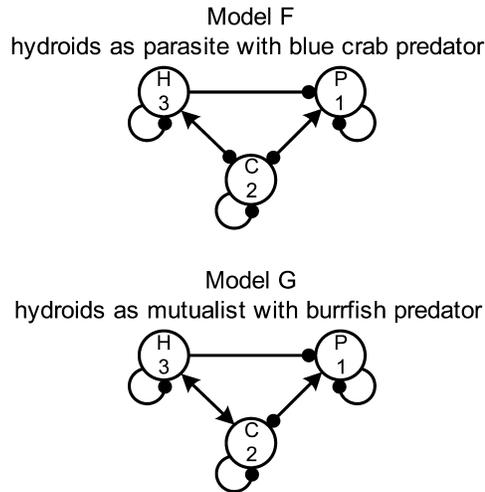


FIGURE 8. ALTERNATIVE MODELS OF HYDROID-HERMIT CRAB SYMBIOSIS

Signed digraph models of interactions between hydroids (H), hermit crabs (C), and predators (P). Models F and G result from ambiguity in the sign of $a_{2,3}$ in the system's community matrix (Equation 18), and correspond to different predators used in laboratory experiments by Damiani (2005).

or below a critical threshold of eutrophication, which leads to changes in relationships among system variables and alternative model structures. Jeppesen (1998) provides a synthesis of studies of Danish shallow lakes, and generally characterizes the shallow lake system by nine trophic guilds and a system variable representing nutrient stores (Figure 9). Against a framework of food web interactions (i.e., only trophic pairwise links) depicted in Model J, there are a number of interactions that are modified by variables within the lake system. Macrophytes have been identified as providing zooplankton a refuge from their cyprinid predators, with zooplankton migrating laterally out of macrophyte beds at night to feed in the water column. In Models H and I, this is treated as a negative link ($-a_{7,2}$) from macrophytes to cyprinids, and a positive link ($+a_{8,2}$) to zooplankton. Anthropogenic additions of phosphorous have shifted many lakes to a eutrophic condition, and lakes with total phosphorous concentrations exceeding $0.1\text{--}0.2\text{ mg L}^{-1}$ generally have a dramatic increase in algal populations and reduced transparency of the water column. Exceeding this threshold appears to modify a number of interactions in the system, such that in the transition from a mesotrophic condition in

Model H to a eutrophic condition in Model I, new links are created and others are severed. We have depicted macrophyte's relationship with nutrients in eutrophic lakes as a saturated Type I response. Macrophytes are depicted as being insensitive to change in nutrient levels, and it is presumed that nutrient's overall self-effect is negative, which corresponds with model vi in Figure 6b. Phytoplankton, which have a turnover rate that is much faster than that of macrophytes, are not depicted as saturated, and the positive link from nutrients is maintained. In the eutrophic model, phytoplankton suppress macrophytes through shading and interfere with the ability of piscivorous fish to see their cyprinid prey, the latter accounting for two additional links in the system, $-a_{6,9}$ and $+a_{7,9}$.

Eutrophic lakes can become highly turbid and have blooms of nuisance algae. Efforts to reverse eutrophication have focused on eliminating anthropogenic sources of nutrients, but even when this has been achieved there can be a lag of decades before nutrient stores are at equilibrium with background rates of inflow. Eutrophic lakes appear to have alternative equilibria, and can either be in a clear-water state (where macrophytes are dominant) or a turbid state (where phytoplankton

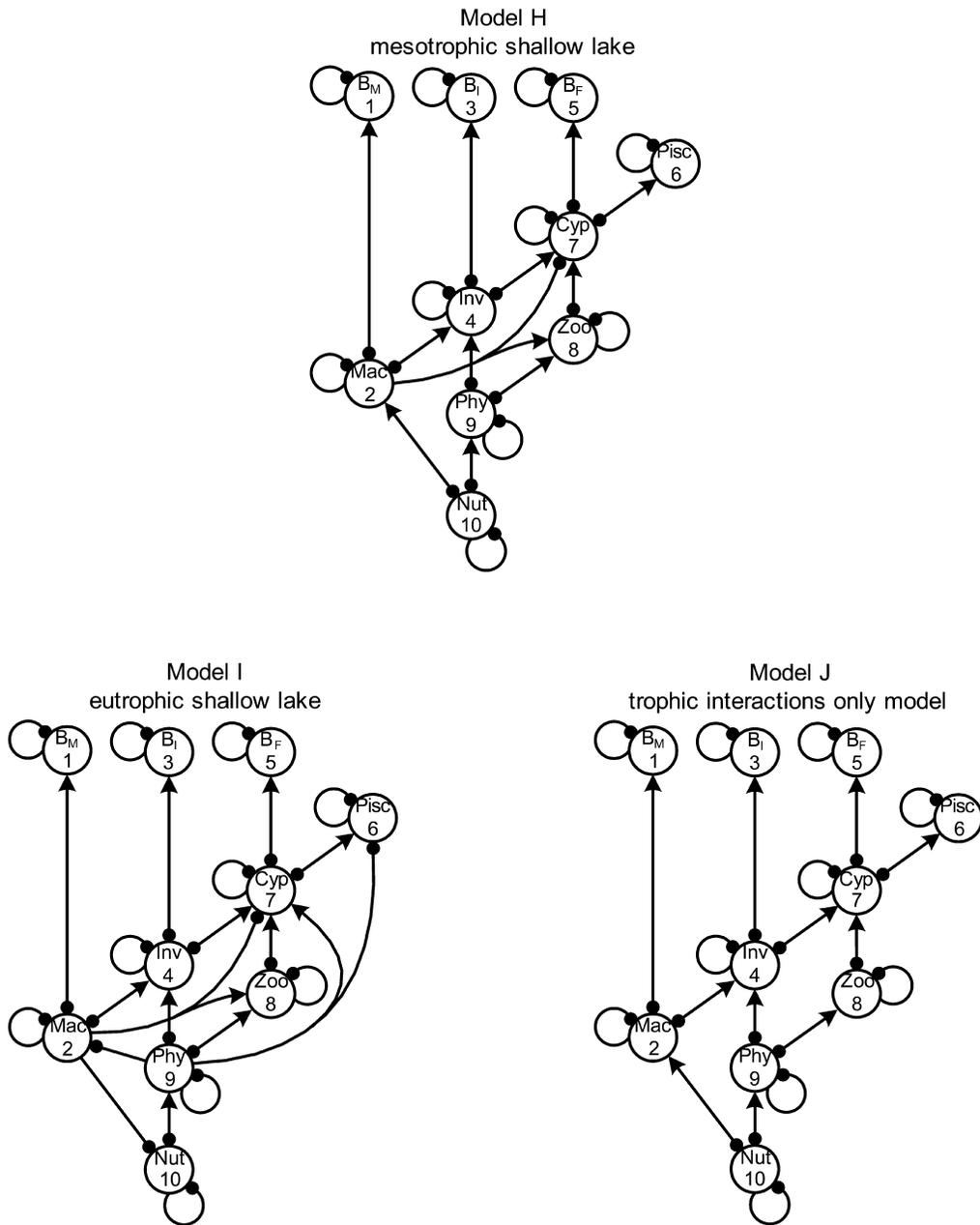


FIGURE 9. ALTERNATIVE MODELS OF DANISH SHALLOW LAKES

Signed digraph models of Danish shallow lakes in mesotrophic and eutrophic condition, as described from studies compiled in Jeppesen (1998); for comparison, model J includes only pairwise trophic interactions.

- B_F: fish-eating birds
- B_I: invertebrate-eating diving ducks
- B_M: macrophyte-eating birds
- Cyp: planktivorous fish (cyprinids)
- Inv: invertebrates (e.g., insects, snails, mussels)
- Mac: submerged macrophytes
- Nut: nutrients
- Phy: phytoplankton
- Pisc: piscivorous fish (pike, large perch)
- Zoo: zooplankton.

are dominant) (Scheffer 1990). Management actions to achieve and maintain a clear-water state under eutrophic conditions have often worked through the system's biological variables, and include removal of cyprinids, the stocking of piscivorous fish, and the propagation and protection of macrophytes. These manipulations can be interpreted as press perturbations to the system, and observed responses can be compared to predictions from the adjoint of Model I's community matrix

$$\text{adj}(-{}^\circ\mathbf{A}_{\text{model I}}) = \begin{bmatrix} 7 & 21 & 6 & -6 & 1 & 1 & -1^* & 9 & -10 & -10^* \\ -21 & 21 & 6 & -6 & 1 & 1 & -1^* & 9 & -10 & -10^* \\ -7 & 7 & 18 & 10 & 3 & 3 & -3 & -1 & -2 & -2^* \\ -7 & 7 & -10 & 10 & 3 & 3 & -3 & -1 & -2 & -2^* \\ 14 & -14 & -4 & 4 & 18 & -10 & 10 & -6 & 16 & 16^* \\ -7 & 7 & -2 & 2 & -5 & 23 & 5^\dagger & 11 & -6 & -6^* \\ 14 & -14 & -4 & 4 & -10 & -10 & 10^* & -6 & 16 & 16^* \\ -14 & 14 & 8 & -8 & 6 & 6 & -6^* & 26 & -4 & -4^* \\ 21 & -21^* & -2 & 2 & -5 & -5 & 5^* & -17 & 22 & 22^* \\ 0 & 0 & -4 & 4 & 4 & 4 & -4^\dagger & 8 & -12 & 16^* \end{bmatrix} \quad (20)$$

The adjoint matrix in Equation 20 is calculated from a community matrix specified with the signed unity (+1, -1, 0) of its interaction terms, which is denoted as ${}^\circ\mathbf{A}$. Specified as such, the adjoint of $-{}^\circ\mathbf{A}$ gives the net number of feedback cycles contributing to a response (Dambacher et al. 2002). A separate calculation can also be made of the absolute number of cycles, both positive and negative, in each adjoint matrix element. Each element of the adjoint matrix can then be divided by the absolute number of feedback cycles within each respective element to give a weighted predictions matrix \mathbf{W} (see Dambacher et al. 2002 and supplemental computer programs for calculation of the adjoint $(-{}^\circ\mathbf{A})$ and \mathbf{W} matrices, as well as analyses for overall feedback, stability, and life expectancy change, available from *Ecological Archives* at <http://esapubs.org/archive/ecol/E083/022/>). Each element of \mathbf{W} represents a ratio of the net to the absolute number of feedback cycles in each response prediction, and can be used to scale the likelihood of sign determinacy for each adjoint matrix element. The sign determinacy of responses with weighted predictions

≥ 0.5 has been shown to generally exceed 90% through simulations using random parameter space (Dambacher et al. 2003).

In Equation 20, we compare Model I's adjoint matrix predictions for eutrophic shallow lakes with responses reported by Jeppesen (1998) to manipulation of macrophytes (column 2), cyprinids (column 7), and nutrient stores (column 10). Response predictions that were measured in field studies are marked by superscripts, with predictions that correctly match field observations marked by an asterisk, and incorrect predictions with low weights (weighted predictions < 0.5) marked by a single dagger (\dagger), and those with a high expected sign determinacy (weighted predictions ≥ 0.5) marked by a double dagger (\ddagger). Of 18 measured responses for eutrophic lakes, 16 were correctly predicted by Model I's adjoint matrix. Of the two wrong predictions, both had weighted prediction values less than 0.3, and thus were of low expected sign determinacy (marked by single daggers). Hence, Model I can be considered consistent with responses observed in the system. Running the same comparison for Model J,

$$\text{adj}(-{}^\circ\mathbf{A}_{\text{model J}}) = \begin{bmatrix} 50 & 27 & 8 & -8 & 1 & 1 & -1^* & 11 & -12 & 15^\ddagger \\ -27 & 27 & 8 & -8 & 1 & 1 & -1^* & 11 & -12 & 15^\ddagger \\ -8 & 8 & 48 & 29 & 6 & 6 & -6 & -11 & 5 & 13^\ddagger \\ -8 & 8 & -29 & 29 & 6 & 6 & -6 & -11 & 5 & 13^\ddagger \\ 1 & -1 & -6 & 6 & 57 & -20 & 20 & 11 & 9 & 8^* \\ 1 & -1 & -6 & 6 & -20 & 57 & 20^\ddagger & 11 & 9 & 8^\ddagger \\ 1 & -1 & -6 & 6 & -20 & -20 & 20^* & 11 & 9 & 8^* \\ 11 & -11 & 11 & -11 & 11 & 11 & -11^* & 44 & 22 & 11^\ddagger \\ 12 & -12^* & 5 & -5 & -9 & -9 & 9^* & -22 & 31 & 19^* \\ 15 & -15 & -13 & 13 & 8 & 8 & -8^\ddagger & 11 & -19 & 43^* \end{bmatrix} \quad (21)$$

which is constructed only from pairwise trophic interactions, we find eight predictions that do not match field observations. All incorrect predictions have high expected sign determinacy (marked by double daggers), thus Model J is largely inconsistent with observed responses.

In Model I's adjoint matrix, correlations among variables present a pattern that is consistent with alternative equilibria main-

TABLE 1
Positive system feedbacks in eutrophic shallow lake model

| | | | |
|----------|-----------------|----------------|---------------|
| Length 3 | 2→4→9→2 (4) | 2→8→9→2 (7) | 2→10→9→2 (9) |
| | 4→9→7→4 (2) | 7→8→9→7 (5) | |
| Length 4 | 2→7→4→9→2 (1) | 2→7→8→9→2* (2) | 2→8→7→4→2 (2) |
| | 2→8→9→4→2 (3) | 2→10→9→4→2 (4) | 4→7→8→9→4 (2) |
| | 4→9→6→7→4 (2) | 4→9→8→7→4 (2) | 6→7→8→9→6 (5) |
| Length 5 | 2→7→8→9→4→2 (1) | | |

- 2: macrophytes
- 4: invertebrates
- 6: piscivorous fish
- 7: planktivorous fish (cyprinids)
- 8: zooplankton
- 9: phytoplankton
- 10: nutrients

Listing of all sequences of cyclical conjunct links forming positive feedback cycles in a system determinant of eutrophic shallow lake model I of Figure 9, where “→” denotes a positive direct effect of one variable on another and “→” denotes a negative direct effect. The number of feedback cycles in which the sequence appears is noted parenthetically.

Positive feedback leads to mutual reinforcement or suppression of variables depending on their position within a sequence of links. For example, in the second sequence of length four*, more of 2 will decrease 7, which increases 8 and decreases 9, resulting in a further increase of 2; alternately, less of 2 leads to more of 7 and 9, and less of 8 and 2.

taining either a clear-water or turbid state. In Equation 20, the sign of responses for macrophytes (read along the second row) are always opposite those for phytoplankton (ninth row). Similarly, responses of cyprinids (seventh row) are perfectly correlated with those of phytoplankton, as is zooplankton (eighth row) with macrophytes. Analysis of Model I’s overall feedback in Table 1 reveals 15 separate paths or sequences of interaction that form cyclical conjunct links of length three, four, and five. Each path constitutes a positive feedback cycle, and positive feedback accounts for 39% of the total number of feedback cycles in the system determinant, that is, 51 cycles of 130 total. In these positive feedback cycles, the relative position of macrophytes, cyprinids, zooplankton, and phytoplankton within each sequence results in a pattern of mutual reinforcement or suppression between variables. When occurring within the same positive feedback cycle, macrophytes and zooplankton always reinforce each other, as do cyprinids and phytoplankton, while macrophytes and zooplankton usually oppose cyprinids and phytoplankton. In general, there are strong correlations for the signs of these influences (Table 2), and this same pattern of influence is reflected in Model I’s adjoint matrix along rows 2, 7, 8, and 9 of Equation

20. As a consequence, input to any one of the variables in Model I has the potential to either shift the system to the alternate state or reinforce the existing one. Model J, however, lacks a consistent pattern of correlation between these four rows in its adjoint matrix, and its system determinant does not have a general pattern or sufficient amount of positive feedback to support alternative equilibria (i.e., while the correlation of influence between variables 2 and 9 is -1.0 , and $+1.0$ for 7 and 9, these correlations are based on only two positive feedback cycles each, all other correlations between 2, 7, 8, and 9 are zero). In all, positive feedback accounts for only 13% of the total number of feedback cycles in Model J’s determinant, that is, 14 cycles of 105 total.

A GENERAL FUNCTIONAL FORM FOR MODIFIED INTERACTIONS

The above examples demonstrate that interactions between species can be modified in various ways, though most modifications can be generally described by the function

$$f_{ij} = I + (\Psi_{ijk} N_k)^\theta, \tag{22}$$

which is patterned after the theta-logistic equation (Gilpin et al. 1976). I determines the existence of the pairwise interaction of

TABLE 2
Correlation of positive feedback effects in eutrophic shallow lake model

| | 7: cyprinids | 8: zooplankton | 9: phytoplankton |
|----------------|--------------|----------------|------------------|
| 2: macrophytes | -0.33 | +1.0 | -1.0 |
| 7: cyprinids | | -0.58 | +1.0 |
| 8: zooplankton | | | -0.85 |

Correlation of sign of influence of four variables on each other in positive feedback cycles of model I's system determinant (Table 1).

species i and j in the absence of species k , Ψ_{ijk} regulates N_k 's effect on the pairwise interaction, and θ shapes the function's symmetry over all values of N_k .

I is dimensionless, and in the examples presented has equaled one, which implies species k 's influence is additive, such that if species k is not also species i or j , then the pairwise interaction exists in its absence. It is conceivable, however, that a pairwise interaction might dissolve in the absence of species k , as when it supplies a habitat feature or substrate that constitutes an irreplaceable context for the interaction of species i and j , in which case its influence is multiplicative and I would equal zero.

Ψ_{ijk} has been treated here as the degree to which species k influences the magnitude of species i and j 's interaction, divided by a parameter or variable with dimension of mass that acts to limit the extent of species k 's influence. For the snowshoe hare example, Ψ_{ijk} in Equation 15 equals $\Psi_{2,3,1} = \Psi_{3,2,1} = v/K_1$, which is the tactical advantage of vegetation divided by vegetation's carrying capacity. For the hydroid-hermit crab example, Ψ_{ijk} in Equation 17 equals $-\rho/N_2$, which is the suppressive influence of a hydroid-colonized shell divided by the total number of shells occupied by hermit crabs.

When θ equals one, then species k 's influence is symmetrical across all levels of its abundance. But if we imagine that the success of a predator increases most dramatically when vegetation grows from a closely cropped state to a level where the predator first becomes concealed, then θ would take on values less than one. Similarly, a θ value less than one applies when the presence of only a few predators is sufficient to drive prey into hiding. Values greater than one describe effects realized only at a relatively high abundance of N_k , such

as when a predator is weakened by an ectoparasite only at a relatively high level of infestation.

While Equation 22 is formulated for an interaction modified by only a single species, it can also be extended to accommodate modification via multiple species. It is not universal, however, as a number of recognized functions vary from this basic form (e.g., Holling equations in Appendix A).

DISCUSSION

While the means by which species interact are diverse, this work demonstrates that both pairwise and modified interactions can be understood within a general and predictive framework via the community matrix, thereby facilitating the disentanglement of direct and indirect effects. Thus, interactions modified via phenotypic plasticity, natural selection, chemical cues, functional responses, or environmental change can be considered alongside those altered by experimental manipulation or management intervention. By formal definition, a species modifying the interaction of two others can have a direct effect as well as an indirect effect on one or both of those species. While this definition does not fit neatly into existing ecological terminology, which recognizes only the indirect effect of a modified interaction, it nonetheless provides a rigorous means to analyze complex interactions in complex systems. Emphasizing a qualitative approach, we have focused on the role that system structure and feedback play in a system's dynamics and in its response to perturbation and intervention. In doing so, we are drawn to consider thresholds that determine alternative model structures, which, in turn, reveal critical parameters and experiments that are most worthy of measurement effort.

In the Danish shallow lakes example, Model I (Figure 9) incorporates a number of modified interactions, and its predictions are consistent with responses observed for a variety of management interventions. Moreover, Model I's structure appears to support the existence of alternative equilibria, and qualitative analysis of its feedback offers a means to understand the mechanisms underpinning the development and maintenance of the clear-water and turbid states. Model J (Figure 9), however, based only on pairwise trophic interactions, is a decidedly poor predictor of documented responses, and does not appear to generate alternative equilibria. The difference in predictability afforded by Models I and J highlights the importance of accounting for modified interactions and supports the dictum that ecosystem dynamics cannot be understood or predicted by food webs alone.

Models of ecological communities are typically based on trophic interactions, the presence of which is easily verified by observation. Nontrophic interactions are difficult to observe and substantiate, however, and thus more likely to be revealed through unexpected experimental results. In the snowshoe hare example, the hypothesis that vegetation enhances hare predation emerges as a consequence of asking what model structure(s) is consistent with observed experimental results. Analysis of a set of alternative models reveals a critical experiment by which to test this hypothesis and advance understanding of the system's structure and dynamics.

In mathematical terms, alternative qualitative models result from ambiguities in the sign structure of the community matrix, which are resolved by distinguishing the relative magnitude of key variables and parameters. These ambiguities can arise from modified interactions, and transition from one model structure to another coincides with passage through a system threshold. In the case of the hydroid-hermit crab system, a threshold was breached by change of the predator species, which effectively altered a key parameter in the system. In the Danish lakes example, the long-term addition of nutrients can be viewed as a massive press perturbation that moves the system far from its original equilibrium. In transition

from a mesotrophic to eutrophic condition, modified interactions change the nature of relationships between variables and, thus, system structure.

A major challenge to the practical use of the community matrix is the requirement or assumption that a system is at or near equilibrium. To address this challenge, one is left to consider, in imprecise terms, whether a perturbation is sufficiently "small," such that a system's dynamics can be approximated by linearized functions while the system remains "close" to a local neighborhood of stability. However, we find that this condition need not be as restrictive as it is typically framed in quantitative analyses, where the goal is to predict change in equilibria with precision. In a qualitative analysis, we are concerned with predicting only the direction of change following a press perturbation, and thus qualitative analyses of the adjoint matrix are valid as long as the new equilibria remain within thresholds that define system structure. All the same, we are unable to predict how equilibria will change if a perturbation moves a system across a threshold. For example, a single model cannot describe the qualitative dynamics of both mesotrophic and eutrophic lakes, rather, a set of alternative models must be considered.

We recognize that it can be a daunting task to sort through all possible alternative models when there are multiple ambiguities in a system's structure. Where equations are at hand, as in the hydroid-hermit crab example, then it may be possible to narrow the choice through interpretation of symbolic inequalities. In the Danish shallow lake example, numerous modified interactions were added to the eutrophic model. For brevity, we chose to consider them all within a single model, but there are at least eight possible permutations. Clearly, there is a need to compare and test predictions from alternative qualitative models, and this is an area that is actively being developed through the use of Bayesian belief networks that have embedded predictions from alternative qualitative models. This approach promises a more structured and rigorous means for using empirical observations in model diagnosis.

On the other hand, there is also an advan-

tage to considering alternative models, as they lay bare our conceptions and assumptions about the world and provide a means to address structural uncertainty in models, a problem typically neglected in ecological studies and resource management (Punt and Hilborn 1997; Varis and Kuikka 1999). Moreover, a comparative analysis of the feedback properties of alternative qualitative models reveals the role that community structure has in determining a system's behavior and deepens our understanding of how the world

works. Analysis of alternative qualitative models extends our ability to understand and predict the dynamics of complex ecological communities through a range of conditions and multiple equilibria.

ACKNOWLEDGMENTS

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APPENDIX A: QUALITATIVE ANALYSIS OF THE HOLLING EQUATIONS

The main text provided a qualitative analysis of Holling's (1959, 1961) functional responses based only on the general form of the functional response curves for a single-prey system. This section provides a brief analysis of the equations themselves for systems where a predator (N_i) is a consumer of one or more prey. While the Holling equations were originally formulated within the context of an individual predator, here they are cast at a population level within a Lotka-Volterra framework. The equations have the commonality that predation intensity is a function of the prey species, and in Equation 2 the system can be generally specified with $f_{ij}(N_2)$ for the single-prey case, or $f_{ij}(N_2, N_3)$ for the two-prey case, thus leading to community matrices of the general form:

$$\mathbf{A} = \begin{bmatrix} 0 & \alpha_{1,2}f_{1,2} + \alpha_{1,2}N_2^* \frac{\partial f_{1,2}}{\partial N_2} \\ -\alpha_{2,1}f_{2,1} & -\alpha_{2,1}N_1^* \frac{\partial f_{2,1}}{\partial N_2} \end{bmatrix},$$

$$\mathbf{A} = \begin{bmatrix} 0 & \alpha_{1,2}f_{1,2} + \sum_{k=2}^3 \alpha_{1,k}N_k^* \frac{\partial f_{1,k}}{\partial N_2} & \alpha_{1,3}f_{1,3} + \sum_{k=2}^3 \alpha_{1,k}N_k^* \frac{\partial f_{1,k}}{\partial N_3} \\ -\alpha_{2,1}f_{2,1} & -\alpha_{2,1}N_1^* \frac{\partial f_{2,1}}{\partial N_2} & -\alpha_{2,1}N_1^* \frac{\partial f_{2,1}}{\partial N_3} \\ -\alpha_{3,1}f_{3,1} & -\alpha_{3,1}N_1^* \frac{\partial f_{3,1}}{\partial N_2} & -\alpha_{3,1}N_1^* \frac{\partial f_{3,1}}{\partial N_3} \end{bmatrix}. \tag{23}$$

In a Type I functional response, a predator's standard rate of consumption increases linearly with prey abundance up to a threshold, beyond which the predator lacks the ability to consume more prey. Usually applied to predators of a single prey, a Type I response extended to include multiple prey will be

$$f_{ij}^{(\text{Type I})} = \begin{cases} 1, & \text{when } \sum_k h_{ik}N_k < 1 \\ \left(\sum_k h_{ik}N_k \right)^{-1}, & \text{when } \sum_k h_{ik}N_k \geq 1 \end{cases}, \tag{24}$$

where i = predator, j = prey, and h_{ik} is the product of the predator's per capita rate of search and attack of prey (i.e., the standard interaction coefficient for prey mortality) and the time required for the predator to subdue, consume, and digest an individual of prey k ; it has dimension of mass⁻¹. In this and all other Holling equations, $f_{ij} = f_{ji}$, thus Equation 24 is used in the growth equation for both the predator and the prey, and the indices for h will be the same in the predator and the prey's growth equations, as in columns 2 and 3 of Equation 26 below. To maintain correct indices in this and subsequent equations, when k is a prey of predator i , then $h_{ik} > 0$, otherwise $h_{ik} = 0$. By this function, the predator is saturated when $\sum_k h_{ik}N_k \geq 1$, and for the case of a predator with a single prey, the saturating prey density equals h_{ik}^{-1} .

For a predator-prey system following a Type I response (Figure 1a), when prey abundance is less than saturating, $\partial f_{ik}/\partial N_j$ equals zero in Equation 23, and no interactions are modified. Community matrices for a one- and two-prey system will simply be

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

$$\mathbf{A} = \begin{bmatrix} 0 & \alpha_{1,2} & \alpha_{1,3} \\ -\alpha_{2,1} & 0 & 0 \\ -\alpha_{3,1} & 0 & 0 \end{bmatrix}. \tag{25}$$

But when the predator is saturated, then $\partial f_{ik}/\partial N_j$ will be negative, and the predator-prey interaction is suppressed; the community matrices then become

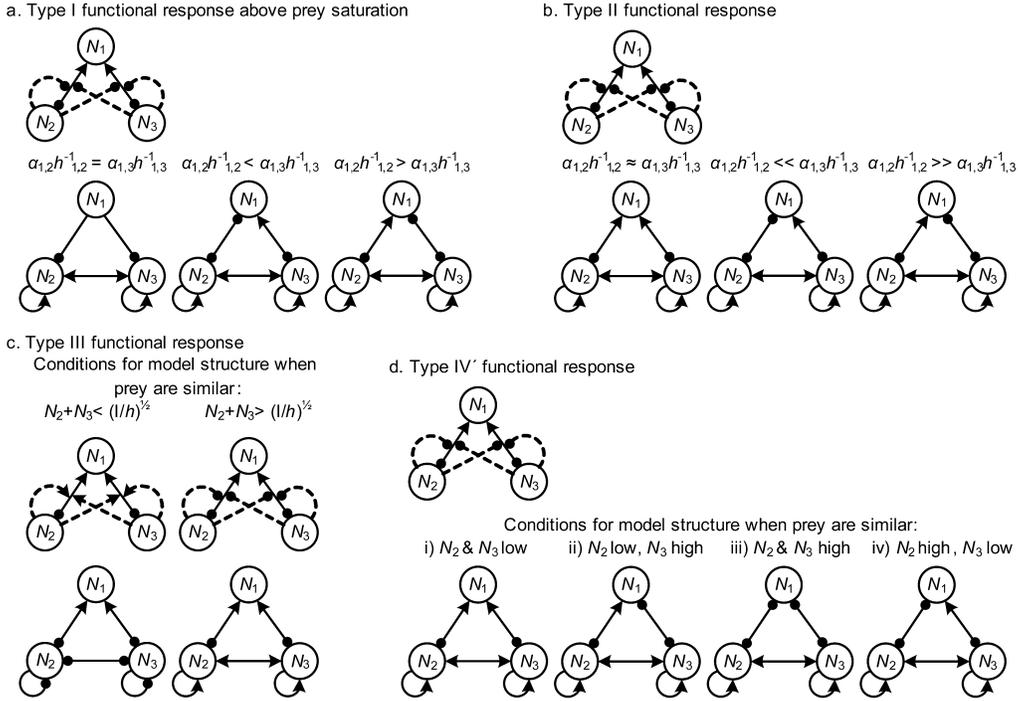


FIGURE A1. ALTERNATIVE MODELS OF FUNCTIONAL RESPONSE IN A TWO-PREY SYSTEM

Signed digraphs of systems with one predator and two prey, where the predator’s rate of prey consumption follows a Holling (1959, 1961) Type I, II, III, or IV’ functional response (Equations 24–30). Conditions for model structure vary according to the magnitude of parameter values and threshold values of prey abundance, similar to single-prey systems, as described in Figure 6. Model structure for a Type IV’ response depends on the relative magnitude of prey abundance, as defined in Figure A2. Prey similarity is defined in terms of their relative benefit to the predator and their respective handling times (i.e., $\alpha_{1,2}h_{1,2} \approx \alpha_{1,3}h_{1,3}$).

$$\begin{aligned}
 \mathbf{A} = & \begin{bmatrix} 0 & 0 \\ -\alpha_{2,1}f_{2,1} & \frac{\alpha_{2,1}N_1^* f_{2,1}}{N_2^*} \end{bmatrix}, \\
 \mathbf{A} = & \begin{bmatrix} 0 & N_3^* f_{1,3}^2 (\alpha_{1,2}h_{1,3} - \alpha_{1,3}h_{1,2}) & N_2^* f_{1,3}^2 (\alpha_{1,3}h_{1,2} - \alpha_{1,2}h_{1,3}) \\ -\alpha_{2,1}f_{2,1} & \alpha_{2,1}N_1^* h_{1,2} f_{2,1}^2 & \alpha_{2,1}N_1^* h_{1,3} f_{2,1}^2 \\ -\alpha_{3,1}f_{3,1} & \alpha_{3,1}N_1^* h_{1,2} f_{3,1}^2 & \alpha_{3,1}N_1^* h_{1,3} f_{3,1}^2 \end{bmatrix}.
 \end{aligned}
 \tag{26}$$

For the single-prey system, when the predator is saturated, its per capita growth equation equals $\alpha_{1,2}N_2(h_{1,2}N_2)^{-1} - r_2$. Here, the prey variable N_2 cancels, and the benefit the predator derives from resource consumption will reside in the growth equation as a fixed rate via the term $\alpha_{1,2}h_{1,2}^{-1}$. This cancellation effectively severs the link from the prey to the predator (i.e., model iv Figure 6b), and the fixed consumption term will act as a density-independent parameter offsetting starvation mortality ($-r$). For the multiple-prey case (Figure A1a), when the predator is satu-

rated, alternative model structures are determined by the relative similarity of the prey species. When prey are equally beneficial and difficult to capture, such that $\alpha_{1,2}h_{1,2}^{-1} = \alpha_{1,3}h_{1,3}^{-1}$, then neither prey will affect the predator’s rate of growth. But when one prey is less beneficial than the other or more burdensome to capture and consume, then it will negatively affect the predator’s growth rate, while the other species will positively affect it. In all instances, however, when the predator is saturated, the two prey will have a mutualistic relationship and gain positive self-effects.

For a Type II functional response,

$$f_{ij}^{(\text{Type II})} = \left(1 + \sum_k h_{ik} N_k \right)^{-1}, \tag{27}$$

the predator specializes in one or a few prey and, in Figure 6a, its per capita rate of consumption is always negative sloped. For functions of this shape, $\partial f_{ik} / \partial N_j$ is always negative, and thus a positive self-effect is imparted to the prey, and they will be mutualistic in their

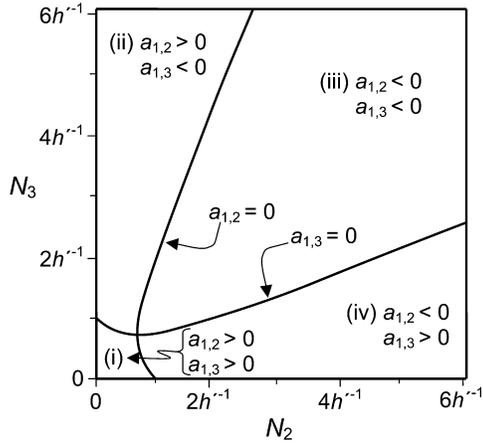


FIGURE A2. PREY-TO-PREDATOR EFFECTS FOR TYPE IV' FUNCTIONAL RESPONSE

Conditions that determine the sign of the relationship between prey N_2 and N_3 , and a common predator N_1 , for a Type IV' functional response (Equation 30), when the prey are similar in terms of their benefit to predators (i.e., $\alpha_{1,2} \approx \alpha_{1,3}$) and their difficulty to subdue and consume (i.e., $h'_{1,2} \approx h'_{1,3}$). The sign of community matrix element $a_{1,2}$ depends on $h'^{-2} + 2N_3^2 - (N_2 + N_3)^2$, and the sign of $a_{1,3}$ depends on the same but with indices swapped. Curves describe prey abundance where $a_{1,2}$ and $a_{1,3}$ equal zero, and their intersection at $N_2 = N_3 = (\sqrt{2h'})^{-1} = 0.707h'^{-1}$ demarcates four general regions of prey abundance that define alternative model structures in Figure A1d. In region i, where the abundance of both prey is relatively low, they will have a positive effect on the predator. In region ii, a linear approximation of the slope of the curve for $a_{1,2} = 0$ is 2.4, and the same would hold in region iv for the slope of $a_{1,3} = 0$ if the x and y axes were switched. Thus, when one prey exceeds the abundance of the other by more than this amount, then it will have a negative effect on the predator, while the less abundant prey will have a positive effect. In region iii, both prey are of a relatively high abundance and both negatively affect the predator.

interaction. For the two-prey case (Figure A1b), three alternative model structures are possible depending on the relative benefit of the prey species to the predator (i.e., $\alpha_{1,2}$ versus $\alpha_{1,3}$) and the relative magnitude of the prey's saturation density (i.e., $h_{1,2}^{-1}$ versus $h_{1,3}^{-1}$). Where the product $\alpha_{ik}h_{ik}^{-1}$ is similar between prey, they both will have a positive direct effect on their shared predator. But where one prey species is less beneficial to the predator or more difficult to handle, then it will have a negative effect on the predator, and the other will have a positive effect.

In a Type III functional response,

$$f_{ij}^{(\text{Type III})} = \frac{I}{\sum_k \text{sgn}(h_{ik})N_k \left(I + \sum_k h_{ik}N_k \sum_k \text{sgn}(h_{ik})N_k \right)^{-1}}, \quad (28)$$

and I is a constant with dimension mass ordinarily set equal to one. In this function, the predator is presumed to be more general in its diet, but requires learning to take advantage of abundant prey that were previously scarce. The predator's per capita rate of consumption peaks at $(I/h)^{1/2}$ (Figure 6a); the prey will have a negative self-effect below this threshold, and a positive self-effect above it. For the two-species case, it is possible to define alternative model structures based on a complex set of conditions that depend on the relative abundance and similarity of prey species. Figure A1c considers the more tractable set, with prey having similar handling times and benefit to the predator. In such instances, the prey will always have a net positive effect on the predator, but can have either a competitive or mutualistic interaction with each other depending on whether their combined abundance is less or greater than $(I/h)^{1/2}$.

In a Type IV functional response, prey have the ability to mount a defense or otherwise inhibit the effectiveness of a predator's attack, and this ability increases with prey density

$$f_{ij}^{(\text{Type IV})} = \left(1 + \sum_k h_{ik}N_k \sum_k h_{ik}^2 N_k^2 \right)^{-1}. \quad (29)$$

Here, h'_{ik} equals $h_{ik}i^{-1}$ and accounts for the relative immunity i that a predator has to the inhibiting effects of the prey, where i is dimensionless and increases with a predator's immunity (Kot 2001). If a predator has a strong immunity to prey defenses, then i will tend toward infinity, and the last term in Equation 29 will effectively vanish, in which case the function converges to a Type II response (Figure A1b). But where i is small and the predator is greatly susceptible to inhibitory effects of the prey, then $\sum_k h_{ik}^2 N_k^2$ will dominate Equation 29, and the effect of the linear middle term will be insignificant. In this latter case, the function converges toward

$$f_{ij}^{(\text{Type IV}')} = \left(1 + \sum_k h_{ik}^2 N_k^2 \right)^{-1}. \quad (30)$$

In both the Type IV and IV' functional response, the standard rate of prey consumption peaks at h'^{-1} , which will be relatively lower than the saturation density h^{-1} (Figure 6a). Beyond this point, prey consumption plummets with increased prey density as prey

mount an increasingly intensive defense. In Equations 29 and 30, $\partial f_{ik}/\partial N_j$ will always be negative, and prey gain self-enhancing feedback. For the single-prey system, the predator receives a positive effect from its prey when prey abundance is less than h^{-1} , but will receive a negative effect when prey abundance exceeds h^{-1} . Equations 29 and 30 have nearly identical dynamics, however, the conditions for system structure of the two-prey system are more easily derived from the Type IV' equation. Again, we consider the more tractable set of conditions for prey that are similar in terms of their benefits to the predator and their difficulty in handling. As in the Type II and saturated Type I responses, the slope of the per capita rate of consumption is always negative, thus the prey gain positive self-effects and have a mutualistic relation-

ship. The effect of the prey on the predator, however, will depend on the relative abundance of each prey species. The sign of $a_{1,2}$ depends on the sign of $h'^{-2} + 2N_3^2 - (N_2 + N_3)^2$, and similarly, the sign of $a_{1,3}$ depends on this same expression but with indices swapped. This interdependency of sign for these prey-to-predator links forms four alternative model structures (Figure A1d) based on the relative abundance of the prey species (Figure A2). Generally, when the abundance of both prey is low ($\leq h'^{-1}$), then both prey will benefit the predator; when both prey are (roughly) equally high, they will both negatively affect the predator. But when one prey exceeds the relative abundance of the other by about 2.4 times, then it will have a negative effect on the predator and the other a positive effect.

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1) In Equation 5, page 230, the sign of $A_{2,1}$ should be negative:

$$A = \begin{bmatrix} 0 & \alpha_{1,2}f_{1,2} & \alpha_{1,2}N_2^* \frac{\partial f_{1,2}}{\partial N_3} \\ -\alpha_{2,1}f_{2,1} & 0 & -\alpha_{2,1}N_1^* \frac{\partial f_{2,1}}{\partial N_3} \\ 0 & 0 & 0 \end{bmatrix}. \quad (5)$$

2) In Equation 16, page 238, subscripts of interaction coefficient in $A_{3,1}$ are switched:

$$A = \begin{bmatrix} -\frac{r_1}{K_1} & -\alpha_{1,2} & 0 \\ \alpha_{2,1} - \alpha_{2,3}N_3^* \left[\frac{v}{K_1} \right] & 0 & -\alpha_{2,3} \left[1 + \frac{v}{K_1}N_1^* \right] \\ \alpha_{3,2}N_2^* \left[\frac{v}{K_1} \right] & \alpha_{3,2} \left[1 + \frac{v}{K_1}N_1^* \right] & -\frac{R_3}{N_3^{*2}} \end{bmatrix}. \quad (16)$$

3) In Equation 17, page 238, right side of hermit crab's growth equation should be multiplied by N_2 , not N_1 :

$$\text{Hermit crabs } \frac{dN_2}{dt} = N_2 \left(-\alpha_{2,1}N_1 \left[1 - \frac{\rho N_3}{N_2} \right] - r_2 \right) + R_2 \left(1 - \frac{\sigma N_3}{N_2} \right). \quad (17)$$

4) In legend for Figure A2, page 248, square root should only be taken for number two, i.e., $N_2 = N_3 = (\sqrt{2}h')^{-1} = 0.707h'^{-1}$.