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Indirect Effects in Ecological Interaction Networks
I. The Chain Rule Approach

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ABSTRACT

A mathematical method for evaluating indirect effects propagated through ecosystems consisting of multiple species is developed. The time-backward expansion of the sensitivity matrix of a system at steady state represents the tracking back of the total effects received by species. Aggregating those portions of the total effect between two species that travel through a common path with various schedules gives the path partitioning of the total effect. From this path partitioning, a chain rule is derived that expresses the indirect effect transmitted through an individual path as the products of direct effects associated with the links constituting the path. The evaluation of indirect effects by this chain rule is applied to example systems to reveal the entire structure of influence propagation through the systems. The results of this application suggest three basic mechanisms through which indirect effects contribute to the complexity and contingency of species interactions: (i) the globalization of influence by bundles of long indirect paths, (ii) the amplification (or reduction) of effects by positive (or negative) cycles, and (iii) the alteration in sign of interactions between a pair of species due to the change in dominance among the effects carried by parallel paths connecting the species.

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1. INTRODUCTION

What happens to each member species of an ecological system when a local disturbance occurs? Not only the species subject to the disturbance and those directly connected to the disturbed species but also those with no direct connections to these species would possibly be affected in significant ways. One extreme case is when the removal of a species in a biotic community leads to the destruction of the whole community; such a species is called a keystone species [1]. These phenomena demonstrate the existence of indirect effects, that is, effects

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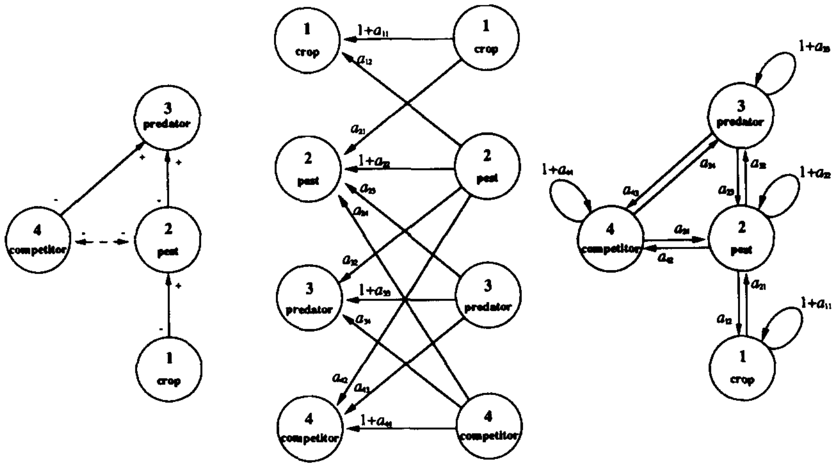
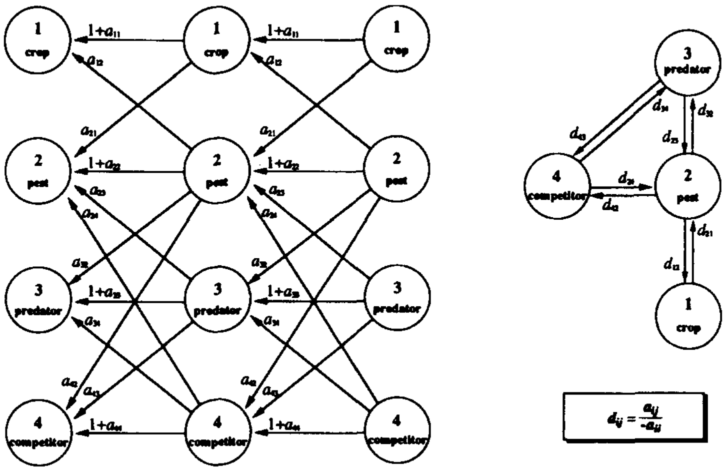


(a) (b) (c)

FIG. 1. (*a*) A hypothetical system for considering the problem of controlling a pest (species 2) that damages an agricultural crop (species 1) when a predator (species 3) and a competitor (species 4) for the pest coexist. Each node represents a species, a directed solid line represents the feeding of the donor node species by the recipient node species, and a dashed line with arrows at both ends represents the competition between the species connected by the line. The signs "+" and "−" at both ends of each line (both solid and dashed) indicate that the interactions between the species connected by the line bring positive and negative effects, respectively, to the aside species. (*b*) The bipartite graph and (*c*) the directed graph (digraph) that represent the structure of immediate effects on one species' abundance caused by an unit inflow added to another species, which is defined by the matrix $(I + A)$, for the hypothetical system of the pest control example. (*d*) The composition of two of the same bipartite graph depicted in Figure 1b, which summarizes all the walks (temporal courses) of length 2, which carry the effects that constitute the third term of (8). (*e*) The graph that represents the structure of the direct effects from one species' abundance to another species', which is determined by direct effect matrix D, for the hypothetical system of the pest control example.

propagated from one species to another through a third member, or more generally through a chain of member species in the network system.

Indirect effects may play an important role in generating the complexity and structural contingency of species interactions in ecological networks. Many instances of unexpected consequences when working with a network of interacting species are known [2]. For example, consider the problem of controlling a pest (species 2) damaging an agricultural crop (species 1), both of which are members of an interaction network (Figure 1a). A direct strike on the pest would not reduce



(d) (e)

FIG. 1. Continued.

its abundance overall as much as the initial response could lead one to expect; the initial reduction in abundance of the pest would cause a reduction in abundance of its predator (species 3) and, at the same time, an increase in abundance of its food (i.e., our objective crop, species 1 in this case), both of which would, in turn, help the pest recover, compensating the initial damage to the pest. Also, exactly the same "experiment" would lead to different and even opposite (from negative to positive, or vice versa) results if only a slight modification is made in the structure of the interaction network, because a small change in structure can greatly alter the propagation pattern of indirect effects. As a result, a pest that is originally troublesome can become either manageable, or conversely even more difficult to control. The difficulty in predicting consequences in such instances illustrates the potential practical and academic importance of indirect effects.

The significance of indirect effects, even if the term is not used, has been recognized and emphasized by many authors, particularly in connection with complex interactions in ecological systems. Indirect effects have been shown to be important in empirical studies [see reference 3 for a review] and also through theoretical investigations [4–16].

Bender et al. [17] distinguish two types of experimental perturbation to ecological systems: *press* perturbation, the type of perturbation introduced and maintained at a predetermined level for a period of time long enough for the system to attain a new steady state (i.e., the step function, or Heaviside's function), and *pulse* perturbation, the type of perturbation introduced for a short interval Δt and immediately removed. Theories on the sensitivity in abundance of constituent species to a press perturbation introduced into an ecological system have been developed [17–19]. This concept of sensitivity represents the total (or ultimate) effect. Thus, its difference from the corresponding direct effect should signify the indirect effect [18]. The smaller difference, however, does not necessarily imply the less indirect effect, but it may be due to the cancellation between the positive and negative components of the indirect effect, which can both be great in magnitude. More generally, to gain insight into the causes of this difference requires the means to analyze how indirect effects are generated and transmitted throughout the interaction network, more specifically, which pathways in the network carry what and how much effect. Levins' [4,5] *loop analysis* provides a means of accounting for total effects not in terms of pathways but rather a certain type of network units, called *loops*. Theoretical analyses along paths of indirect effects have been more recently developed for several specific forms of model systems, revealing novel features of interactions for those systems and demonstrating the importance of elucidating the propagation of indirect effects along individual paths [7–10].

Here we present a mathematical method, applicable to any ecological system of interacting species (the term "species" is here used to represent any constituent unit for an ecological system of concern, e.g., trophic guild or "trophic species" in a food web [20]), for revealing the entire structure of direct and indirect effects propagated through an interaction network under press perturbation [21,22]. Specifically, a chain rule that characterizes the nature of indirect effects occurring in interaction networks is derived. We then apply the method to hypothetical systems and suggest the mechanisms through which indirect effects may contribute to generating the complexity and structural contingency of species interactions in ecological networks.

2. REVEALING INDIRECT EFFECTS STRUCTURE: THE BASIC THEORY

In this section, we derive a mathematical method for the analysis of indirect effects propagated from one species to another in an ecological network subject to press perturbation. In preparation, however, we have first to review some results on inflow and parameter sensitivity analyses [19], which evaluate the total (net) changes in the abundance of each member species of an ecological system caused, respectively, by a unit inflow added to (a unit increment in the growth rate of) a component species and a unit increase in the value of a parameter involved in a local process of the ecological system. They are directly relevant to the present study.

2.1. *PRELIMINARIES: RELEVANT RESULTS OF SENSITIVITY ANALYSIS*

Consider an ecological network consisting of n species that interact with one another, such as the community considered in the pest control example (Figure 1a). Let x_i denote the abundance of component species i. Assume that the growth rate of each species i is a function of the component species: $f_i(x_1, x_2, \ldots, x_n)$. Suppose now that the system is in a steady state, $(x_1^*, x_2^*, \ldots, x_n^*)$, which is determined by the following set of equations:

$$f_i(x_1^*, x_2^*, \cdots, x_n^*) = 0, \qquad (i = 1, 2, \ldots, n). \tag{1}$$

Suppose then that a small amount of inflow z_i is added to species i. This addition of inflows $\mathbf{z} = (z_1, z_2, \ldots, z_n)$ moves the system to a new steady state, $(x_1(\mathbf{z}), x_2(\mathbf{z}), \ldots, x_n(\mathbf{z}))$, that is determined by the following set of equations:

$$f_i(x_1(\mathbf{z}), x_2(\mathbf{z}), \cdots, x_n(\mathbf{z})) + z_i = 0, \qquad (i = 1, 2, \ldots, n). \tag{2}$$

Let $a_{ij} = \partial f_i / \partial x_j$ evaluated at the original steady state [i.e., $(x_1(\mathbf{z}), x_2(\mathbf{z}), \ldots, x_n(\mathbf{z}))$ with $\mathbf{z} = 0$ or $z_i = 0$ for all i], and let

$$s_{ij} = \frac{\partial x_i(z_1, z_2, \cdots, z_n)}{\partial z_j}, \tag{3}$$

which is evaluated at $z_j = 0$ for all j, represent the inflow sensitivity of abundance x_i due to the change in additional inflow z_j (i.e., the change in the abundance of species i caused by a unit increment in the growth rate of species j). Let $A = [a_{ij}]$ and $S = [s_{ij}]$, where $i, j = 1, 2, \ldots, n$. Then, by differentiating (2), we have the following relationship [18]:

$$S = -A^{-1}. \tag{4}$$

[See [19] for an alternative derivation of (4).] Matrix A is often referred to in the literature as "community matrix," and S is called "sensitivity matrix" [19].

Suppose now that some parameter p is involved in the system dynamics, and that the steady state is determined as a function of p by the balance equations

$$f_i(x_1(p), x_2(p), \ldots, x_n(p); p) = 0, \tag{5}$$

for $i=1,2,\ldots,n$. Then, it follows [19] that

$$\begin{bmatrix} \dfrac{dx_1}{dp} \\ \vdots \\ \dfrac{dx_n}{dp} \end{bmatrix} = -A^{-1} \begin{bmatrix} \dfrac{\partial f_1}{\partial p} \\ \vdots \\ \dfrac{\partial f_n}{\partial p} \end{bmatrix} = S \begin{bmatrix} \dfrac{\partial f_1}{\partial p} \\ \vdots \\ \dfrac{\partial f_n}{\partial p} \end{bmatrix}, \tag{6}$$

where the derivatives are evaluated at $p=0$. This implies a chain rule:

$$\frac{\mathrm{d}x_i}{\mathrm{d}p} = \sum_{j=1}^{n} s_{ij} \frac{\partial f_j}{\partial p} = \sum_{j=1}^{n} \frac{\partial x_i}{\partial z_j} \frac{\partial f_j}{\partial p}. \tag{7}$$

Equation (6) shows that the sensitivity of x_i with respect to parameter p can be decomposed into the part represented by the elements of S and the part represented by $\partial f_j / \partial p$; the former is global in nature, involving the entire network (in the matrix inversion A^{-1}), whereas the latter is local in nature, involving the direct dependency on p of the growth rate of each individual species. Thus, the indirect effect aspect of parameter sensitivity can be reduced to that of inflow sensitivity S. Therefore, we focus on inflow-sensitivity in the rest of this article.

2.2. *TEMPORAL UNFOLDING OF TOTAL EFFECTS*

Each element s_{ij} of sensitivity matrix S represents the total effect on species i (in terms of change in steady state abundance of species i) due to a unit rate of continuous causes introduced in species j throughout the past time (in terms of a unit increment in growth rate of species j), which Bender et al. [17] called a press perturbation, in contrast to a pulse perturbation. This total effect on i's abundance caused by a unit inflow added to j can be viewed as the sum of the effects that propagate through all the paths connecting j to i with various time schedules; that is, one can imagine the *age distribution* as well as *path distribution*, within the total effect, s_{ij}.

In a discrete time framework, which is easier for intuitive visualization, the *temporal unfolding* (i.e., the tracing back in time along alternative paths), or age distribution, of total effects, s_{ij}, where $i,j=1,2,\ldots,n$, can be given in the form of matrix series expansion:

$$\begin{aligned} S &= -A^{-1} = I + (I+A) + (I+A)^2 + \cdots \\ &= \sum_{i=-\infty}^{0} B^{-t}, \end{aligned} \tag{8}$$

where $B = I + A$. The (i, j) element is given as

$$s_{ij} = \delta_{ij} + b_{ij} + \sum_{k=1}^{n} b_{ik} b_{kj} + \cdots \tag{9}$$

where δ_{ij} is Kronecker's delta and $b_{ij} = \delta_{ij} + a_{ij}$ (i.e., $B = [b_{ij}]$). The first term of the righthand side of (9) corresponds to the initial impact (a unit increment in growth rate of each species), and the second term b_{ij} represents the immediate effect on i from an impact introduced to j, that is, the effect arriving at i at present ($t = 0$) that is caused by an impact made on j at the immediately previous time ($t = -1$). In particular, b_{ij} in the case of $i = j$ (i.e., $b_{jj} = 1 + a_{jj}$) represents the portion of the impact made on j at the previous time ($t = -1$) that remains in j at present ($t = 0$). The bipartite graph and the directed graph (digraph) that represent the structure of these immediate effects on one species' abundance caused by a unit inflow added to another species for the hypothetical system of the pest control example is depicted in Figure 1, b and c, respectively. The third term is the sum of the effects, each of which, evaluated as $b_{ik} b_{kj}$, originates in an impact made on j at two units of time before ($t = -2$) and travels through alternative courses, $j \to k \to i$, where k may be identical with j or i, in two units of time, arriving at i at present ($t = 0$) (Figure 1d). In general, the $(m+1)$th term of the righthand side of (9) is the sum of the effects, each of which, evaluated as $b_{ik_{m-1}} \ldots b_{k_2 k_1} b_{k_1 j}$, orginates in an impact made on j at m units of time before ($t = -m$) and follows a temporal course or "walk", $j \to k_1 \to k_2 \to \cdots \to k_{m-1} \to i$, in m units of time, arriving at i at present ($t = 0$). Note that, as is illustrated in Figure 2 (left), a walk represents a cause-effect chain in which the *effect* of a preceding cause becomes a *cause* for subsequent effects.

Within a sequence of species, such as $j \to k_1 \to k_2 \to \cdots \to k_{m-1} \to i$, representing a walk from species j to i, any sequence of consecutive positions occupied by an identical species implies that the effect after the walk stays in that species for the corresponding number of time units. Thus, the path taken by the effect is obtained by omitting from (the sequence representing) the walk any subsequence of identical species (which represents a retention of the effect). For example, in the hypothetical system of the pest control example, the effect after the walk, $1 \to 1 \to 2 \to 2 \to 2 \to 3 \to 3$, stays at species 1 for one unit of time, then moves to 2, where it stays for two units of time, and further moves to 3, where it stays for one unit of time (Figure 2, left). The path this effect takes is represented by the subsequence $1 \to 2 \to 3$ (Figure 2, right). The length of a walk represents the time period (the number of time units) that it takes for the effect to travel (6 for the example walk,

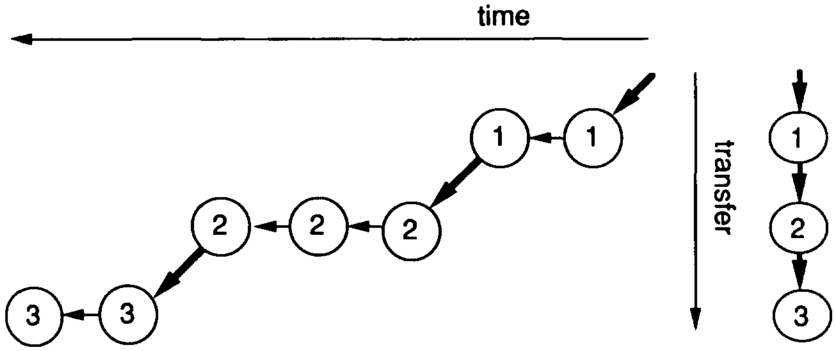


FIG. 2. A sample walk, 1 → 1 → 2 → 2 → 2 → 3 → 3, in the hypothetical system of the pest control example, to illustrate a cause-effect chain in which an *effect* from preceding causes becomes a cause for subsequent effects (left), and its corresponding path, 1 → 2 → 3 (right).

1 → 1 → 2 → 2 → 3 → 3), whereas that of a path represents the number of interspecific transfers that the effect experiences (2 for the example path, 1 → 2 → 3).

Note that the matrix series in (8) converges if and only if the absolute values of all the eigenvalues of matrix $(I + A)$ are < 1, under which the steady state of the system is locally stable.

Similar developments can be made for the continuous time case. In the continuous time framework, the temporal unfolding of total effects, s_{ij}, can be given as follows:

$$S = -A^{-1} = \int_{-\infty}^{0} e^{-At}\,dt. \tag{10}$$

Note that, like the discrete time case, the matrix integral in (10) converges only if the real parts of all the eigenvalues of matrix A are negative, under which the steady state of the system is locally stable in the continuous time framework. [This is because the integral on the righthand side of (10) is calculated as $[-A^{-1}e^{-At}]_{-\infty}^{0} = -A^{-1}(I - \lim_{t\to\infty} e^{At})$, which converges to $-A^{-1}$ (because e^{At} converges to 0) if and only if the real parts of all the eigenvalues of matrix A are negative.] The notion of age structure of total effects from one species to another is also valid in the continuous time case. Indeed, the age distribution of the total effects is expresses by density function e^{-At}, that is, the (i, j) element of $e^{-At}dt$ $(= e^{A|t|}dt$, where $t \leqslant 0)$ represents the sum of effects that originate in the impacts made on species j by a unit rate of continuous causes during the time period of $[t, t + dt]$, and have followed alternative paths from j to i, arriving at i at present ($t = 0$). [This is verified as follows: for the continuous time case, the dynamics of the system is governed by equation $\dot{\mathbf{x}} = \mathbf{f}(\mathbf{x})$, where $\mathbf{x} = (x_1, x_2, \ldots, x_n)$ and $\mathbf{f} = (f_1, f_2, \ldots, f_n)$. Thus, the dynamics of a small deviation $\boldsymbol{\xi}$ from a steady state $\mathbf{x}^*$ is determined by linear equation $\dot{\boldsymbol{\xi}} = A\boldsymbol{\xi}$, whose solution is given as $\boldsymbol{\xi}(t) = e^{At}\boldsymbol{\xi}(0)$. The ith element of this solution when $\boldsymbol{\xi}(0)$ is a unit vector with one for the jth element, i.e., the (i, j) element of e^{-At}, represents the sum of effects that originate in a unit impact initially made on j, and arrive at i after t units of time.]

2.3. *PATH PARTITIONING OF TOTAL EFFECTS: A CHAIN RULE FOR INDIRECT EFFECTS*

In the temporal unfolding of the total effect on i's abundance caused by a unit inflow added to j, aggregating those portions of the total effect that travel through an identical path connecting j to i with different time schedules gives the path partitioning of the total effect.

In the first step of this aggregation procedure, we evaluate the portion of the total effect associated with the direct path (or link) connecting j to $i, j \to i$, where $j \neq i$, by summing all those portions of the total effect that travel through this link with different time schedules, In the discrete time case, these portions are those that follow the walks of the form $(j \to)^{m_0} j \to i(\to i)^{m_1}$, where $(\ )^m$ implies the repetition of the content by m times. The effect after each walk, $(j \to)^{m_0} j \to i(\to i)^{m_1}$, is evaluated as $(1 + a_{ii})^{m_1} a_{ij} (1 + a_{jj})^{m_0}$, thus the portion of the total effect associated with the link, $j \to i$, is given by the following summation:

$$\begin{aligned}
&\sum_{m_1=0}^{\infty} \sum_{m_0=0}^{\infty} (1 + a_{ii})^{m_1} a_{ij} (1 + a_{jj})^{m_0} \\
&\quad = \sum_{m_1=0}^{\infty} (1 + a_{ii})^{m_1} a_{ij} \sum_{m_0=0}^{\infty} (1 + a_{jj})^{m_0} \\
&\quad = \frac{a_{ij}}{-a_{ii}} \frac{1}{-a_{jj}}.
\end{aligned} \tag{11}$$

The continuous-time version of this calculation leads to the same result as follows:

$$\begin{aligned}
&\int_0^{\infty} \mathrm{d}t_1 \int_0^{\infty} \mathrm{d}t_0\, e^{a_{ii}t_1} a_{ij} e^{a_{jj}t_0} \\
&\quad = \left(\int_0^{\infty} e^{a_{ii}t_1}\, \mathrm{d}t_1 \right) a_{ij} \left(\int_0^{\infty} e^{a_{jj}t_0}\, \mathrm{d}t_0 \right) \\
&\quad = \frac{a_{ij}}{-a_{ii}} \frac{1}{-a_{jj}}.
\end{aligned} \tag{12}$$

This quantity, $a_{ij}/(a_{ii}a_{jj})$, represents the *direct* effect to i's abundance from j's inflow:

$$\left[\begin{array}{c}\text{direct effect from } j\text{'s inflow to } i\text{'s abundance}\\ \text{for } i \neq j\end{array}\right] = \frac{a_{ij}}{-a_{ii}} \frac{1}{-a_{jj}}. \quad (13)$$

The part $1/(-a_{jj})$ of this quantity corresponds to the sum of the effects (i.e., the ultimate impacts observed at present) on species j's abundance caused by a unit rate of inflow added to the same species j throughout the past time, which is referred to as the *retention coefficient* of j. On the other hand, the part $-a_{ij}/a_{ii}$ represents the sum of all the effects on i's abundance caused by a unit increase of j's abundance and transmitted through the link connecting j to i, that is, the direct effect from j's abundance to i's abundance (strictly, this interpretation of $-a_{ij}/a_{ii}$ requires a new mathematical framework, which will be given, together with the full justification of this interpretation, in a companion paper [23]):

$$\left[\begin{array}{c}\text{direct effect from } j\text{'s abundance to } i\text{'s abundance}\\ \text{for } i \neq j\end{array}\right] = d_{ij} = \frac{a_{ij}}{-a_{ii}}. \quad (14)$$

This direct effect from j's abundance to i's abundance can be said to equal the corresponding immediate effect, a_{ij}, multiplied by the recipient's retention coefficient, $-1/a_{ii}$. Let $d_{jj}=0$ for $j=1,2,\cdots,n$, and matrix $D=[d_{ij}]$, where $i,j=1,2,\cdots,n$, is referred to as the *direct effect matrix*. The digraph that represents the structure of these direct effects on one species' abundance caused by a unit inflow added to another species for the hypothetical system of the pest control example is depicted in Figure 1e.

The effect from j's inflow to i's abundance through a particular path, $j \to k_1 \to k_2 \to \cdots \to k_{i-1} \to i$, is given by summing all those pieces of the total effect on i's abundance caused by a unit inflow added to j that travel this path with different time schedules (i.e., that take the walks sharing this path):

$$\begin{aligned}&\sum_{m_p=0}^{\infty} \cdots \sum_{m_1=0}^{\infty} \sum_{m_0=0}^{\infty} (1+a_{ii})^{m_p} a_{ik_{p-1}} \cdots (1+a_{k_1k_1})^{m_1} a_{k_1j} (1+a_{jj})^{m_0}\\ &= \sum_{m_p=0}^{\infty} (1+a_{ii})^{m_p} a_{ik_{p-1}} \cdots \sum_{m_1=0}^{\infty} (1+a_{k_1k_1})^{m_1} a_{k_1j} \sum_{m_0=0}^{\infty} (1+a_{jj})^{m_0}\\ &= \frac{a_{ik_{p-1}}}{-a_{ii}} \cdots \frac{a_{k_1j}}{-a_{k_1k_1}} \frac{1}{-a_{jj}}. \end{aligned} \quad (15)$$

The continuous time version of this calculation leads to the same result:

$$\begin{aligned}
&\int_0^\infty dt_p \cdots \int_0^\infty dt_1 \int_0^\infty dt_0 e^{a_{jj} t_p} a_{ik_{p-1}} \cdots e^{a_{k_1 k_1} t_1} a_{k_1 j} e^{a_{jj} t_0} \\
&\quad = \left(\int_0^\infty e^{a_{jj} t_p}\, dt_p \right) a_{ik_{p-1}} \cdots \left(\int_0^\infty e^{a_{k_1 k_1} t_1}\, dt_1 \right) a_{k_1 j} \left(\int_0^\infty e^{a_{jj} t_0}\, dt_0 \right) \\
&\quad = \frac{a_{ik_{p-1}}}{-a_{ii}} \cdots \frac{a_{k_1 j}}{-a_{k_1 k_1}} \frac{1}{-a_{jj}}.
\end{aligned} \tag{16}$$

Therefore, the *indirect* effect from j's inflow to i's abundance through a particular path equals the retention coefficient of the donor j, $1/(-a_{jj})$, multiplied by the product of the direct effects transmitted through those links that make up the path; thus, a chain rule follows:

$$\begin{aligned}
&\left[\begin{array}{c} \text{indirect effect from } j\text{'s inflow to } i\text{'s abundance} \\ \text{through a path } j \to k_1 \to k_2 \to \cdots \to k_{l-1} \to i \end{array} \right] \\
&\quad = d_{ik_{l-1}} \cdots d_{k_2 k_1} d_{k_1 j} \frac{1}{-a_{jj}}.
\end{aligned} \tag{17}$$

From chain rule (17), it follows that the sum of the effects from j's inflow to i's abundance through all the paths of length l connecting j to i is given as the (i, j) element of matrix $D^l R$, where R is a diagonal matrix with retention coefficient $-1/a_{jj}$. Therefore, the sum of the effects from j's inflow to i's abundance through all the paths of all length connecting j to i, which equals s_{ij}, the total effect on i's abundance caused by a unit inflow added to j, is given as the (i, j) element of the following matrix series:

$$S = R + DR + D^2 R + \cdots = (I + D + D^2 + \cdots) R. \tag{18}$$

Equation (18) gives an alternative matrix series expansion of S to the temporal expansion in (8). The matrix series expansion in (18) represents the *path partitioning* of the total effects represented by S. That is, the (i, j) element of the matrix series in (18) indicates the partitioning of the total effect s_{ij} from j's inflow to i's abundance into the paths of different length connecting j to i.

3. INDIRECT EFFECT MECHANISMS FOR GENERATING COMPLEX INTERACTIONS

The general formulation of indirect effects developed above, when applied to specific systems, may provide a useful means for identifying and understanding the specific mechanisms that generate the complexity and structural contingency of species interactions in those systems. We first illustrate the point with several examples of hypothetical systems. Motivated by those examples, we then identify three general mechanisms through which indirect effects contribute to generating the complexity and contingency of species interactions in an ecological network.

The application of the mathematical method for indirect effect analysis developed above for the following example systems should also demonstrate that the method generates the same answers as previously studies did, but under a unified perspective, providing a more general and coherent understanding of the nature of indirect effects in ecological interaction networks.

3.1. *EXAMPLES*

Example 1. Consider a system consisting of two species (species 2 and 4) with no direct interactions and their common predator (species 3) depicted in Figure 3a, which is identical in structure to a subsystem [consisting of the pest (species 2), its competitor (species 4) and their common predator (species 3)] of the system considered in the pest control example (Figure 1a). Holt [8] shows that the two species with no direct interactions may interact negatively with each other through their common predator and calls this indirect interaction *apparent competition*. Assume that the community matrix A at a steady state of the system is given as

$$A = \begin{bmatrix} -\alpha_{22} & -\alpha_{23} & 0 \\ \alpha_{32} & -\alpha_{33} & \alpha_{34} \\ 0 & -\alpha_{43} & -\alpha_{44} \end{bmatrix}, \tag{19}$$

where $\alpha_{ij} > 0$ for any i and j. Then, matrix $B = I + A$ summarizes the immediate effects between the member species of the system (Figure 3b). The direct effects between pairs of species are then given by the corresponding direct effect matrix (Figure 3c):

$$D = [d_{ij}] = \begin{bmatrix} 0 & \dfrac{-\alpha_{23}}{\alpha_{22}} & 0 \\ \dfrac{\alpha_{32}}{\alpha_{33}} & 0 & \dfrac{\alpha_{34}}{\alpha_{33}} \\ 0 & \dfrac{-\alpha_{43}}{\alpha_{44}} & 0 \end{bmatrix}. \tag{20}$$

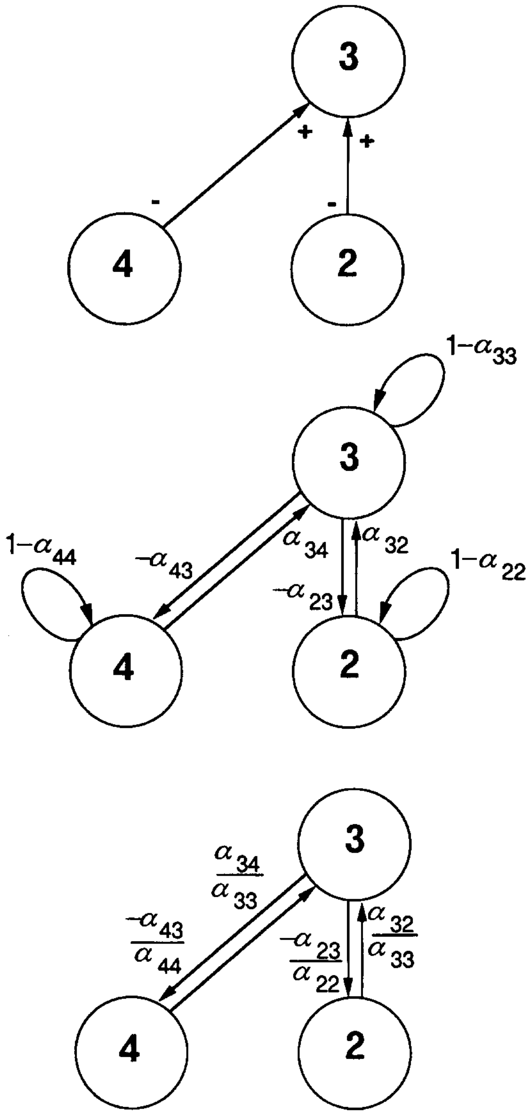


FIG. 3. (*a*) A system consisting of two species with no direct interaction and their common predator. The digraphs represent (*b*) the immediate effect structure and (*c*) the direct effects structure of the system.

Although species 2 and 4 do not directly interact with each other, they do indirectly through their common predator (species 3), as we verify below.

A unit increment in inflow to species 4 will have a negative effect on species 2's abundance through path 4 → 3 → 2: $-(\alpha_{23}/\alpha_{22})(\alpha_{34}/\alpha_{33})(1/\alpha_{44}) < 0$. But this is not the total effect from species 4 to 2. The sum of the effects carried by the paths from species 4 to 2 represented in the form, 4 → 3(→ 4 → 3)* → 2, where ( )* represents the repetition of the contents in any number of times, is evaluated as

$$\frac{-\alpha_{23}}{\alpha_{22}}\sum_{k=0}^{\infty}\left(\frac{\alpha_{34}}{\alpha_{33}}\frac{-\alpha_{43}}{\alpha_{44}}\right)^{k}\frac{\alpha_{34}}{\alpha_{33}}\frac{1}{\alpha_{44}}=\frac{-\alpha_{23}}{\alpha_{22}}\frac{1}{1+\dfrac{\alpha_{34}}{\alpha_{33}}\dfrac{\alpha_{43}}{\alpha_{44}}}\frac{\alpha_{34}}{\alpha_{33}}\frac{1}{\alpha_{44}}$$

$$=\frac{1}{1+\gamma_{43}}\left(-\frac{\alpha_{23}}{\alpha_{22}}\frac{\alpha_{34}}{\alpha_{33}}\frac{1}{\alpha_{44}}\right), \qquad (21)$$

where $\gamma_{ij}=|c_{ij}|$ with c_{ij} representing the effect associated with cycle $j \to i \to j$ (denoted by C_{ij}) that is, $c_{ij}=(a_{ji}/a_{jj})(a_{ij}/a_{ii})$. This sum (21) is still negative, but smaller in magnitude than the effect through path 4 → 3 → 2 alone, which is evaluated as $-(\alpha_{23}/\alpha_{22})(\alpha_{34}/\alpha_{33})(1/\alpha_{44})$, due to the dwindling in passing through intermediate cycle C_{34} (associated with negative effect, $c_{43}=-\gamma_{43}$) by the factor $1/(1+\gamma_{43})(<1)$. This sum is still not the entire effect from species 4 to 2; it is only the total of the effects carried by the *first-passage* paths from species 4 to 2, the paths starting at species 4 and arriving at species 2 for the first time. The *recycling effects*, the effects carried by the *subsequent-passage* paths (i.e., the paths starting from species 4 and coming to species 2 once, then leaving and returning to species 2 several times, e.g., 4 → 3 → 2 → 3 → 2 → 3 → 4 → 3 → 2) must also be taken into account to evaluate the total effect from species 4 to 2. The paths connecting species 4 to 2, including those that carry the recycling effects, are expressed in the general form 4 → 3(→ 4 → 3)* → 2[→ 3(→ 4 → 3)* → 2]*, where 2[→ 3(→ 4 → 3)* → 2]* represents the cycles around the recipient species 2. Thus, the total effect from species 4's inflow increment on species 2's abundance is given as

$$\sum_{k=0}^{\infty}\left(\frac{-\alpha_{23}}{\alpha_{22}}\frac{1}{1+\dfrac{\alpha_{34}}{\alpha_{33}}\dfrac{\alpha_{43}}{\alpha_{44}}}\frac{\alpha_{32}}{\alpha_{33}}\right)^{k}\frac{\alpha_{23}}{\alpha_{22}}\frac{1}{1+\dfrac{\alpha_{34}}{\alpha_{33}}\dfrac{\alpha_{43}}{\alpha_{44}}}\frac{-\alpha_{34}}{\alpha_{33}}\frac{1}{\alpha_{44}}$$

$$=\frac{1}{1+\dfrac{\gamma_{32}}{1+\gamma_{43}}}\frac{1}{1+\gamma_{43}}\left(-\frac{\alpha_{23}}{\alpha_{22}}\frac{\alpha_{34}}{\alpha_{33}}\frac{1}{\alpha_{44}}\right), \qquad (22)$$

which is still negative but gets even smaller in magnitude than the sum of the first-passage effects from species 4 to 2.

Therefore, a unit increase in inflow to species 4 indirectly has a negative effect on species 2's abundance, which corresponds to apparent competition, but the simple product $-(\alpha_{23}/\alpha_{22})(\alpha_{34}/\alpha_{33})(1/\alpha_{44})$ would overestimate in magnitude the actual total effect. Note here that the numerical value for this total effect from species 4 to 2 can alternatively be calculated by the matrix inversion according to (4), which, however, does not provide any insight into the mechanisms for producing the total (i.e., ultimate) effects.

We can make an exactly symmetric argument for the effects from species 2 to 4, by reversing the direction. Species 2 (the pest) has a negative effect on species 4 indirectly through their common predator, which is evaluated by the following expression obtained by exchanging 2 and 4 in (22):

$$\frac{1}{1+\dfrac{\gamma_{34}}{1+\gamma_{23}}}\,\frac{1}{1+\gamma_{23}}\left(-\frac{\alpha_{43}}{\alpha_{44}}\frac{\alpha_{32}}{\alpha_{33}}\frac{1}{\alpha_{22}}\right). \tag{23}$$

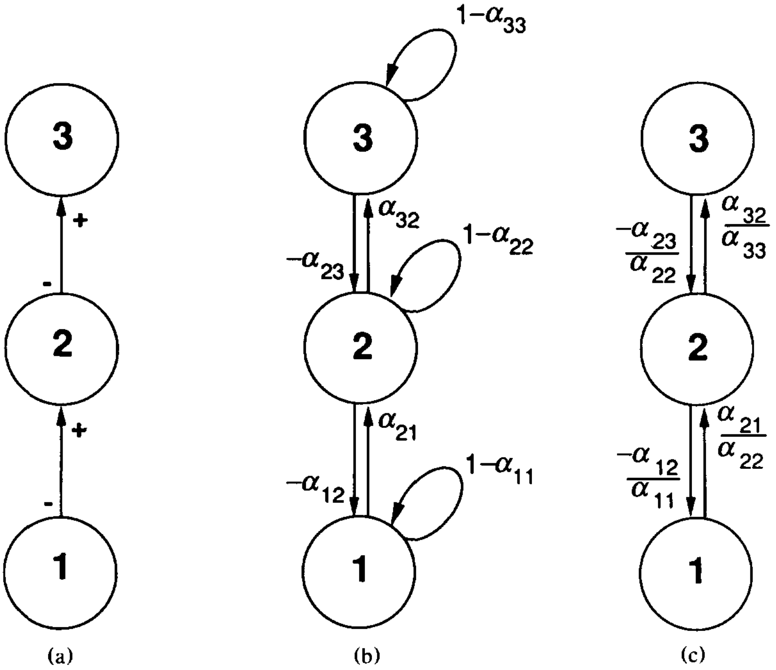
Example 2. Consider a food chain of three trophic levels (Figure 4a), which is identical in structure to a subsystem (consisting of the crop, the pest, and its predator) of the system in the pest control example (Figure 1a). Assume that the community matrix A is given as

$$A=[a_{ij}]=\begin{bmatrix} -\alpha_{11} & -\alpha_{12} & 0 \\ \alpha_{21} & -\alpha_{22} & -\alpha_{23} \\ 0 & \alpha_{32} & -\alpha_{33} \end{bmatrix}, \tag{24}$$

where $\alpha_{ij} > 0$ for any i and j. The immediate and direct effects between species are then given by $B = A + I$ (Figure 4b) and D (Figure 4c), respectively, where

$$D=[d_{ij}]=\begin{bmatrix} 0 & \dfrac{-\alpha_{12}}{\alpha_{11}} & 0 \\ \dfrac{\alpha_{21}}{\alpha_{22}} & 0 & \dfrac{-\alpha_{23}}{\alpha_{22}} \\ 0 & \dfrac{\alpha_{32}}{\alpha_{33}} & 0 \end{bmatrix}. \tag{25}$$

Although the top predator (species 3) and the primary producer (species 1) do not directly interact with each other, they *do* indirectly through the middle species in the food chain (species 2), just as species 2 and 4 do through species 3 in Example 1.



(a) (b) (c)

FIG. 4. (*a*) A food chain. The digraphs represent (*b*) the immediate effect structure and (*c*) the direct effects structure of the system.

A unit increment in inflow to species 1 will have an impact on species 3's abundance through path 1 → 2 → 3, which is evaluated as $(\alpha_{32}/\alpha_{33})(\alpha_{21}/\alpha_{22})(1/\alpha_{11}) > 0$. But this is not the total effect from species 1 to 3. The sum of the effects carried by the first-passage paths from species 1 to 3 is evaluated as

$$\frac{\alpha_{32}}{\alpha_{33}}\sum_{k=0}^{\infty}\left(-\frac{\alpha_{21}}{\alpha_{22}}\frac{\alpha_{12}}{\alpha_{11}}\right)^{k}\frac{\alpha_{21}}{\alpha_{22}}\frac{1}{\alpha_{11}}=\frac{\alpha_{32}}{\alpha_{33}}\frac{1}{1+\gamma_{12}}\frac{\alpha_{21}}{\alpha_{22}}\frac{1}{\alpha_{11}}, \tag{26}$$

which is still positive, but smaller than $(\alpha_{32}/\alpha_{33})(\alpha_{21}/\alpha_{22})(1/\alpha_{11})$. Furthermore, the total effect, including recycling effect carried by the subsequent-passage paths, from species 1 to 3 is given as

$$\begin{aligned}\sum_{k=0}^{\infty}&\left(\frac{\alpha_{32}}{\alpha_{33}}\frac{1}{1+\gamma_{12}}\frac{-\alpha_{23}}{\alpha_{22}}\right)^{k}\frac{\alpha_{32}}{\alpha_{33}}\frac{1}{1+\gamma_{12}}\frac{\alpha_{21}}{\alpha_{22}}\frac{1}{\alpha_{11}}\\&=\frac{1}{1+\dfrac{\alpha_{32}}{\alpha_{33}}\dfrac{1}{1+\gamma_{12}}\dfrac{\alpha_{23}}{\alpha_{22}}}\frac{\alpha_{32}}{\alpha_{33}}\frac{1}{1+\gamma_{12}}\frac{\alpha_{21}}{\alpha_{22}}\frac{1}{\alpha_{11}},\end{aligned} \tag{27}$$

which is still positive but even smaller than the sum of the first passage effects.

Therefore, an increase in inflow to 1 indirectly has a positive effect on species 3's abundance, which corresponds to what is called *bottom-up effect* (e.g., [24]), but the simple product $(\alpha_{32}/\alpha_{33})(\alpha_{21}/\alpha_{22})(1/\alpha_{11})$ would overestimate the actual total effect from species 1 to 3. Similarly, species 3 has an indirect effect on species 1 through species 2, a so-called *top-down effect* (e.g., [24]), evaluated as

$$\frac{1}{1+\dfrac{\alpha_{12}}{\alpha_{11}}\dfrac{1}{1+\gamma_{32}}\dfrac{\alpha_{21}}{\alpha_{22}}}\frac{\alpha_{12}}{\alpha_{11}}\frac{1}{1+\gamma_{32}}\frac{\alpha_{23}}{\alpha_{22}}\frac{1}{\alpha_{33}}. \tag{28}$$

This effect from species 3 to 1 is positive but less than the simple product $(\alpha_{12}/\alpha_{11})(\alpha_{23}/\alpha_{22})(1/\alpha_{33})$.

Example 3. Consider the pest control problem mentioned earlier (Figure 1a). Assume that the dynamics of the pest control system is governed by the set of equations

$$\dot{x}_i = x_i\left(\epsilon_i + \sum_{k=1}^{4} c_{ik}x_k\right), \tag{29}$$

where $i = 1,2,3,4$, and that the removal or addition of species i is made in the rate proportional to the species' abundance, $y_i x_i$. Thus the steady state of the system with these removals or additions is determined by the balance equations

$$x_i\left(\epsilon_i + \sum_{k=1}^{4} r_{ik}x_k + y_i\right) = 0. \tag{30}$$

Then, according to formula (7), we have $\mathrm{d}x_i/\mathrm{d}y_j = s_{ij}x_j^*$. Therefore, a modified version of the chain rule (17) follows for this case:

$$\left[\begin{array}{l}\text{indirect effect from the removal of } j \text{ in a unit ratio } (y_j = -1)\\ \text{to } i\text{'s abundance through a path } j \to k_1 \to k_2 \to \cdots \to k_{l-1} \to i\end{array}\right]$$

$$= -d_{ik_{l-1}} \cdots d_{k_2k_1} d_{k_1j}\frac{1}{-a_{jj}}x_j^*, \tag{31}$$

where $d_{ij} = a_{ij}/(-a_{ii}) = x_i^* r_{ij}/(-x_j^* r_{ii}) = r_{ij}/(-r_{ii})$ and $x_i^*/(-a_{ii}) = x_i^*/(-x_i^* r_{ii}) = -1/r_{ii}$. Thus it can also be expressed as

$$\left[\begin{array}{l}\text{indirect effect from the removal of } j \text{ in a unit ratio } (y_j = -1)\\ \text{to } i\text{'s abundance through a path } j \to k_1 \to k_2 \to \cdots \to k_{l-1} \to i\end{array}\right]$$

$$= -\frac{r_{ik_{l-1}}}{-r_{ii}} \cdots \frac{r_{k_2k_2}}{-r_{k_2k_2}} \frac{r_{k_1j}}{-r_{k_1k_1}} \frac{1}{-r_{jj}}. \tag{32}$$

The latter expression shows that the indirect effect of a unit ratio of removal $(y_j = -1)$ that is brought to the abundance of species i via a path (thus the total effect of the removal made on i's abundance) does not depend on the steady state values x_i^* $(i = 1,2,3,4)$. This fact allows comparison between different subsystems of the pest control system in terms of the influence propagation structure. Let α_{ij} here denote the magnitude of the interaction coefficient $r_{ij}, |r_{ij}|$.

First, consider a subsystem consisting of the crop (species 1) and pest (species 2) alone (model I in Figure 5). What happens if species 2 (the target pest in this example) is directly damaged due to its removal? The direct damage made on the pest (species 2) by its unit ratio of removal $(y_2 = -1)$ is evaluated as $-1/\alpha_{22}$. This damage, however, will be compensated by the boomerang effects that are repeatedly brought back to species 2 via the cycle C_{12} (i.e., $2 \to 1 \to 2$). The boomerang effect of first return via simple cycle C_{12} is evaluated as $c_{12}(-1/\alpha_{22}) = (\gamma_{12}/\alpha_{22}) > 0$. This simple cycle is the only first-passage path from species 2 back to itself. The second-passage path from species 2 back to itself (i.e., the path that starts from species 2, passes through species 2 once, and then ends up with species 2) is given by concatenating two of the same cycle, C_{12}, that is, $C_{12}C_{12} = (C_{12})^2$. Thus, the boomerang effect from a unit ratio of removal of species 2 back to itself via this second-passage path amounts to $(c_{12})^2(-1/\alpha_{22})$. In general, the kth-passage path from species 2 back to itself is given by concatenating k of the cycle, $(C_{12})^k$, and the boomerang effect from a unit ratio of removal of species 2 back to itself via this kth-passage path amounts to $(c_{12})^k(-1/\alpha_{22})$. Thus, the total effects from a unit ratio of removal of species 2 back to itself are given as

$$\frac{-1}{\alpha_{22}} + \sum_{k=1}^{\infty} (c_{12})^k \frac{-1}{\alpha_{22}} = \frac{-1}{\alpha_{22}} + \frac{1}{1+\gamma_{12}} \frac{\gamma_{12}}{\alpha_{22}}. \tag{33}$$

From this, it can be seen that the damage on the pest directly made by a unit ratio of removal [the first term of (33)] is in fact moderated by the

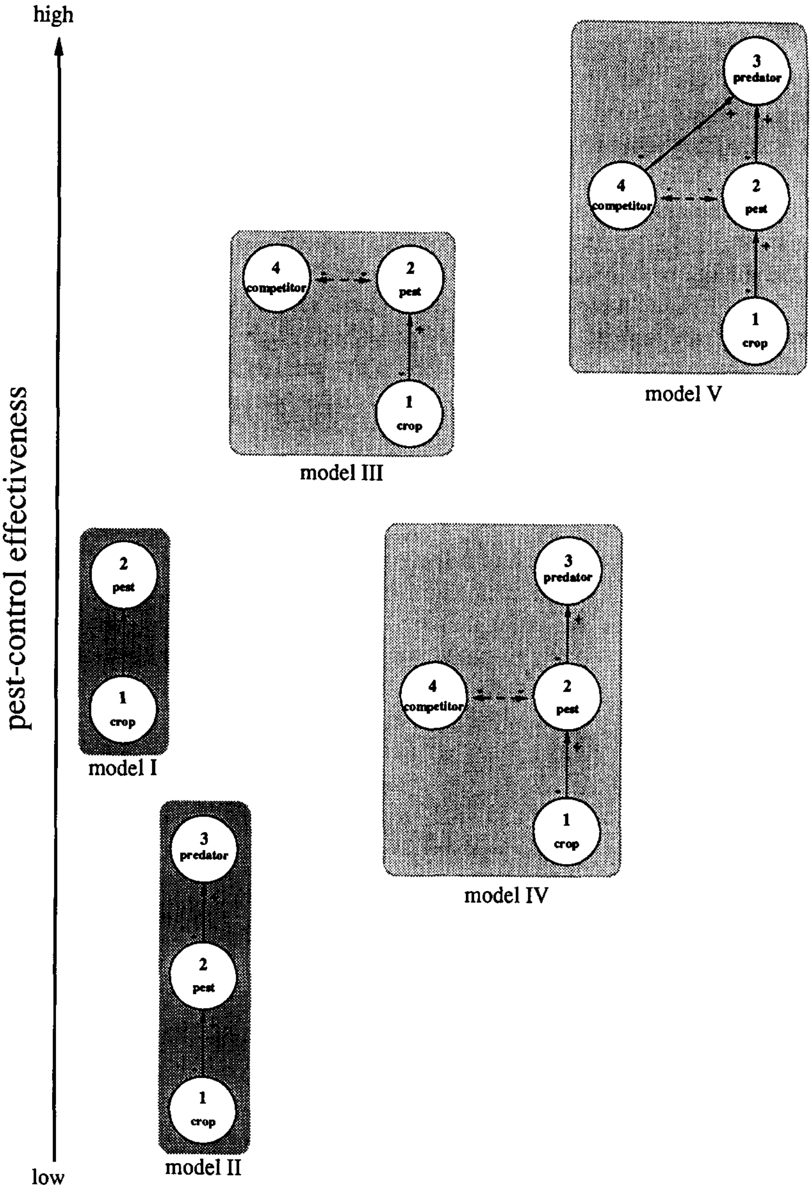


FIG. 5. A summary of the comparison, in terms of the effectiveness of a unit "press" removal of pest in controlling the pest, of alternative subsystem models of the hypothetical pest control system depicted in Fig. 1a. Model I consists of the crop (species 1) and its pest (species 2), model II adds a predator (species 3) for the pest, model III has a competitor (species 4), instead of the predator, for the pest, and model IV has both a predator and competitor. Model V is the full system depicted in Fig. 1a, in which the predator preys on both the pest and its competitor.

positive boomerang effects brought back to the pest via the sequence of cycles $(C_{12})^k$, $k = 1, 2, \cdots$, [the second term of (33)], though this positive effect is smaller by the factor of $1/(1+\gamma_{12})$ than the one via the first-passage cycle alone.

Second, consider the same system (model I) but with predator (species 3) for the pest (species 2) added (model II in Figure 5). The direct damage made on the pest (species 2) by its unit ratio of removal, $-1/\alpha_{22}$, will be compensated by the boomerang effects repeatedly brought back to species 2 via the two cycles, $C_{12}(2 \to 1 \to 2)$ and $C_{32}(2 \to 3 \to 2)$. The boomerang effects of first return via simple cycles C_{12} and C_{32} are evaluated as $(c_{12} + c_{32})(-1/\alpha_{22}) = (\gamma_{12} + \gamma_{32})/\alpha_{22} > 0$. These two simple cycles are the only first-passage paths from species 2 back to itself. The second-passage paths from species 2 back to itself are given by concatenating two cycles, each of which is either C_{12} or C_{32}, with all (four in this case) possible combinations, that is, $C_{12}C_{12}$, $C_{12}C_{32}$,$C_{32}C_{12}$, and $C_{32}C_{32}$, which can be summarized in the form $(C_{12} \vee C_{32})(C_{12} \vee C_{32})$ or $(C_{12} \vee C_{32})^2$, where the symbol "$\vee$" represents the choice between the alternative paths on both sides. Thus, the boomerang effects from a unit ratio of removal of species 2 back to itself via these second-passage paths amount to $(c_{12} + c_{32})^2(-1/\alpha_{22})$. In general, the kth-passage paths from species 2 back to itself are given by concatenating k cycles, each of which is either C_{12} or C_{32}, with all (2^k in this case) possible combinations, which can be summarized as $(C_{12} \vee C_{32})^k$, and the boomerang effects from a unit ratio of removal of a species 2 back to itself via these kth-passage paths amount to $(c_{12} + c_{32})^k(-1/\alpha_{22})$. Thus, the total effects from a unit ratio of removal of species 2 back to itself are given as

$$\frac{-1}{\alpha_{22}} + \sum_{k=1}^{\infty} (c_{12} - c_{32})^k \frac{-1}{\alpha_{22}} = \frac{-1}{\alpha_{22}} + \frac{1}{1+(\gamma_{12}+\gamma_{32})} \frac{\gamma_{12}+\gamma_{32}}{\alpha_{22}}. \quad (34)$$

From this, the compensation of the direct damage on the pest [the first term of (34)] by the positive boomerang effects brought back to the pest via the sequence of cycles, $(C_{12} \vee C_{32})^k$, $k = 1, 2, \cdots$ [the second term of (34)], is more than the case without the predator. Thus, the pest control by a constant rate of removal of the pest is less effective in the setting of model II than in model I (Figure 5). Furthermore, (34) implies that the stronger the feeding interactions $(c_{12} + c_{32})$ are in magnitude, the less effective is the control of the pest by direct removal.

Third, consider model I with the competitor (species 4), instead of the predator (species 3), for the pest added (model III in Figure 5). The direct damage made on the pest by its unit ratio of removal, $-1/\alpha_{22}$, will be moderated by the boomerang effects repeatedly brought back to species 2 via C_{12} but enhanced by those via C_{42}. The boomerang effects of first return via simple cycles C_{12} and C_{42} are evaluated as $(c_{12}+c_{42})(-1/\alpha_{22})=(\gamma_{12}-\gamma_{42})/\alpha_{22}$. These two simple cycles are the only first-passage paths from species 2 back to itself. Thus, just as in the case of model II, the total effects from a unit ratio of removal of species 2 back to itself are given as

$$\begin{aligned}&\frac{-1}{\alpha_{22}}+\sum_{k=1}^{\infty}(c_{12}+c_{42})^k\frac{-1}{\alpha_{22}}\\&=\frac{-1}{\alpha_{22}}+\frac{1}{1+(\gamma_{12}-\gamma_{42})}\frac{\gamma_{12}-\gamma_{42}}{\alpha_{22}}.\end{aligned}\tag{35}$$

From this, the compensation of the damage on the pest directly made by a unit ratio of removal [the first term of Equation (35)] by the boomerang effects to the pest via the sequence of cycles, $(C_{12} \vee C_{42})^k$, $k=1,2,\ldots$ [the second term of (35)], is less than in the case without the pest's competitor. Furthermore, if the boomerang effects via the competitor are greater in magnitude than those via the crop, that is, $\gamma_{42}>\gamma_{12}$, then the direct damage on the pest is enhanced rather than moderated, and these total (negative) boomerang effects are greater in magnitude by the factor of $1/(1+(\gamma_{12}-\gamma_{42}))$ than those via the first-passage paths alone. Therefore, the pest control by a constant rate of removal of the pest is more effective in the setting of model III than in model I (Figure 5).

Fourth, consider the first system with the competitor (species 4) and predator (species 3) for the pest both added (model IV in Figure 5). The direct damage made on the pest by its unit ratio of removal, $-1/\alpha_{22}$, will be moderated by the boomerang effects repeatedly brought back to species 2 via C_{12} and C_{32} but enhanced by those via C_{42}. The boomerang effects of first return via simple cycles C_{12}, C_{32}, and C_{42} are evaluated as $(c_{12}+c_{32}+c_{42})(-1/\alpha_{22})=(\gamma_{12}+\gamma_{32}-\gamma_{42})/\alpha_{22}$. These three simple cycles are the only first-passage paths from species 2 back to itself. Thus, following the same logic as has been used in the preceding cases (models I–III), the total effects from a unit ratio of removal of species 2 back to itself are given as

$$\begin{aligned}&\frac{-1}{\alpha_{22}}+\sum_{k=1}^{\infty}(c_{12}+c_{32}+c_{42})^k\frac{-1}{\alpha_{22}}\\&=\frac{-1}{\alpha_{22}}+\frac{1}{1+(\gamma_{12}+\gamma_{32}-\gamma_{42})}\frac{\gamma_{12}+\gamma_{32}-\gamma_{42}}{\alpha_{22}}.\end{aligned}\tag{36}$$

From this, it can be seen that the effectiveness of the pest control with model IV, measured by the total (ultimate) damage on the pest made by a unit ratio of removal of the pest, should be between those in models II and III (Figure 5).

Finally, consider the full picture of the pest control example depicted in Figure 1a, that is, the system consisting of the same members as model IV but in which the predator of the pest also preys on the pest's competitor (model V in Figure 5). The direct damage made on the pest by its unit ratio of removal, $-1/\alpha_{22}$, will be moderated by the boomerang effects repeatedly brought back to species 2 via C_{12} and the group of cycles of the form $2 \to 3(\to 4 \to 3)^* \to 2$, which are C_{32} with $(C_{43})^k$ added in the middle (Figure 6). But, it will be enhanced by the boomerang effects vial three groups of cycles, $2 \to 4(\to 3 \to 4)^* \to 2$, $2 \to 3(\to 4 \to 3)^* \to 4 \to 2$, and $2 \to 4(\to 3 \to 4)^* \to 3 \to 2$, which are, respectively, C_{42}, C_{432}, and C_{342} with $(C_{43})^k$ added in the middle, where C_{ijk} denotes cycle $k \to j \to i \to k$ (Figure 6). The boomerang effects of first return via these cycles are evaluated as

$$\left(c_{12} + \frac{1}{1-c_{43}}c_{32} + \frac{1}{1-c_{34}}c_{42} + \frac{1}{1-c_{43}}c_{432} + \frac{1}{1-c_{34}}c_{342}\right)\frac{-1}{\alpha_{22}}$$
$$= \left[\gamma_{12} + \frac{1}{1+\gamma_{43}}\gamma_{32} - \frac{1}{1+\gamma_{43}}\gamma_{42} - \frac{1}{1+\gamma_{43}}\gamma_{432} - \frac{1}{1+\gamma_{43}}\gamma_{342}\right]\frac{1}{\alpha_{22}}. \tag{37}$$

where $\gamma_{ijk} = |c_{ijk}|$ with c_{ijk} representing the effect associated with C_{ijk}, that is, $c_{ijk} = (a_{ki}/a_{kk})(a_{ij}/a_{ii})(a_{jk}/a_{jj})$. These cycles are the only first-passage paths from species 2 back to itself. Thus, from the same reasoning as in the previous cases (model I–IV), it follows that the total effects from a unit ratio of removal of species 2 back to itself are given as

$$\frac{-1}{\alpha_{22}} + \sum_{k=1}^{\infty}\left(c_{12} + \frac{1}{1-c_{43}}c_{32} + \frac{1}{1-c_{34}}c_{42} + \frac{1}{1-c_{43}}c_{432} + \frac{1}{1-c_{34}}c_{342}\right)^k$$
$$\times \frac{-1}{\alpha_{22}}$$
$$= \frac{-1}{\alpha_{22}}$$
$$+ \frac{\gamma_{12} + \frac{1}{1+\gamma_{43}}\gamma_{32} - \frac{1}{1+\gamma_{43}}\gamma_{42} - \frac{1}{1+\gamma_{43}}\gamma_{432} - \frac{1}{1+\gamma_{43}}\gamma_{342}}{1 + \left(\gamma_{12} + \frac{1}{1+\gamma_{43}}\gamma_{32} - \frac{1}{1+\gamma_{43}}\gamma_{42} - \frac{1}{1+\gamma_{43}}\gamma_{432} - \frac{1}{1+\gamma_{43}}\gamma_{342}\right)}$$
$$\times \frac{1}{\alpha_{22}}. \tag{38}$$

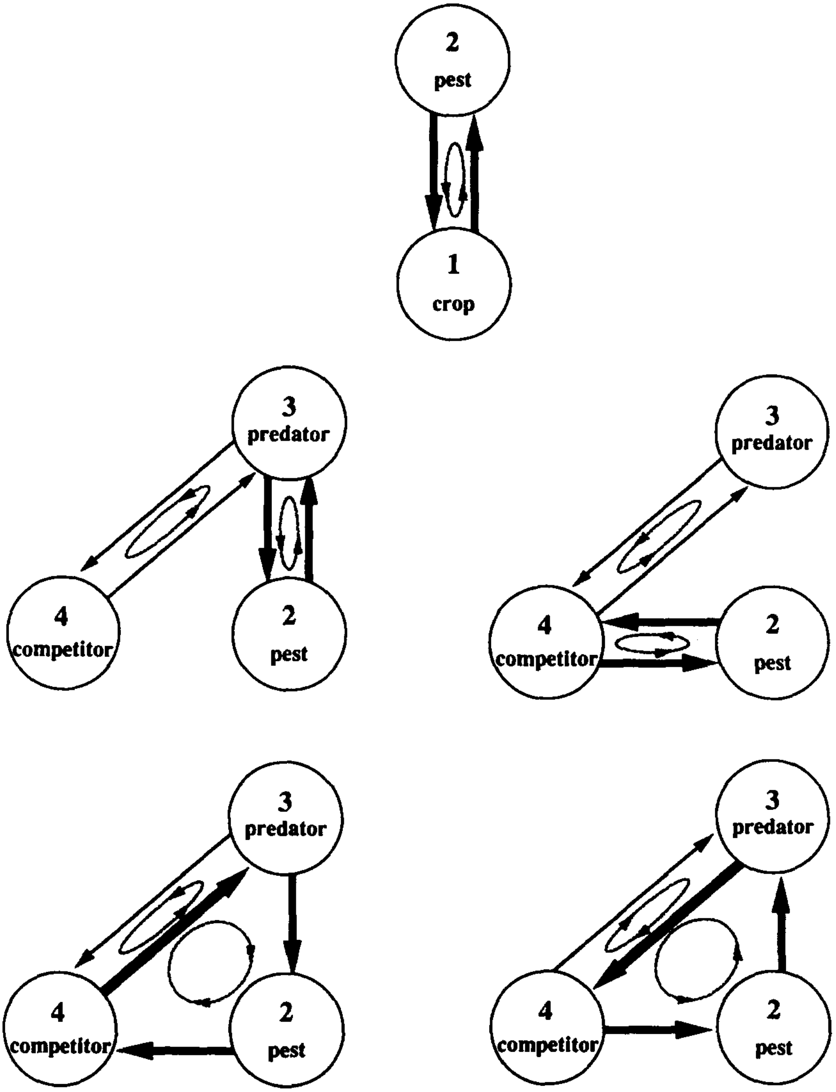


FIG. 6. The alternative first-passage paths (cycles) connecting the pest back to itself for model V in Figure 5. These paths (cycles) consists of a primary cycle (formed by those links that are represented in the figure with thick lines) connecting the pest back to itself, together with secondary cycles added in any number in the middle of the primary cycle.

Note that the addition of the links between species 3 and 4 produces a pair of cycles of length three in both directions, C_{432} and C_{342}, which bring about positive feedbacks with the magnitude of γ_{432} and γ_{432}, respectively. From (38), it can be shown that with these key links, it is possible for the total (ultimate) damage on the pest due to a unit ratio of removal of the pest in the setting of model V to exceed even that of model III (Figure 5), unless $\gamma_{432} = \gamma_{432}$, that is, the two cycles C_{432} and C_{342} in the opposite directions carry exactly the same magnitude of effects (see Appendix for a proof). Alternatively, the necessary and sufficient condition for the pest control in the setting of model V to be more effective than that of model III is given as follows: either two inequalities $|d_{24}d_{43}| < |d_{23}|$ and $|d_{34}d_{42}| > |d_{32}|$ both hold, or the opposite inequalities $|d_{24}d_{43}| > |d_{23}|$ and $|d_{24}d_{43}| < |d_{23}|$ both hold (see Appendix for a proof). This condition can be interpreted as follows: for the direct versus indirect effects (via species 4) between species 2 and 3, their relative dominance in magnitude is reversed in the two opposite directions (i.e., if direct effects dominate over indirect ones in one direction, then the opposite is the case for the reversed direction).

Example 4. Suppose a system consisting of three competitors (Figure 7a). Assume that the community matrix A is given as

$$A = [a_{ij}] = \begin{bmatrix} -\alpha_{11} & -\alpha_{12} & -\alpha_{13} \\ -\alpha_{21} & -\alpha_{22} & -\alpha_{23} \\ -\alpha_{31} & -\alpha_{32} & -\alpha_{33} \end{bmatrix}, \tag{39}$$

where $\alpha_{ij} > 0$ for any i and j. The immediate and direct effects between species are then given by $B = A + I$ (Figure 7b) and D (Figure 7c), respectively, where

$$D = [d_{ij}] = \begin{bmatrix} 0 & \dfrac{-\alpha_{12}}{\alpha_{11}} & \dfrac{-\alpha_{13}}{\alpha_{11}} \\ \dfrac{-\alpha_{21}}{\alpha_{22}} & 0 & \dfrac{-\alpha_{23}}{\alpha_{22}} \\ \dfrac{-\alpha_{31}}{\alpha_{33}} & \dfrac{-\alpha_{32}}{\alpha_{33}} & 0 \end{bmatrix}. \tag{40}$$

Although the direct effect of a unit increment in inflow to species 1 made on species 3's abundance is negative, $(-\alpha_{31}/\alpha_{33})(1/\alpha_{11}) < 0$, the indirect effects make a difference. The indirect effects carried by the first-passage paths from species 1 to 3 are evaluated as

$$\frac{-\alpha_{32}}{\alpha_{33}} \sum_{k=0}^{\infty} \left(\frac{\alpha_{21}}{\alpha_{22}} \frac{\alpha_{12}}{\alpha_{11}} \right)^k \frac{-\alpha_{21}}{\alpha_{22}} \frac{1}{\alpha_{11}} = \frac{\alpha_{32}}{\alpha_{33}} \frac{1}{1-\gamma_{12}} \frac{\alpha_{21}}{\alpha_{22}} \frac{1}{\alpha_{11}}, \tag{41}$$

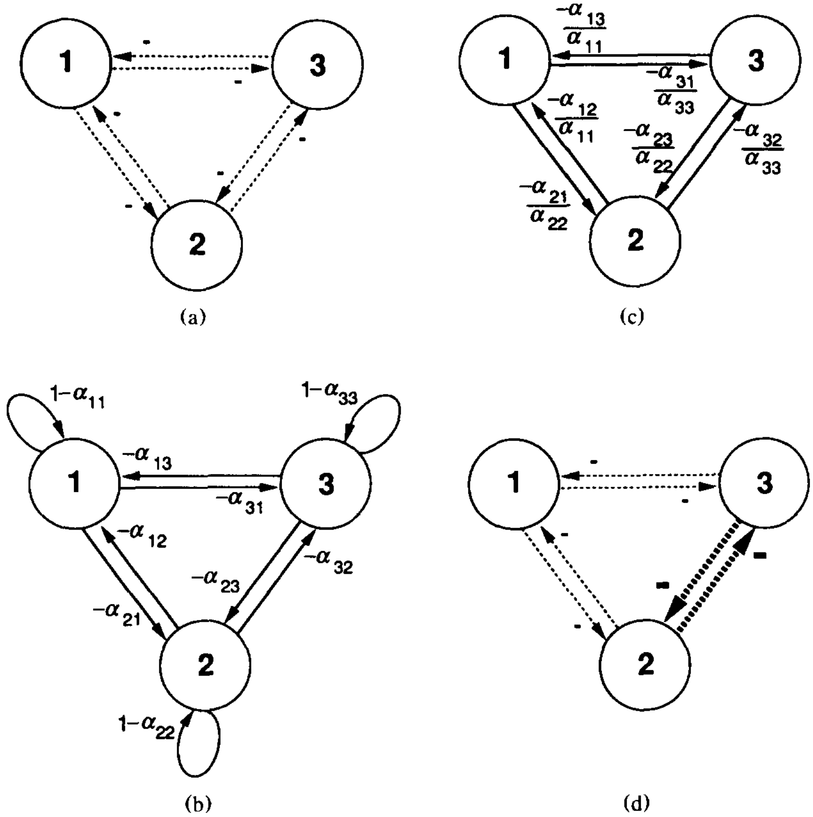


FIG. 7. (*a*) A hypothetical system consisting of three competitors. The digraphs represent (*b*) the immediate effect structure and (*c*) the direct effects structure of the system. (*d*) If the competition between species 2 and 3 increases, then competitive negative interactions between species 1 and 3 may be transformed into positive mutualistic ones.

which is positive. The total (net) effects from species 1 to 3 are the sum of these positive indirect effects and negative direct ones, multiplied by the cycling coefficient, $1/(1+\alpha_{33})$, where α_{33} denotes the first-passage effects from 3 to itself. Thus, if the indirect effect given by (41) is greater in magnitude than the direct effect, species 1 gives in net a positive influence on species 3, in spite of its apparent (direct) negative interactions with species 3. For example, if the competition between species 2 and 3 increases for some reason, then competitive negative interactions between species 1 and 3 may be transformed into positive mutualistic ones (Figure 7d).

3.2. *THREE BASIC MECHANISMS*

These examples suggest the following three basic mechanisms through which indirect effects contribute to generating complex and contingent interactions among species in an ecological network.

(1) *Influence globalization and diffusing.* It is clearly demonstrated, particularly in Example 3, that as the size of a system grows, the number and length of paths available to transmit influences among constituent species drastically increase. The influence of local events should spread out through the system over these paths. Thus, longer paths, branching and intersecting with one another, provide a mechanism for making global influence of local causality. Among a bundle of parallel paths connecting two species, no single path (causal chain) is solely responsible for their interactions but rather any path is responsible, making diffusive the "controlling" of one species by another.

(2) *Effect amplification and reduction by cycles.* A point, repeatedly appearing throughout the above examples, can be captured in its most general form by a simple mathematical relationship (Figure 8):

$$effect_{out} = (1 + c + c^2 + \cdots)effect_{in} = \frac{1}{1-c}effect_{in}, \qquad (42)$$

where $effect_{in}$ denotes an effect that is coming into a cycle (more strictly, a group of parallel cycles, which are here described as a cycle for simplicity), $effect_{out}$ is the accumulated sum of effects originating in

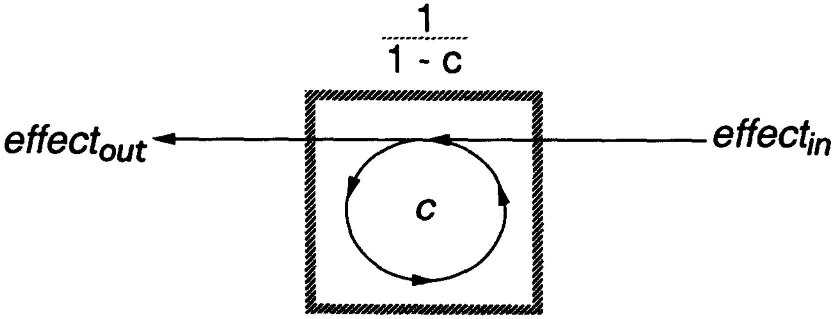


FIG. 8. An illustration of the effect of amplification and reduction by cycles in the most general form. An effect coming into a cycle, $effect_{in}$, generates (is transformed into) the accumulated sum of effects coming out of the cycle, $effect_{out}$, which is $effect_{in}$ multiplied by $1/(1-c)$, where c is the first return effect associated with the cycle. The cycle amplifies an effect coming in if $1 > c > 0$, while reducing it if $0 > c > -1$.

effect$_{in}$ and coming out of the cycle, and c is the first return effect associated with the cycle, which equals the product of the direct effects ($d_{ij} = -a_{ij}/a_{ii}$) associated with the direct links constituting the cycle (for example, for a cycle $3 \rightarrow 4 \rightarrow 3$, $c = d_{34}d_{43}$, and for a group of cycles, c equals the sum of the products associated with the cycles). Relation (42) indicates that a cycle does not change the sign but only the magnitude of any effect passing through it, and that a positive cycle (i.e., a cycle with a positive value for its first return effect c) amplifies, while a negative cycle dampens (reduces), the effect.

(3) *Interaction sign switching by competitive parallel paths.* As demonstrated in Example 4, the net effect from one species to another can be changed even qualitatively, that is, in its sign, when the dominance in magnitude between the positive and negative effects carried by parallel paths connecting these species is altered. That is, if the sum of the effects carried by positive paths connecting one species to another (where a positive path is such that the product of the direct effects associated with the direct links constituting it is positive) is greater than that for negative paths connecting those species, then the net effect between these species is positive; in the opposite cause, the net effect is negative. Thus, one can imagine that an increase only in the magnitude of a direct link between two species involved in one of the positive paths connecting species A to B may well change the net (total) effect from species A to B, from a negative one into a positive one.

4. CONCLUDING REMARKS

The theory of indirect effects developed above may also be used to design interaction networks for management problems, such as pest control and fishery, because it allows one to not only prevent negative (undesirable) results, specifically by identifying key paths responsible for such results [e.g., the predation cycle, $C_{32}(2 \rightarrow 3 \rightarrow 2)$, in the pest control example, i.e., Example 3 in Section 3], but to also more actively discover new paths, possibly a bundle of long (distant) indirect effect paths through which more effective control can be exerted.

In identifying or discovering such effective paths, both in negative and positive ways, the key task is clearly to assess the nature of each individual path, in terms of the changes in magnitude and sign that any given effect should experience while it passes along the path. The chain rule derived above provides a useful means for this task, which can be applied to any form of interactive network, however complex the structure. Furthermore, the three basic mechanisms for generating complex interactions that have been identified above may provide a general guide in this assessment.

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APPENDIX

From (38), the total effects on the pest made by a unit ratio of removal in the setting of model V of Example 3 exceeds (toward the negative direction) that of model III if and only if

$$\gamma_{12} - \gamma_{42} > \gamma_{12} + \frac{1}{1+\gamma_{43}}\gamma_{32} - \frac{1}{1+\gamma_{43}}\gamma_{42} - \frac{1}{1+\gamma_{43}}\gamma_{432} - \frac{1}{1+\gamma_{43}}\gamma_{342}, \tag{A.1}$$

that is, $\gamma_{43}\gamma_{42} + \gamma_{32} < \gamma_{432} + \gamma_{342}$. This may be rewritten as

$$\begin{aligned} &\alpha_{24}\alpha_{43}\alpha_{32}\alpha_{44} + \alpha_{23}\alpha_{34}\alpha_{42}\alpha_{44} - \alpha_{23}\alpha_{32}\alpha_{44}\alpha_{44} - \alpha_{24}\alpha_{42}\alpha_{34}\alpha_{43} \\ &\quad = (\alpha_{24}\alpha_{43} - \alpha_{23}\alpha_{44})\,\alpha_{32}\alpha_{44} + (\alpha_{23}\alpha_{44} - \alpha_{24}\alpha_{43})\,\alpha_{42}\,\alpha_{34} \\ &\quad = (\alpha_{24}\alpha_{43} - \alpha_{23}\alpha_{44})(\alpha_{32}\alpha_{44} - \alpha_{42}\,\alpha_{34}) > 0, \end{aligned} \tag{A.2}$$

This implies either

$$\alpha_{24}\alpha_{43} - \alpha_{23}\alpha_{44} > 0 \quad \text{and} \quad \alpha_{32}\alpha_{44} - \alpha_{42}\,\alpha_{34} > 0 \tag{A.3}$$

or

$$\alpha_{24}\alpha_{43} - \alpha_{23}\alpha_{44} < 0 \quad \text{and} \quad \alpha_{32}\alpha_{44} - \alpha_{42}\,\alpha_{34} < 0. \tag{A.4}$$

Condition (A.3) is rewritten as

$$\frac{\alpha_{24}\alpha_{43}}{\alpha_{23}} > \alpha_{44} > \frac{\alpha_{42}\alpha_{34}}{\alpha_{32}}, \tag{A.5}$$

whereas (A.4) is rewritten as

$$\frac{\alpha_{24}\alpha_{43}}{\alpha_{23}} < \alpha_{44} < \frac{\alpha_{42}\alpha_{34}}{\alpha_{32}}. \tag{A.6}$$

Now, (A.5) implies $\alpha_{24}\alpha_{43}/\alpha_{23} > \alpha_{42}\alpha_{34}/\alpha_{32}$, that is, $\alpha_{24}\alpha_{43}\alpha_{32} > \alpha_{23}\alpha_{34}\alpha_{42}$, thus, $\gamma_{432} > \gamma_{342}$. Similarly, (A.6) implies $\gamma_{432} < \gamma_{342}$. Therefore, (A.5) or (A.6) implies $\gamma_{432} \neq \gamma_{342}$. Inversely, if $\gamma_{432} \neq \gamma_{342}$, thus $\alpha_{24}\alpha_{43}/\alpha_{23} \neq \alpha_{42}\alpha_{34}/\alpha_{32}$; then choosing α_{44} between the two sides of this inequality, we have either (A.5) or (A.6). Therefore, $\gamma_{432} \neq \gamma_{342}$ is necessary and sufficient condition that it is possible for the total effects on the pest in the case of model V to exceed (toward the negative direction) that of model III.

Alternatively, (A.5) can be rewritten as

$$\frac{\dfrac{\alpha_{24}}{\alpha_{22}}\,\dfrac{\alpha_{43}}{\alpha_{44}}}{\dfrac{\alpha_{23}}{\alpha_{22}}} > 1 > \frac{\dfrac{\alpha_{42}}{\alpha_{44}}\,\dfrac{\alpha_{34}}{\alpha_{33}}}{\dfrac{\alpha_{32}}{\alpha_{33}}}, \qquad \text{(A.7)}$$

which implies $(\alpha_{24}/\alpha_{22})(\alpha_{43}/\alpha_{44}) > \alpha_{23}/\alpha_{22}$ and $\alpha_{32}/\alpha_{33} > (\alpha_{42}/\alpha_{44})(\alpha_{34}/\alpha_{33})$, that is, $|d_{24}d_{43}| > |d_{23}|$ and $|d_{24}d_{43}| > |d_{23}|$. Similarly, (A.6) implies $|d_{24}d_{43}| > |d_{23}|$ and $|d_{24}d_{43}| > |d_{23}|$. Therefore, the necessary and sufficient condition for the pest control in the setting of model V to be more effective than in that of model III is given as follows: either two inequalities $|d_{24}d_{43}| < |d_{23}|$ and $|d_{34}d_{42}| > |d_{32}|$ both hold, or the opposite inequalities $|d_{24}d_{43}| > |d_{23}|$ and $|d_{24}d_{43}| > |d_{23}|$ both hold.

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