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I.C.T.P., P.O. BOX 586, 34100 TRIESTE, ITALY, CABLE: CENTRATOM TRIESTE

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"Indirect Effects in Ecological Networks"

M. HIGASHI
Ryukoku University
Faculty of Science and Technology
Otsu 520-21
Japan

These are preliminary lecture notes, intended only for distribution to participants.

A lecture note for the third "Autumn Course on Mathematical Ecology" participants

INDIRECT EFFECTS IN ECOLOGICAL NETWORKS

Masahiko Higashi† & Hisao Nakajima††

†Ryukoku University, Otsu 520-21, Japan
††Ritsumeikan University, Kyoto 603, Japan

1. Introduction

1.1. Mechanism for complex causality in an ecosystem

What happens to each component constituting an ecosystem when a local disturbance takes place within the system? The abundance of some species would decrease, or even go extinct, but some other would increase its abundance.

As an example, consider the problem of controlling a pest (species 1) damaging an agricultural crop (species 5), both members of an ecological interaction network (Fig. 1).

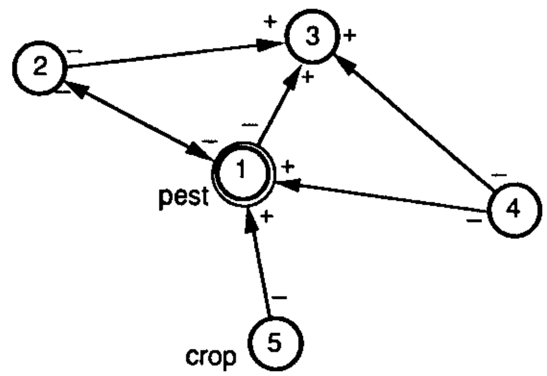


Fig. 1. Pest control example

A direct strike on the pest will not bring so much effect to reduce its abundance, because the reduction in abundance of the pest species will cause both a reduction in its predator's abundance and an increase in its food (resource), including our objective crop, which will in turn bring about a recovery of the pest. Further, if the treatment for introducing that direct impact on the pest affects other members of the community, as it is very likely in real situations, the net result could be even more disappointing. For instance, a damage made by this treatment on the competitor (species 2) of the pest would indirectly benefit the pest, and this positive effect on the pest would dominate over the negative effect that originates in the direct strike on it and subsequently get mild due to indirect effects brought back from its predators and resources.

Exactly the same cause would lead to quite different, and even opposite (from negative to positive, or vice versa), results if the structure of a given system is modified, or if the system is put in a larger network. A pest that is difficult to cope with would become manageable, or, on contrary, it would get worse. Thus, the causal relationships between components of a system vary depending on the network that connects those components.

The main purpose of this note is to present a mathematical method for analyzing the entire structure of influences that are generated by a change in the growth rate of a component species or some parameters involved in a local process within an ecosystem, and propagated, as indirect effects, through the interaction network of the system. As the pest control example illustrates, this analysis of indirect effects should elucidate, for a given system, why and how those particular impacts take place on the system components (e.g., less effective control, or even undesirable enhancement, of the pest) when a particular local cause is introduced into a part of the system (e.g., direct strike on the pest, or that of both the pest and its competitor). Further, this analysis can be used to predict the outcomes under new situations that would happen in future. This implies, for management problems such as pest control, fishery, and so on, that one can not only prevent negative (undesirable) results but, more actively, discover new paths through which more effective control can be exerted. Also, the analysis of the entire structure of influence propagated through an ecosystem network will provide an insight into the organization of the ecosystem; specifically, it may effectively distinguish the particular niche that each constituent species occupies in the system under specific circumstances.

1.2. Review of inflow and parameter sensitivity analyses

As preparation, we review basic results on the inflow and parameter sensitivity analyses (Nakajima 1988), which evaluate the total (net) change in the abundance of each component species of an ecosystem caused by a unit of change in the growth rate

(net production) of a component species and a unit of change in the value of a parameter involved in a local process of the ecosystem, respectively.

Consider an ecological network consisting of n component species (each may represent a species population, trophic guild, or some other unit of ecological interaction at the level of concern) that interact one another. Let x_i denote the abundance of component species i. Assume that growth rate of each species i is a function of standing stocks: $g_i(x_1, x_2, ..., x_n)$. Suppose now the system is in a steady state. At a steady state, the growth rate of each compartment i is zero:

$$g_i(x1, x2, ..., x_n) = 0 \tag{1.1}$$

for $i = 1, 2, ..., n$.

a. Inflow sensitivity

Suppose now that a small amount of inflow z_i is introduced into species i. This addition of z_i moves the system to a new steady state that is determined by:

$$g_i(x_1(z_i), x_2(z_i), ..., x_n(z_i)) + z_i = 0 \tag{1.2}$$

for $i = 1, 2, ..., n$. By taking the derivatives of this set of equations with respect to z_j at the steady state, we have:

$$\sum_{k=1}^{n} a_{ik}s_{kj} = -\delta_{ij} \tag{1.3}$$

where

$$a_{ik} = \frac{\partial g_i}{\partial x_k} \tag{1.4}$$

evaluated at the steady state, and

$$s_{kj} = \frac{dx_k(0)}{dz_j} \tag{1.5}$$

In matrix form,

$$A\,S = -I \tag{1.6}$$

where $A = [a_{ik}]$, $S = [s_{ij}]$, and I is identity matrix. From this, it follows that

$$S = -A^{-1} \tag{1.7}$$

Matrix A is often in literature referred to as community matrix, and we call S sensitivity matrix, whose element s_{ij} represents the change in the abundance of species i caused by a unit of change in the growth rate of species j.

b. Parameter sensitivity

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 equation:

$$g_i(x_1(p), x_2(p), \ldots, x_n(p); p) = 0 \tag{1.8}$$

for $i = 1, 2, \ldots, n$. By taking the derivatives of this set of equations with respect to p, we have the following:

$$\sum_{k=1}^{n} a_{ik}\frac{dx_k}{dp} = -\frac{\partial g_i}{\partial p} \tag{1.9}$$

In matrix form,

$$A\begin{bmatrix}\frac{dx_1}{dp}\\ \vdots \\ \frac{dx_n}{dp}\end{bmatrix} = -\begin{bmatrix}\frac{\partial g_1}{\partial p}\\ \vdots \\ \frac{\partial g_n}{\partial p}\end{bmatrix} \tag{1.10}$$

From this, it follows:

$$\begin{bmatrix}\frac{dx_1}{dp}\\ \vdots \\ \frac{dx_n}{dp}\end{bmatrix} = -A^{-1}\begin{bmatrix}\frac{\partial f_1}{\partial p}\\ \vdots \\ \frac{\partial f_n}{\partial p}\end{bmatrix} = S\cdot\begin{bmatrix}\frac{\partial f_1}{\partial p}\\ \vdots \\ \frac{\partial f_n}{\partial p}\end{bmatrix} \tag{1.11}$$

This implies a kind of chain rule:

$$\frac{dx_i}{dp} = \sum_{k=1}^{n} s_{ij}\frac{\partial g_j}{\partial p} = \sum_{k=1}^{n} \frac{dx_i}{dz_j}\frac{\partial g_j}{\partial p} \tag{1.12}$$

Equation (1.11) shows that the sensitivity of x_i with respect to parameter p can be decomposed into the part represented by S and the part represented by $\partial g_j/\partial p$; the former part is global in nature, involving the entire network (in the matrix inversion), whereas the latter is local in nature, each involving the dependency on p of the growth rate of only one individual species. Thus, the indirect effect analysis of parameter sensitivity can be reduced to that of inflow sensitivity S. Therefore, we will focus on the latter in the rest of the present note.

2. Chain rule approach

2.1. Temporal expansion of the total effects

Each element s_{ij} of sensitivity matrix S represents the total effects (in terms of change in steady state abundance) on species i from a unit of cause (in terms of a unit of change in growth rate) from species j. This total effects can be viewed as the sum of the effects brought by paths connecting j to i throughout time; that is, one can imagine "age distribution" within this total effects, s_{ij} (Fig. 2).

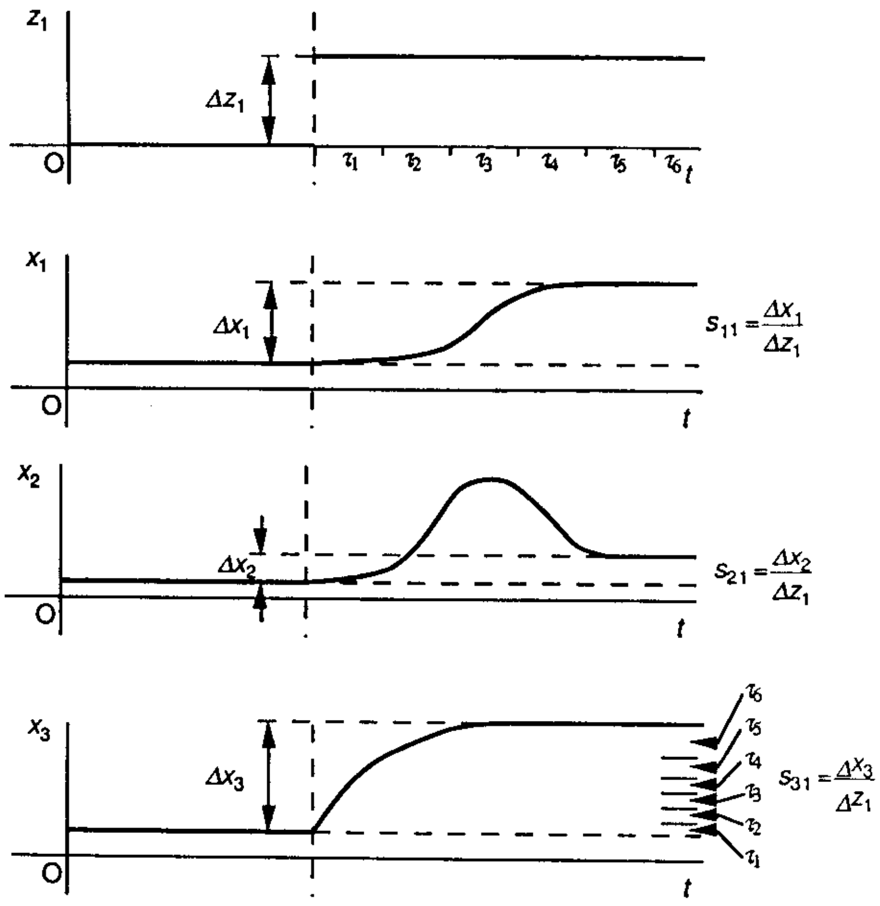


Fig. 2. An illustration of inflow sensitivity as the total effect on the abundance of each species caused by a unit of change in the abundance of specific species (species 1 in this example), and the "age structure" within those total effects.

a. Discrete time case

In discrete time framework, which is easier for intuitive visualization, the temporal expansion, or age distribution, of total effects, s_{ij}, can be given in the form of the matrix expansion:

$$S = -A^{-1} = I + (I+A) + (I+A)^2 + \dots \quad (2.1)$$

The (i,j) element is given as:

$$s_{ij} = \delta_{ij} + b_{ij} + \sum_{k=1}^{n} b_{ik} b_{kj} + \cdots \quad (2.2)$$

where $b_{ij} = \delta_{ij} + a_{ij}$. The first term corresponds to the initial impact (a unit of change in growth rate of each species), the second the effects arriving at i at present (t=0) that is caused by the impact made on j at the previous time (t=-1), and the third term is the sum of effects that originate in the impact made on j at two units of time before (t=-2) and travel through paths $j \rightarrow k \rightarrow i$ in two units of time, arriving at i at present (t=0), and so on (Box 1).

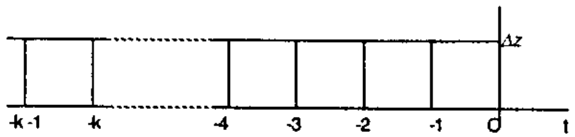
Box 1

$$x(t+1)= x(t) + g_i \ , \qquad i=1,\dots,n$$

Linearization of Dynamical Equation

$$x_i(t) = x_i^* + \xi_i(t) \ , \qquad i=1,\dots,n$$

$$\xi_i(t+1) = \xi_i(t) + \sum_{j=1}^{n} a_{ij}\xi_j(t), \qquad i=1,\dots,n$$



$$I\Delta z$$

$$+(I+A)\Delta z$$

$$+(I+A)^2\Delta z$$

$$+(I+A)^3\Delta z$$

$$+(I+A)^k\Delta z$$

↓

Total effect

$$\sum_{k=0}^{\infty}(I+A)^k\Delta z = -A^{-1}\Delta z$$

b. Continuous time case

In continuous time framework, the temporal expansion of total effects, s_{ij}, can be given in the form of the matrix expansion (Box 2):

$$S = -A^{-1} = \int_{-\infty}^{0} e^{-At}dt \qquad (2.3)$$

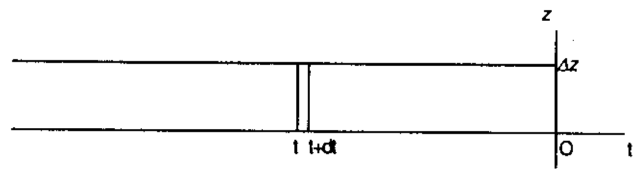
Box 2

$$\dot{x}_i = g_i \ , \qquad i=1,\dots,n$$

Linearization of Dynamical Equation

$$x_i(t) = x_i^* + \xi_i(t) \ , \qquad i=1,\dots,n$$

$$\dot{\xi}_i = \sum_{j=1}^{n} a_{ij}\xi_j, \qquad i=1,\dots,n$$



Effect from change Δz in the past time interval [t, t+dt] $\quad e^{-At}dt\,\Delta z$

↓

Total effect $\quad \int_{-\infty}^{0} e^{-At}dt\,\Delta z = -A^{-1}\Delta z$

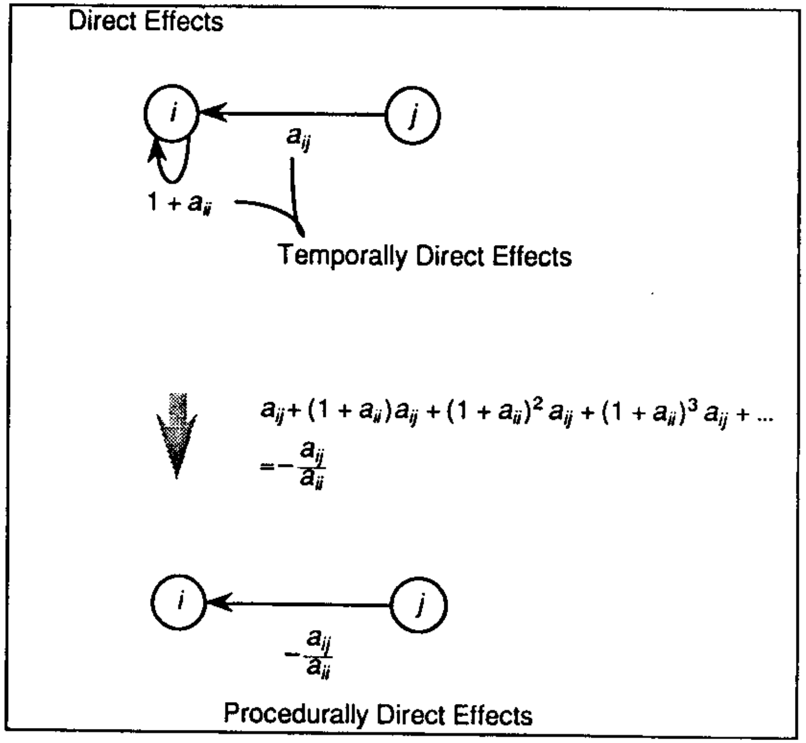
2.2. Partitioning of the total effects according to their route paths

In the following, for the sake of simplicity, we will focus on the case of discrete time, though the conclusions hold for the continuous time case.

By re-aggregating the pieces of effect from j to i according to the routes they take to travel from j to i, we get route-partitioning of the total effects from j to i, s_{ij}. The first step for this procedure is to group together all the effects associated with direct link from j to i ($j \neq i$). This sum amounts to $-a_{ij}/a_{ii}$, and it is referred to as the procedurally (route) direct effect from j *to* i (Box 3). Let d_{ij} denote this procedurally direct effect from j *to* i. Thus,

$$d_{ij} = \begin{cases} \frac{a_{ij}}{-a_{ii}} & (i \neq j) \\ 0 & (i = j) \end{cases} \qquad (2.4)$$

Box 3



Let $D = [d_{ij}]$ denote the matrix of procedurally direct effect. In terms of procedurally direct effects, the total of effects (generated by a unit of impact on j) associated with any particular route, $j \to k \to h \to \cdots \to m \to i$, is given as:

$$\frac{a_{im}}{-a_{ii}} \cdots \frac{a_{hk}}{-a_{hh}} \frac{a_{kj}}{-a_{kk}} \frac{1}{-a_{jj}} \qquad (2.5)$$

Therefore, the total of effects carried by paths of length k connecting j to i is given as the (i, j) th element of matrix $D^k C$, where C is a diagonal matrix with $-1/a_{ii}$ as (i, i)th element, and the total effects from j to i, s_{ij}, is given as the (i, j) th element of matrix series, $IC + DC + D^2C + \cdots = (I + D + D^2 + \cdots)C = (I - D)^{-1}C$. Thus,

$$S = IC + DC + D^2C + \cdots = (I + D + D^2 + \cdots)C = (I - D)^{-1}C \qquad (2.6)$$

2.3. A theory of indirect effects propagation analogous to Markov chain theory

The results that we have derived so far suggest that the multiplication of elements of matrix D along with a specific path of concern gives the total effect that is carried by that path. In this sense, matrix D, which can be derived from community matrix A (thus, from sensitivity matrix $S = -A^{-1}$), characterizes the topological structure without temporality of influences propagated, as indirect effects, through the interaction network of an ecosystem. On the other hand, matrix A characterizes the temporal pattern of the propagation of influences through the network.

For the influence propagation process through an ecological network, characterized by matrix A, we may construct a theory analogous to Markov chain theory. Specifically, suppose that matrix A is corresponded to the transition matrix $P = [p_{ij}]$ of a Markov chain. Then, the procedurally direct effect from j to i, represented by each element d_{ij} of matrix D, corresponds to the residence time in state j on a visit directly from state i. The total effect from j to i, represented by each element s_{ij} of matrix $S = -A^{-1}$, corresponds to the total number of visits to state j that the Markov chain makes when it starts from state i. Also, corresponding to the probability of the Markov chain ever reaching to j starting from i, s_{ij}/s_{ii} represents the first-passage effects, i.e., the total of effects originating in j that arrive at i for the first time. In other words, the difference, $s_{ij} - s_{ij}/s_{ii}$, represents the recycled (revisiting) effects, i.e., the components of the total effects that passed through j at least once in the past and has returned to j. Thus,

[Total effects from j to i] = [first passage effects] + [revisiting effects]
$s_{ij} = s_{ij}/s_{ii} + (s_{ij} - s_{ij}/s_{ii})$

3. Conjugate variables approach

In this section, we explore a completely different approach to the analysis of indirect effects propagated in the network of ecological interactions. The basic idea of this approach lies in viewing each pair of variables (x_i, z_i) as conjugate variables, and the selection of a set of n independent variables by picking up one variable from each conjugate pair; the rest of variables are viewed as dependent variables. Viewing the steady state condition

$$g_i(x_1, x_2, ..., x_n) + z_i = 0 \qquad (3.1)$$

for $i = 1, 2, ..., n.$, as the set of equations that define the relationship among $2n$ variables, x_i, z_i, ($i = 1, 2, ..., n$), for a given selection of independent variables, one can take n partial derivatives with respect to each of the selected n independent variables.

For example (Box 4) , if we choose as independent variables z_i for all i , then we can derive the inflow sensitivities s_{ij}. If we instead choose as independent variables, for instance, (z_1, z_2, x_3,..., z_n), then what we can derive, for instance,

$$\left(\frac{\partial x_2}{\partial z_1}\right)_{z_2,\, x_3,\, z_4, \cdots,\, z_n} = s_{21} + s_{23}\left(\frac{\partial z_3}{\partial z_1}\right) \qquad (3.2)$$

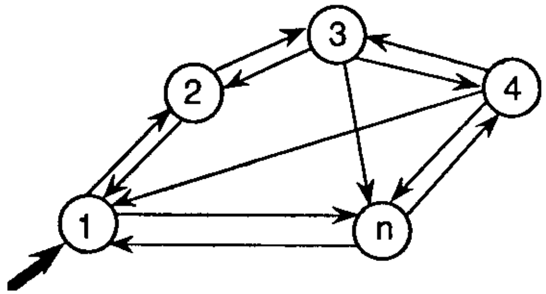
This quantity represents the component of total effects from species 1 to 3 that does not pass through species 3, because the abundance of species 3 is fixed in this derivative. Notice that for fixing the abundances of a particular set of species, we must select as the independent variables for those species abundance variables x_i rather than inflow variables z_i.

To derive procedurally direct effect from j to i, we should select as independent variables abundance variables for all species except the target species to which the effects are coming. For instance, selecting as independent variables (x_1, z_2, x_3,..., x_n), we can derive the procedurally direct effects from j to 2 ($j \neq 2$) as $-a_{2j}/a_{22}$ (Box 5)

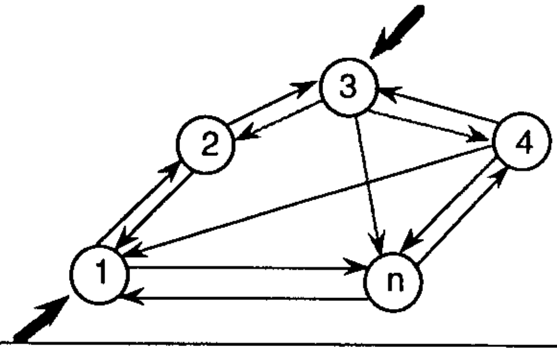
Box 4

Example of Combination of Independent Variables

$$\begin{pmatrix} x_1, x_2, x_3, ..., x_n \\ \boxed{z_1}, \boxed{z_2}, \boxed{z_3}, ..., \boxed{z_n} \end{pmatrix} \longrightarrow \left(\frac{\partial x_1}{\partial z_2}\right)_{z_1,\, z_3, ..., z_n} = s_{12}$$



$$\begin{pmatrix} x_1, x_2, \boxed{x_3}, ..., x_n \\ \boxed{z_1}, \boxed{z_2}, z_3, ..., \boxed{z_n} \end{pmatrix} \longrightarrow \left(\frac{\partial x_2}{\partial z_1}\right)_{z_2, x_3, z_4, ..., z_n}$$



Box 5

Procedurally Direct Effects Estimated by Conjugate variables Approach

$$\begin{pmatrix} \boxed{x_1}, x_2, \boxed{x_3}, \ldots, \boxed{x_n} \\ z_1, \boxed{z_2}, z_3, \ldots, z_n \end{pmatrix} \longrightarrow \left(\frac{\partial x_2}{\partial x_1}\right)_{z_2, x_3, x_4, \ldots, x_n} = -\frac{a_{12}}{a_{11}}$$