Overview of Network Environ Analysis: A systems analysis technique for understanding complex ecological systems

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Synopsis

Network Environ Analysis, based on network theory, reveals the quantitative and qualitative relations between ecological objects interacting with each other in a system. The primary result from the method provides input and output "environs", which are internal partitions of the objects within system flows. In addition, application of Network Environ Analysis on empirical datasets and ecosystem models has revealed several important and unexpected results that have been identified and summarized in the literature as network environ properties. Network Environ Analysis requires data including the intercompartmental flows, compartmental storages, and boundary input and output flows. Software is available to perform this analysis. This article reviews the theoretical underpinning of the analysis and briefly introduces some the main properties such as indirect effects ratio, network homogenization, and network mutualism. References for further reading are provided.

Keywords: Systems ecology, connectivity, energy flows, network analysis, indirect effects, mutualism

Introduction

Environ Analysis is in a more general class of methods called Ecological Network Analysis (ENA) which uses network theory to study the interactions between organisms or populations within their environment. Bernard Patten was the originator of the environ analysis approach in the late 1970s and along with his colleagues have expanded the analysis to reveal many insightful, holistic properties of ecosystem organization. ENA follows along the synecology perspective introduced by EP Odum which is mostly concerned with interrelations of material, energy and information among system components (Table 1).

ENA starts with the assumption that a system can be represented as a network of nodes (compartments, objects, etc.) and the connections between them (links, flows, etc.). In ecological systems, the connections are usually based on the flow of energy, matter, or nutrients between the system compartments. If such a flow exists, then there is a direct transaction between the two connected compartments.

Synecology	Autecology
• Holistic	• Reductionistic
• Ecology of relationships among the various organisms and populations	• Ecology of individual organisms and populations
• Mostly concerned with communication of material, energy and information among system components	• Mostly concerned with the elements themselves

Table 1 - Two main paradigms used for ecological investigations

These direct transactions give rise to both direct and indirect relations between all the objects in the system. Network analysis provides a systems-oriented perspective as it is based on uncovering patterns and relations among all the objects in a system.

Theoretical Development of Environ Analysis

Patten was motivated to develop Environ Analysis to attempt to answer the question, "What is environment?". In order to study environment as a formal object, a system boundary is a necessary condition to avoid the issue of infinite regress, because in principle one could trace the environment of each object back in history to the big bang origins. The realization of a boundary is, in fact, one of the three foundational principles in his seminal paper introducing the environ theory concept (Patten 1978). The necessary boundary demarcates two environments, the unbound external environment, which indeed includes all space–time objects in the universe, and the second internal, containing the environmental compartments of interest. This quantifiable, internal environment for each system object is termed "environ", and is the study of Environ Analysis. An object's environ stops at the system boundary, but as ecosystems are open systems, they require exchanges across the boundary into and out of the system. Therefore, input and output boundary flows are necessary to maintain the system's far-from-equilibrium organization. Objects and connections that reside wholly in the external environment are not germane to the analysis.

Another foundational principle of environ analysis theory is that each object in the system itself has two "environs" one receiving and one generating flows in the system. In other words, an object's input environ includes those flows from within the system boundary leading up to the object, and an output environ, those flows emanating from the object back to the other system objects before exiting the system boundary. This alters the perception from internal–external to receiving–generating. Thus, the object, while distinct in time and space, is more clearly embedded in and responsive to the couplings with other objects within the network. This shifts the focus from the objects themselves to the relations they maintain; or from parts to processes (or what Ilya Prigogine called from "*Being to Becoming*").

The third foundational principle of Network Environ Analysis is that individual environs (and the flow carried within each one) are unique such that the system comprises the set union of all environs, which in turn partition the system level of organization. This partitioning allows one to classify environ flow into what have been called different modes: mode 0) boundary input; 1) first passage flow received by an object from other objects in the system (i.e., not boundary flow), but also not cycled flow (in other words first time flow reaches an object); 2) cycled flow that returns to a compartment before leaving the system; 3) dissipative flow in that it has left the focal object not to return, but does not directly cross a system boundary (i.e., it flows to another within system object); and 4) boundary out.

The modes have been used to understand better the general role of cycling and the flow contributions from each object to the other, which has had application in showing a complementarity of several of the holistic, thermodynamic-based ecological indicators (see Fath *et al*. 2001).

Holistic Reductionism

On one level network Environ Analysis could be referred to as a holistic/reductionistic approach. It is holistic because it considers simultaneously the whole influence of all system objects, yet it is reductionistic in that the fine details of all object transactions are entailed in the analysis. The network data requirements include the complete flow–storage quantities for each identified link and node (note flow and storage are interchangeable as determined by the turnover rate).

Data can be acquired from empirical observations, literature estimates, model simulation results, or balancing procedures, when all but a few are unknown. This difficulty in obtaining data has resulted in a dearth of available complete network datasets. Due to this lack of requisite data for fully quantified food webs, researchers have developed community assembly rules that are heuristics to construct ecological food webs. Assembly rules are in general a set of rules that will generate a connectance matrix for a number of N species.

Common assembly rules that have been developed are random or constant connectance, cascade, niche, modified niche, and cyber-ecosystem each with its own assumptions and limitations (see Halnes *et al.* 2007). In all but the last case, the assembly rules construct only the structural food web topology. The cyber-ecosystem methodology also includes a procedure for quantifying the flows along each link. It uses a meta-structure of six functional groups: Producer (P), Herbivore (H), Carnivore (C), Omnivore (O), Detritus (D), and Detrital Feeders (F), within which random connections link species based on these definitional constraints.

Example Network

To demonstrate basic Environ Analysis, a commonly studied ecosystem network model first proposed by Tilly (1968) is used as an example. Figure 1 shows the network structure and includes the storages and flow values between compartments. The network has 5 compartments or nodes (x_i, for i=1 to 5) representing: X1) Plants, X2) Detritus, X3) Bacteria, X4) Detritus Feeders, and X5) Carnivores, respectively. Compartments are connected by transaction of the energy flows between them. These pairwise couplings are the basis for the internal network structure.

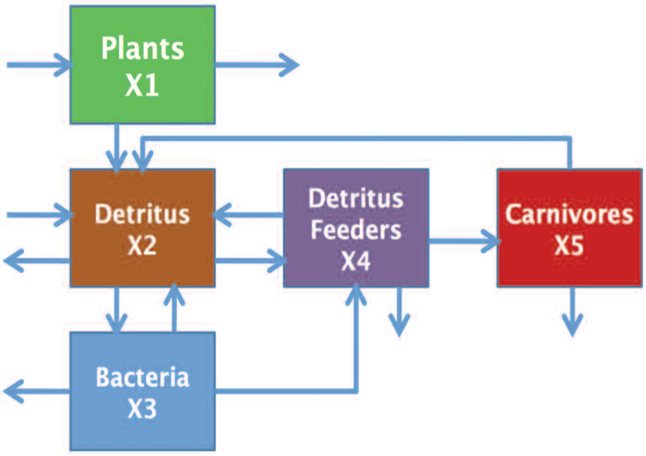

Figure 1 - Cone Spring Network Model (after Finn 1976); Five compartment model used to demonstrate Eviron Analysis notation and methodology.

This basic information regarding the storages, flows, and boundary flows provides all the necessary information to conduct Environ Analysis. Environ Analysis has been classified into a structural analysis-dealing only with the network topology, and three functional analyses-flow, storage, and utility-which require the numerical values for flow and storage in the network (Table 2).

Structural Analysis

A structural connectance matrix, or adjacency matrix, **A**, is a binary representation of the connections such that $a_{ij}=1$ if there is a connection from j to i, and a zero otherwise (Eq 1).

$$A=\begin{bmatrix} 0 & 0 & 0 & 0 & 0 \\ 1 & 0 & 1 & 1 & 1 \\ 0 & 1 & 0 & 0 & 0 \\ 0 & 1 & 1 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 \end{bmatrix} \tag{1}$$

Using this adjacency matrix one can calculate the number of pathways between compartments along paths of various lengths, in that the power of the matrix is equivalent to the path length. For example, the A^2 matrix below shows that there is exactly one path of length two from X1 to X5 and zeros paths of length two from X1 to X6, etc. A few powers are given below for inspection. Note, that while taking longer path sequences the numbers of path connections between compartments increases in well connected networks (except row 1 remains zero since there are no return paths to the X1). In fact, they grow so rapidly (note, by the time we look at A^{20} there are upwards of 78,000 unique paths!) that it is this abundance of pathways that give rise to the important contribution of indirect influence described below in the functional properties.

STRUCTURAL ANALYSIS	FUNCTIONAL ANALYSES
Path Analysis enumerates pathways in a network (connectance, cyclicity, etc.)	*Flow Analysis*: $g_{ij} = f_{ij}/T_j$ Identifies flow intensities along indirect pathways
	Storage Analysis: $c_{ij} = f_{ij}/x_j$ Id entifies storage intensities along indirect pathways
	Utility Analysis: $d_{ij} = (f_{ij}–f_{ji})/T_i$ Identifies utility intensities along indirect pathways

Table 2 - Basic methodologies for Network Environ Analysis

$$A^2 = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 \\ 0 & 2 & 1 & 1 & 0 \\ 1 & 0 & 1 & 1 & 1 \\ 1 & 1 & 1 & 1 & 1 \\ 0 & 1 & 1 & 0 & 0 \end{bmatrix} \quad A^3 = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 \\ 2 & 2 & 3 & 2 & 2 \\ 0 & 2 & 1 & 1 & 0 \\ 1 & 2 & 2 & 2 & 1 \\ 1 & 1 & 1 & 1 & 1 \end{bmatrix}$$

$$A^4 = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 \\ 2 & 5 & 4 & 4 & 2 \\ 2 & 2 & 3 & 2 & 2 \\ 2 & 4 & 4 & 3 & 2 \\ 1 & 2 & 2 & 2 & 1 \end{bmatrix} \quad A^5 = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 \\ 5 & 8 & 9 & 7 & 5 \\ 2 & 5 & 4 & 4 & 2 \\ 4 & 7 & 7 & 6 & 4 \\ 2 & 4 & 4 & 3 & 2 \end{bmatrix}$$

$$A^{10} = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 \\ 96 & 178 & 177 & 149 & 96 \\ 53 & 96 & 97 & 81 & 53 \\ 81 & 149 & 149 & 125 & 81 \\ 44 & 81 & 81 & 68 & 44 \end{bmatrix} \quad A^{20} = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 \\ 42762 & 78653 & 78652 & 66012 & 42762 \\ 23250 & 42762 & 42763 & 35890 & 23250 \\ 35890 & 66012 & 66012 & 55403 & 35890 \\ 19513 & 35890 & 35890 & 30122 & 19513 \end{bmatrix}$$

There are many structural properties of the network which can be determined from this analysis. Table 3 provides a few for Cone Spring ecosystem such as connectance, link density, in-degree, out-degree, and path proliferation (the rate of increase in number of paths).

Structural property	Value
# links	8
Connectance	0.32
Link density	1.6
In-degree (row sum)	[0 4 1 2 1]
Out-degree (column sum)	[1 2 2 2 1]
Path proliferation	1.84

Table 3 - Structural network properties

Functional Analysis

Storage and flows must have consistent units (although it is possible to consider multi-unit networks). Typically, units for storages are given in amount of energy or biomass per given area or volume (e.g., g/m^2), and units for flows are the same but as a rate (e.g., g/(m^2*day)). The generic intercompartmental flows for Figure 1 are given in the following flow matrix, **F**:

$$F = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 \\ f_{21} & 0 & f_{23} & f_{24} & f_{25} \\ 0 & f_{32} & 0 & 0 & 0 \\ 0 & f_{42} & f_{43} & 0 & 0 \\ 0 & 0 & 0 & f_{54} & 0 \end{bmatrix} \qquad (2)$$

which for this specific example becomes:

$$F = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 \\ 8881 & 0 & 1600 & 200 & 167 \\ 0 & 5205 & 0 & 0 & 0 \\ 0 & 2309 & 75 & 0 & 0 \\ 0 & 0 & 0 & 370 & 0 \end{bmatrix}$$

Note the orientation of flow from j to i is used because that makes the direction of ecological relation from i to j. For example, if i preys on j, the flow of energy is from j to i. All compartments experience dissipative flow losses (y_i, for i=1 to 5), and here the first compartment receives external flow input, z_1, (arrows starting or ending not on another compartment represent boundary flows). For this example, these can be given as:

$$y = [y_1\ y_2\ y_3\ y_4\ y_5] \qquad (3)$$

and

$$z = \begin{bmatrix} z_1 \\ z_2 \\ 0 \\ 0 \\ 0 \end{bmatrix} \qquad (4)$$

which are, respectively:

y = [2303 3969 3530 1814 203]

$$z = \begin{bmatrix} 11184 \\ 635 \\ 0 \\ 0 \\ 0 \end{bmatrix}$$

Total throughflow of each compartment is an important variable, which is the sum of flows into, $T_i^{in} = z_i + \sum_j^n f_{ij}$, or out of, $T_i^{out} = y_i + \sum_j^n f_{ji}$ the ith compartment.

At steady state, compartmental inflows and outflows are equal such that $dx_i/dt = 0$, and therefore, incoming and outgoing throughflows are equal also: $T_i^{in} = T_i^{out} = T_i$. In vector notation, compartmental throughflows are given by:

$$T = \begin{bmatrix} T_1 \\ T_2 \\ T_3 \\ T_4 \\ T_5 \end{bmatrix} \qquad (5)$$

The sum of all throughflows is called Total System Throughflow (TST) and is an important measure of the total energy (power) passing through the network. For Cone Spring ecosystem TST = 30626 kcal m^{-2} yr^{-1}.

The technical aspects of environ analysis are explained in detail elsewhere, so rather than repeat those here, the remainder of the entry highlights some of the important results from environ analysis. But first, one issue that must be covered is the way in which network analysis identifies and quantifies indirect pathways and flow contributions. Indirectness originates from transfers or interactions that occur non-directly, and are mediated by other within system compartments. These transfers could travel two, three, four, or many links before reaching the target destination. For example, the flow analysis starts with the calculation of the non-dimensional flow intensity matrix, **G**, where $g_{ij}=f_{ij}/T_j$. The **G** matrix corresponding to Figure 1 would look as follows:

$$G=\begin{bmatrix} 0 & 0 & 0 & 0 & 0 \\ 0.7941 & 0 & 0.3074 & 0.0839 & 0.4514 \\ 0 & 0.4533 & 0 & 0 & 0 \\ 0 & 0.2011 & 0.0144 & 0 & 0 \\ 0 & 0 & 0 & 0.1552 & 0 \end{bmatrix} \tag{6}$$

These values represent the fraction of flow along each link normalized by the total throughflow at the donating compartment. These elements give the direct, measurable flow intensities (or probabilities) between any two nodes j to i. To identify the flow intensities along indirect paths (e.g., j–>k–>i), one need only consider the matrix **G** raised to the power equal to the path length in question. For example, $\mathbf{G}^2$ gives the flow intensities along all paths of length 2, $\mathbf{G}^3$ along all paths of length 3, etc. This well-known matrix algebra result is the primary tool to uncover system indirectness. In fact, it turns out that due to the way in which the **G** matrix is constructed all elements in $\mathbf{G}^m$ go to zero as m–> ∞. Therefore, it is possible to sum the terms of $\mathbf{G}^m$ to acquire an "integral" flow matrix (called **N**), which gives the flow contribution from all path lengths.

$$N = G^0 + G^1 + G^2 + G^3 + \ldots = \sum_{m=0}^{\infty} G^m = (I - G)^{-1} \tag{7}$$

where $\mathbf{G}^0$=I, the identity matrix, $\mathbf{G}^1$ the direct flows, and $\mathbf{G}^m$ for m>1 are all the indirect flows intensities. Note, that the elements of **G** and **N** are non-dimensional; to retrieve back the actual throughflows, one need only multiply the integral matrix by the input vector: T=**N**z. In other words, N redistributes the input, z, throughout each compartment to recover the total flow through that compartment. Similarly, one could acquire any of the direct or indirect flows by multiplying $\mathbf{G}^m$z for any m.

$$N=\begin{bmatrix} 1.0 & 0 & 0 & 0 & 0 \\ 0.9582 & 1.2067 & 0.3736 & 0.1858 & 0.5446 \\ 0.4343 & 0.5470 & 1.1694 & 0.0842 & 0.2469 \\ 0.1989 & 0.2505 & 0.0920 & 1.0386 & 01131 \\ 0.0309 & 0.0389 & 0.0143 & 0.1612 & 1.0175 \end{bmatrix}$$

A similar argument is made to develop integral storage and utility matrices.

$$\textit{storage}\ Q = P^0 + P^1 + P^2 + P^3 + \ldots = \sum_{m=0}^{\infty} P^m = (I - P)^{-1} \tag{8}$$

$$\textit{utility}\ U = D^0 + D^1 + D^2 + D^3 + \ldots = \sum_{m=0}^{\infty} D^m = (I - D)^{-1} \tag{9}$$

where $p_{ij}=(f_{ij}/x_j)\Delta t$, and $d_{ij}=(f_{ij}-f_{ji})/T_i$.

Network Properties

Patten has developed a series of "ecological network properties" which summarize the results of environ analysis. These have all been described in the literature (for an overview of the 13 main ones, see Jørgensen *et al*. 2007, Chapter 5). The properties have been used to assess the current state of ecosystem networks and to compare the state of different networks. Furthermore, while interpreting some of the properties as ecological goal functions, it has been possible to identify the structural or parametric configurations that positively affect the network property values as a way to detect or anticipate network changes. For example, certain network alterations, such as increased cycling, lead to greater total system energy throughflow and energy storage, so one could expect that if possible ecological networks are evolving or adapting to such configurations.
This leads to a new area of research on evolving networks. In this section, a brief overview is given for four of these properties: dominance of indirect effects (or non-locality), network homogenization, network mutualism, and environs themselves.

Dominance of indirect effects

This property compares the contribution of flow along indirect pathways with those along direct ones. Indirect effects are any that require an intermediary node to mediate the transfer and can be of any length. The strength of indirectness has been measured in a ratio of the sum of the indirect flows intensities divided by the direct flow intensities:

$$\frac{\sum_{i,j=1}^{n} \left(n_{ij} - g_{ij} - \delta_{ij}\right)}{\sum_{i,j=1}^{n} g_{ij}} \tag{10}$$

where δ_{ij}, the Kronecker Delta, = 1 if and only if i=j and is 0 otherwise. When the ratio is greater than one, then dominance of indirect effects is said to occur. Analysis of many different models has shown that this ratio is often greater than one, revealing the non-intuitive result that indirect effects have greater contribution than direct effects. Thus, each compartment influences each other, often significantly, by many indirect, non-obvious pathways. The implications of this important result are clear in that each compartment is embedded in and dependent on the rest of the network for its situation, thus calling for a true systems approach to understand such things as feedback and distributed control in the network.

In this particular network the direct and indirect flows are about equal, with slightly more direct. Therefore, the ratio of indirect to direct is slightly less than one (i/d = 0.913). Still, the cycling index demonstrates that over 9% of the flow is cycled (FCI = 0.092). This is because of the total system throughflow, the boundary flow is 11819, first passage flow is 15991 and cycled flow is 2816.

Network homogenization

The homogenization property yields a comparison of resource distribution between the direct and integral flow intensity matrices. Due to the contribution of indirect pathways, it was observed that flow in the integral matrix was more evenly distributed than that in the direct matrix. A statistical comparison of resources distribution can be made by calculating the coefficient of variation of each of the two matrices. For example, the coefficient of variation of the direct flow intensity matrix **G** is given by:

$$CV(G) = \frac{\sum_{j=1}^{n}\sum_{i=1}^{n}(\bar{g}_{ij} - g_{ij})^2}{(n-1)\bar{g}} \tag{11}$$

Network homogenization occurs when the coefficient of variation of **N** is less than the coefficient of variation of **G** because this says that the network flow is more evenly distributed in the integral matrix. The test statistic employed here looks at whether or not the ratio CV(**G**)/CV(**N**) exceeds one.

For this ecosystem the homogenization ratio is 1.875. The interpretation again is clear that the view of flow in ecosystems is not as discrete as it appears because in fact the material is well-mixed (i.e., homogenized) and has traveled through and continues to travel through many, if not, most parts of the system.

Network mutualism

Turning now to the utility analysis, the net flow, utility matrix, **D**, can be used to determine quantitatively and qualitatively the relations between any two components in the network such as predation, mutualism, or competition. Entries in the direct utility matrix, **D**, or integral utility matrix, **U,** can be positive or negative (-1 _< d_{ij}, u_{ij} <1). The elements of **D** represent the direct relation between that (i, j) pairing; for the example in Figure 1, this produces the following:

$$D = \begin{bmatrix} 0 & -\frac{f_{12}}{T_1} & 0 & 0 & 0 \\ \frac{f_{21}}{T_2} & 0 & -\frac{f_{23}}{T_2} & -\frac{f_{24}}{T_2} & \frac{f_{25}}{T_2} \\ 0 & \frac{f_{32}}{T_3} & 0 & -\frac{f_{34}}{T_3} & 0 \\ 0 & \frac{f_{42}}{T_4} & \frac{f_{43}}{T_4} & 0 & -\frac{f_{45}}{T_4} \\ 0 & -\frac{f_{52}}{T_5} & 0 & \frac{f_{54}}{T_5} & 0 \end{bmatrix}$$

$$D = \begin{bmatrix} 0 & -0.7941 & 0 & 0 & 0 \\ 0.7734 & 0 & -0.3139 & -0.1837 & 0.0145 \\ 0 & 0.69261 & 0 & -0.0144 & 0 \\ 0 & 0.8846 & 0.0315 & 0 & -0.1552 \\ 0 & -0.4514 & 0 & 1.0000 & 0 \end{bmatrix} \tag{12}$$

The direct matrix **D**, being zero-sum, always has the same number of positive and negative signs.

$$\mathrm{sgn}(D) = \begin{bmatrix} 0 & - & 0 & 0 & 0 \\ + & 0 & - & - & + \\ 0 & + & 0 & - & 0 \\ 0 & + & + & 0 & - \\ 0 & - & 0 & + & 0 \end{bmatrix} \tag{13}$$

The elements of **U** provide the integral, system-determined relations. There is one caveat that must be mentioned and that is that integral matrix, contributing indirect flows, makes sense in light of the power series converging. One test that has been proposed for this is based on the eigenvalues of the D matrix. It has been proven that if the absolute value of the largest eigenvalue is less than one, then convergence is guaranteed. It turns out that for the Cone Spring ecosystem, the absolute value of the largest eigenvalue is slightly more than one at 1.0156. It is still an open research question as to interpretation and alternative approaches.

For this example, which is didactic in nature, I will proceed with the integral matrix (which is still calculable from matrix inversion) nonetheless. Therefore, continuing the example, we get the following integral utility matrix and relations between compartments:

$$U = \begin{bmatrix} 0.6894 & -0.4016 & 0.1279 & 0.0572 & -0.0147 \\ 0.3912 & 0.5058 & -0.1610 & -0.072 & 0.0.185 \\ 0.2662 & 0.3441 & 0.8900 & -0.0615 & 0.0.145 \\ 0.3305 & 0.4273 & -0.1089 & 0.8044 & -0.1186 \\ 0.1540 & 0.1991 & -0.0362 & 0.8370 & 0.8730 \end{bmatrix}$$

$$\text{sgn}(U) = \begin{bmatrix} + & - & + & + & - \\ + & + & - & - & + \\ + & + & + & - & + \\ + & + & - & + & - \\ + & + & - & + & + \end{bmatrix} \qquad (14)$$

Unlike, the direct relations, this is not zero-sum. Instead, we see that there are 17 positive signs (including the diagonal) and 8 negatives signs. If there are a greater number of positive signs than negative signs in the integral utility matrix, then network mutualism is said to occur.

Here, the ratio is 2.125. Network mutualism reveals the preponderance of positive mutualistic relations in the system. Specifically, here, we can identify 3 cases of indirect mutualism and 7 of exploitation (Table 4). There are no competition relations in this network.

Environ Analysis

The last property mentioned here is the signature property, the quantitative environ, both in the input and output orientation. Since each compartment has two distinct environs there are in fact 2n environs in total. The output environ, **E**, for the ith node is calculated as:

$$E = (G - I)\hat{N} \qquad (15)$$

where is the diagonalized matrix of the ith column of **N**. When assembled, the result is the output oriented flow from each compartment to each other compartment in the system and across the system boundary.

Input environs are calculated as:

$$E' = \hat{N}_1'(G' - I) \qquad (16)$$

where, $g'_{ij}=f_{ij}/T_i$, and $N'=(I–G')^{-1}$.

Direct	*Integral*
$(sd_{21}, sd_{12}) = (+, -)$ → exploitation	$(su_{21}, su_{12}) = (+, -)$ → exploitation
$(sd_{31}, sd_{13}) = (0, 0)$ → neutralism	$(su_{31}, su_{13}) = (+, +)$ → mutualism
$(sd_{41}, sd_{14}) = (0, 0)$ → neutralism	$(su_{41}, su_{14}) = (+, +)$ → mutualism
$(sd_{51}, sd_{15}) = (0, 0)$ → neutralism	$(su_{51}, su_{15}) = (+, -)$ → exploitation
$(sd_{32}, sd_{23}) = (+, -)$ → exploitation	$(su_{32}, su_{23}) = (+, -)$ → exploitation
$(sd_{42}, sd_{24}) = (+, -)$ → exploitation	$(su_{42}, su_{24}) = (+, -)$ → exploitation
$(sd_{52}, sd_{25}) = (-,+)$ → exploited	$(su_{52}, su_{25}) = (+, +)$ → mutualism
$(sd_{43}, sd_{34}) = (+, -)$ → exploitation	$(su_{43}, su_{34}) = (-, +)$ → exploited
$(sd_{53}, sd_{35}) = (0, 0)$ → neutralism	$(su_{53}, su_{35}) = (-, +)$ → exploited
$(sd_{54}, sd_{45}) = (+, -)$ → exploitation	$(su_{54}, su_{45}) = (+, -)$ → exploitation

Table 4 - Direct and integral relations in sample network from Figure 1.

These results comprise the foundation of Network Environ Analysis since they allow for the quantification of all within system interactions, both direct and indirect, on a compartment-by-compartment basis.

Summary

A practical objective of ecological network analysis in general, and environ analysis in particular, is to trace material and energy flow–storage through the complex network of system interactions.

The Network Environ approach has been a fruitful way of holistically investigating ecosystem. In particular, a series of "network properties" such as indirect effects ratio, homogenization, and mutualism have been observed using this analysis, which consider the role of each entity embedded in a larger system.

Biographical sketch

Brian D. Fath is Professor in the Department of Biological Sciences at Towson University (Maryland, USA).

He teaches courses in ecosystem ecology, environmental biology, networks, and human ecology and sustainability. Dr. Fath has also taught courses on ecological networks and modeling in Portugal, Croatia, Denmark, China, France, and Germany. He holds a Fulbright Distinguished Chair position at Parthenope University of Naples, Italy for spring 2012.

Since 2002, he has been a summer Research Scholar within the Advanced Systems Analysis Program at the International Institute for Applied Systems Analysis in Laxenburg, Austria, where he is also co-scientific coordinator for their Young Scientist Summer Program. He has published around 100 research papers, reports, and book chapters in journals such as the Journal of Theoretical Biology, Ecological Modelling, BioSystems, Ecological Complexity, Environmental Modelling and Software, and Ecosystems.

He co-authored the books *A New Ecology: Systems Perspective* and *Ecological Modelling* (4th edition) and is Associate Editor-in-Chief for *Encyclopedia of Ecology*.

He is also Editor-in-Chief for the journal Ecological Modelling; President of the North American Chapter of International Society for *Ecological Modelling*; and Chair of Baltimore County Commission on Environmental Quality.

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