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Review of the Foundations of Network Environ Analysis

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ABSTRACT

This article introduces and summarizes the foundations of network environ analysis and describes four primary properties resulting from this research. These properties—*dominance of indirect effects* (Higashi and Patten 1986), *network amplification* (Patten and others 1990), *network homogenization* (Patten and others 1990), and *network synergism* (Patten 1991)—provide insight into the behavior of holistic network interactions. In short, amplification, homogenization, and indirect effects demonstrate the influence of the indirect flows in a system to show that energy or matter cycling allows flow to return to the same component many times and tend to become evenly distributed within the network. Synergism relates direct and indirect, qualitative relations to show that network organization is, on the whole, more mutualistic than is apparent from direct interactions alone. Using network analysis, objects can be studied as part of a connected system and the indirect effects can be identified and quantified. This is a fundamentally different way of investigating ecosystems, and it gives a quantitative foundation to the widely held perception of the interconnectedness of nature.

Key words: ecological modeling; environ analysis; indirect effects; network analysis; synergism; systems analysis.

INTRODUCTION

Network analysis is a powerful, general analytical tool that makes it possible to study objects as part of a connected system and to identify and quantify the direct and indirect effects in that system. It is based on the conservative transactions of a consistent currency through the components in an interconnected network. In ecosystem models, this currency is usually energy or matter. This methodology can also be used to determine many other important ecosystem properties such as cycling index, total throughflow, turnover rate and time, and relational interactions between any two components in a system. Network analysis is an area that is growing and gaining acceptance as a way to answer important questions about the connectivity of system components. Several edited volumes advancing this approach are available [for example, see Platt and others (1981), Ulanowicz and Platt (1985), Wulff and others (1989), Higashi and Burns (1991), and Patten and Jørgensen (1996)]. One software implementation, ECOPATH (Christensen and Pauly 1992) now records over 800 registered users in more than 90 countries, and over 100 published models are based on it (Christensen 1998).

Network analysis is an environmental application of input-output analysis. Input-output analysis was developed by Leontief (1936, 1951, 1966) to analyze the interdependence of industries in an economy (Miller and Blair 1985). In ecology, there have been several somewhat independent lines of research in this field. Hannon (1973) first used input-output analysis to investigate the interdependence of organisms in an ecosystem to determine the total energy flows that directly and indirectly link the component to its ecosystem. He has added other significant contributions to network analysis theory. For example, he proposed that network analysis could be used as a goal function in that ecosystems operate to maximize their total direct and indirect storages (Hannon 1979). He also introduced dynamic analysis as a way to identify control in an ecosystem (Hannon 1986). Herendeen (1981)

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Corresponding author, e-mail: bfath@smokey.forestry.uga.edu applied the network formulation to determine energy intensity in ecological and economic systems. His contributions include using network analysis to compare goal functions (Herendeen 1989; Brown and Herendeen 1996) such as exergy (Jørgensen and Mejer 1983; Jørgensen 1986), ascendancy (Ulanowicz 1980, 1986), and emergy (Odum 1983, 1988). Levine (1977) developed his own approach to network analysis, using it to calculate trophic level distribution (Levine 1980) and introducing a dynamic formulation of input-output analysis for determination of effects on a harvested ecosystem (Levine 1988). Ulanowicz (1986, 1997) emphasized a combination of transactive (i.e., energy or matter) flows and information theory called ascendancy. He, too, used network analysis to investigate mixed trophic levels and relational (nontransactive) interactions between components (Ulanowicz and Kemp 1979; Ulanowicz and Puccia 1990). Patten (1978, 1982) and subsequent coworkers developed a line of ecological network analysis called *environ analysis*. It is this last approach that is the focus of this report.

Patten and colleagues (1976), drawing heavily on the mathematical general systems theory of Zadeh (Zadeh and Desoer 1963), introduced the *holon* (Koestler 1967) as a subsystem at any level in a system hierarchy, and recognized that a holon has two distinct *environments*. Looking backward in time defines the environment that produces the input, or the input environment. Looking forward in time defines the environment that is affected by the system's output, or output environment. These two environments later were implemented quantitatively as input and output environs (Patten 1978). Starting with Zadeh's basic idea of causation as a determinate and nonanticipatory relation between two entities, Patten and colleagues (1976) constructed a theory for causal bonds, causal sequences, and causal networks. The causal networks were used to speculate on the ecosystem as a coevolutionary object. Based on the input-output duality, the Leontief-Hannon analysis was reoriented so as to also calculate the output generated by each unit of input (Finn 1976). Finn (1976) also developed standard methods to calculate the total system throughflow, average path length, and a cycling index that has been widely used in ecology.

The foundations of network environ analysis were set when Patten (1978) applied the previously developed general systems theory to ecological systems and established three key ideas toward an environmental system theory. First, every object within a system has two environments that, within the system boundaries, could be specified and quantified as *environs*. Second, an environmental (external) reference state is needed to account for the internal causation of a system. In other words, an object is embedded in and linked to its surrounding environment, and depends on this surrounding environment for its internal identity and structural and functional completeness. Third, the propagation of flow along each pathway is uniquely targeted for and derived from a particular component. Therefore, all transactive flows are accounted for and none are double counted. More precisely, the set unions of the input and output environs of the different objects are mutually disjoint and exhaustive. Therefore, the transactive flow along each pathway is unique and targeted for a particular component. This foundation has been used to develop several lines of research based on the pathways, flows, storages, and net flows of static ecosystem models and has resulted in the identification of the network properties described below. The environ approach to network analysis is distinct from others in the following ways: (a) environment, expressed as both input and output environs, is explicit and central; (b) matrix power series, as decompositions of inverse matrices analogous to Leontief's original inverse, are employed and emphasized in each of the analyses; other approaches use the inverse, but not the power series; (c) structural pathway analysis to enumerate the number of pathways; and (d) input and output orientation of flows and net flows to both throughflows and storages, making eight total functional analyses.

ENVIRONMENT AND ENVIRONS

Environment is used broadly to represent many different ideas, depending on the situation. In network environ analysis, environment has two interpretations, depending on scale. Within the boundaries of a predefined system, an object's local environment consists of all the other objects in the system with which it directly and indirectly interacts. In this context, each object is seen as a partition of two mutually exclusive halves, one comprising the inflow and the other outflow (von Uexküll 1926). This differs from the standard organism-environment context that separates the organism from its environment (Figure 1a). The traditional view reflects years of reductionist science in which objects are studied as entities separated from their natural environment. Even ecology, which is the study of organism-environment relationships, focuses on the impact of environment on discrete biota and vice versa, but less explicitly on the biotic object as an integrated part of a flowing and complete ecosystem. Kareiva (1994) reviewed 1253

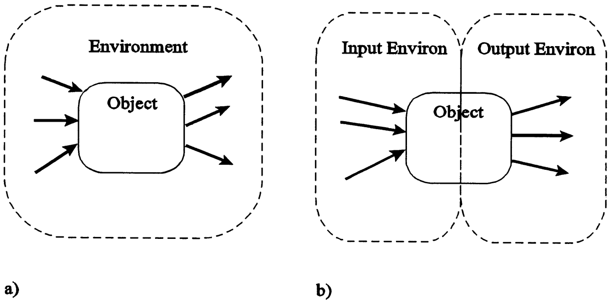

Figure 1. Environment-object duality a versus input-output environ duality (b). In (a), an object is conceptually separate from the environment, creating a disjoint duality. In (b), the object duality is based on its role as a receiver and generator of interactions with an environment to which it is inexorably connected.

articles published in *Ecology* between 1981 and 1990 and almost 1000 of these dealt with four or fewer species; this is hardly representative of holistic investigation of the environment and its organisms. In network environ analysis, each component consists of two system-bounded *environs*: one acts on the defining component, and the other is acted upon by the component (Figure 1b) (Patten 1978). Therefore, the component itself is part of two environs, one received and one generated. The input or received environ is the terminus of all the within-system interactions leading up to the component, and the output environ is generated by new flows and future interactions. In this view, an object is inexorably linked to its surrounding world through its afferent input and efferent output environs.

The second interpretation of environment refers to objects and processes outside the predefined system boundaries, that is, external to a model. The within-system objects and transactions are imbedded in a larger context represented by the environment. Here, environ represents the local component interactions as mediated by input and output transactions. An input environ includes transactions from components within the system boundaries and from the environment across the boundary. Similarly, an output environ includes transactions to other components and to the system-level environment. A conceptual model should contain all relevant entities within the ecosystem boundaries. Other interactions are included as 'black box' input to or output from the system to the environment. In Figure 2, a simple three-component model is used to show the dichotomy between environs and environment. This figure also shows that within the system boundaries the outputs from one component become inputs to others, and inputs to components influence outputs from others.

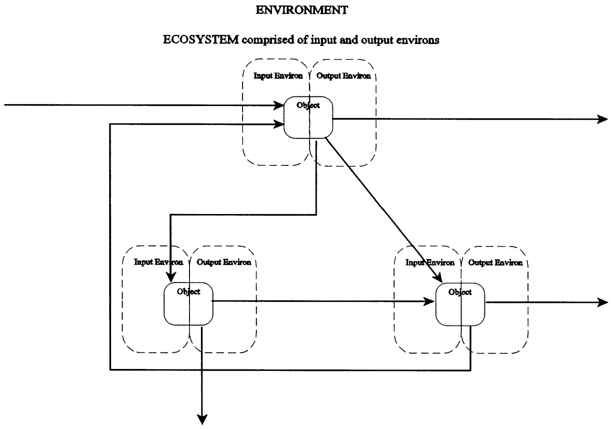

Figure 2. A simple three-component model is used to demonstrate coupling of input-output linkages between connected components. This figure also emphasizes that component environs are embedded in a larger environment with which they can exchange energy and matter.

Network analysis supports another paradigm shift from the storage objects to the flows. Although we are interested in both flows and storages, these are in fact homologous because storages are related to flows through storage turnover. Flows connect the output environ of one component with the input environ of a second to create structure and dominate overall system behavior. The orientation is more holistic because the flows create the system pattern that binds components together. Also, the flow values that correspond to a particular system structure and function are sufficient to determine certain network properties reflected in the behavior of that system. Thus, we analyze ecosystems in a holistic manner to measure the contribution of indirect effects to system behavior.

Behavior, Structure, and Function

In addition to the preceding description of environs and environment, it is important to keep in mind that, based on physical constraints, there are three types of systems: isolated, closed, and open (White and others 1992). Isolated systems have no energy or matter transfer with their environment, and closed systems exchange energy but not matter. Open systems transfer both energy and matter with their environment. Every biological entity is an open system. Nonisolated systems are not at thermodynamic equilibrium, because they receive, transfer, and dissipate energy. Ecological systems exist because of this energy or chemical gradient that is needed to maintain life, so at a minimum all ecological systems are nonisolated. Since most ecosystems also exchange matter, they can, for all practical purposes, be considered open systems. The energy gradient causes all open systems to exhibit behavior; therefore, all ecological systems exhibit behavior.

Behavior, structure, and function are three key concepts in network environ analysis. *Webster's Dictionary* (1961) defines *behavior* as an 'observable activity when measurable in terms of quantifiable effects on the environment whether arising from internal or external stimulus.' This fits nicely with the concept of output in state-space theory. This theory provides the mathematical framework necessary to compute a component's response to inputs. In this theory, inputs (Z_t) received into a state (X_t) create a new state (X_{t+1})and produce associated outputs (Y_{t+1}). These phenomena are represented in two basic equations of state-space theory: the state transition function [Eq. (1)] and the response function [Eq. (2)] (Zadeh and Desoer 1963):

$$Z_t \times X_t \rightarrow X_{t+1} \quad (1)$$

$$Z_t \times X_t \rightarrow Y_{t+1} \quad (2)$$

The connection to state-space theory is useful because it offers an already developed mathematical theory that can be applied in understanding system behavior. If the receiving state connects to a second state, then the output becomes the input to the connected state and the process repeats. An input environ gives rise to a new state and an output environ. When the system is well connected, the influence of the output created at one instant in time from a particular state moves through the network and can potentially cycle around [as function circles (von Uexküll 1926)] and reenter the original generating component at a later time. This direct and indirect feedback of outputs into inputs is the basis of coevolutionary behavior in network theory (Patten and others 1976; Patten 1981; Patten and Auble 1981). The pervasiveness of coevolutionary processes occurs by the shaping and reshaping of an organism's input environment through its own output. Organisms modify their environment (niche construction) through their output environ. This is very similar to niche creation (Odling-Smee 1995; Laland and others 1996; Odling-Smee and others 1996) in which organisms modify their environment and generate conditions more suitable for survival. Coevolution is just one of many by-products from the state-space interpretation. The measurable output environ, as influenced by its input environ, constitutes the consequences of behavior system.

Behavior, as described by the response function and reflected in the output environ, is determined by both system structure and function. Dictionary definitions are again helpful starting places. *Structure* is defined as 'the elements or parts of an entity or the position of such elements or parts in their external relationship to each other,' and *function* is 'the normal and specific contribution of any . . . part' (Webster's 1961). Again, these are equivalent to their conceptual and mathematical meanings in environ analysis. Here, structure is the relative position of one component to another as determined by the network connections, and function is the quantity and type of energy or material that passes along these connections. This terminology differs slightly, yet importantly, from that commonly used in other disciplines such as physiology, where structure refers to the hard-wired physical characteristics of an organism and function refers to the operation of the structure. For example, the structure of a bat wing describes the relative position and composition of the bones, tendons, hair, and so on, and the wing's function is its role in the mammal's flight. The important distinction with function is that in network analysis its meaning is not purpose, but process as in the exchange of energy or matter. These words have such common and transdisciplinary usage that it is important that their definitions be clear. Here, we are interested in structure and function as two related quantities at a lower level of organization underlying system behavior expressed at a higher level of organization.

IMPLEMENTATION OF NETWORK ANALYSIS

Network analysis is predicated on a conceptual flow-storage model of an (eco)system [*eco* is in parentheses because the theory is applicable to any system that can be represented as a combination of conservative flows (transactions) and components]. A quantified functional diagram based on a conceptual model of the ecosystem will contain both the structural and functional information. A main advantage of network analysis is that it allows for investigation of direct and indirect interdependencies and relationships between components of a system without removing them from the system. This is the meaning of *holism* (components operating in systems), and understanding ecosystem behavior and its underlying relations requires such a perspective.

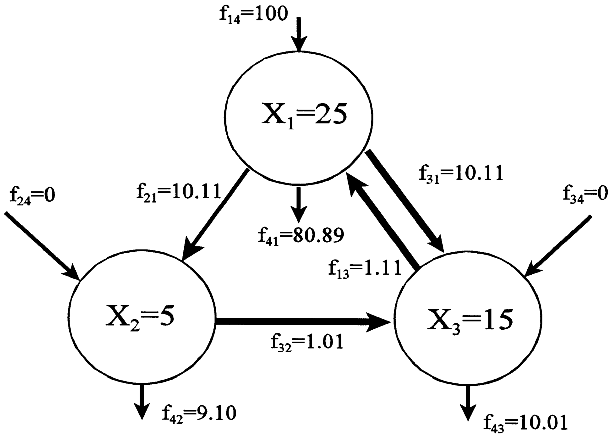

Figure 3. The input-output conceptual model of Figure 2 is quantified with specific flow and storage values. A functional digraph with this level of detail is sufficient to proceed with the network environ analysis.

Structural Analysis

Mathematically, system structure is represented as a graph of component interconnections. An adjacency matrix, A = (a_{ij}), is a one-to-one mapping of the graph. It has a 1 in elements (i,j) and (j,i) if and only if a connection exists between the two components i and j. Directed flow is represented by a *directed graph* (or *digraph*). By convention in the environ analysis literature, the adjacency matrix of a flow digraph has a 1 in the (i,j) position if and only if there is a flow from j to i. Row (i) to column (j) transfers are reserved for the utility part of environ analysis. In this, relations directed from i to j give rise to transactions directed from j to i. For example, in the trophic relation i eats j, the physical flow of material is from j to i. In ecological models, nontrophic flows (such as from a living compartment to detritus) are also represented in the digraph because they represent pathways for material to travel in the network. However, when dealing with certain properties, it is important to differentiate between trophic and nontrophic processes. Whipple (1995) investigated a method to count the pathways without augmenting the trophic level. The digraph in Figure 3 shows the energy transactions in a hypothetical three-component ecological model. The structural information in the digraph is represented identically in matrix format in Eq. (3):

$$\mathbf{A} = \begin{bmatrix} 0 & 0 & 1 \\ 1 & 0 & 0 \\ 1 & 1 & 0 \end{bmatrix} \tag{3}$$

Having the structural information in the adjacency matrix format makes it possible to perform the mathematical manipulations in the path analysis.

An important concept in structural analysis is that of a *cycle*: a path that ends at the same node where it began. Cycles can be embedded within other cycles, and they contribute to the complexity of networks in two ways. First, cycles increase the total number of pathways between two components for a given path length. Second, cycles play a major role in increasing the number pathways between two nodes as path length increases. The simplest cycle is of length 1 and is called a *loop* (or *self-loop*). In environ analysis, self-loops are used to represent storage (Patten 1981, 1982) and interpreted as nonflow at that component. Self-loops are implicit in the storage, but are not algebraically considered in the three functional analyses described next.

Functional Analysis

System function is reflected in the amount of mass-energy transaction between components. Function is, therefore, a dimensional quantity. In the case of ecological models, transactions usually have the dimensions of mass or energy per unit area and unit time (M/L^2T), or mass-energy per unit volume and unit time (M/L^3T). A dimensional flow matrix, F = (f_{ij}), has flow from j to i in these dimensions in its (i,j) element. An infinite number of possible flow matrices are associated with each structure since flows are measured in real numbers. Equation (4) is one example of a steady-state flow matrix corresponding to the adjacency matrix in Eq. (3) and based on the flows in Fig. 3.:

$$\mathbf{F} = \begin{bmatrix} 0 & 0 & 1.11 \\ 10.11 & 0 & 0 \\ 10.11 & 1.01 & 0 \end{bmatrix} \tag{4}$$

Input into the system is represented by an $n \times 1$ column vector, z. Here, let z = $[100, 0, 0]^T$. When this system is at steady state, a $1 \times n$ row vector, y, can be used to represent the outflow from each component. For Figure 3, y = [80.89, 9.10, 10.01]. Other information necessary to proceed with storage-oriented functional analysis are steady-state storage values for the components. Notationally, this is represented as an $n \times 1$ column vector, x [Eq. (5)]:

$$\mathbf{x} = \begin{bmatrix} 25 \\ 5 \\ 15 \end{bmatrix} \tag{5}$$

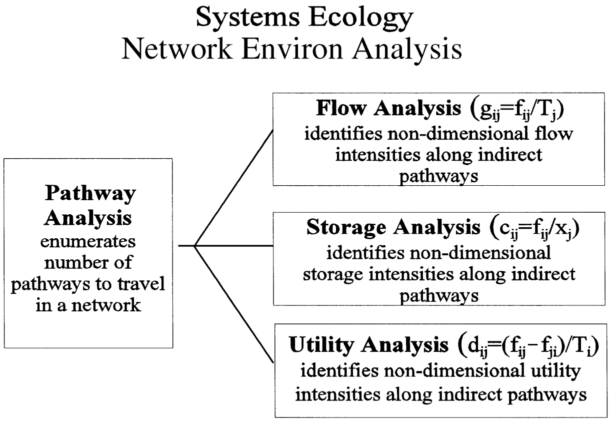

Figure 4. Diagram of systems ecology network analysis. The structural path analysis, which enumerates the number of pathways in a network, is the basis for the three functional analyses: storage, flow, and utility. Each of the functional analyses is derived from a different relationship of the flow-storage data and is used to determine different properties of the system.

Together, the functional flow and storage values transform the structural digraph into a operational systems model (Figure 3). The combination of system structure and function underlies system behavior and is sufficient to determine the values of the network properties. Behavior, in particular that contributed by indirect effects, can be identified by using network analysis.

In network ecology, structure and function are analyzed using mathematical models based on flows and storages as described. Structural *path analysis* enumerates associated pathways (Patten and others 1982). Three types of functional analyses are *flow analysis* (Hannon 1973), *storage analysis* (Matis and Patten 1981), and *utility analysis* (Patten 1991). Each of the functional analyses is based on a different nondimensional normalization of the dimensional flows in the network (Figure 4). Flows with given dimensions are divided by one or more constants having reciprocal dimensions. This makes the values dimensionless and relative to a standard scale, between 0 and 1 for flow and storage analyses, and between −1 and 1 for utility analysis. The result of normalization is interpreted as a flow or net flow intensity. Either throughflows or storages are used to scale the values. In retrospective flow analysis as originally developed by Leontief and most used in ecological applications, flows from j to i, f_{ij}, are normalized by the total steady-state throughflow [Eq.(6)] at donor component j, ($g_{ij} = f_{ij}/T_j$):

$$T_j = \sum_{i=0}^{n} f_{ij} = \sum_{i=0}^{n} f_{ji} \tag{6}$$

In the reverse orientation, flows from j to i, f_{ij}, are normalized by the total steady-state throughflow at recipient component i, ($g'_{ij} = f_{ij}/T_i$). The input and output flows are represented by f_{0j} and f_{j0}, respectively, where zeros denote the system level environment. Similar dual relationships are developed for the storage analysis. In storage analysis, the flows are normalized by the steady-state storage at the originating component j, ($c_{ij} = f_{ij}/x_j$), and receiving component i, ($c'_{ij} = f_{ij}/x_i$). A time step is needed to make this dimensionless and bounded between 0 and 1, ($p_{ij} = i_{ij} + c_{ij}\Delta t$ and $p'_{ij} = i_{ij} + c'_{ij}\Delta t$, in this equation. where i_{ij} are the elements of the identity matrix). And, in utility analysis, the net flow between i and j is normalized by the steady-state throughflow at i, [$d_{ij} = (f_{ij} - f_{ji})/T_i$]. A storage based utility analysis [$d(s)_{ij} = (f_{ij} - f_{ji})/x_i$] has yet to be explored. Flow analysis identifies properties of networks, such as cycling rates and indirect contributions (Hannon 1973; Finn 1976; Patten and others 1982; Ulanowicz 1986; Higashi and Patten 1989). Storage analysis evaluates retention time, turnover rates, and the system stability (Matis and Patten 1981). Utility analysis identifies direct and indirect qualitative relationships (such as competition and mutualism) in a network (Ulanowicz and Puccia 1990; Patten 1991, 1992). Together, these four analyses, one structural and three functional, allow for the investigation of the role of networks, indirect effects, and environment on an object's behavior.

Indirect Effects

Networks of interacting components exist everywhere in nature because ecological systems are not isolated systems. Recently, much attention has been given to indirect effects in ecosystem processes [for instance, see Lawlor (1979), Strauss (1991), Billick and Case (1994), Menge (1995), Abrams and others (1996), and Rosemond (1996)]. For example, Menge (1995) identified 83 subtypes of indirect effects in a rocky intertidal community and found that they accounted for about 40% of the change in community structure. Billick and Case (1994) distinguished between higher-order interactions and indirect effects, identifying three types of higher-order interactions and two definitions of indirect effects. Abrams (1991) proposed a distinction between short-term and long-term indirect effects. In a review article, Strauss (1991) identified four types of indirect effects based on species abundance, behavior, environment, and response. She stated that indirect effects may be important and 'that species may be able to adapt to indirect effects and that communities, cemented together by such interactions, may themselves succeed and fail based on the dynamics of all species taken in toto‘ (p. 207), but that ‘intimate knowledge and detailed experimentation within individual systems‘ (p. 209) may be the only way to determine the importance of indirect effects. From these examples, it is becoming empirically clear that, as previously identified theoretically, indirect effects play an important role, but experimental design and differing definitions of indirect effects affect results.

There is much confusion and ambiguity among the many definitions proposed for indirect effects. The distinction between direct and indirect effects used in environ theory is that direct effects are those associated with flows of material between adjacently connected components in a system, whereas indirect flows are those in which the originating and terminating nodes are nonadjacent by reason of nonadjacent flow in either space or time. This is similar to the definition used by Miller (1994) and by Miller and Travis (1996), except that they do not include temporal indirectness, but only spatial indirectness. In both spatial and temporal cases, indirect effects are mediated by transactions that relate the originating and terminating components. For example, in a three-component food chain with flow i → j → k, the direct flows are i → j and j → k. A second-order (path length 2), indirect flow is i → k. Although there is no direct transaction linking k and i, there is a relational linkage. If analyzed separately as two two-component networks (k → j and j → i), this relation would not be evident. It is only apparent when the three-component network is analyzed as one system. From this, it is evident that understanding ecosystem behavior and in-system relations requires the holistic perspective.

Core Methodology

Path analysis identifies the direct and indirect pathways in a network. As stated above, an adjacency matrix is a matrix of zeros and ones, with a 1 in the *i*th row and *j*th column if and only if there is a flow from j to i. When the adjacency matrix is raised to a particular power, the elements of the new matrix are equal to the number of pathways of a length commensurate with the power [for example, see Patten and others (1982) and Patten (1985)]. For instance, the number of paths to travel from node j to node i in two steps is given in the (i,j) element of A^2. A step is a connection in the path. Similarly, the number of paths of length 3 from j to i is the (i,j) element of A^3, and the number of paths of length m from j to i is the (i,j) element of A^m. For example, we see in the last matrix of Eq. (7) below that there are two ways to get from component 1 to component 3 in exactly four steps. Referring to Figure 3, these two paths are 1 → 2 → 3 → 1 → 3 and 1 → 3 → 1 → 2 → 3:

$$\mathbf{A}^2 = \begin{bmatrix} 1 & 1 & 0 \\ 0 & 0 & 1 \\ 1 & 0 & 1 \end{bmatrix}, \quad \mathbf{A}^3 = \begin{bmatrix} 1 & 0 & 1 \\ 1 & 1 & 0 \\ 1 & 1 & 1 \end{bmatrix}, \quad \mathbf{A}^4 = \begin{bmatrix} 1 & 1 & 1 \\ 1 & 0 & 1 \\ 2 & 1 & 1 \end{bmatrix}, \tag{7}$$

In a well-connected system like this, the number of paths between the components continues to increase as path length increases. The indirect pathways are enumerated in the higher-order powers of the adjacency matrix, and the summation of all paths of all orders is given by the divergent power series:

Paths:

$$\underbrace{\mathbf{B}}_{\text{integral}} = \underbrace{\mathbf{I}}_{\substack{\text{initial}\\ \text{state}}} + \underbrace{\mathbf{A}}_{\text{direct}} + \underbrace{\mathbf{A}^2 + \mathbf{A}^3 + \mathbf{A}^4 +}_{\text{indirect}} \cdots \tag{8}$$

The same premise for enumerating indirect pathways is used in the functional analyses. When normalized direct transaction matrices are raised to a particular power, this gives the functional influence (expressed nondimensionally) associated with all paths of lengths commensurate with the power. Network properties are based on an interpretation of the infinite power series associated with the nondimensional quantity of interest (flow, storage, or utility), where the higher-powered terms in the series correspond to the indirect contributions of those orders. Integral interaction matrices are found by summing convergent infinite power series of the direct interaction matrices [Eqs. (9)].

$$\begin{aligned} &\text{Flow:} && \mathbf{N} = \mathbf{I} + \mathbf{G} + \mathbf{G}^2 + \mathbf{G}^3 + \mathbf{G}^4 + \cdots \\ &\text{Storage:} && \mathbf{Q} = \mathbf{I} + \mathbf{P} + \mathbf{P}^2 + \mathbf{P}^3 + \mathbf{P}^4 + \cdots \\ &\text{Utility:} && \underbrace{\mathbf{U}}_{\text{integral}} = \underbrace{\mathbf{I}}_{\substack{\text{initial}\\ \text{input}}} + \underbrace{\mathbf{D}}_{\text{direct}} + \underbrace{\mathbf{D}^2 + \mathbf{D}^3 + \mathbf{D}^4 + \cdots}_{\text{indirect}} \end{aligned} \tag{9}$$

The definitions of the direct interaction matrices are given earlier as $g_{ij} = f_{ij}/T_j$, $p_{ij} = i_{ij} + c_{ij}\Delta t$ (with $c_{ij} =$

Table 1. Four Emergent Network Hypotheses and Mathematical Tests to Determine Their Existence

Property	Definition	Test
Dominance of indirect effects	A system receives more influence from indirect processes than from direct processes	$\frac{i}{d} = \frac{\sum_{i=1}^{n}\sum_{j=1}^{n}(n_{ij} - i_{ij} - g_{ij})}{\sum_{i=1}^{n}\sum_{j=1}^{n} g_{ij}}$
Amplification	Components in a network get back more than they put in	$n_{ij} > 1 \quad \text{for} \quad i \neq j$
Homogenization	Action of the network makes the flow distribution more uniform	$CV(G) + \frac{\sum_{j=1}^{n}\sum_{i=1}^{n}(\bar{g} - g_{ij})^2}{(n-1)\bar{g}}$
Synergism	Systemwide relations in the network are inherently positive	$\frac{b}{c} = \frac{\sum + \text{utility}}{\left\lvert \sum - \text{utility} \right\rvert}$

f_{ij}/x_j), and $d_{ij} = (f_{ij} - f_{ji})/T_i$, respectively (Figure 4). Note, the same power series procedure is used for the retrospective input oriented flow and storage matrices and the storage utility matrix.

Given that these series converge, the summed indirect effects can also be determined using matrix inversion:

$$\begin{aligned} \text{Flow:} \quad & \mathbf{N} = (\mathbf{I} - \mathbf{G})^{-1} \\ \text{Storage:} \quad & \mathbf{Q} = (\mathbf{I} - \mathbf{P})^{-1} \qquad (10) \\ \text{Utility:} \quad & \mathbf{U} = (\mathbf{I} - \mathbf{D})^{-1} \end{aligned}$$

For example, the direct flow intensity is a measure of the flow normalized by the total throughflow, T_j, at j: $G = (g_{ij}) = f_{ij}/T_j$. In Eqs. (9), the integral flow matrix, N, which accounts for the contribution of all direct and indirect interactions, is found by summing all powers of G. N is interpreted to be an integral flow matrix because its elements represent the total nondimensional flow expressed across all path lengths. A simple test shows that the integral matrix multiplied by the input vector returns the throughflow vector, $T = Nz$. This confirms that each of the elements in N, both direct and indirect, contributes at steady state to the overall throughflow in the network. This can also be inferred for the more complicated nonsteady-state case. The integral storage and utility matrices are similarly derived. In the storage case, the confirmation is given by $x = (Q\Delta t)z$, where Δt is the discrete time interval. For the retrospective analyses, the verification formulas are $T = N'y^T$ and $x = (Q' \Delta t)y^T$, where y is the output vector. The utilities of different orders are the benefits (net gain) and costs (net losses) associated with the flows of those orders. Thus, the power series methodology allows for a quantitative description of indirect effects as mediated by the flows, storages, and net flows in well-connected networks.

FOUR EMERGENT NETWORK HYPOTHESES

Of the three analyses in Eqs. (9), the flow and utility analyses have been used to identify four network properties (Table 1): *dominance of indirect effects* (Higashi and Patten 1986), *amplification* (Patten and others 1990), and *homogenization* (Patten and others 1990) follow from the flow analysis, and *synergism* (Patten 1991) follows from utility analysis. These four properties are the core hypotheses of theoretical systems ecology research using environ analysis (Patten 1999).

Dominant Indirect Effects

Dominance of indirect effects was the first property established from flow analysis (Higashi and Patten 1986, 1989). An element in the direct flow matrix is the normalized amount of direct flow between two components, whereas an element in the integral flow matrix represents the total (direct plus indirect) normalized flow. When the sum of elements of the direct matrix is compared with that of the indirect (integral minus direct and initial), there is often a greater contribution from indirect processes than from direct. Higashi and Patten (1989) identified six conditions that contribute to increasing indirect effects: system size, connectivity, looping (storage), cycling, feedback, and strength of direct effects. Indirect processes, as carried by higher-order interactions, can exert dominance in the system. This reinforces the notion that an object's behavior is embedded deeply within the network and the context in which it interacts with its surroundings. System behavior is holistically determined by both direct and indirect effects, but in general is dominated by the latter.

Network Amplification

The amplification hypothesis arose from the observation that terms in the integral flow matrix could be >1 in magnitude (Patten and others 1990). The values of the *direct* flow intensity matrix, G, are strictly <1 because the elements are interpreted as the probability or efficiency of transfer from one component to another. The occurrence of values >1 in the *integral* matrix calls for a new interpretation. Integral flow matrix values represent the average number of times a unit of flow derived from a particular source reaches another particular component (Kemeny and Snell 1960; Barber 1978). If the system is well connected and cycling occurs, then it is possible for a particle to enter, exit, and reenter the same component. When transactions along all the pathways are summed in the integral flow matrix, the values can be >1 when cycling is strong. Amplification is said to occur when any off-diagonal elements of the integral flow matrix are >1. This property has been demonstrated in small, highly aggregated models, but Fath (1998) showed that it does not regularly occur in large-scale models. Recent work suggests that it may be more strongly expressed in storage analysis, and this assessment is currently under way. Biologically, network amplification is significant because it indicates that the summed total amount of flow through a compartment can be greater than the total amount of input into the network. The component ‘sees‘ more material over time than is input into the system due to the cycling action in the network. In a complex food web, limiting nutrients [and energy (Patten 1985)] may cycle through the same component several, and possibly many, times before exiting the system. Network amplification quantifies the number of times that resources from different sources enter a component before exiting.

Network Homogenization

Network homogenization (Patten and others 1990) also arose from comparison of the integral flow matrix, N, with the direct flow matrix, G. This property asserts that values within a column, which represent the leading-edge of the output environ [or output niche (Patten and Auble 1981)], and values within a row (input niche of the input environ) tend to be similar in magnitude. At least they appear more similar to each other than the same comparison of the rows and columns in the direct flow matrix. Resources become well mixed by cycling in the network, giving rise to a more homogeneous distribution of flow. Therefore, ecosystems are composed of material (both energy and matter) that has been highly mixed and cycled. This is a departure from the traditional view derived from Lindeman (1942) trophic dynamics. A quantitative measure using the coefficient of variation was developed to show statistically that homogenization is a common property in well-connected systems (Fath 1998).

Network Synergism

Network synergism (Patten 1991, 1992) is based on utility analysis. Here, direct utilities are compared with integral values. Utility analysis is based on the normalized net flow between components. Positive and negative net flows are distinguished as benefits and costs, respectively. Benefit-cost ratios, which equal 1 for direct utilities, are >1 for integral utilities (Fath and Patten 1998). This is network synergism. Associated with it is a shift toward positive interactions (mutualism). This is revealed by defining interactions in terms of ordered sign pairs associated with the utilities in positions (i,j) and (j,i) in the direct versus integral utility matrices. The direct matrix indicates a qualitative relation as either (0,0), (+,−), or (−,+). When the indirect power series analysis is applied, the qualitative relationships are based on the interactions of all pathways and interactions. The integral matrix includes additional qualitative relations such as mutualism (+,+) and competition (−,−). Here, again, we see the action of the network altering the direct impression of system behavior. In the integral utility, matrices, pairwise system relations are more positive than in direct matrices, providing a synergistic context in which components interact. In isolation, this beneficial effect of coupling would be lost.

ASSUMPTIONS AND LIMITATIONS OF NETWORK ENVIRON ANALYSIS

Much of the analysis to develop these properties was done using models in which energy was the currency of flow in the system. Because of inherent thermodynamic losses, energy flow models generally have a higher percentage of flow lost to the environment through dissipation and respiration. Therefore, these models tend to have a relatively low cycling index (we have seen in general that this value is around 5%–15%). Many of the network properties are directly related to the level of cycling, so by investigating only energy flow models we actually underestimate these properties. Nutrient-based models are more likely to exhibit properties such as network amplification.

Another issue to consider in evaluating these properties is that of scale and aggregation. The question of how to represent a model and whether to split or lump compartments depends on the degree of understanding of the system and the questions of interest. This problem is more generally referred to as the *modeling problem* because each system can be represented in an infinite number of conceptual models. Clearly, the conceptual model underlying the analysis has an effect on the network properties because they are properties of models and not of reality, per se. In particular, the properties change based on the scale selected because of cycling. Large-scale, sparsely connected models tend to have a low cycling index, which means they are less likely to exhibit these properties. Here, we recommend that the level of resolution should be internally consistent.

One of the main limitations of these analyses is that the models are at static steady state. Static steady state is an important condition because not only are internal flows constant, but external inputs driving the system are also constant. It is due to this external push that the system is moved away from thermodynamic equilibrium and exhibits emergent properties based on cycling. The described network properties are based on a constant steady-state input and throughflow; therefore, rapidly changing systems are not yet amenable to this approach. However, static matrices capture the underlying principles that also apply in more complicated dynamic cases.

DIRECTIONS FOR FUTURE RESEARCH

Environ theory and analysis represent a strong theory of the environment, which is a fundamental attribute of every open system. Therefore, its potential for wide scientific application is great. Future research in network environ analysis should proceed along three general lines: further theoretical development, as a bridge to other areas of research, and direct application to management scenarios.

New Theory

There is still much to be done to develop the basic theory. New avenues for theoretical development could include further investigation of identified properties and discovery of additional properties. In particular, storage analysis has not been as thoroughly investigated. None of the four properties identified in this report were derived from storage analysis, though each has storage-analysis counterparts. Another area for new theoretical development could be indirect effects in input environ. Currently, the indirect-effects formulation uses the output environ only. An input measure to complement the output one would follow naturally from the dual object-environment concept underpinning this theory. Comparative aspects of environs have not yet been investigated. For example, input and output environs of a component could be compared to determine to what extent the component takes from versus gives to the ecosystem; or all input environs, and also output environs, could be compared across components to determine their degree of specialization, generalization, keystoneness, and so on. The comparative properties of ecosystems, both within and across different ecosystems, could be developed to reveal organizational characteristics. The list of ecosystem properties that could be explored through environ analysis is potentially very long indeed. When properties emerge, they should be founded on the same type of analytical base as demonstrated here.

Transdisciplinary Bridge

The second possibility is to use network analysis as a bridge to other fields and other applications. Taking the position that nature, including humanity, is organized as scale-sorted networks, the network approach has promise in many areas. Conceptual models contain only relational information of interactions between system components. Any time that relations in a conceptual model can be quantified with a consistent currency exchanged conservatively between components, the network approach is applicable. In ecosystem models, the currency is usually energy or nutrients, but there is nothing in the environ methodology that precludes the use of other informational or physiologically based units, such as inheritance or sexual characteristics. The only requirement is that the substances exchanged be conserved. The formalisms in which environ theory is grounded provide a strong framework that could be expanded to tie together concepts from biology, mathematics, ecology, economics, semiotics, cybernetics, information theory, and other disciplines.

Applications

The third and greatest challenge is finding a way to make network environ analysis operational. Links need to be made so that, as methodology is developed, it can become a practical tool for ecologists and environmental managers. Once a conceptual model has been developed, the number crunching is relatively easy, at least for the static case, and could be provided in a user-friendly software package. ECOPATH II (Christensen and Pauly 1992) and NETWRK4 (Ulanowicz and Kay 1991) are two programs already available for use in ecological network analyses. Such methodology makes it possible to describe quantitatively how objects are connected by structure and pass function through their many pathways to produce behavior. Network relationships, however real and determining they may be, are very obscure and take extensive mathematical manipulations to reveal. A network-oriented ecosystem theory can guide ecologists and other scientists, but it needs operational outlets to permeate and become useful in wide applications, including management decision making.

One area in particular that has a broad base for potential application is the utility analysis, which can be used to study scale-segregated relational interactions because it captures both top-down and bottom-up effects. Two different network-based approaches have already been tried (Herendeen 1995; Fath 1998). More importantly, utility analysis can be used to identify both direct and indirect relational aspects between two components in a network. An environmental management project, which will use utility analysis, is currently in development. It involves modeling ecosystems of the Northwest Atlantic with a view to interactions between cod and seals. The local cod fishery has been closed since 1992 due to overfishing. However, the cod fishery has not rebounded as expected, and it is suspected that cod populations are being suppressed by seals. A plan is being considered by the Canadian government that would cull thousands of seals in an effort to strengthen the cod fishery. This type of simplistic cause-and-effect relation may or may not be correct. A network approach to the interaction between seals and exploited fisheries of the Benguela ecosystem has already indicated that it is not. Yodzis (1998) concluded his study of this issue by network methods with the statement that ‘a cull of seals is more likely to be detrimental to total yields from all exploited species than it is to be beneficial.‘ In the Northwest Atlantic case, it is possible that cod and seals are indirect mutualists, and not necessarily prey and predators or competitors. The utility analysis applied to a network ecosystem model could demonstrate this.

CONCLUSIONS

An ecosystem is a continuous whole of interactions, relationships, and processes, such as growth, death, feeding, mating, and metabolizing. In reality, there is no break between an entity in nature and its surrounding environment (Bohm 1976). As scientists, however, we create conceptual models that partition the environment into its various parts and separate the observer from the observed. These models can be hierarchical and therefore may be considered at many levels of organization, such as individual, population, landscape, or ecosystem. The challenge is to find a way to analyze component interactions yet maintain the influence of the interacting network. In this article, we have reviewed network environ analysis as one tool to meet that objective. Network analysis, more generally, is a branch of ecology that deals with applying mathematical methodologies to flow-storage models to identify holistic and emergent properties of ecosystem behavior. Network environ analysis, in particular, is appropriate for this because it implements the concepts of environment and captures objects’ external relationships as input and output environs.

If indirect effects are dominant as proposed by Higashi and Patten (1989), then the importance of context, of how and where an object is positioned in relation to its environment, is relevant. The whole set of network interactions is potentially more important in determining the system behavior than are the direct transactions. In a holistic, synthetic discipline such as ecology, it is important to have tools available to determine indirect effects and techniques to investigate the system behavior without removing the components from the network. An awareness of the indirect effects garnered from network analysis aids in the design of ecosystem projects, experiments, and simulation models. The final use and test of this methodology is through verification with field data.

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