

9.04 Quantitative Methods for Ecological Network Analysis and Its Application to Coastal Ecosystems*

RE Ulanowicz, University of Florida, Gainesville, FL, USA; University of Maryland Center for Environmental Science, Solomons, MD, USA

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Abstract

In recent years, the description of system networks has been gaining in popularity as an alternative to conventional dynamical analysis. Although network description elsewhere treats only simple graphs and digraphs, ecosystem theory has enjoyed a legacy of analyzing quantitative digraphs. Ecological network analysis spans all levels of system description. Indirect influences of individual species upon one another can readily be measured. Trophic groupings and clusters of cycling can be identified and quantified. Whole system attributes, for example, organization and flexibility can be gauged. It is even possible to provide specific directions for remediating ecosystems so as to improve their sustainability.

9.04.1 An Alternative to Mechanism

Over the years, ecological modeling has produced numerous successes (Ulanowicz, 2009a). Fisheries managers, for example, have found Leslie matrix models (Caswell, 1989) to be useful for setting harvest quotas for fish stocks and game species. Models of single species or single processes have also been useful for purposes of prediction and interpolation (Jassby and Platt, 1976). Similarly, models that are driven by physical forces, such as hydrodynamic simulations (e.g., Wang and Johnson, 2000), have enjoyed widespread application. When chemical processes drive the distribution of living organisms, such as often occurs in models of water quality (Biswas, 1981), useful predictions can result. Various models that employ cellular automata have been instrumental in testing and articulating hypotheses in disciplines such as landscape ecology (Sanderson and Harris, 2000) and individual-based modeling (DeAngelis and Gross, 1992).

Problems arise, however, as soon as the scope of the modeling exercise encompasses more than one biological process. In most cases, models of multiple interacting processes are less than robust and of marginal utility (Platt et al., 1981). Not that such exercises are completely without merit: multiple process models oftentimes generate hypotheses about whole ecological communities. However, actually using them to test hypotheses is quite another matter, because the dynamics of multiple process models usually bear little resemblance to actual

ecosystems behaviors, unless (as mentioned) the community being modeled is dominated by a single physical or chemical factor.

Such difficulties notwithstanding, there remains a pressing need for the study of whole ecosystem behavior – how collections of interacting ecological processes are linked together and affect one another (Lewin, 1984). One way to address multiple biological processes is to forego the specification of dynamics and see what can be learned about the system by focusing on the observed configurations of system processes. That is, one effectively truncates the modeling process after the first two steps – identification and parsing. Identification refers to the choice of the ecosystem elements that are deemed of interest (Halfon, 1979). The cast in any ecological scenario will necessarily reflect the particular interests of the individual carrying out the study – as will the suite of interactions among those components (parsing).

The assumptions that comprise these two steps can be represented as a set of boxes (nodes) that are connected by lines (arcs) denoting the pertinent interactions. A surprising amount can be learned about how the system is functioning from the topology of the resulting graph or network of interactions. In the past decade or so, patterns of connections have been classified for any number of systems (Barabási, 2002), and knowing whether a system is connected, for example, in a power law fashion or via a small world topology reveals much about how the system behaves.

Simply knowing that two components interact constitutes useful information. More is provided by signifying the

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direction of the interaction. For example, an influence by A upon B can be denoted by connecting A with B by an arrow that terminates in B ($A \rightarrow B$). Should B also actively affect A, that interaction would be denoted by a second arrow, $B \rightarrow A$. The ensuing picture of boxes and arrows is called a directed graph, or digraph. The last two decades have seen numerous efforts to classify ecosystems according to their representations as digraphs – work that falls under the rubric of food-web theory (e.g., Yodzis, 1989; Cohen et al., 1990; Polis and Winemiller, 1995).

A digraph is said to be binary in that a connection from A to B either exists or does not. All connections in digraphs are considered equiponderant, which is almost never the actual case. Some connections are always greater in effect than others, and often by large orders of magnitude. If some measure can be assigned to each connection that quantifies the differences among the connections, the result is called a weighted digraph.

Examples of the progression graph \rightarrow digraph \rightarrow weighted digraph are presented in Figure 1. The weighted digraph is obviously the most information-rich depiction, because either of the simpler forms of graphs can be derived from a weighted representation simply by ignoring appropriate information. Because one can always proceed from the weighted digraph to one of the simpler forms, but not necessarily in the reverse direction, the remainder of this chapter will be devoted to analyses of weighted digraphs. It is noted without further remark that considerations of the simpler graphs could, in some cases, result in misleading inferences.

One final classification of networks occurs when the weights assigned to the interactions represent the transfer of some conservative physical medium, such as energy or a form of matter (e.g., carbon, nitrogen, or phosphorus). Such weighted digraphs are known as flow networks. Flow networks can be assumed to balance around each node (i.e., the sum of inputs to a given node equals the sum of its outputs), but strict balance is not required by some of the analyses that will be discussed.

9.04.2 Requirements

The flow networks most familiar to ecologists are trophic in nature. That is, the network represents the answers to two questions: (1) who eats whom? and (2) at what rates? Each node of the network will be said to represent a taxon – that is, either an individual, a population of a given species or some aggregation of species populations according to guild, habitat, or trophic position. Having decided upon a list of appropriate taxa, one must then determine for each taxon which of the other taxa are included in its diet.

Up to this point the digraph for n taxa can be represented as an $n \times n$ square matrix of ones and zeroes. A one appears as the entry for row i and column j whenever material flows from prey i to predator j ; otherwise the i - j th component is set to zero. (Some investigators prefer that the predators appear in the rows and the prey in the columns, i.e., the matrix is the transpose of that described here.) This binary array is called the adjacency matrix. The advantage of representing networks as matrices is that one may then invoke operations from linear algebra to treat in systematic fashion communities of arbitrarily large dimension and complexity.

A defining characteristic of an ecosystem is that it is never closed. There is always exchange of material and energy with the rest of the world. Such exogenous transfers must be part of any bookkeeping scheme. Henceforth, all exogenous (external) inputs to a particular taxon will be bundled into a single flow. (This assumption is made without loss of generality, because different types of inputs could always be treated separately, whenever necessary.) Examples of external inputs include primary production, immigration, and inbound advection of material or energy. An exogenous input is represented by an arrow that has no visible taxon as its origin but which terminates in the particular receiving node (Figure 2).

Unlike inputs, two different categories of exogenous outputs will be distinguished: the first type consists of the export of material or energy that is still useful to other comparable ecosystems. Such exports might represent emigration, harvesting by humans, or advection out of the system. Similar to the inputs, export flows will be represented by arrows that originate in the appropriate taxon but which terminate in no node (Figure 2). To be distinguished from useful exports, some energy will be dissipated into heat (respiration), or some material will be degraded into its lowest energetic form (e.g., reduction of N to N_2 , or C to CO_2). Following Odum (1971), dissipations will be depicted by the conventional ground symbol of electrical circuit diagrams (Figure 2).

Under this typology, the maximum number of flows among n taxa becomes $n^2 + 3n$. Whenever $n > 20$, the number of transfers is usually much lower, and typically is less than 15% of n^2 . That is, real ecosystems are usually represented by sparse matrices.

With flow matrices, the weightings become the rates of exchange among the taxa. Typically, the medium is energy or a particular chemical element, such as C, N, P, or S. The convention in ecological network analysis (ENA) is that each network represents a particular medium (although some investigators allow several (e.g., Hannon et al., 1991)). (The treatment of several parallel networks of interacting media will be treated in Section 9.04.8.)

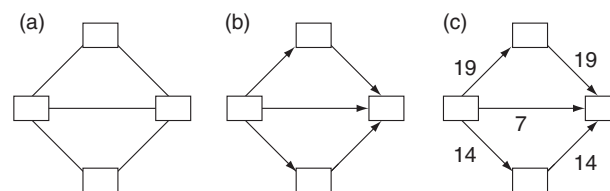


Figure 1 The nested hierarchy of networks: (a) graph; (b) digraph; (c) weighted digraph. Reproduced with permission from Ulanowicz, R.E., 2009b. A Third Window: Natural Life beyond Newton and Darwin. Templeton Foundation Press, West Conshohocken, PA.

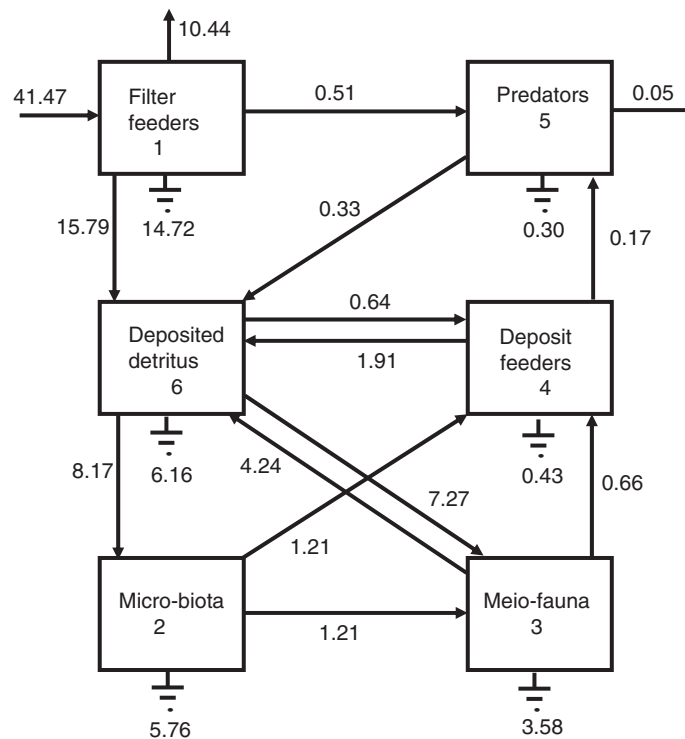


Figure 2 The trophic exchanges of energy ($\text{kcal m}^{-2} \text{yr}^{-1}$) in the Oyster Reef community (Dame and Patten, 1981). Arrows not originating from a box represent exogenous inputs. Arrows not terminating in a box portray exogenous outputs. Ground symbols represent dissipations.

To quantify the various rates, a transfer from prey i to predator j will be denoted as T_{ij} . The rate of exogenous input to taxon i will be designated as X_i , and the rate of removal of useful medium from taxon i to the outside world will be called E_i . Dissipation by i will be Ω_i . Whenever rates are aggregated over a sufficiently long interval, medium is likely to balance around each compartment. That is, around each taxon, i ,

$$X_i + \sum_{j=1}^n T_{ji} = \sum_{k=1}^n T_{ik} + E_i + \Omega_i \quad [1]$$

or

$$X_i + T_i = T_i + E_i + \Omega_i$$

where a dot in the subscript indicates summation over that index. When reckoned over shorter intervals, however, inputs and outputs around each taxon may not balance. (The analysis of cycling and the whole-system information indices that follow does not require balance around each compartment. The input-output (I-O) and trophic level analyses, however, will be distorted by any imbalances.)

In the best of all possible worlds, an investigator has access to field measurements on each rate of transfer. For some rates, such as primary production, such data are often available, but direct measurement of all flows is usually infeasible. One must resort, therefore, to indirect means of estimating the magnitudes of most rates.

One helpful assumption for estimating unknown flows is that the inputs and outputs balance around each taxon. Even then, the estimation of magnitudes in a balanced flow network remains an art form that cannot be formalized in all cases.

Because it is more difficult to measure metabolic rates in the field than the sizes of populations, a common approach has been to assess first the stock of a taxon (in terms of the chosen medium) and to multiply that density by the appropriate tabulated metabolic quotients to obtain the desired rates. For example, if the density of microzooplankton is measured as 150 mgC m^{-2} and published metabolic constants show their average consumption rate to be 160% per diem, then the total demand by these organisms should be roughly $87\,600 \text{ mgC m}^{-2} \text{yr}^{-1}$. Respiration, excretion, and natural mortality for this population can be similarly reckoned. Overall consumption by predators would then be estimated by difference between total inputs and metabolic losses. With estimates of overall demands and availabilities now at hand, balancing the network becomes the task of matching the corresponding ends of the individual flow arrows.

Perhaps the most popular automated balancing routine available to the public has been ECOPATH (Christensen and Pauly, 1992), which was built on an optimization routine by Polovina (1985). Other optimization routines have been written by Vezina and Platt (1988) and Kavanagh et al. (2004). The main difficulty with optimization algorithms, however, is that they almost always nullify one or more of the flows that are known to be nonzero. Some way of balancing the network that keeps all known exchanges nonzero and in proper proportion would be preferable. That is, one seeks a method of balancing the network that imposes the fewest external assumptions.

Two such least-inference schemes are now available (Ulanowicz and Scharler, 2008). In the first routine, MATBLD, the initial magnitude of a flow is set to be jointly proportional to the availability of the given prey and the

demand by the particular predator. If the adjacency matrix of flows were fully connected (all ones), this joint apportionment scheme would immediately yield a balanced network. As mentioned, however, ecosystem networks are almost always sparsely connected, so one must inflate the estimates according to joint proportion by a common factor in order to yield a total system activity ($T_{..}$) that is commensurate with the collective demands by all components. Such uniform inflation does not necessarily balance the network, and one must bring the system into balance by some automated scheme, such as linear donor-control (Allesina and Bondavalli, 2003.)

The second, possibly more promising algorithm, is called MATLOD. It begins by assigning the same miniscule amount of flow to all nonzero connections and progressively loads the flow matrix by incrementing each active flow by the same, very small amount. If the current increment exhausts the availability of that prey or if it satisfies the total demand by that predator, the flow in question is eliminated from further increments. Matrix loading halts when no further flow remains to be incremented. This iteration technique resembles the filling of a mold in reverse. The elimination of any remaining imbalance is achieved via the Allesina and Bondavalli (2003) equilibration routine.

When started with the same data, networks balanced using MATBLD do not differ from those created by MATLOD to any statistically significant degree; neither do the results of either method diverge from published networks to any statistically significant degree (Ulanowicz and Scharler, 2008).

The minimal information required to create a balanced, weighted digraph of trophic interactions thus consists of field estimates of the respective population densities, the predator-prey topology, and the appropriate values of the physiological quotients. As most of these items are known for a wide variety of ecological systems, it should now be possible to create a host of quantified digraphs for a diversity of ecosystems. The issue now becomes how to analyze such networks in order to respond to the usual questions posed by ecological managers.

9.04.3 Issues Needing Attention

The estimated weighted digraphs just discussed are essentially snapshots of the suite of trophic transfers. They do not explicitly address the underlying dynamics. They are rich, however, in implicit information on how the system is functioning – just as X-rays of the body provide snapshots that, in turn, provide myriad clues about physiological functions in the body (e.g., the presence of stones in the kidneys might indicate some disorder in the metabolism of calcium). Similarly, weighted digraphs of ecosystems are rich in information about the status of the ensemble at a number of levels.

At the level of the individual population, one is interested not only in how that compartment interacts with each of its direct prey and predators, but also in how each of those populations relates in turn to others in the overall ecosystem. In other words, even though a species interacts immediately with only a limited number of other organisms, it communicates indirectly with a much larger number of elements of the ecosystem. The fact that networks can be represented in terms of matrices provides a major advantage toward assessing these indirect relationships. Whence, matrix algebra can be invoked

to quantify indirect effects across a myriad of network pathways – an endeavor that has been termed I–O analysis.

In particular, it is possible via successive application of matrix multiplication to gauge how many times, on average, medium has been transferred along its way from primary production to the taxon of interest, that is, the average trophic position of the given taxon. Obversely, the same calculations reveal the proportions of that taxon's activity that has arrived along trophic pathways of various integer lengths. That is, what percentage of the taxon's activity is supported by pathways of length one (herbivory), of length two (carnivory), and so forth? It then becomes a matter of bookkeeping to consolidate all the activities of all compartments at any given integer level into a virtual representation of that trophic stage. In the absence of cycles, these stages all fit together as a classical trophic chain or pyramid. Even when complicated by cycles, the reduction of a complicated food web into a didactic chain is usually possible.

Although they complicate trophic analysis, cycles of medium are of special interest, because they are usually connected with controls in ecosystems. Endogenous control in noncentralized systems is usually expressed via feedback, and feedback implies the existence of cycles. Hence, how many cycles are contained in a particular ecosystem network, what are the constituents of each loop, and how are they all put together become pressing questions, the answers to which should help illumine how the system behaves. Unlike with I–O and trophic analyses, uncovering the details of cycling in ecosystems is not effected by matrix operations *per se*, but by representing networks in terms of matrices, one provides a format conducive to the systematic delineation of cycling structure.

Finally, there remains the question of how the ecosystem as a whole behaves. Can its degree of organization be quantified? Can one also quantify the flexibility of the system to persist in the face of novel perturbations? What are the prospects for the sustainability of a particular system? Where are the controlling bottlenecks in system functioning? How can system dysfunction be remediated? To approach these questions, it should be pointed out that by identifying the various compartments of an ecosystem, the investigator articulates the differences among the taxa. Gregory Bateson defined information as “the difference that makes a difference.” It should come as no surprise; therefore, that information theory is a most appropriate tool for answering such whole-system issues.

9.04.4 Input–Output Analysis

That networks can be represented as matrices is serendipitous, because diagrams otherwise grow too complex to be able to follow the pathways and magnitudes of indirect effects. A convenient starting point for I–O analysis is the definition of the matrix of dietary proportions, $[G]$. The elements of $[G]$ are calculated using the elements of the flow matrix, $[T]$, and the input vector, (X) . Each T_{ij} of $[T]$ is normalized by the total input to the receiving compartment, j :

$$g_{ij} = \frac{T_{ij}}{(T_{.j} + X_j)} \quad [2]$$

so that the element g_{ij} of $[G]$ becomes the fraction which i comprises of the total input into j . In other words, element i

in column j of $[G]$ describes the percentage of i in the diet of j . Hence, $[G]$ is known as the matrix of dietary coefficients.

Most fortuitously, the algebraic powers of $[G]$ reveal the fractions of the diet of j that flows to i along pathways of length corresponding to the integer power to which $[G]$ is raised. Its algebraic powers have very didactic meanings as regards trophic functioning. Those meanings are illustrated by the very simple network in [Figure 3](#). The six nonzero values of T_{ij} become the six corresponding nonzero elements of $[G]$:

$$[G] = \begin{bmatrix} 0 & g_{12} & g_{13} & g_{14} \\ 0 & 0 & g_{23} & g_{24} \\ 0 & 0 & 0 & g_{34} \\ 0 & 0 & 0 & 0 \end{bmatrix}$$

The second power of $[G]$ is obtained via matrix multiplication of $[G]$ by itself,

$$[G]^2 = \begin{bmatrix} 0 & 0 & g_{12}g_{23} & (g_{12}g_{24} + g_{13}g_{34}) \\ 0 & 0 & 0 & g_{23}g_{34} \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix}$$

One notices that each of the nonzero elements of $[G]^2$ consists of terms that represent all of the pathways of length 2 that connect i with j . For example, elements 1–3 of $[G]^2$ reveal how much gets to 3 from 1 over the single two-step pathway $1 \rightarrow 2 \rightarrow 3$. Element 14 of $[G]^2$ is made up of two terms, each representing a two-step pathway from 1 to 4. The first term gives the fraction of total input to 4 that flows over the pathway $1 \rightarrow 2 \rightarrow 4$, whereas the second term reports the fraction of input to 4 that has traversed the route $1 \rightarrow 3 \rightarrow 4$.

Multiplying $[G]^2$ yet again by $[G]$ produces the matrix $[G]^3$:

$$[G]^3 = \begin{bmatrix} 0 & 0 & 0 & g_{12}g_{23}g_{34} \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix}$$

There is only one nonzero element of $[G]^3$ and it represents the sole pathway of length 3 in the network, $1 \rightarrow 2 \rightarrow 3 \rightarrow 4$. The powers of $[G]$ truncate with $[G]^4 = [0]$, because there exist no pathways longer than 3 in this network.

The reader is invited to experiment with other simple graphs to convince herself/himself that the elements of the m th power of $[G]$ are formed by contributions from all pathways of exactly length m and no others.

The way in which $[G]$ was normalized guarantees that each $g_{ij} \leq 1$, making it highly probable that elements in the higher

powers of $[G]$ will grow progressively smaller. The question thus arises whether or not the infinite series

$$[I] + [G] + [G]^2 + [G]^3 + [G]^4 + \dots$$

converges to a finite limit. (The matrix $[I] \{=[G]^0\}$ is called the identity matrix. It consists of ones for $i=j$ and zeroes elsewhere.) [Simon and Hawkins \(1949\)](#) demonstrated that the normalization procedure in eqn [2] guarantees that the infinite series of matrix powers does converge to a finite limit, namely,

$$\lim \{[I] + [G] + [G]^2 + [G]^3 + [G]^4 + \dots\} \rightarrow [I - G]^{-1}$$

This limit, the matrix inverse of $[I - G]$, is called the Leontief structure matrix, $[S]$. The i - j th component of $[S]$ reveals the fraction of the total input into j that left i and traveled over all pathways of all lengths to satisfy a final demand upon j of one unit. Final demand is a pivotal concept in economic theory, and the $[S]$ matrix provided economists with estimates of how much production was required by each economic sector in order to satisfy any prescribed vector of final demands. [Leontief \(1951\)](#) formulated the beginnings of what eventually was called I-O theory. [Hannon \(1973\)](#) introduced Leontief's methods into ecology.

The homologs of final demands in economics are the respirations in ecology. Although respiration is important to ecologists, the intermediate transfers among system components interest them more. That is, ecologists give priority to knowing how much of what arrives at j can be traced to a particular activity i . [Szyrmer and Ulanowicz \(1987\)](#) demonstrated how such intermediate transfers can be estimated by a simple transformation of the $[S]$ matrix. Szyrmer called the transformed matrix the total dependency matrix, $[D]$. The elements of the $[D]$ matrix are calculated from $[S]$ and the original flows $[T]$ as

$$d_{ij} = (s_{ij} - \delta_{ij}) \left(\frac{T_{i.}}{s_{ii}T_{.j}} \right)$$

where δ_{ij} are the elements of the identity matrix. All indices run from 0 to $(n+2)$, and the T_{0j} represent the exogenous inputs to j , $T_{i,(n+1)}$ are the useable exports from i to other systems of comparable scale, and $T_{i,(n+2)}$ are the dissipative losses from i . Effectively, d_{ij} answers the question, "What fraction of the total diet of j passes through i along its way to j ?" Thus, the j th column of $[D]$ becomes the indirect diet of j – the respective amounts by which j depends upon the activity of each element in the ecosystem. Because medium from i can visit several compartments along its way to j , the elements of the j th column sum to ≥ 1 , and that sum also signifies the effective trophic position of j .

It is possible to use the matrix of indirect diets to differentiate trophic roles. For example, the Chesapeake mesohaline ecosystem is host to two piscivorous predators, striped bass (*Morone saxatilis*) and bluefish (*Pomotatus saltatrix*). One would expect heavy competition between them. [Baird and Ulanowicz \(1989\)](#), however, calculated their indirect diets, revealing (among others) the following indirect dependencies: (1) striped bass on zooplankton 65.8%; (2) bluefish on zooplankton 28.7%; (3) striped bass on polychaetes 1.8%; and (4) bluefish on polychaetes 48.0%.

These apportionments revealed significant stratification of trophic resources between the predators. Striped Bass ultimately

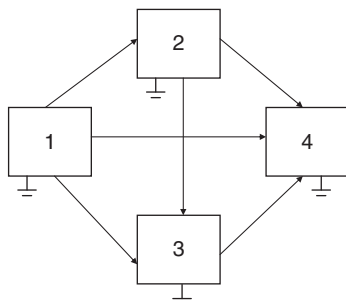


Figure 3 A simple hypothetical network of four components.

showed a high dependency on pelagic production, whereas Bluefish derived their resources more from benthic secondary production.

Instead of normalizing $[T]$ down its columns to get σ , one could have as well normalized across the rows of $[T]$, which would have resulted in a matrix of host coefficients, $[F]$:

$$f_{ij} = \frac{T_{ij}}{(T_{i.} + E_i + \Omega_i)}$$

That is, the component, f_{ij} , of $[F]$ reveals the fraction of the total activity of any compartment i that flows directly to some other element j . The corresponding output structure matrix, $[\Sigma] = (I - F^T)^{-1}$, was originally formulated by Augustinovic (1970) to estimate how much of the activity of any sector j is generated by a single unit of primary input to i . (The superscript T indicates matrix transpose, i.e., the matrix that results when the rows of a matrix are exchanged with its columns [i.e., $(f_{ij})^T = f_{ji}$].) $[\Sigma]$ is the obverse set of indicators to $[S]$. Primary inputs are of substantial interest to ecologists, but many might prefer to know the intermediate contributions of each compartment to all the others, that is, how much of what leaves i eventually flows as input to j . As with the dietary coefficients, Szyrmer defined a total contribution matrix, $[C]$, with the elements

$$c_{ij} = (\sigma_{ji} - f_{ji}) \left(\frac{T_{i.}}{\sigma_{ii} T_{.j}} \right)$$

where σ_{ij} is the i - j th element of $[\Sigma]$.

It is sometimes useful to regard the elements of the total contribution matrix as representing the efficiencies with which the medium flows from any one compartment to any given other. Suppose, for example, that one desired an indicator of overall ecosystem efficiency, that is, how much primary production eventually reaches the upper trophic components. In this regard, Ulanowicz (1984) wanted to compare the trophic efficiencies of two tidal marsh ecosystems situated near the Crystal River nuclear power plant on the west coast of Florida. The first network straddled the thermal outfall from the plant ($\Delta T \approx 6^\circ \text{C}$), while the second (control) marsh was beyond the influence of the thermal effluent. Calculation of the total contribution coefficients of primary production to the Gulf Killifish (*Fundulus grandis*) and to two Needlefish (*Strongylura marina* and *Strongylura notata*) revealed the following:

	Control	ΔT	
Gulf Killifish	0.147×10^{-3}	0.67×10^{-3}	(-54%)
Needlefish	0.338×10^{-3}	0.140×10^{-3}	(-59%)

The impact of the thermal effluent was obvious. Heated water lowered the overall efficiency of the ecosystem for producing top carnivores by ~50–60%.

A frequent criticism of I–O methodology is that it pertains only to steady-state or temporally averaged networks. Several attempts have been made to expand I–O theory to treat time-varying systems. Matis et al. (1979), for example, regarded any imbalance simply as another category of input or output (depending on the direction of the imbalance). Matis and Patten (1981) scaled the flows by the storages of their source

compartments and inflated the diagonal flows to better reflect their relative storage times. Another alternative is to apply information-theoretic methods to a time series of network snapshots depicting the dynamics over an interval (See Section 9.04.8).

Still another deficiency of I–O analysis in the eyes of many is that it pertains to only positive flows of the medium. Beyond contributions and dependencies, ecologists are also interested in how the negative effects of predation might propagate throughout the system. Fortunately, the same linear algebra used to quantify positive contributions can evaluate as well the net positive or negative trophic impact that any one species has on any other (Ulanowicz and Puccia, 1990). One notes that g_{ij} quantifies the positive impact of prey i upon predator j . By contrast, f_{ji} measures the negative impact that i has on j . Consequently, the overall effect of i on j should be related to the difference $g_{ij} - f_{ji}$. Unfortunately, because f_{ji} has been normalized by the total output from i , rather than just the predatory losses that i sustains, it underestimates the magnitude of negative impact by j on i . Accordingly, f_{ji} should be renormalized by its secondary production alone, rather than by its total outflow. The renormalized predator impacts are labeled f_{ij}^* , where

$$f_{ij}^* = \frac{T_{ij}}{\sum_{m=1}^{nl} T_{im}}$$

and the index m is summed over only the subset of living components (nl in number) of the full suite of n ecosystem components. As a result, a more accurate measure of the net direct effect that i has on j becomes

$$q_{ij} = g_{ij} - f_{ji}^*$$

where $-1 \leq q_{ij} \leq 1$.

In almost all instances, the power series of $[Q]$ converges in the manner that the corresponding infinite series of the powers of $[G]$ converged. That is,

$$\lim \{[I] + [Q] + [Q]^2 + [Q]^3 + [Q]^4 + \dots\} \rightarrow [I - Q]^{-1}$$

In rare (usually degenerate) instances, the matrix $[I - Q]$ can be singular, and then the series does not converge.

The net trophic impact (direct and indirect) of any given compartment i upon any chosen other, j , is the i - j th component of the matrix of net total impacts, $[M]$. It is calculated as $\{[I - Q]^{-1} - [I]\}$. For any connected graph, all n^2 elements of $[M]$ will be nonzero. Such a jumble of impacts would be difficult to interpret (e.g., Hillebrand and Shurin, 2005) failing a systematic way of presenting the results. The original algorithm for calculating these indirect trophic influences (IMPACTS) allows the user to focus upon a particular compartment and ranks the impacts of all the other species upon that taxon, so that the major influences are easy to spot at either end of the ranking.

Patten (1982, 'On the quantitative dominance of indirect effects in ecosystems', unpublished paper presented at the Third International Conference on State-of-the-Art in Ecological Modeling, Colorado State University, 24–28 May, Fort Collins, CO) posited a tendency for negative, competitive direct interactions to become positive indirect influences. Using the non-normalized form of f_{ij} , Fath and Patten (1998) counted a higher ratio of positive elements in $[M]$ than are present in the direct effects matrix, $[Q]$. As noted above, the

lack of renormalization (to f_{ij}^*) would tend to inflate positive effects in $[M]$. Nevertheless, it is easy to identify instances when negative direct interactions become positive indirect influences, even under the more conservative normalization used above (Bondavalli and Ulanowicz, 1999).

9.04.5 Trophic Analysis

It has been mentioned how the powers of the $[G]$ matrix elaborate flow in terms of integral trophic steps. It stands to reason, therefore, that the powers of $[G]$ can be employed to quantify the trophic status of an ecosystem network.

It happens that the notion of trophic level began with a very simple depiction of the ecosystem as a trophic chain or pyramid. At the first level, energy is fixed by primary producers (plants), and some (but never all) of that energy is transmitted to plant eaters (herbivores) at the second level. Subsequent transfer is made to carnivores at the third trophic level, then to the top carnivores at the fourth, etc. Rarely is any mention made of tertiary carnivores and beyond. Earlier, it was presumed that thermodynamic losses of energy and material during each transfer curtailed trophic chains to no more than five steps, but that assumption was shown to be problematic (Pimm and Lawton, 1977).

Of course, nature is hardly ever as simple as a straight chain or pyramid, and the actual web of interactions usually proves to be quite complicated (Hillebrand and Shurin, 2005.) One seeks, therefore, a systematic method for making sense of the general situation. While some species are, in fact, obligate autotrophs or herbivores, many of the heterotrophs feed at several levels, so that no assignment of taxa to integral trophic levels seems obvious. Cousins (1985), for example, remarked as how a hawk usually feeds at five separate trophic levels. Although some urge that the concept of a trophic level be dropped as a useless fiction, the properties of the powers of $[G]$ give reason to hope that some sense can be made of Darwin's 'entangled bank'.

Levine (1980) observed that the sum of any column of the structure matrix, $[S]$, was related to the number of trophic transfers that medium had experienced on its way to that given compartment. This sum is generally not an integer, but Levine suggested that one regard it as an average level at which the taxon is feeding. In the hypothetical example shown in Figure 4, compartments 1, 2, and 3 are arrayed in chain-like fashion. Compartment 4, however, receives only 5 of its 50 units of activity at the fourth trophic level. Otherwise, 30%

of its sustenance arrives the third level and 60% at the second. Hence, its effective trophic level can be reckoned as $(0.6 \times 2) + (0.3 \times 3) + (0.1 \times 4) = 2.5$. In the $[S]$ matrix corresponding to this network, the first three columns sum to 1.0, 2.0, and 3.0, respectively, and the sum down the fourth column is 2.5, as just calculated. This calculation applies to the most complicated flow topologies. Christian and Luczkovich (1999) used Levine's notion of effective trophic level to establish the direction of causality (bottom-up vs. top-down) in seagrass communities in St. Mark's Refuge, Florida. Pauly et al. (1998) used it to demonstrate how world fisheries in the last decades have been 'fishing down' stocks, that is, decimating higher trophic level species and relying more on lower level populations.

Now that it is possible to attach several trophic levels to a particular compartment, one asks whether the reverse might also be feasible – that is, can the activity of a given compartment be apportioned among several integral trophic levels (Ulanowicz and Kemp, 1979)? In this regard, one notes that the fraction by which compartment i feeds directly upon primary sources is

$$g_{oi} = \frac{T_{oi}}{\sum_{m=0}^n T_{mi}}$$

so that the fractions for all n components can be arrayed as a row vector, call it $(L_1)^T = (g_o)^T$. Each element of this row vector reveals the fraction of the activity of the respective taxon that can be attributed to primary production. To calculate the amounts by which each taxon feeds as a herbivore, it is necessary only to multiply $[G]$ by $(L_1)^T$ from the left to generate a new row vector, $(L_2)^T = (L_1)^T [G]$. In like manner, the fractions by which each compartment feeds as a carnivore (acts at the third level) become $(L_3)^T = (L_2)^T [G]$. By mathematical induction, the fractions at the m th trophic level become $(L_m)^T = (L_1)^T [G]^{m-1}$. Whenever cycles are absent from a network, the sequence of row vectors, $(L_1)^T, (L_2)^T, (L_3)^T, \dots$, truncates (become all zeroes) within $n-1$ steps. As a result, whenever cycling is absent, it becomes possible to define an unambiguous Lindeman trophic transformation matrix, $[L]$, such that the i th row of $[L]$ is constituted by $(L_i)^T$. The fraction by which taxon j feeds at the i th trophic level is given by matrix component L_{ij} . Furthermore, reading across the row i reveals the composition of i th virtual trophic level.

Applying this construction to the simple network in Figure 4 yields as the Lindeman trophic transformation matrix,

$$[L] = \begin{bmatrix} 1. & 0. & 0. & 0. \\ 0. & 1. & 0. & 0.6 \\ 0. & 0. & 1. & 0.3 \\ 0. & 0. & 0. & 0.1 \end{bmatrix}$$

Reading down the columns, one sees that the first three compartments act wholly at one of the first three trophic levels, but that compartment 4 is partitioned as described earlier. Looking across the rows reveals the apportionments of the various components to the virtual integer levels. For example, virtual trophic level 3 consists of all of the activity of taxon 3 and 30% of the activity of taxon 4.

Reality is not hypothetical, however, and almost all real trophic networks contain cycles. Although this is true, Pimm (1982) nevertheless observed that cycles confined strictly to

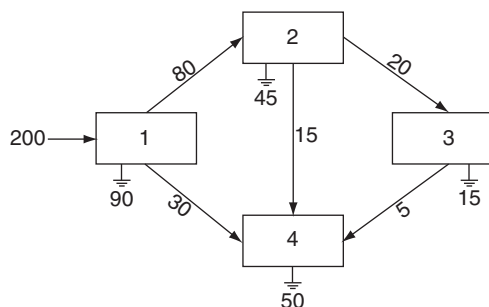


Figure 4 A hypothetical trophic network. Units are arbitrary.

living, feeding taxa remain quite rare and are usually small in magnitude. Reading Pimm's statement the other way around, virtually all cycles in ecosystems contain at least one nonliving compartment. By ordering the ecosystem's components so as to place all living compartments (say there are nl of them) first, the $nl \times nl$ submatrix of transfers among the living compartments should contain very few cycles, all consisting of flows of insignificant magnitude. It will be shown below how cycles can be removed from networks without affecting the balance around any constituent. It becomes possible, then, to remove such feeding cycles without significantly altering the $nl \times nl$ submatrix of predatory flows. An $nl \times nl$ Lindeman transformation matrix $[L]$ can then be constructed using the $nl \times nl$ submatrix of $[T]$ from which cycles of predatory exchanges have been removed (Ulanowicz, 1995).

To sort out the manifold predatory flows in the ecosystem, one regards $[L]$ as a conventional transform in linear algebra. That is, $[L]$ can act upon the known input vector (X) to define a vector of canonical inputs, (Ψ) (Greek uppercase psi):

$$(\Psi) = [L](X)$$

Similarly, canonical forms for the useful exports, (E), and disipations, (R), become

$$(Y) = [L](E)$$

and

$$(P) = [L](R)$$

respectively.

One then seeks to create a canonical matrix of flows $[\Theta]$ by transforming the matrix of original flows, $[T]$, in conventional fashion:

$$[\Theta] = [L][T][L]^T.$$

Unfortunately, $[L]$ is not orthonormal, so that the transformed matrix of flows, $[\Theta]$, is not diagonal in form. The situation can be redeemed, however, because $[\Theta]$ possesses a peculiar form of symmetry that allows one to rework it into a surrogate diagonal matrix, $[\Xi]$. $[\Xi]$ has as its i th diagonal element the sum of the i th row of $[\Theta]$ and zeroes elsewhere, that is, $\xi_{ii} = \sum_k \theta_{ik}$, and $\xi_{ij} = 0$ otherwise. Then in analogy to eqn [1], one may balance each virtual trophic level, λ , as follows:

$$\Psi_\lambda + \xi_\lambda = \xi_{(\lambda+1)} + v_\lambda + \omega_\lambda$$

Proceeding in this way, the Lindeman matrix $[L]$ shown above for the simple network in Figure 4 transforms that network into the equivalent straight chain in Figure 5.

Although the canonical transformation just described works whenever there are no cycles in the entire network, significant cycles are present in almost every real ecosystem network and involve mostly the nonliving compartments. Arranging the n compartments so that the nl living taxa always appear first facilitates the removal of all (insignificant) cycles among only

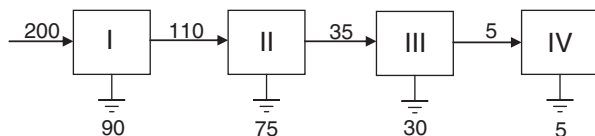


Figure 5 The Lindeman spine of the network in Figure 4.

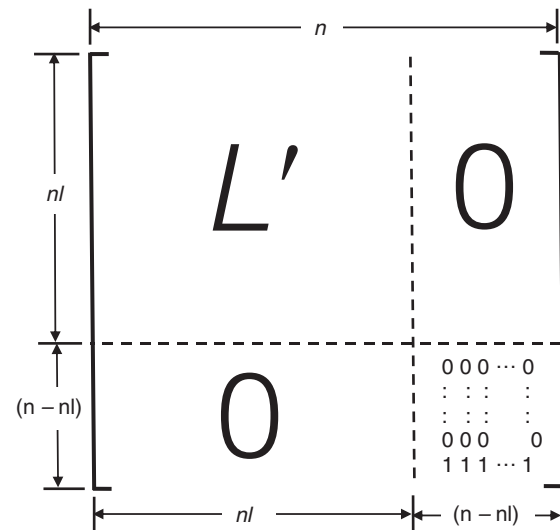


Figure 6 The partitioned expansion of the $[L']$ matrix.

predators. This arrangement allows one to create an $nl \times nl$ Lindeman matrix, $[L']$, from the revised $nl \times nl$ acyclic submatrix. To create a Lindeman transformation for the entire system, one places $[L']$ into the upper left hand corner of the expanded $n \times n$ matrix, $[L]$, as in Figure 6. The remainder of matrix is filled out with zeroes, except for the final $[n - nl]$ elements of the n th row, all of which are set equal to one.

The ensuing matrix $[\Xi]$ creates what is called a 'Lindeman spine' of chain-like flows. The remainder of the $[L]$ matrix aggregates all the nonliving compartments into a single non-living pool in such a way that maintains balance around each virtual component. Applying this method to the network in Figure 2 produces the Lindeman spine in Figure 7 along with its associated detrital flows.

Transforming general networks into canonical trophic chains allows the investigator to compare trophic dynamics among disparate ecosystems or to monitor changes in the same ecosystem over time. It should be mentioned that one often encounters canonical trophic chains that are longer than five steps, seemingly at odds with the observation of Pimm and Lawton (1977) that trophic chains do not exceed five steps. Closer inspection, however, shows that the magnitudes of transfers beyond the fifth level are miniscule. Whipple and Patten (1993) write about activities at very high trophic levels (e.g., >10), but the magnitudes associated with such levels make it improbable that more than a few molecules reach such elevated levels. As an indicator of ecosystem perturbation, one notes that environmental perturbations usually act to shorten the length of the canonical chain by disproportionately diminishing flows at higher levels (Ulanowicz, 1984).

In addition to these I-O methods, Bernard Patten and associates have developed what they called the environ theory of ecosystems (Patten, 1978, 1982; Patten and Auble, 1981; Fath and Patten, 1999). By an 'environ' is meant the entire tree of flows antecedent to a particular compartment, or, alternatively, the subsequent dendrite of medium exiting a compartment. That is, an input environ is the quantitative description of where the current biomass has appeared since it entered the system and the pathways along which it flowed to

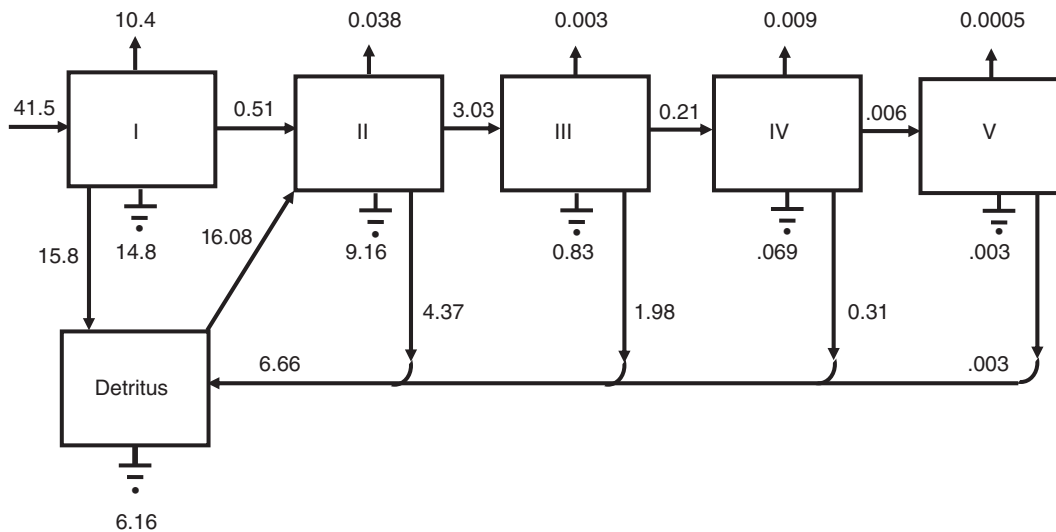


Figure 7 The canonical representation of the Oyster Reef network (Figure 2).

arrive at the node in question. Similarly, an output environ describes which other nodes will receive the material in question and the routes it will take to get there. Any given network can be decomposed into a suite of input and output environs. Environs are useful for scoping out the possible causes and effects of any changes in a particular population. One significant result of environ theory is that indirect effects are very frequently more significant than direct interactions.

A useful survey of I-O and trophic methods of network analysis can be found in [Higashi and Burns \(1991\)](#) and [Higashi et al. \(1991\)](#).

9.04.6 Analysis of Cycling

As mentioned in the last section, medium does not simply pass straight through an ecosystem. Scarcity and crowding make it inevitable that some of the same material be reused by the biota. Within the confines of a given locality, chances are that the same medium will be used more than once by the same biotic species. That is, the system engages in recycling, or more simply, cycling of medium.

Words such as scarcity and inevitable hint that cycling in ecosystems is associated with controls that guide the processing of medium by biotic species. Ecosystems are likely to develop means for retaining chemical elements that are both scarce and necessary. One such means is autocatalysis, which rewards each participant for its role in keeping the scarce medium in circulation ([Ulanowicz, 2009b](#)). Hence, a significant focus of the study of ecosystem dynamics should be the pattern and magnitudes by which medium is being recycled. That is, one needs to know the topology of pathways over which medium is recycled as well as some idea of how much material is cycled around each loop.

It was the latter, quantitative issue that was first received attention in ecology. [Odum \(1969\)](#) identified the magnitude of cycling as one of his 24 criteria defining mature or developed ecosystems. [Patten et al. \(1976\)](#) and [Finn \(1976\)](#), therefore, set about to use I-O analysis (earlier introduced to ecology by [Hannon, 1973](#)) to quantify the aggregate intensity of cycling in a system. Finn reasoned that each diagonal element in the

Leontief structure matrix, $[S]$, is related to the probability that a quantum of medium will visit the same designated compartment more than once. He suggested that the degree of recycling in the given network be quantified by multiplying each diagonal element by the total activity (throughput) of that particular taxon and then summing all such products (i.e., $T_{cyc} = \sum_i [T_i S_{ii}]$). Over time the ratio of this sum to the total system throughflow ($T_{..}$) became known as the Finn cycling index ($FCI = [T_{cyc}/T_{..}]$).

As noted earlier, [Szyrmer and Ulanowicz \(1987\)](#) elaborated upon Leontief's accounting scheme and noted that the diagonal elements of both the total dependency matrix, $[D]$, and the total contribution matrix, $[C]$, were identical. Furthermore, these diagonals, rather than the diagonals of $[S]$, more accurately represent the probability that a given quantum leaves a particular taxon and returns to it. They recommended that the diagonal elements of either $[C]$ or $[D]$ be used in lieu of those of $[S]$ in Finn's calculations. ([Han, 1997](#) independently recapitulated Szyrmer's calculations.) [Allesina and Ulanowicz \(2004\)](#) remarked how previous estimates of cycling ignored some of the compound cycling that is inherent in the off-diagonal terms. They developed a tedious method to calculate the full amount involved in cycling. Fortunately, their revised estimates amounted to the same 14% in all the cases examined. In effect, the original index continues to be a useful estimate, when appropriately modified (L.G. Latham, personal communication).

The problem with the Finn index is that its magnitude does not always reflect the developmental status of an ecosystem. [Ulanowicz \(1984\)](#), for example, showed that perturbing an ecosystem could lead to an increase the FCI (see also [Wulff and Ulanowicz, 1989](#)). [Ulanowicz \(1984\)](#) suggested that augmented cycling was a homeostatic response of an ecosystem to stress. Impacts tended to shake loose medium from storage in the biomass of higher taxa, and the system responds in homeostatic fashion to prevent, insofar as possible, the loss of the resource by cycling it among the lower trophic taxa.

To understand better the increase of the Finn index in response to stress requires detailed knowledge of how the pattern of recycling changes under stress. It happens that longer, slower cycles involving the higher taxa are usually replaced under perturbation by shorter, faster cycles among

lower trophic components. Discerning this shift requires knowing the exact topology of cycling (Ulanowicz, 1983, 1986).

The first task in elaborating the topology of cycling is the identification of all simple cycles in a network. Simple cycles are those in which any element appears only once. Writing an algorithm to find all the simple cycles in a network would appear, at first glance, to be straightforward. For example, one could perform a depth-first search with backtracking (Tarjan 1972; Mateti and Deo, 1976). A backtracking algorithm starts with ordering the nodes in some convenient way (to be described) and then repeats the same order of n nodes at n levels as depicted in Table 1.

The search begins at the first node in the zeroth level (designated as the pivot element) and the nodes in the next higher level are examined from left to right until a network connection is found. One then advances to that node in the next level and initiates searching (left to right) the level above to find a connection at yet a higher level. As one moves up to higher levels, the last node visited in each previous level is temporarily stored in a vector array that defines the current pathway. Before advancing to any higher level, one checks the destination there to make sure that this node does not appear in the current pathway. (The search is for simple cycles.)

One climbs to as high a level as possible, until halted by one of two conditions: (1) If the link encountered in the next level is to the pivot (starting) element, then a simple-directed cycle has been found. The cycle constituents are recorded from the current pathway, and the search continues. (2) If the search is from node k at level m and all possibilities in level $m+1$ have been exhausted (i.e., one reaches the far-right extreme), then one backtracks to the node in the current pathway at the $(m-1)$ th level and reinitiates searching the m th level, beginning with the $(k+1)$ st node. When further backtracking becomes impossible, all cycles passing through the pivot element have been identified. The pivot element may be eliminated from further consideration (thereby decreasing the dimension of the subsequent search).

As an illustration, the backtracking algorithm is applied to the Oyster Reef (Dame and Patten, 1981) network in Figure 2. Cycles can be found most efficiently if the nodes are ordered in a propitious sequence. Ideally, one wishes to consider first those nodes most likely to participate in cycling. One way of estimating that likelihood is to count the number of cycle arcs incident to each node. A cycle arc is one that completes one or more cycles (Knuth, 1973). To count up the incident cycle arcs, one first determines all of the other nodes that can be reached from the given node. (The reachable nodes can be located in n^2 or fewer steps.) One then counts up the connections from each reachable node directly back to the given node (another n steps). The consequent sum is the number of cycle arcs incident to the given node.

Table 1 The order of the nodes in a depth-first search

	n	[1]	[2]	[3]	...	[n]
L
e
v	2	[1]	[2]	[3]	...	[n]
e	1	[1]	[2]	[3]	...	[n]
l	0	[1]	[2]	[3]	...	[n]
Compartment						

Performing these operations on the Oyster Reef network, one counts 3 cycle arcs each incident to compartments 4 and 6. There are 2 cycle arcs into compartment 3 and one each into compartments 2 and 5. Compartment 1 possesses no incident cycle arcs and thus can be eliminated from the search. A propitious order in which to consider the compartments thus becomes 4, 6, 3, 2, 5. The following mnemonic array may help to keep track of the order of operations:

L	4	4	6	3	2	5
e	3	4	6	3	2	5
v	2	4	6	3	2	5
e	1	4	6	3	2	5
l	0	4	6	3	2	5
Compartment						

One begins with pivot element 4 in level 0 and searches level 1 from left to right, following the instructions in the text above. The order of the significant operations in the search and the current pathways they generate are as follows:

Operation	Current pathway
Begin at pivot element in level 0	4
Advance to level 1	4-6
Report cycle 1	4-6-4
Advance to level 2	4-6-3
Report cycle 2	4-6-3-4
Backtrack to level 1	4-6
Advance to level 2	4-6-2
Report cycle 3	4-6-2-4
Advance to level 3	4-6-2-3
Report cycle 4	4-6-2-3-4
Backtrack to level 2	4-6-2
Backtrack to level 1	4-6
Backtrack to level 0	4
Advance to level 1	4-5
Advance to level 2	4-5-6
Report cycle 5	4-5-6-4
Advance to level 3	4-5-6-3
Report cycle 6	4-5-6-3-4
Advance in level 3	4-5-6-2
Report cycle 7	4-5-6-2-4
Advance to level 4	4-5-6-2-3
Report cycle 8	4-5-6-2-3-4
Backtrack to level 3	4-5-6-2
Backtrack to level 2	4-5-6
Backtrack to level 1	4-5
Backtrack to level 0	4
Advance in level 0	6
(All cycles with 4 have been found)	
Advance to level 1	6-3
Report cycle 9	6-3-6
Backtrack to level 0	6
Advance to level 1	6-2
Advance to level 2	6-2-3
Report cycle 10	6-2-3-6
Backtrack to level 1	6-2
Backtrack to level 0	6
Advance in level 0	3
(All cycles with 6 have been found)	
Advance in level 0	2
Advance in level 0	5
Further backtracking impossible.	END

One sees that the Oyster Reef network contains 10 simple cycles. If the components had been considered in the order given in Figure 2, the first pivot element would have been 1, and considerable time would have been wasted searching for cycles that simply do not exist. It is obvious that reordering the pivot elements can significantly diminish the time it takes to complete the full search.

In principle, the time spent searching networks is combinatoric in magnitude (i.e., it varies as n -factorial). This means that years of computer time can be spent searching networks of even moderate dimension. Reasonable computational times cannot be guaranteed for the method just described. As mentioned, however, ecological networks of moderate dimension are

rather sparse, that is, they typically possess 15% or fewer non-zero arcs. This, in combination with the component ordering scheme outlined above, makes the identification of simple cycles feasible for most estimated ecosystem flow networks.

Having identified all simple cycles in a network, one now seeks to separate cycled from straight-through flows, that is, subtract the cycled flows from the original network. Subtracting an isolated cycle from out of its supporting network is rather straightforward. One first finds the link with the smallest magnitude ($D \rightarrow A$ in Figure 8(a)).

Then the magnitude of that smallest link is subtracted from the weight of each link in the cycle. Doing so separates the target cycle (e.g., $A \rightarrow B \rightarrow C \rightarrow D \rightarrow A$) from the supporting

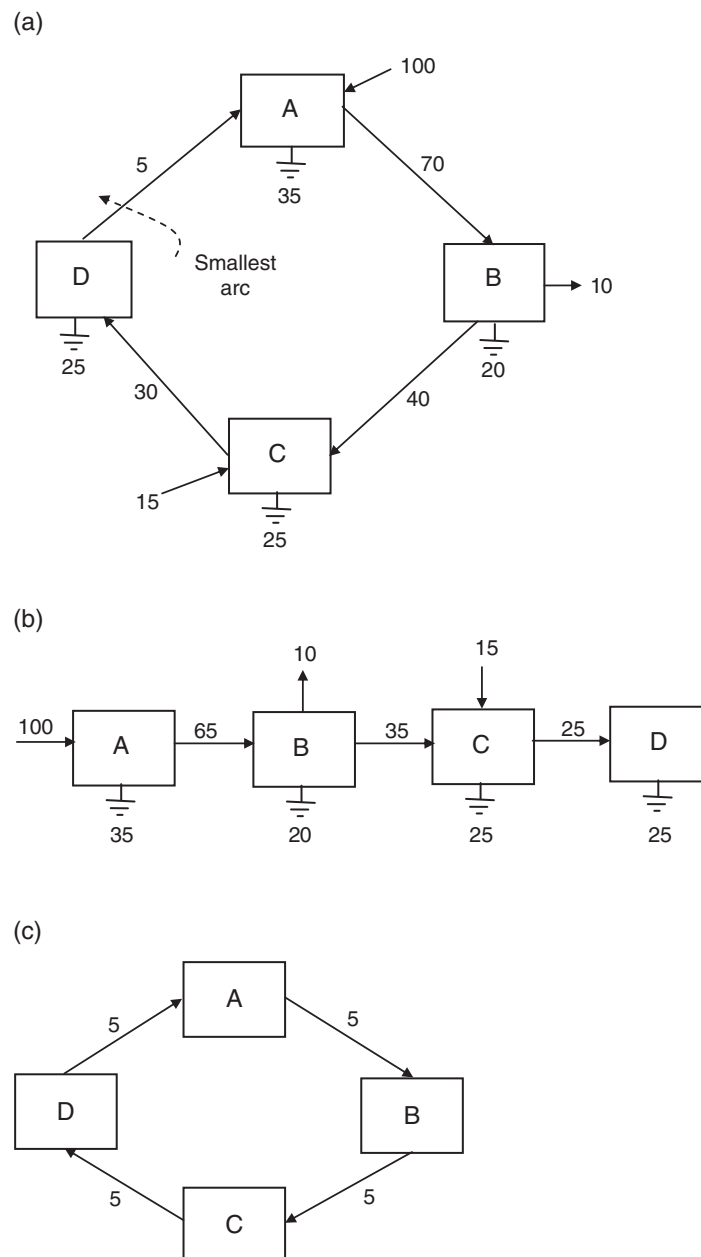


Figure 8 (a) Hypothetical network consisting of one simple cycle. (b) Single-pass flows through the network. (c) Cycling within the network. Note that (a) = (b) + (c).

straight-through pathway (Figure 8(b)). Each link of the cycle bears the magnitude of the smallest arc in the original cycle (Figure 8(c)) and the balance around each of the nodes in the residual fragment (Figure 8(b)) has been maintained.

This method of cycle extraction will work only when none of the simple cycles in the network overlaps. In most whole-system networks, however, the number of simple cycles far outnumber the total number of flows comprising the network. Hence, some cycles must share the same smallest link. The collection of simple cycles that shares the same smallest link is henceforth called a nexus. It is also likely that all cycles comprising a nexus are controlled by their shared smallest link. Removing that smallest link by subtracting it from any one cycle of the nexus would also negate all the other cycles in the nexus, but choosing any particular cycle is likely to be arbitrary. It would seem preferable and more realistic to devise a rational method for apportioning the magnitude of the smallest link over all the cycles of the nexus.

Some reflection will reveal that there are an infinite number of ways of apportioning the least flow over all cycles of the nexus. For example, one could simply divide the magnitude of the smallest link by the number of cycles in the nexus and uniformly subtract that amount from each arc of all the nexus cycles. However, this uniform distribution seems arbitrary as well. Another reasonable allocation might be to apportion the least flow to each nexus cycle in relation to the fraction of the total nexus activity that is comprised by that cycle. Perhaps more reasonable still would be to use the $[F]$ matrix to calculate the probability that a quantum of medium anywhere in a simple cycle will complete that particular pathway and return to its starting point. (That probability is simply the product of all the f_{ij} in the particular cycle pathway.) One then divides that probability of completion by the sum of all other such probabilities for all of the cycles in the nexus. That fraction of the smallest magnitude is then subtracted from each arc in the given cycle. Once the subtraction is done for all cycles in the nexus, the smallest link will zero-out, but the balance around all nodes will remain intact (William Silvert, personal communication).

After removing all cycles from the starting network, one is left with an acyclic tree of once-through flows. The separation procedure ensures that none of the inputs, exports, or dissipations in the system have been altered. (For every amount that has been subtracted from an input to a node, an equal magnitude was also removed from an output of the same node.) A network of all the medium being cycled can be constructed either by simple addition of the cycles that have been removed, or by subtracting the residual tree from the starting network. Figure 9(a) shows the residual, acyclic network from the Oyster Reef example (Figure 2) and Figure 9(b) the complementary web of purely cyclical flows.

Although the partitioning of a graph into its cyclic and acyclic components is an abstract exercise, it also has its practical side. Baird and Ulanowicz (1989), for example, extracted all the cycles from the mesohaline Chesapeake Bay ecosystem (Figure 10) and were surprised to find that the aggregated cycling was comprised of two nonoverlapping graphs. One cluster cycled among only planktonic species (those that move passively with water currents), while the other encompassed both benthic (bottom-dwelling) compartments and nektonic (actively moving through the water) species. The

two constellations of cycling represent independent domains of control – an apparently common characteristic of estuaries (Allesina et al., 2005). Another item of interest was that none of the filter-feeding compartments, be they on the bottom or among the fishes, participated in any of the recycling. Instead, their function in this context appeared to be the transfer of resources from the pelagic realm into the benthic-nektonic domain. It was also of particular interest that two compartments of pelagic microbes that are normally included among the microbial loop of open oceanic waters were not among any of the cycles in the Chesapeake system. In the Chesapeake, these compartments seemed instead to be transferring carbon (which is fixed by excessive plant growth in Chesapeake Bay) out of the ecosystem.

9.04.7 Whole System Status

The methods discussed thus far treat either particular system components, or a subsystem of the whole, but ecosystem managers increasingly are wanting to know how an ecosystem is performing *in toto*. Funding agencies more often are seeking research that addresses environmental problems in the context of the whole ecosystem (NSF, 1999). As mentioned in the introduction, the conventional response to the need for whole-ecosystem research has been to simulate the system using a mechanistic mathematical model. Such models, however, are usually lacking in prediction ability and often do not provide a convenient metric by which to gauge system status. As an alternative, investigators have developed several whole-system indices of an *ad hoc* nature, for example, the popular and useful index of biotic integrity (IBI) of Karr et al. (1986). More suitable would be indices that are founded upon solid theoretical considerations. As the subject of this chapter is ecological networks, it is only appropriate to ask whether some quantitative attribute of ecosystem networks might be appropriate with which to gauge ecosystem performance.

Before embarking upon the quest for whole-system metrics, it should be remarked that ecosystems are significantly affected by what is missing, very often as much as by what is present (Ulanowicz et al., 2009). Whether or not a given predator is missing in a habitat will have great bearing on whether a particular prey will thrive there. The significance of absence is mentioned, because most treatments of ecosystem behaviors derive from methodology created for physics and chemistry. Bateson (1972) pointed out, however, that physics treats overwhelmingly only that which is present. Very little in physics addresses that which is missing. (Rare exceptions include the Pauli exclusion principle and Heisenberg's uncertainty.)

The approach to quantifying that which is missing is called information theory (IT). Conventional descriptions of information theory usually begin with the rubrics of communication. IT, however, has applications far beyond communications theory, and can be invoked to measure the relative degrees of constraint and flexibility inherent in a system.

That information theory begins by quantifying that which is missing is evident in Boltzmann's famous definition of surprisal:

$$s = -k \log(p)$$

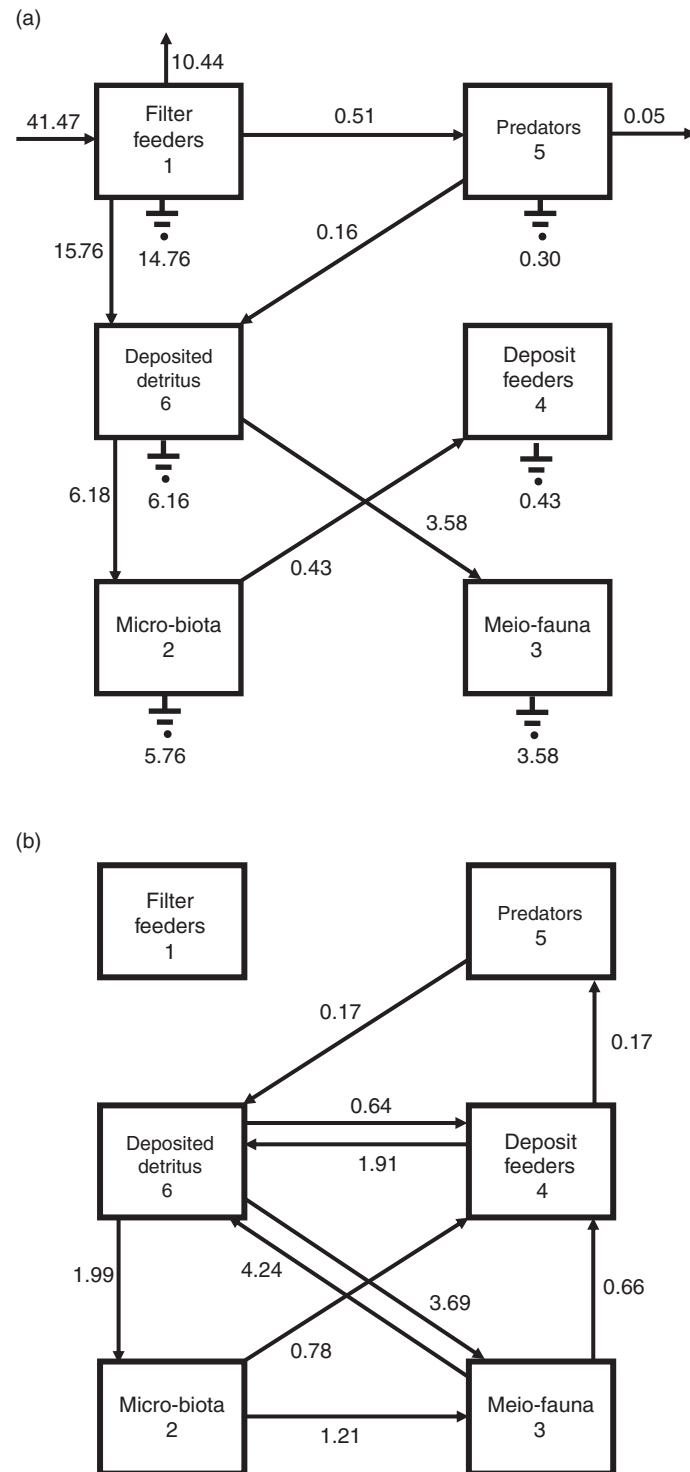


Figure 9 (a) The residual throughflow in the Oyster Reef ecosystem (Figure 2). (b) The aggregate cycled flows in the same system.

where s is one's surprisal at seeing an event that occurs with probability p , and k is an appropriate (positive) scalar constant. Because the probability, p , falls between 0 and 1, we may conclude that the negative sign in the definition is a mathematical convenience that guarantees that s will remain positive (and such may have been Boltzmann's motivation). However in terms of sheer logic, this equation clearly defines s to measure the degree

to which p is not. That is, if p is the weight one gives to the presence of something, then s becomes a measure of its absence. (Here the reader might ask why the absence of event i is not represented more directly by $(1 - p_i)$. The advantage and necessity of using the logarithm will soon become apparent.) If p is very small, then the ensuing large magnitude of s reflects the circumstance that most of the time we do *not* see the event in question.

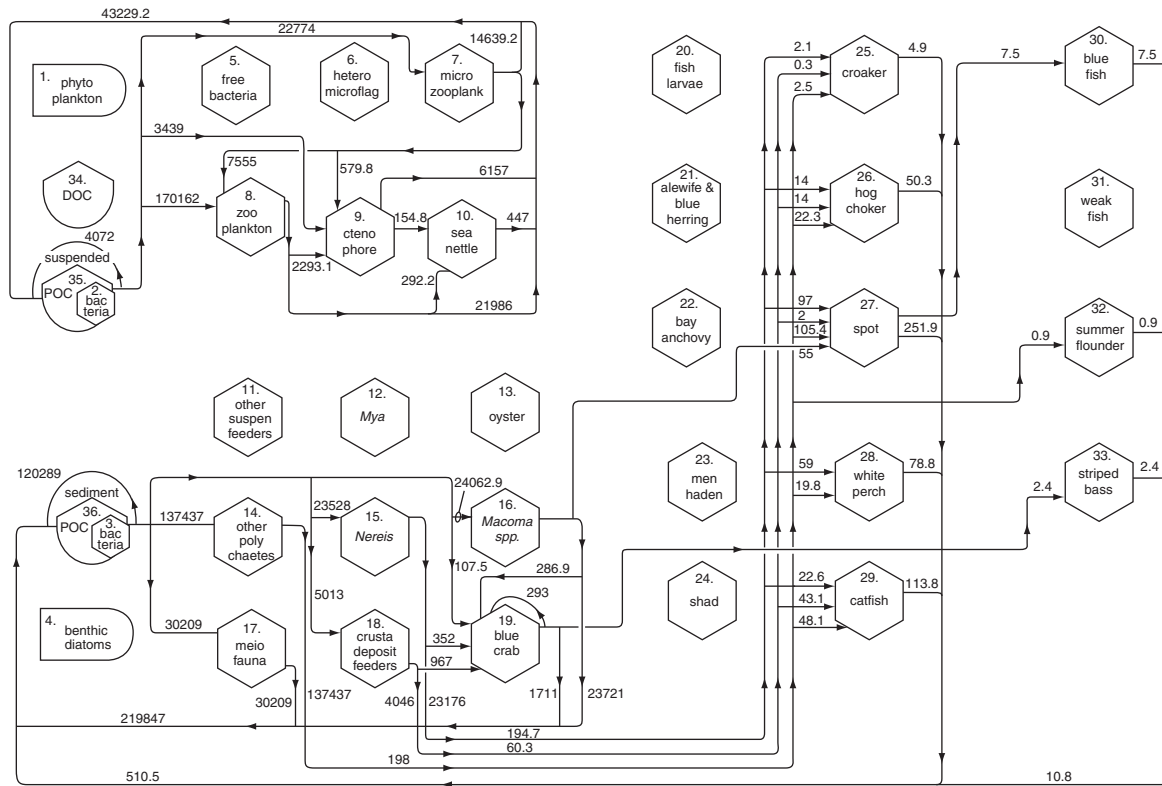


Figure 10 The composite cycling that occurs in the Chesapeake Mesohaline ecosystem. Reproduced with permission from Baird, D., Ulanowicz, R.E., 1989. The seasonal dynamics of the Chesapeake Bay ecosystem. *Ecological Monographs* 59, 329–364.

Boltzmann's gift to science – the feasibility of quantifying what is not – remains largely unappreciated. It ranks alongside the contribution of the Arabian mathematicians who invented the number 0. One can build upon Boltzmann's invention to demonstrate that IT literally opens new vistas to which classical physics remains blind. Moreover, the interplay between presence and absence becomes crucial to whether a system survives or disappears, that is, to its sustainability. In particular, it is the very absence of order (in the form of a diversity of processes) that makes it possible for a system to persist (sustain itself) over the long run (Ulanowicz, 2009c).

That the Boltzmann definition actually quantifies absence provides an insight that few appreciate – namely, that the product of the measure of the presence of event i (p_i) by the magnitude of its absence (s_i) yields a quantity that represents the indeterminacy (h_i) of the event in question,

$$h_i = -kp_i \log(p_i) \quad [3]$$

When $p_i \approx 1$, event i is almost certain, and $h_i \approx 0$; then when $p_i \approx 0$, the event is almost surely absent, so that again $h_i \approx 0$. It is only for intermediate, less determinate values of p_i that h_i becomes appreciable, achieving its maximum at $p_i = (1/e)$.

It is helpful to reinterpret eqn [3] as it relates to evolutionary change and sustainability. When $p_i \approx 1$, the event in question is almost constantly present and exhibits little change ($h_i \approx 0$). Conversely, when $p_i \approx 0$, the event in question has great potential to change matters ($s_i \approx 1$), but it hardly ever appears in the system dynamics (so that, again, $h_i \approx 0$). It is only when p_i is intermediate that the event is both present frequently enough and has sufficient potential for change. Whence, h_i represents

the capacity for event i to be a significant player in system change or evolution. With regard to the entire ensemble of events, one can aggregate all the indeterminacies:

$$H = \sum_i h_i = -k \sum_i p_i \log(p_i) \quad [4]$$

to achieve a metric of the total capacity of the system to undergo change. Whether such change will be coordinated or mostly stochastic depends upon whether or not the various events i can affect each other and by how much.

Most readers will recognize eqn [4] as the familiar Shannon–Wiener index of diversity. The quest for measures of whole-ecosystem status was provided major impetus by MacArthur (1955) when he applied Shannon's information measure to quantify the diversity of flows, H , in an ecosystem network:

$$H = -k \sum_{ij} \left(\frac{T_{ij}}{T_{..}} \right) \log \left(\frac{T_{ij}}{T_{..}} \right)$$

where k is a scalar constant, and $T_{..}$ denotes the sum of T_{ij} over all combinations i and j . In this case, the p_i in eqn [4] becomes the probability that a randomly selected quantum of medium is in transit between compartments i and j , and it is estimated by the quotient $(T_{ij}/T_{..})$.

MacArthur's goal was to probe for a connection between the diversity of a system's flows, as measured by eqn [4], and the stability of that system. His attempt was the first in a long line of efforts to link a system's diversity with its stability (Woodwell and Smith, 1969) that dominated systems ecology during the 1960s.

Not long after MacArthur's effort, attention shifted away from the difficult-to-measure flows to the more accessible stocks of biomass, and biological diversity, D , was recast as

$$D = -k \sum_i \left(\frac{B_i}{B} \right) \log \left(\frac{B_i}{B} \right)$$

where B_i is the biomass (or number) in compartment i , and B is the sum of all the B_i .

Unfortunately, the fervor to establish a theoretical connection between the two systems attributes came to a sudden halt as soon as May (1972) demonstrated that in randomly assembled linear dynamical systems, a higher biodiversity was more likely to result in instability. Caught in abrupt embarrassment, most ecologists immediately foreswore any further efforts to apply information theory to ecology – a prejudice that lingers among many ecologists today. As a consequence, when Rutledge et al. (1976) returned to MacArthur's original focus upon flows, and reinterpreted their diversity in a Bayesian manner, hardly anyone was paying attention. Rutledge et al. (1976) were able to decompose MacArthur's index into two complementary terms using the notion of conditional probability. Taking $(T_{ij}/T_{..})$ as the estimate of the unconditional probability that a flow occurs from i to j , $(T_{ij}/T_{.j})$ then becomes the estimator of the conditional probability that any quantum of flow continues on to compartment j , given that it had originated from component i . This allows H to be decomposed as

$$H = \text{AMI} + H_c \quad [5]$$

where

$$\text{AMI} = k \sum_{ij} \left(\frac{T_{ij}}{T_{..}} \right) \log \left(\frac{T_{ij} T_{..}}{T_{.i} T_{.j}} \right)$$

and

$$H_c = -k \sum_{ij} \left(\frac{T_{ij}}{T_{..}} \right) \log \left(\frac{T_{ij}^2}{T_{.i} T_{.j}} \right)$$

AMI is called the average mutual information inherent in the flow structure, while H_c is the residual (conditional) diversity/freedom (commonly known as the conditional entropy in information theory). Both are non-negative.

It is important to stress that information is not being used here in the usual context of communications theory, but rather in the more generalized sense of constraint. In that context, MacArthur's overall complexity of flow structure has been decomposed into a component that gauges how orderly and coherently the flows are connected (constrained) and one that measures the residual disorder and/or freedom.

Rutledge et al. (1976) focused upon H_c as a more didactic measure of ecosystem maturity (*sensu* Odum, 1969) than MacArthur's index had provided. Ulanowicz (1980), however, became more interested in the AMI, because he was impressed by Atlan's (1974) argument that AMI can provide a useful measure of the organization inherent in a system. Ulanowicz suggested that AMI is an indicator of the developmental status of an ecosystem, because it reflects the average degree of constraint that channels an arbitrary quantum of currency from any one compartment to the next (Ulanowicz, 1997; Latham and Scully, 2002).

Unfortunately, AMI bears no physical dimensions. Given a particular value of the AMI, one cannot tell whether the index is representing a microbial community in a Petri dish or an ecological community on the Serengeti Plain. Tribus and McIrvine (1971) had commented that the lack of physical dimensions on information measures gives rise to ambiguity about their importance. As a remedy, they suggested that the scalar constant, k (usually set equal to one and then forgotten), becomes the vehicle that imparts physical dimensions to the information index. Following Tribus' lead, Ulanowicz set $k = T_{..}$ (the total system throughput) and named the resulting product the system network ascendancy, A , where

$$A = \sum_{ij} T_{ij} \log \left(\frac{T_{ij} T_{..}}{T_{.i} T_{.j}} \right)$$

Ascendancy was formulated to combine the total activity, or power generated by the system ($T_{..}$), with its organization in the sense of how effectively component processes are linked (AMI) (Latham and Scully, 2002). (The alternative spelling 'ascendency' is used here to distinguish the quantitative measure from the conventional meaning of 'ascendency'.) As a result, it quantifies how well the system is processing the given medium. It is perhaps easiest to think of ascendancy as 'organized power', because the measure represents power that is flowing within the system toward particular ends, as distinct from power that is dissipated willy-nilly (Ulanowicz, 2009b). Almost half a century earlier, Lotka (1922) had suggested that the capacity of a system to prevail in evolution is related to its ability to capture useful power. Ascendancy can be regarded as a refinement of Lotka's supposition that takes into account how power is actually being channeled within a system. In Figure 11(a), for example, power is exchanged in relatively confused fashion among the components (nodes) of the network. By contrast, in Figure 11(b), the flows out of or into any given compartment are more selective and determinate (constrained). In addition, the magnitudes of the flows are greater (as indicated by thicker arrows). The increased power flowing in Figure 11(b) is realized in a more organized way; whence the ascendancy of network b exceeds that of a .

When he first created the ascendancy measure, Ulanowicz (1980) was thinking that an ecosystem would develop so as to maximize its ascendancy. He later abandoned that presumption as being too mechanical and deterministic (Mueller and Leupelt, 1998). He now refers to the propensity for ecosystems to increase in ascendancy (Ulanowicz, 1997).

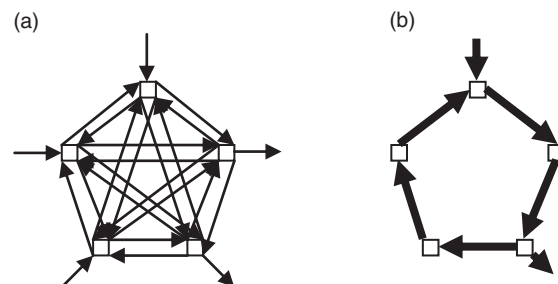


Figure 11 (a) A network of flows having a relatively confused pattern of transfers. (b) Another network where the flows of power are more determinate (greater ascendancy). Reproduced with permission from Ulanowicz, R.E., 2009b. A Third Window: Natural Life beyond Newton and Darwin. Templeton Foundation Press, West Conshohocken, PA.

One may impart physical dimensions to H_c (the complement of AMI) by also multiplying it by $(T_{..})$. The result is what Ulanowicz and Norden (1990) called the system overhead, Φ :

$$\Phi = - \sum_{i,j} T_{ij} \log \left(\frac{T_{ij}^2}{T_{i.} T_{.j}} \right)$$

In fact, H itself can be scaled by $T_{..}$ to create what is termed the system's 'development capacity', C :

$$C = - \sum_{i,j} T_{ij} \log \left(\frac{T_{ij}}{T_{..}} \right) \quad [6]$$

Accordingly, the scaled version of relationship eqn [5] becomes

$$C = A + \Phi \quad [7]$$

The complementary relationship of the terms in eqn [7] suggests that any increase in ascendancy usually comes at the expense of overhead, Φ . One is led to ask whether there are any limits as to how far ascendancy can displace system overhead without endangering system persistence. Systems with high ascendancy that retain little overhead appear rigidly linked and almost mechanical. Holling (1986) calls such systems 'brittle' and vulnerable to collapse. Such vulnerability proceeds from a lack of sufficient freedom and flexibility (overhead) remaining to the system to adapt to novel perturbations. It follows that the health or integrity of an ecosystem requires adequate amounts of both ascendancy and overhead (Ulanowicz, 2000a).

To help gauge where a balance of constraint and flexibility might lie, one notes that

$$\frac{0 \leq A}{C \leq 1}$$

The ratio $a = A/C$, therefore, becomes a convenient (and normalized) measure of the degree of system order. The actual pattern of order in any instance is the result of two opposing tendencies (Ulanowicz, 2009a). In an inchoate system (one with low a), there are manifold opportunities for selective constraints (such as autocatalytic cycles) to arise. This tendency for a to increase persists over all values of a . The role of overhead, Φ , however, changes over the range of a . As just mentioned, in systems with little order (low a), the randomness inherent in Φ is what provides the opportunities for constraints to appear (Ulanowicz, 2009b). In systems that are already highly developed ($a \approx 1$), however, the dominant action of Φ is to disrupt established constraints, often resulting in the sudden loss of organized performance (the system resets to much a lower a). At high a , then, Φ strongly opposes additional increase in a . Presumably, a critical balance between the countervailing roles of Φ exists for some value of a .

It is important to stress that ecological reality is not simply the unfolding of a mechanical clockwork. It is more a matter of opposition between order-generating tendencies and dissipative inefficiencies. Noise, inefficiencies, and incoherencies play as large a role in how ecosystems behave as do constraints and efficient performance.

Exactly how this agonism plays out and where the balance between A and Φ lies are matters of both theoretical and practical concern. Theoretical considerations are addressed in Ulanowicz (2009c). As for actual data on how ecosystems are distributed over the domain of a , quantified networks of real ecosystems

scatter across the interval $0 < a < 1$, skewed slightly toward higher values, but with a notable concentration between $a = 0.3$ and 0.5 (Ulanowicz, 2009c). Robert Christian (personal communication) noted that the outlying systems (those closer to either 0 or 1) are all represented by networks of small dimension. Whenever ecosystems were parsed in more detail (say, $n > 12$), however, their values of a would join the cluster.

Figure 12 is a plot of data on 17 ecosystems (mostly from estuarine and coastal habitats). The ordinate is a hypothesized, normalized measure of the fitness for an ecosystem to persist, F , and is defined as $F = -ea \ln(a)$, where e is the natural base for logarithms (see Ulanowicz, 2009c).

An implication that can be drawn from Figure 12 is that networks distant from the maximum at $a = (1/e)$ are not sustainable. They either have too little organization (a small) or are too inflexible (a large.) In order for an ecosystem to persist, it should exhibit a value of a in the neighborhood of maximum fitness. The question then arises, if a system is not at the maximum, how can it be directed toward the maximum – that is, toward a more sustainable configuration? This question can be answered by defining the robustness, R , of a system as the product of its fitness, F , and its total activity $(T_{..})$:

$$R = T_{..} F$$

Now, taking the derivatives of the robustness, R , with respect to each flow, T_{ij} , yields the marginal contribution of each unit of flow T_{ij} toward the sustainability of the system:

$$\frac{\partial R}{\partial T_{ij}} = F + T_{..} \frac{\partial F}{\partial T_{ij}}$$

$$\frac{\partial R}{\partial T_{ij}} = F + T_{..} F' \frac{\partial a}{\partial T_{ij}}$$

$$\frac{\partial R}{\partial T_{ij}} = F + \frac{T_{..} F'}{C} \left\{ \log \left[\frac{T_{ij} T_{..}}{T_{i.} T_{.j}} \right] + a \log \left[\frac{T_{ij}^2}{T_{i.} T_{.j}} \right] \right\}$$

Where F' is the derivative of F with respect to a , that is,

$$F' = -e \left[\frac{\log(a)}{\log(e)} + 1 \right]$$

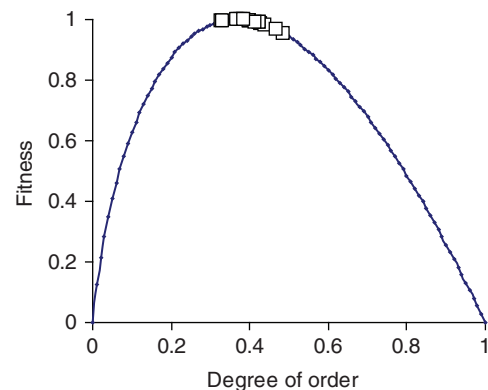


Figure 12 The degrees of order and corresponding magnitudes of fitness for the subset of 17 ecosystem flow networks that consist of more than 12 compartments. Ulanowicz, R.E., 2009c. Increasing entropy: Heat death or perpetual harmonies? International Journal of Design and Nature and Ecodynamics 42 (2), 83–96.

One notices that because $F = 1$ and $F' = 0$ at $a = (1/e)$, the marginal contribution of each T_{ij} at the maximum is 1. If a particular derivative is less than 1.0, then the system would be moved in the direction of the maximum by decreasing that flow. Conversely, if the marginal contribution of T_{ij} is greater than one, systemic sustainability should be improved by increasing the magnitude of that arc.

As an example, the derivatives of the robustness are calculated for each flow in the Oyster Reef network of Figure 2 as depicted in Figure 13. Because $a = 0.436$, the system is only slightly beyond the maximum, and incremental changes in the various flows would move the system to the left toward the maximum in Figure 12.

A more didactic demonstration of the application of these vectors toward sustainability would be to hypothetically inflate primary production in the system and shunt all the extra production through the detritus on to the microbiota, where it is respired out of the system – that is, it makes the system highly eutrophic. Such a shunt radically increases a to a value of 0.687. The corresponding values of the marginal contributions are given in parentheses below the values of the flows in Figure 14. One sees from those marginal values that each link in the primary route of eutrophication possesses negative marginal values (especially the one for primary production). Most of the other flows now have positive marginal values, and some, such as feeding by predators and deposit feeders, are quite significant. According to these results, remediation should entail depressing primary production in combination with channeling material away from the eutrophication pathway and into the consumer ecosystem. Such is precisely the strategy that has been recommended for eutrophic estuaries (Newell, 1988; Ulanowicz and Tuttle, 1992).

It should be clear that the relative values of A and Φ are significant indicators of the status of an ecosystem. For example, a key property of flow networks is their degree of connectivity, or how many links, on average, flow into or out of a typical node (sometimes called the link density). Ulanowicz and Wolff (1991) demonstrated that a convenient measure of the effective link density is achieved by raising e (the natural base of logarithms) to the power ($H_c/2$). They were able to demonstrate that this index, which is valid for any weighted digraph, converges to intuitive integer values for simple examples. Bersier et al. (2002) saw major significance in how properties of weighted digraphs can generalize those of binary topologies. They used the link-density relationship to bridge quantitative network analysis with the more popular food-web analysis that deals only in binary networks. For each and every index that has been defined in food-web analysis, Bersier et al. were able to construct an information-theoretic weighted homolog. Of special importance, they were able to demonstrate that the measures pertaining to weighted digraphs converge more rapidly to the intended properties than do the original, *ad hoc* food-web measures.

Zorach and Ulanowicz (2003) have been able to pursue the connection between H_c and link density to even greater depth. They were able to demonstrate that raising e to the power ($H_c/2$) yields precisely the weighted geometric mean of the link density that one calculates using conventional algebra. Following dimensional considerations, they inferred that raising e to the power AMI should provide an estimate of the number of trophic roles in the network (i.e., it should correspond roughly to the effective number of trophic levels, or the trophic depth of the network).

Although A and Φ quantify the status of the whole network, one is often interested in details about how subgroups of taxa

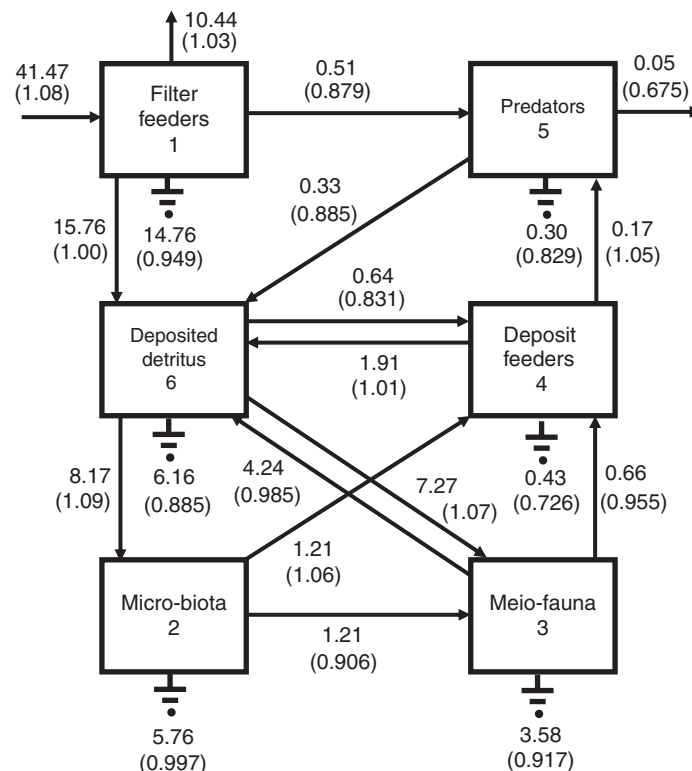


Figure 13 The values of the marginal contributions (in parentheses) of the flows in the Oyster Reef community (Figure 2).

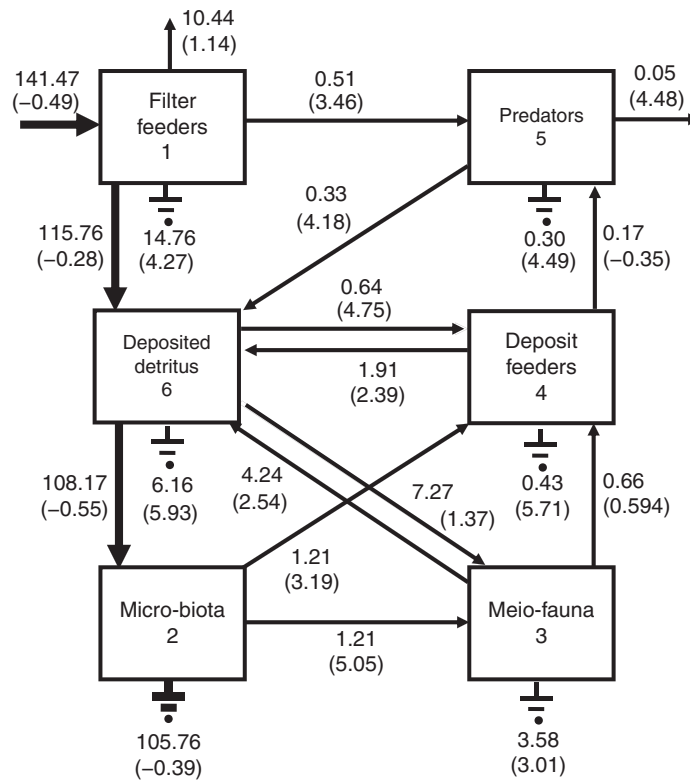


Figure 14 Hypothetical eutrophication in the Oyster Reef community, represented by adding 100 units to the pathway $\rightarrow 1 \rightarrow 6 \rightarrow 2 \rightarrow$. The revised marginal contributions appear in parentheses.

or individual populations are behaving. To address such questions, it helps to decompose Λ and Φ further. For example, one may be interested in only the internal workings of the system. To focus on the inside of the system, one defines an internal ascendancy, A_I , that is confined solely to the internal exchanges between the n system components:

$$A_I = \sum_{i,j=1}^n T_{ij} \log \left(\frac{T_{ij} T_{..}}{T_{i.} T_{.j}} \right)$$

The fraction of the development capacity that is comprised by A_I is then purported to be an index of the internal development of the given ecosystem. This ratio has been used to compare ecosystems that were similarly parsed (Wulff and Ulanowicz, 1989; Baird et al., 1991; Christian et al., 2003; Baird et al., 2004).

Likewise, it is sometimes helpful to know the contributions to the overhead that are generated by different types of flows. As noted earlier, there are four basic categories of flow in ecosystems: internal exchanges, exogenous inputs, useful outputs, and dissipations. Accordingly, the overhead separates neatly into four respective components (Ulanowicz and Norden, 1990):

$$\Lambda = - \sum_{i=1}^n \sum_{j=1}^n T_{ij} \log \left(\frac{T_{ij}^2}{T_{i.} T_{.j}} \right)$$

$$\Phi_I = - \sum_{j=1}^n T_{0j} \log \left(\frac{T_{0j}^2}{T_{0.} T_{.j}} \right)$$

$$\Phi_E = - \sum_{i=1}^n T_{i,n+1} \log \left(\frac{T_{i,n+1}^2}{T_{i.} T_{.,n+1}} \right)$$

$$\Phi_D = - \sum_{i=1}^n T_{i,n+2} \log \left(\frac{T_{i,n+2}^2}{T_{i.} T_{.,n+2}} \right)$$

where Λ is called the redundancy of flows in the system, because it provides a measure of the multiplicity of, or parallelism in, flow pathways between any two arbitrary system components. Φ_I is the overhead due to imports, and Φ_E and Φ_D are the overheads that can be traced to exports and dissipations, respectively. Often, disturbances will increase the ratio Λ/C (Ulanowicz, 1984), indicating that the response of a system to disturbance usually increases its ability to resist further perturbations (the LeChâtelier–Braun principle as applied to ecology). Heymans (2003) and Heymans et al. (2007) employed the internal overhead to gauge the potential of a system for adaptation and resilience.

One criticism of network analysis in general is that all attention seems to be focused on flows to the neglect of stocks. It has been argued here that ecosystem dynamics depend largely on the configurations of flows within them, but there most certainly remain situations where the magnitudes of stocks affect system dynamics. In order to introduce stock size into the information dynamics, the stock in compartment i will be denoted by B_i . To relate B_i to flows into and out of i , one notes that the *a priori* probability that any quantum of medium in transit has originated from compartment i is $(B_i/B_{..})$. Similarly, the corresponding (unconditional) probability that a particle of flowing medium will enter j is $(B_j/B_{..})$. Thus, the *a priori* joint probability that any quantum of flowing medium is en route from i to j becomes $(B_i B_j / B_{..}^2)$. The observed, or *a posteriori* frequency of such flow from i to j is measured as $(T_{ij}/T_{..})$. The

Kullback (1959) index can be employed to calculate the average difference between these *a priori* and *a posteriori* probabilities, I_B , to be

$$I_B = k \sum_{ij} \left(\frac{T_{ij}}{T_{..}} \right) \log \left(\frac{T_{ij} B_{..}^2}{T_{..} B_{.i} B_{.j}} \right)$$

As with the flow ascendancy, one may scale I_B by $T_{..}$ to yield the biomass-inclusive form of the ascendancy, A_B (Ulanowicz and Abarca-Arenas, 1997), as

$$A_B = \sum_{ij} T_{ij} \log \left(\frac{T_{ij} B_{..}^2}{T_{..} B_{.i} B_{.j}} \right)$$

How the overall system status might change with infinitesimal additions to the biomass of taxon p , B_p , is reckoned by taking the partial derivative of A_B with respect to B_p :

$$\frac{\partial A_B}{\partial B_p} = 2 \left(\frac{T_{..}}{B_{..}} - \frac{1}{2} \frac{T_{.p} + T_{p.}}{B_p} \right)$$

Examination of this result shows that the sensitivity is proportional to the amount by which the average turnover rate of medium in compartment p is exceeded by the overall turnover rate ($T_{..}/B_{..}$). The system appears to be more sensitive to those components having slower turnover rates.

One might ask further, "Which prey resource, r , is most important as a source of medium to predator p ?" As with the biomasses, the limiting source can be identified by taking the partial derivative of A_B with respect to each prey, r , of taxon p . Because A_B is a first-order homogeneous function in the T_{ij} (Courant, 1936: 108), one may invoke Euler's relation to arrive at the simple result:

$$\frac{\partial A_B}{\partial T_{rp}} = \log \left(\frac{T_{rp} B_{..}^2}{T_{..} B_{.r} B_{.p}} \right)$$

According to this formula, one arrives at the intuitively satisfying conclusion that the controlling resource is the one that is being depleted of medium at the fastest rate relative to its available remaining stock (i.e., the one with the highest ratio ($T_{rp}/B_{.r}$)). In the next section, these sensitivities will be used to identify points of control by various nutrients in an estuarine ecosystem.

9.04.8 Higher Dimensional Considerations

The utility of the sensitivities just presented would be enhanced if they could be used to discriminate among the dynamics of several media flowing simultaneously. Furthermore, until now network analysis has been applied only to a single snapshot of the system. It is not difficult, however, to depict temporal ecosystem dynamics as a motion picture or a time series of such network snapshots. Nor is it far-fetched to envision a tessellation of networks, each pertaining to a small segment of the physical space occupied by the ecosystem. While it remains difficult in general to extend the I-O, trophic and cycle analyses to encompass heterogeneities in time, space, and media, widening the scope of information-theoretic indices presents no conceptual obstacles.

If, for example, T_{ijk} denotes the flow of medium from taxon i to taxon j during time interval k , then the temporal

capacity, C_T , immediately follows as a straightforward generalization of eqn [6]:

$$C_T = - \sum_{ijk} T_{ijk} \log \left(\frac{T_{ijk}}{T_{...}} \right)$$

In defining the corresponding temporal ascendancy, however, one must choose among several possibilities. In schematic terms, C_T can be decomposed into numerous terms, as suggested by Venn diagrams (Blachman, 1961). In two dimensions the situation is unambiguous (Figure 15).

The left circle in Figure 15 represents the diversity of source flows (from prey), whereas the right one represents the diversity of sinks (to predators). The overlap between the circles represents the AMI. The combined nonoverlapping areas comprise the conditional uncertainty, H_c .

The overlaps in three dimensions are multiple, however. Figure 16 consists of the pattern of Figure 15 repeated 3 times. If the three circles represent the diversities of sources, sinks, and time, then there are three bilateral regions of overlap, representing the mutual information between sources and sinks, sources and time, and sinks and time, respectively. In addition, however, these overlaps themselves intersect, yielding at least four distinct regions: there is the central area where all three domains intersect (AMI_3) and the three adjoining regions where only a single pair each overlaps (λ_1 , λ_2 , and λ_3 in the figure). As to which region should represent the information factor in three-dimensional (3D) ascendancy, one could choose the innermost circular triangle (AMI_3 ; which is designated as the 3D AMI in information theory), but this formula has the disadvantage of sometimes being negative in value.

In terms of the T_{ijk} , AMI_3 can be calculated (Abramson, 1963) as

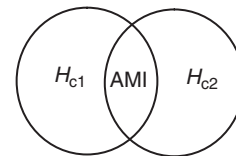


Figure 15 2D Venn diagram showing the AMI as the intersection of the uncertainties of sources and sinks. The conditional uncertainty, $H_c = H_{c1} + H_{c2}$.

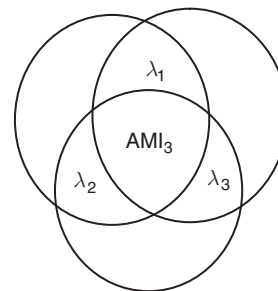


Figure 16 The intersection of the three domains of sources, sinks, and time. The central area of overlap (AMI_3) represents the 3D average mutual information, but the three areas of bilateral overlap (λ_1 , λ_2 , λ_3) also contribute to the overall system organization.

$$AMI_3 = \sum_{i,j,k} \left(\frac{T_{ijk}}{T_{...}} \right) \log \left(\frac{T_{ijk}^2 T_{...}}{T_{i..} T_{.j.} T_{..k}} \right)$$

It represents the simultaneous coherence among sources and sinks over time. It does not, however, encompass all the coherence present in the system. In particular, the leaflets ($\lambda_1, \lambda_2, \lambda_3$) that adjoin AMI_3 represent bilateral coherencies that do not correlate with the third remaining variable. To be inclusive of all coherencies in the system, Pahl-Wostl (1995) suggested that the appropriate measure is the overlap of all bilateral AMIs (i.e., the trefoil-like region $AMI_3 + \lambda_1 + \lambda_2 + \lambda_3$). Calling this conjunction AMI_T , one calculates its magnitude in terms of the T_{ijk} as

$$AMI_T = \sum_{i,j,k} \left(\frac{T_{ijk}}{T_{...}} \right) \log \left(\frac{T_{ijk}^2 T_{...}}{T_{ij.} T_{i.k.} T_{.jk}} \right)$$

Unlike AMI_3 , AMI_T is guaranteed to be ≥ 0 . Scaling AMI_T by $T_{...}$ yields the temporal ascendency A_T :

$$A_T = \sum_{i,j,k} T_{ijk} \log \left(\frac{T_{ijk}^2 T_{...}}{T_{ij.} T_{i.k.} T_{.jk}} \right)$$

Having resolved 3D ambiguities, the extension of capacity and ascendency by induction into four or more dimensions becomes relatively straightforward. Probably, the most inclusive domain an ecologist is likely to consider would consist of five dimensions – donor, recipient, time, space, and medium. Accordingly, transfer T_{ijklm} will represent the flow from taxon i to taxon j during time interval k at spatial location l of medium m . (Space is considered as only a single dimension, because any 2D and 3D partitioning of a finite domain of physical space always can be enumerated by a single index (in the same fashion that multi-dimensional arrays are stored as a single sequence by computer machine code).) The corresponding 5D ascendency, A_O , would then be

$$A_O = \sum_{i,j,k,l,m} T_{ijklm} \log \left(\frac{T_{ijklm}^4 T_{.....}}{T_{.jklm} T_{i..klm} T_{ij..lm} T_{ijk..m} T_{ijkl.}} \right)$$

This ascendency remains homogeneous (*sensu* Euler) in the flows. As before, this property allows one to calculate readily the 5D sensitivities as

$$\frac{\partial A_O}{\partial T_{pqrst}} = \log \left(\frac{T_{pqrst}^4 T_{.....}}{T_{.qrst} T_{p..rst} T_{pq..st} T_{pqr..t} T_{pqrs.}} \right)$$

The corresponding biomass-inclusive overall ascendency, A_{OB} , then takes the form

$$A_{OB} = \sum_{i,j,k,l,m} T_{ijklm} \log \left(\frac{T_{ijklm} B_{.....}^2}{B_{iklm} B_{jklm} T_{.....}} \right)$$

where B_{iklm} is the biomass of medium m in taxon i at time k in spatial segment l . The corresponding sensitivities become

$$\frac{\partial A_{OB}}{\partial B_{prst}} = 2 \left[\frac{T_{.....}}{B_{.....}} - \frac{1}{2} \left(\frac{T_{p..rst}}{B_{prst}} + \frac{T_{pqrs.}}{B_{prst}} \right) \right] \quad [8]$$

and

$$\frac{\partial A_{OB}}{\partial T_{pqrst}} = \log \left(\frac{T_{pqrst} B_{.....}^2}{B_{prst} B_{qrst} T_{.....}} \right) \quad [9]$$

In those cases for which data are available on multiple media, Ulanowicz and Baird (1999) have demonstrated analytically that the largest biomass sensitivity coefficients eqn [8] correspond to that medium which is present in least proportionate amount, that is, in the sense of von Liebig (1854). Liebig's law, however, provides no way of identifying the most limiting source of that nutrient. The controlling source is given by the largest value of eqn [9]. Ulanowicz and Baird (1999) applied eqns [8] and [9] to parallel networks of several media to elucidate a new and systematic way of depicting nutrient dynamics in ecosystems. They assembled sufficient data to estimate the trophic exchanges of carbon, nitrogen, and phosphorus (C, N, and P) in the ecosystem of the mesohaline reach of Chesapeake Bay over the four seasons of a typical year (no spatial variation). They used the 4D version of eqn [8] to identify the limiting medium for each taxon and found that N was limiting primary production during the summer season (as has long been known). During that same season, however, P was controlling bacterial production and secondary production by nekton (mobile fishes). Applying eqn [9] to their networks, the investigators were able to diagram (graphical) trees that depict the hierarchy of nutrient controls during each season (Figure 17).

The nutrient limitation analysis can be used as well for purposes of comparison. For example, data at very similar resolution to those estimated for the Chesapeake are available on the chief components of the Sylt-Romero Bight ecosystem (Daniel Baird, personal communication). The analysis of C, N, and P for this system reveals that a very similar pattern of nutrient controls is operating in both estuarine ecosystems, although they are separated by thousands of kilometers and more than 10° of latitude. Primary production in both systems is limited by nitrogen, whereas most heterotrophs in both habitats are controlled by phosphorus. There is more of a tendency in the Sylt system for bottom dwellers to be starved for N: crabs and demersal fish appear to be controlled by N in the Sylt, while their counterparts in the Chesapeake are limited by carbon and phosphorus, respectively. Likewise, sediment bacteria are wanting N in the Sylt and P in the Chesapeake. It is curious that the nutrient limitation of crabs is reversed the next trophic level down, that is, crabs lack C in the Chesapeake and N in the Sylt.

A_{OB} was also applied by Ulanowicz (2000b) to animal migration across a simple 10×10 spatial grid. He simulated (using cellular automata) the hypothetical migration of population across this landscape to generate data to show how information theoretic measures could be applied to landscape ecology. Kikawada (1998) extended Ulanowicz's analysis to include simultaneous trophic interactions, and Krivov and Ulanowicz (2003) addressed the most general configuration of network dynamics pertaining to several chemical elements distributed across a landscape. Of note to hydrodynamicists, the calculus discussed here can even be applied to quantify the degree of organization inherent in fluid dynamics (Ulanowicz and Zickel, 2005).

9.04.9 Summary and Conclusions

The network perspective was prompted by the observed shortcomings of the mechanical worldview – how mechanical descriptions of coupled processes usually fail to mimic

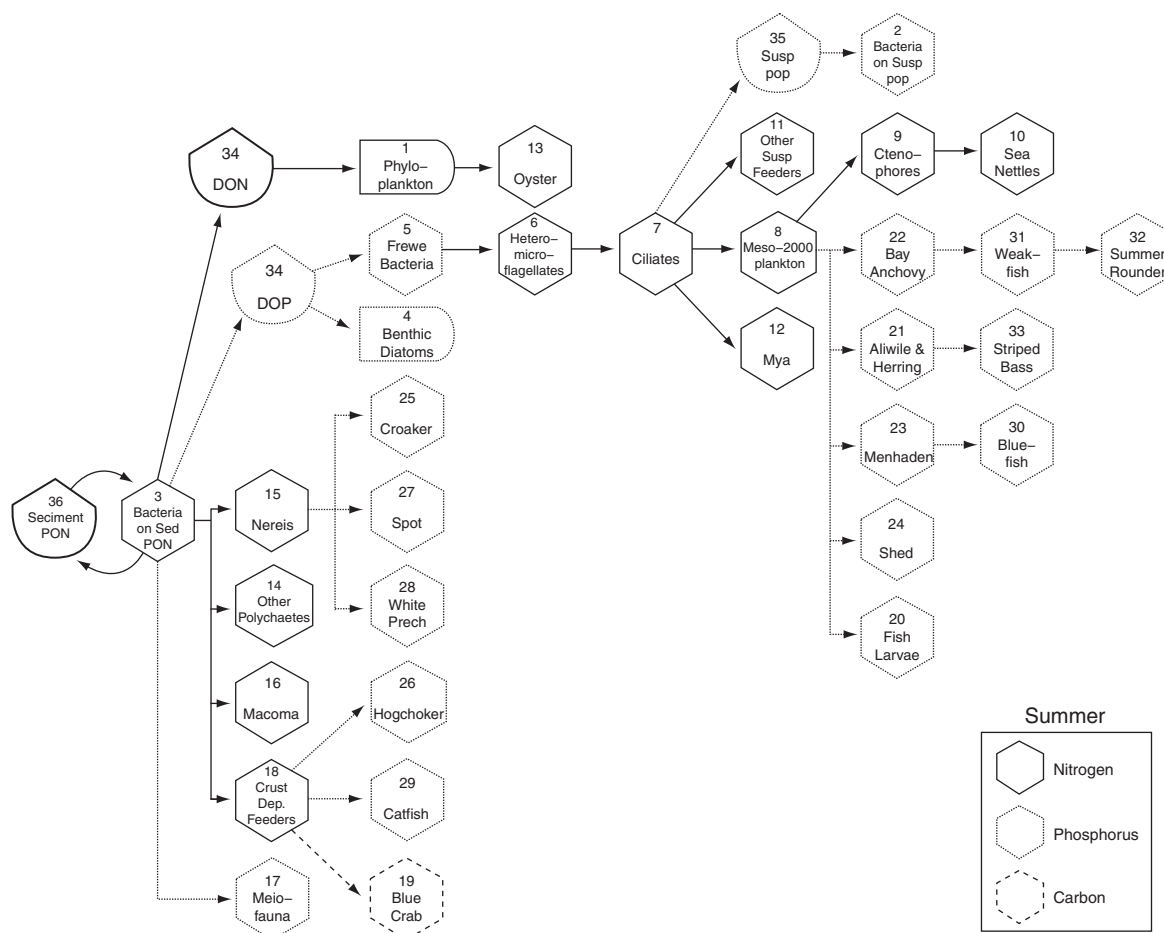


Figure 17 A schematic of the prevailing nutrient controls in the Chesapeake mesohaline ecosystem during springtime. Compartments and flows controlled by nitrogen are indicated by solid lines; those controlled by phosphorous by short dotted line; and those by carbon by long dotted lines.

ecosystem behaviors. In the course of searching for ways around this obstacle, network tools have been developed that do not merely circumvent the problem, but actually open entirely new perspectives on the process of life (Ulanowicz, 1997).

In retrospect, this outcome should not have been a surprise. An electron, for example, possesses its own internal nature (Sungchul Ji, personal communication). If one uses one set of apparatus to observe an electron, the entity will appear as a particle with a certain mass. If one focuses a different set of observational tools upon an electron, it will appear rather as a wave packet. As every physicist knows, the nature of the electron is dual. Its perceived nature depends upon the method of observation.

In a more general way, the same thing is true of an ecosystem. If one approaches a living community with the tools of quiescent material and laws, one can observe only the more mechanical aspects of the system. If, however, one adopts a process-oriented perspective (such as is afforded by network analysis), then the dynamics of life can be observed more directly, and the (restricted) role of noise becomes far more apparent. The process viewpoint allows for a truly evolutionary description of what transpires in living systems.

In particular, living systems now appear to be the outcome of the opposing tendencies toward order and dissipation, not

simply the unfolding of a mechanical scheme (Ulanowicz, 2009b). The focus in the network perspective is upon causality via configurations of processes, rather than laws working on inert material.

That the lens of process affords a most exciting new philosophical viewpoint on living systems does not at all detract from the utilitarian value of network analysis. In the absence of mechanical models, one can still say much, both qualitative and quantitative, about how estuarine and coastal systems are operating. One can use networks to identify configurations that order dynamics, to locate bottlenecks in the sequence of processes, to quantify the developmental status of a particular system in relation to others, to trace indirect effects, to evaluate trophic status, to assess how the ecological community as a whole might be made more sustainable, and so on.

Network analysis belongs in the toolbox of every manager of estuarine and coastal ecosystems.

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