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In network ecology one constructs and analyzes topological models to understand the intricacies of material and energy flows within ecosystems. These models (i.e. networks) consist of compartments (nodes) that contain a designated form of material or energy, the flows between these compartments, and those between the compartments and the external world. Emphasis is on the analysis of the constructed networks. The term that is most often associated with the practice of this discipline is ecological network analysis (ENA; also called ecosystem network analysis). In actuality, the method is more than a single analysis. ENA includes several algorithms designed to aid the understanding of the flow structure of the network and, by inference, the corresponding ecosystem. These algorithms are particularly valuable to ecologists in categorizing compartments and groups of compartments, defining indirect relationships between compartments, and indexing system-level attributes. This entry introduces the reader to network ecology and ecosystem network analysis in the following ways:

- 1. It familiarizes the reader with the origins of network ecology and ENA, and explains the construction of trophic flow networks.
- 2. It describes two commonly used software packages for network analysis.
- 3. Using one of these packages as a guide, it describes a selected group of algorithms with special attention on system-level attributes.
- 4. It discusses both the opportunities beyond the analysis of trophic dynamics and the limitations and concerns associated with the technique.

# Origins

Although the use of networks to describe the flow structure of **ecosystems** dates to the first half of the twentieth century [6], the use of formal algorithms in what is now called ecological network analysis did not begin to develop until the 1970s [7]. At that time it became obvious that mechanical simulation modeling was limited in its capacities to represent actual ecosystem dynamics [10]. In the light of this conclusion, the Scientific Committee on Ocean Research (SCOR) of the United Nations formed Working Groups 59 (Mathematical Models in Biological Oceanography) and 73 (Ecosystem Theory in Relation to Biological Oceanography). These groups urged ecologists to shift attention from stocks and biomasses towards a greater emphasis upon the measurement and analysis of ecological processes in general, and upon trophic transfers in particular [4]. Out of this movement arose the systematic analysis of ecological flow networks [18] and the protocols for network ecology.

# **Trophic Flow Networks**

Trophic flow networks answer two questions: 'Who eats whom?' and 'At what rates?'. Often, networks are depicted as box and arrow diagrams, with each box representing an ecosystem component (e.g. population, guild or detritus) and the arrows connecting them indicating the directed flows of a particular medium (material or energy). Also depicted on such diagrams are various transfers of the system elements to or from the external world, e.g. primary productions, respirations and other exports and losses (Figure 1). With large food webs (greater than about 40 compartments) (*see* **Community food webs**), such graphical representation becomes too complicated to interpret visually, and one usually resorts to matrix and vector representations of the network.

How does one put together such a network? While the magnitudes of some fluxes are available for most ecosystems, in virtually no biotic community have all the transfers been measured directly. One may combine the **biomass** densities (e.g. grams of carbon per square meter) of the various components with tabulated data on physiological ratios, such as consumption/biomass, respiration/biomass, assimilation efficiency, etc. Then, with a knowledge of the diet composition, one may estimate the various flows. Often this is done in spreadsheet format, to keep running tabs on the approximate balance of medium around each compartment. Alternatively, one may employ one of the software packages mentioned below to assist with balancing the network.

# Software for Analysis

Two software packages provide calculations for ENA and are most commonly used by ecologists: NET-WRK developed by Ulanowicz (http://www.cbl.

umces.edu/~ulan/ntwk/network.html) and Ecopath developed by Christensen and Pauly (http: //www.ecopath.org/). Each has undergone multiple revisions and contains somewhat different algorithms, assumptions, benefits and limitations. NET-WRK lists output under the following major headings. Structure Analysis provides matrices and vectors designed to quantify both direct and indirect relationships of compartments and fates of imported material. Trophic Structure Analysis provides information about the food web in the context of Lindeman's trophic structure [8]. Biogeochemical Cycle Analysis evaluates the characteristics of cycles within the system. Information Analysis focuses on system-level attributes characteristic of the growth and development of the system.

Ecopath is an alternative application for network analysis. (Its Windows versions may be considered more user friendly than NETWRK.) Ecopath was intended for application to fisheries, as reflected by some of its terminology [2]. Ecopath includes some of the same algorithms as NETWRK, but also exhibits some differences. In particular, the information needed to begin calculating flows is somewhat different. In NETWRK all flows are provided as input, whereas in Ecopath the flows are often calculated from ratios, proportions and biomass information.

#### **Selected Network Analysis Algorithms**

ENA is based on the premise that network representations may be so complex as seemingly to defy rational analysis. With mathematical tools one can glean highly useful insights, at several levels of resolution, into the functioning of the ecosystem. Selected analyses are summarized in this section as they appear in NETWRK. Some of the analyses provide insight into how components inter-relate, and some refer to system-level attributes. These are by no means the only analyses that can be employed, nor the only ways they can be used.

A total contribution matrix is computed in the structure analysis. It is used to evaluate the fraction that any compartment's throughput (i.e. total flow into or out of the compartment) contributes to any other compartment's activity. This contribution is derived from the matrix of exchanges among the compartments. The matrix coefficients represent connections between compartments that may be either direct or indirect. That is, no direct connection is necessary for a contribution to occur. For example, as shown in Figure 1, zooplankton are seen to eat phytoplankton. The connection between fish larvae and phytoplankton is indirect, however, and is mediated by intermediate feeding by zooplankton. The matrix includes the relative contributions of both the direct connections (e.g. the fraction of production from phytoplankton to zooplankton), as well as the indirect connections (e.g. the fraction of production from phytoplankton to fish larvae).

The total dependency matrix as calculated in structure analysis evaluates the fraction of a compartment's throughput that resided at some point in another compartment. As such, this analysis provides a mirror to total contribution. It can be used to assess the extended diet of consumers.

Through a series of vectors and matrices, input environs analysis computes the contributions of each import to other system flow. Each import is considered separately. This analysis could be used, for example, to determine the fate of primary production from either benthic diatoms or phytoplankton as it passes through and out of the ecosystem (*see* Benthic ecology).

Algorithms for trophic structure analysis provide a formalized description of energy flow (sensu Lindeman [8]). Primary production and detritus formation are considered to be trophic level 1 activities. Herbivory and detritivory are considered to occur at level 2, and primary carnivory acts at level 3. Higher trophic levels represent higher levels of carnivory. Matrices and vectors are assembled from computations of the various flows at each level (i.e. feeding, detrital production, respiration, import and export). These could be portrayed as a flow diagram of canonical (i.e. integer) trophic levels (Figure 2). Individual taxa, however, may feed across these canonical trophic levels. The effective trophic level of each consumer is determined from the distribution of the trophic levels of its various prey or diet. Thus, a population that feeds as a herbivore for half of its trophic needs (at level 2) and as a primary carnivore for the other half (at level 3) would have an effective trophic level of 2.5.

Biogeochemical cycle analysis evaluates the nature of flows associated with cycles within the network [12]. A cycle is a series of transfers that, in combination, pass material from a compartment, through one or more other compartments, and return



standing crops are indicated within the compartments in milligrams per square meter, and the indicated carbon flows are in milligrams of carbon per square meter per year. Reproduced by permission of the Ecological Society of America; from Baird and Ulanowicz (1989), The seasonal dynamics of the Chesapeake Bay ecosystem, *Ecological Monographs* **59**, 329–364 Figure 1 Schematic representation of the annual carbon flows among the 36 principal components of the Chesapeake Bay mesohaline ecosystem [1]. Carbon



Figure 2 The trophic chain corresponding to the network in Figure 1. Percentages in the boxes represent the effective trophic efficiencies. Units of flows and numbering of the compartments are the same as in Figure 1. Reproduced by permission of the Ecological Society of America; from Baird and Ulanowicz (1989), The seasonal dynamics of the Chesapeake Bay ecosystem, *Ecological Monographs* **59**, 329–364

material to the original one. In fact, this is a positive feedback or autocatalytic loop. The transfer within a cycle that has the smallest flux is called the weak arc, and a group of cycles sharing the same weak arc is called a nexus. One may infer that the weak arc is potentially the controlling flow within a cycle. Thereby, all cycles in a nexus share a common control. In the example shown in Figure 1, a cycle exists as the following: carbon is passed from particulate organic carbon (POC) (compartment no.35) to attached bacteria (no.2) to zooplankton (no.8) and back to POC. The smallest flux is the consumption of bacteria by zooplankton, and this is designated the weak arc. There is also a cycle from 35 to 2 to 8 to ctenophores (no.9) and back again to 35, and its smallest flow is from 2 to 8. The two cycles form a nexus. The cycling of carbon through both cycles may be controlled by their common weak arc. If all flows within the cycles were to be reduced by the amount in flow from bacteria to zooplankton, then both cycles would be broken. If zooplankton feeding were to increase, then one might also infer that both cycles would have greater flow (see Nutrient cvcling).

As cycles may have different lengths (i.e. different numbers of transfers per cycle) and quantities of flow, the system is characterized not only by the number of cycles, but also by the distribution of flow according to cycle length. The total flow associated with these cycles represents cycled flow. This summed flow can be compared with the total flows in the system (i.e. total system throughput equals the sum of all inputs, outputs, and interactions). The cycled flow as a fraction of total system throughput is commonly called the *Finn cycling index* [5].

Information analysis consists of a set of whole-system indicators that reflect those agencies

potentially responsible for changes in network structures [13]. These indices stem from the role of chance and historical contingency in effecting change. Whenever such indeterminacy is accompanied by indirect mutualism, as one might encounter in any autocatalytic configuration of processes (i.e. positive feedback loops or cycles), then the resulting system dynamics can depart significantly from conventional scenarios. Ulanowicz [15] argues that an autocatalytic configuration affected by chance disturbances can exhibit a host of attributes that, taken as a whole, portray a nonmechanical system response. Such attributes include selection, growth enhancement, symmetry breaking, centripetality of resources, inducement of competition between autocatalytic clusters, and partial autonomy.

The combined effects of such autocatalytic behavior can be both extensive (size-dependent) and intensive (size-independent) in nature. As for the extensive effect of autocatalysis, it is simply to increase the overall level of system activity. Intensively (or topologically), the result of indirect mutualism is to prune the web of flows in a way that reinforces those links that most effectively participate in the autocatalytic scheme. The extensive effect can be quantified readily by summing up the magnitudes of all the existing trophic exchanges into the total system throughput, T.

The effect of pruning is a little more difficult to quantify; fortunately, information theory is useful here. As a system is pruned, it becomes progressively more constrained. That is, on average each compartment communicates with fewer other compartments at greater relative amplitudes. In information theory, such focus upon a few outcomes is quantified in a negative fashion. That is, one begins by quantifying the maximal complexity, H, that a collection of processes can exhibit as the familiar Shannon–Wiener index applied to the individual flows (*see* **Diversity measures**). However, these processes are not randomly construed. Rather they are constrained by any number of biotic mechanisms to communicate in a particular pattern. The amount by which the constraints encumber the potential complexity, *H*, is called the *average mutual information* (AMI).

The observation that autocatalytic activity can be both extensive and intensive prompts one to scale the last two dimensionless (intensive) measures by the extensive measure, T. When network complexity has been scaled by T, the result ( $T \times$ H) is called the system capacity, C. Once the AMI has been scaled similarly, the ensuing quantity is called the system ascendency, A. It can be demonstrated that  $C \ge A \ge 0$ . This set of inequalities insures that the difference C - A always remains nonnegative and is called the system overhead, denoted by  $\Phi$ . In contrast to the ascendency, which measures the amount of complexity that is expressed as constrained flow structure, the overhead assigns a number to the residual flexibility that the system retains.

These various indices provide an investigator with ways to gauge and characterize system changes. For example, when a system is perturbed, a frequent result is that the ascendency falls abruptly. That is, one can quantify the negative impact of a perturbation at the level of the whole system in terms of the consequent drop in ascendency. Furthermore, one can define the well-known process of eutrophication as any response to system enrichment that increases system ascendency via an increase in T that more than compensates for a drop in AMI [14]. This quantitative definition allows one to distinguish between simple enrichment (which does not induce a drop in AMI) and the less desirable circumstance, eutrophication (which does).

These indices have been extended to incorporate other aspects of ecosystem ecology. One can also use the relationships among C, A and  $\Phi$  to help quantify what until now have been the anecdotal concepts of ecosystem health [9] and integrity [16]. In brief, A represents the level of system performance, or how healthily the community seems to be functioning. While overhead might appear at first to be a measure of dysfunction, one notes that

some degree of disorganization is necessary if a system is to adapt to unforeseen disturbances. Whence,  $\Phi$  becomes a surrogate for the system's potential resilience in the face of novel perturbation. As integrity requires both that a system perform well and that it remain robust in response to injury, the sum of the ascendency and the overhead, *C*, becomes an appropriate measure of ecological integrity. The four-dimensional counterparts to *A*,  $\Phi$  and *C* follow from information theory and have been used to evaluate time-dependent change [11]. Using another modification of the indices, one is able to pinpoint those flows that limit nutrients to other parts of the food web [17].

NETWRK and Ecopath share some analyses, but not all. The Trophic Structure Analysis and Information Analysis sections are common to the outputs of both NETWRK and Ecopath. In place of the Structure Analysis in NETWRK, Ecopath provides a Mixed Trophic Impact Matrix that gauges the sum of both positive impacts (e.g. food source or predator of a competitor) and negative impacts (e.g. competitor or predator) of each compartment on every other one. (Actually, such an analysis is also available as a companion to the NETWRK software package.) Instead of characterizing the cycling structure of the network, Ecopath focuses on the pathway structure. The number of different ways in which energy or matter can flow from a primary producer or prey to a predator at any trophic level is described. Also, the amount of primary production needed to support each consumer is calculated. Ecopath provides an omnivory index that calculates the variance of the trophic levels of a consumer's diet. Omnivores that feed over several levels have a higher index than consumers that feed over fewer levels. Finally, note that Ecopath includes sensitivity analyses and numerous aids for the user.

#### **Beyond Trophic Networks**

Most network studies have focused on trophic flows, but other kinds of material exchanges can be studied in a similar manner. Nutrient cycles have also been analyzed [3, 5]. Although the same software can be used to perform nutrient analyses, some results pertaining to nutrient cycles become difficult to interpret because of differences that may exist between nutrient cycle and trophic network structures. In nutrient cycling networks, the emphasis

on inorganic or abiotic forms of the nutrient may cause the construction of a network with a greatly aggregated food web. This restricts the application of the trophic structure and information analyses. Also, carbon cycling in trophic networks generally involves only organic forms (e.g. organisms or detritus) with carbon dioxide being outside the system (*see* Forest carbon cycling). Nutrient cycle networks may include several inorganic and organic forms as compartments, changing the meaning of the cycling indices.

#### **Concerns and Limitations**

Perhaps the most important source of concern for network analysis is the lack of data with which to construct networks. Each compartment must be identified by its standing stock and by its connections with its environment. There is the qualitative concern that each connection be properly positioned (e.g. are all food items represented?), along with the quantitative concern that the values for standing stocks and flows are appropriate. Some flows may have been derived from more than one parameter, and an estimate is needed for each parameter. Direct measurement of each stock, flow or parameter is rare. It is more likely that some large fraction of the values will come from various literature sources, and are general estimates. The consequences of using information from such sources are rarely assessed. Furthermore, little evaluation is made of the ramifications of stochasticity or uncertainty upon the network analysis.

Because ENA is not a single analysis, or even a single class of algorithms, it is difficult to discuss the issue of sensitivity in a blanket fashion. One general limitation is that most of the analyses are based on linear algebra (see Matrix population models) and, therefore, are not prone to the complexities associated with nonlinearities. Different analyses are sensitive to different aspects of model structure. The two aspects of structure are (a) the number and position of flows and compartments (topology) and (b) the magnitudes of flows and compartments. Both are important in almost every network analysis. The Biogeochemical Cycle Analysis of NETWRK and the Pathway Structure Analyses of Ecopath are, however, generally more dependent on the number and position of flows and compartments.

Other analyses are more sensitive to the quantities of flow.

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(See also Bioaccumulation; Community, ecological; Compartmental analysis; Ecosystem element cycling; Pelagic ecology; Population dynamics)

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