Systems Ecology: Ecological Network Analysis ☆

Brian D Fath, Towson University, Towson, MD, United States and International Institute for Applied Systems Analysis, Laxenburg, Austria
Ursula M Scharler, University of KwaZulu-Natal, Durban, South Africa

Introduction

Ecological Network Analysis (ENA) uses network theory to study the interactions between organisms or populations within their environment. ENA follows along the synecology perspective introduced by EP Odum which is predominantly concerned with inter-relations of material, energy, and information among system components. Bernard Patten was the originator of the environ analysis approach in the mid-to-late 1970s and along with colleagues expanded the analysis to reveal many insightful, holistic properties of ecosystem organization. During about the same time, Robert Ulanowicz developed several system's measures for networks motivated by information theory to analyze the system flows. This approach has been applied in ecological and socio-economic settings.

ENA starts with the assumption that a system can be represented as a network of nodes (compartments, vertices, components, storages, objects, etc.) and the connections between them (links, arcs, flows, etc.). In ecological systems, the connections are usually based on the flow of energy or matter (water, nutrients, etc.) between the system compartments, and in socioeconomic networks of money, trade, water, or social interactions. If such a flow exists, then there is a direct transaction between the two connected compartments. These direct transactions give rise to both direct and indirect relations between all the objects in the system. Network analysis provides a systems-oriented perspective because it is based on uncovering patterns and relations among all the objects in a system. Therefore, it gives a view on how system components are tied to a larger web of interactions.

Theoretical Developments of Ecological Network Analysis

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

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

The third foundational principle is that individual environs (and the flow carried within each one) are unique such that the system comprises the set union of all environs, which in turn partition the system level of organization. This partitioning allows one to classify environ flow into what have been called different modes: (1) boundary input; (2) first passage flow received by a compartment from other compartments in the system [i.e., not boundary flow, but also not cycled flow (in other words first time flow reaching a compartment)]; (3) cycled flow that returns to a compartment before leaving the system; (4) dissipative flow in that it has left the focal compartment not to return, but does not directly cross a system boundary (i.e., it flows to another within system compartment); and (5) boundary output. The modes have been used to understand better the general role of cycling and the flow contributions from each object to the other, which has had application in showing a complementarity of several of the holistic, thermodynamic-based ecological indicators (see Fath et al., 2001).

The link to thermodynamics has been incorporated into several other ecosystem measures and methodologies, used to calculate structural and functional systems indicators from the number and weight of links, or from the flows and associated

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biomass, or size, of nodes. Many of these have their roots in macroecological considerations, and were conceived by the desire to quantify the growth, succession and development of ecosystems (e.g., Ulanowicz, 1986), within the framework of "process ecology." Process ecology focuses less on the biomass (storage) of species, which often in conjunction with abundance is the main focus of ecologists. Rather, processes such as the biomass (or energy, nutrients, etc.) fluxes between species (nodes), recycling of material, decomposition, or production are the main focus. These lead to emerging properties on the ecosystem level, which links it to macro-ecology.

Data Requirements and Community Assembly Rules

On one level Ecological Network Analysis could be referred to as a holistic/reductionistic approach. It is holistic because it considers simultaneously the whole influence of all system objects, yet it is reductionistic in that the fine details of all transactions are entailed in the analysis. In other words, it is the opposite of a black box model. The network data requirements are considerable, which include the complete flow–storage quantities for each identified link and node (note flow and storage are interchangeable as determined by the turnover rate). Data can be acquired from empirical observations, literature estimates, model simulation results, or balancing procedures, when all but a few are unknown. While there is difficulty in obtaining complete network datasets, a number of ecosystem network models are available from various databases [see EcoPath (http://sirs.agro-campus-ouest.fr/EcoBase/), Ulanowicz (https://www.cbl.umces.edu/~ulan/ntwk/network.html), or Borrett (http://people.uncw.edu/borretts/research.html)].Due to this lack of requisite data for fully quantified food webs, researchers have developed community assembly rules that are heuristics to construct ecological food webs. Assembly rules are in general a set of rules that will generate a connectance matrix for a number of N species. Common assembly rules that have been developed are random or constant connectance, cascade, niche, modified niche, and cyber-ecosystem each with its own assumptions and limitations (see Halnes et al. (2007) for a review of these methods). In all but the last case, the assembly rules construct only the structural food web topology. The cyber-ecosystem methodology (Fath, 2004) also includes a procedure for quantifying the flows along each link. It uses a meta-structure of six functional groups: Producer (P), Herbivore (H), Carnivore (C), Omnivore (O), Detritus (D), and Detrital Feeders (F), within which random connections link species based on these definitional constraints.

Methods and Sample Network

To demonstrate a few network analysis methodologies it is best to proceed with an example. Consider the network in **Fig. 1**, which has five compartments or nodes (x_i, for $i = 1$ to 5). Compartments are connected by transaction of the energy–matter substance flowing between them. These pair-wise couplings are the basis for the internal network structure. A structural connectance matrix, or adjacency matrix, $\mathbf{A}$, is a binary representation of the connections such that $a_{ij} = 1$ if there is a connection from j to i, and a zero otherwise (Eq. **1**).

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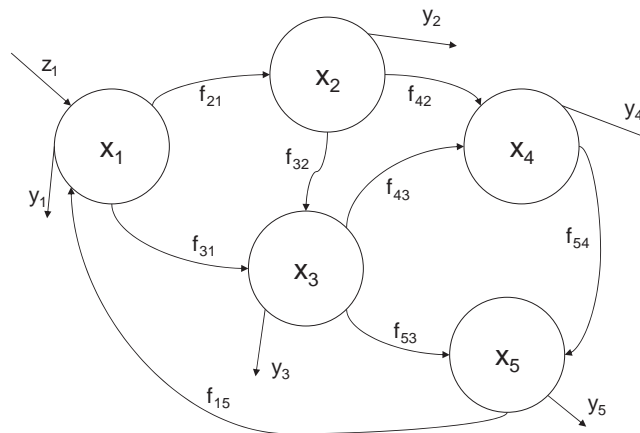

Fig. 1 Sample Network with five compartments use to demonstrate Environ Analysis notation and methodology.

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

$$\mathbf{F} = \begin{bmatrix} 0 & 0 & 0 & 0 & f_{15} \\ f_{21} & 0 & 0 & 0 & 0 \\ f_{31} & f_{32} & 0 & 0 & 0 \\ 0 & f_{42} & f_{43} & 0 & 0 \\ 0 & 0 & f_{53} & f_{54} & 0 \end{bmatrix} \tag{2}$$

Note that the orientation of flow from j to i is used in Environ Analysis because that makes the direction of ecological relation from i to j. For example, if i preys on j, the flow of energy is from j to i. To the contrary, other types of ecological network analyses direct the flow of energy from i to j when predator j feeds on i. It is therefore important to check the matrix setup before embarking on an analysis. All compartments experience dissipative flow losses (y_i, for $i = 1$ to 5), and here the first compartment receives external flow input, z_1 (arrows starting or ending not on another compartment represent boundary flows). For this example, these can be given as:

$$y = [y_1 \ y_2 \ y_3 \ y_4 \ y_5] \tag{3}$$

and

$$z = \begin{bmatrix} z_1 \\ 0 \\ 0 \\ 0 \\ 0 \end{bmatrix} \tag{4}$$

In this approach, there is no distinction between the types of outflow; whereas with other approach it is split into useable export and respiration loss. Total throughflow of each compartment is an important variable, which is the sum of flows into, $T_i^{in} = z_i + \sum_j^n f_{ij}$, or out of, $T_i^{out} = y_i + \sum_j^n f_{ji}$ the ith compartment. At steady state, compartmental inflows and outflows are equal such that $dx_i/dt = 0$, and therefore, incoming and outgoing throughflows are equal also: $T_i^{in} = T_i^{out} = T_i$. In vector notation, compartmental throughflows are given by:

$$T = \begin{bmatrix} T_1 \\ T_2 \\ T_3 \\ T_4 \\ T_5 \end{bmatrix} \tag{5}$$

The sum of flows in a network can also be depicted as total system throughput, which is defined as the sum of flows in the system including ingoing and outgoing boundary flows, and all internal flows from i to j, $\text{TSTput} = \sum_{j=1}^{n} \sum_{i=1}^{n} f_{ij} + \sum_{i=1}^{n} E_i + \sum_{i=1}^{n} R_i + \sum_{j=1}^{n} z_j$ where E is the export of usable material, and R the respiration losses across the system boundary.

This basic information regarding the storages, flows, and boundary flows provides all the necessary information to conduct Ecological Network Analysis. Environ Analysis has been classified into a structural analysis—dealing only with the network topology, and three functional analyses—flow, storage, and utility—which require the numerical values for flow and storage in the network (**Table 1**). Some of the analyses have been developed in tandem (e.g., utility analysis and mixed trophic impacts analysis) and their differences and similarities are pointed out below. In addition, an illustration of ascendency analysis follows.

The technical aspects of environ analysis are explained in detail elsewhere, so rather than repeat those here, the remainder of the entry highlights some of the important results from environ analysis. But first, one issue that must be covered is the way in which network analysis identifies and quantifies indirect pathways and flow contributions. Indirectness originates from transfers or interactions that occur nondirectly, and are mediated by other within system compartments. These transfers could travel two, three, four, or many links before reaching the target destination. For example, the flow analysis starts with the calculation of the

Table 1   Basic methodologies for Network Environ Analysis

Structural analysis	Functional analyses
Path Analysis: a_{ij} Enumerates pathways in a network (connectance, cyclicity, etc.)	*Flow analysis:* $b_{ij} = f_{ij}/T_j$ Identifies flow intensities along indirect pathways *Storage analysis:* $c_{ij} = f_{ij}/x_j$ Identifies storage intensities along indirect pathways *Utility analysis:* $d_{ij} = (f_{ij} - f_{ji})/T_i$ Identifies utility intensities along indirect pathways

nondimensional flow intensity matrix, **B**, where $b_{ij} = f_{ij}/T_j$. The generalized, **B** matrix corresponding to **Fig. 1** would look as follows:

$$\mathbf{B} = \begin{bmatrix} 0 & 0 & 0 & 0 & b_{15} \\ b_{21} & 0 & 0 & 0 & 0 \\ b_{31} & b_{32} & 0 & 0 & 0 \\ 0 & b_{42} & b_{43} & 0 & 0 \\ 0 & 0 & b_{53} & b_{54} & 0 \end{bmatrix} \tag{6}$$

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

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

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

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

$$\text{Storage}: \quad Q = P^0 + P^1 + P^2 + P^3 + \cdots = \sum_{m=0}^{\infty} P^m = (I - P)^{-1} \tag{8}$$

$$\text{Utility}: \quad U = D^0 + D^1 + D^2 + D^3 + \cdots = \sum_{m=0}^{\infty} D^m = (I - D)^{-1} \tag{9}$$

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

Network Properties

Patten has developed a series of "ecological network properties" which summarize the results of environ analysis. These have all been described in the literature (for an overview, see Patten, 2016; Jørgensen et al., 2007). The properties have been used to assess the current state of ecosystem networks and to compare the state of different networks. Furthermore, while interpreting some of the properties as ecological goal functions, it has been possible to identify the structural or parametric configurations that positively affect the network property values as a way to detect or anticipate network changes. For example, certain network alterations, such as increased cycling, lead to greater total system energy throughflow and energy storage, so one could expect that if possible ecological networks are evolving or adapting to such configurations. This leads to a new area of research on evolving networks. In this section, a brief overview is given for four of these properties: dominance of indirect effects (or nonlocality), network homogenization, network mutualism, and environs themselves.

Dominance of Indirect Effects

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

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

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

Network homogenization

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

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

$$CV(B) = \frac{\sum_{i,j=1}^{n} \left(\overline{b}_{ij} - b_{ij}\right)^2}{(n-1)\overline{b}} \tag{12}$$

Network homogenization occurs when the coefficient of variation of **N** is less than the coefficient of variation of **B** because this says that the network flow is more evenly distributed in the integral matrix. The test statistic employed here looks at whether or not the ratio $CV(\mathbf{B})/CV(\mathbf{N})$ exceeds one. The interpretation again is clear that the view of flow in ecosystems is not as discrete as it appears because in fact the material is well-mixed (i.e., homogenized) and has traveled through and continues to travel through many, if not, most parts of the system.

Network mutualism

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

$$\mathbf{D} = \begin{bmatrix} 0 & -\frac{f_{21}}{T_2} & -\frac{f_{31}}{T_3} & 0 & \frac{f_{15}}{T_5} \\ \frac{f_{21}}{T_2} & 0 & -\frac{f_{32}}{T_3} & -\frac{f_{42}}{T_4} & 0 \\ \frac{f_{31}}{T_3} & \frac{f_{32}}{T_3} & 0 & -\frac{f_{43}}{T_4} & -\frac{f_{53}}{T_5} \\ 0 & \frac{f_{42}}{T_4} & \frac{f_{43}}{T_4} & 0 & -\frac{f_{54}}{T_5} \\ -\frac{f_{15}}{T_5} & 0 & \frac{f_{53}}{T_5} & \frac{f_{54}}{T_5} & 0 \end{bmatrix} \tag{13}$$

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

$$\text{sgn }(\mathbf{D}) = \begin{bmatrix} 0 & - & - & 0 & + \\ + & 0 & - & - & 0 \\ + & + & 0 & - & - \\ 0 & + & + & 0 & - \\ - & 0 & + & + & 0 \end{bmatrix} \tag{14}$$

The elements of **U** provide the integral, system-determined relations. Kazanci and Adams (2017) recently showed that convergence of the D matrix can always be achieved. Continuing the example, and now including flow values derived from 10% transfer efficiency along each link ($b_{ij} = 0.10$, if $a_{ij} = 1$, and $b_{ij} = 0$ otherwise), we get the following integral relations between compartments:

$$\text{sgn }(\mathbf{U}) = \begin{bmatrix} + & - & - & + & + \\ + & + & - & - & + \\ + & - & + & - & - \\ + & + & + & + & - \\ + & + & + & + & + \end{bmatrix} \tag{15}$$

Unlike, the direct relations, this is not zero-sum. Instead, we see that there are 17 positive signs (including the diagonal) and 8 negatives signs. If there are a greater number of positive signs than negative signs in the integral utility matrix, then network mutualism is said to occur. Network mutualism reveals the preponderance of positive mutualistic relations in the system. Specifically, here, we can identify two cases of indirect mutualism, seven of exploitation, and one competition (**Table 2**).

Table 2   Direct and integral relations in sample network from **Fig. 1**

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

Mixed Trophic Impacts Analysis (MTI)

Utility analysis (UA) and MTI have been developed in parallel. Essentially both analyses strive to elucidate the type of interactions between two nodes, both along direct and indirect pathways. Their similarities and differences have been defined in Scharler *et al.* (2009), and below is given a brief outline. At the start of the analyses, the orientation of fluxes between nodes differs in the **F** matrix between UA and MTI analysis, as pointed out above. Next, the imports across the system boundary are taken into account in the UA analysis (D^0) but not in the MTI analysis (Q^0 omitted), leading to more negative numbers along the diagonal in the M matrix of the MTI analysis. The signs of the relations over direct and indirect effects are used in both the MTI and UA analyses as qualitative descriptions of node relation. In UA, however, the fractions of the matrix are also re-dimensionalized by their total throughflow. All respiration flows are excluded in the calculation of impacts in the MTI analysis (Ulanowicz and Puccia, 1990). In UA they are included in the total system throughflow for each compartment. Lastly, the impacts to detritus are taken as zero in the MTI analysis, as the detritus nodes do not compete for these flows in contrast to living nodes, which actively impact their source nodes. In the UA analysis, on the other hand, a detritus node has a negative impact on the source node. This variation in weighting may give a reason for the different outcomes. Bearing these differences in mind, applying an MTI analysis to the example illustrated for the UA analysis above yields the following results.

In the MTI approach the positive effect of a prey on its predator is expressed as:

$$g_{ij} = f_{ij} / \sum_{k=1}^{n} f_{kj}, \tag{16}$$

where k represents all diets of j, and g_{ij} ranges from 0 to 1. The negative impact of the predator on its prey, is defined as:

$$h_{ij} = f_{ij} / \sum_{m=1}^{n} f_{im}, \tag{17}$$

where m represents all consumers of i (note, in the original MTI literature this matrix is called f_{ij}, but is renamed here h_{ij} to avoid confusion with the notation defined above).

The direct net impact (q_{ij}) of a network compartment on another is depicted as the difference of the positive impact the prey has on the predator (g_{ij}) minus the negative impact the predator has on its prey (h_{ij}):

$$q_{ij} = g_{ij} - h_{ji} \tag{18}$$

The indirect interactions (M) are calculated, similar to the Utility Analysis, by summing the powers of the matrices describing indirect steps over various path lengths. Note that imports across the system boundary are not part of the MTI analysis.

$$M = Q + Q^2 + Q^3 + Q^4 + \dots \tag{19}$$

where Q, as defined in Eq. (18), is the matrix of the direct impacts of i upon j (path length of one), Q^2 the indirect impacts of i upon j over a path length of 2, Q^3 the indirect impacts of i upon j over a path length of 3, etc. Assuming the infinite power series converges, Eq. (19) can be written using the commonly known closed form solution as:

$$M = (I - Q)^{-1} - I \tag{20}$$

For the above example, the Q matrix of direct interactions, and M matrix for the integrated interactions are as follows:

Direct (Q)	Integral (M)
$(sd_{12}, sd_{21}) = (+, -) \rightarrow$ exploitation	$(sd_{12}, sd_{21}) = (+, -) \rightarrow$ exploitation
$(sd_{13}, sd_{31}) = (+, -) \rightarrow$ exploitation	$(sd_{13}, sd_{31}) = (+, +) \rightarrow$ mutualism
$(sd_{14}, sd_{41}) = (0, 0) \rightarrow$ neutralism	$(sd_{14}, sd_{41}) = (+, +) \rightarrow$ mutualism
$(sd_{15}, sd_{51}) = (-, +) \rightarrow$ exploited	$(sd_{15}, sd_{51}) = (-, +) \rightarrow$ exploited
$(sd_{23}, sd_{32}) = (+, -) \rightarrow$ exploitation	$(sd_{23}, sd_{32}) = (-, -) \rightarrow$ competition
$(sd_{24}, sd_{42}) = (+, -) \rightarrow$ exploitation	$(sd_{24}, sd_{42}) = (+, -) \rightarrow$ exploitation

$(sd_{25}, sd_{52}) = (0, 0) \rightarrow$ neutralism	$(sd_{25}, sd_{52}) = (+, +) \rightarrow$ mutualism
$(sd_{34}, sd_{43}) = (+, -) \rightarrow$ exploitation	$(sd_{34}, sd_{43}) = (-, -) \rightarrow$ competition
$(sd_{35}, sd_{53}) = (+, -) \rightarrow$ exploitation	$(sd_{35}, sd_{53}) = (+, +) \rightarrow$ mutualism
$(sd_{45}, sd_{54}) = (+, -) \rightarrow$ exploitation	$(sd_{45}, sd_{54}) = (+, -) \rightarrow$ exploitation

Environ analysis

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

$$E = (B - I)\hat{N}_i \tag{21}$$

where $\hat{N}_i$ is the diagonalized matrix of the ith column of **N**. When assembled, the result is the output oriented flow from each compartment to each other compartment in the system and across the system boundary. Input environs are calculated as:

$$E = \hat{N}'_i(B' - I) \tag{22}$$

where, $b'_{ij} = f_{ij}/T_i$, and $N' = (I - B')^{-1}$. These results comprise the foundation of Network Environ Analysis since they allow for the quantification of all within system interactions, both direct and indirect, on a compartment-by-compartment basis.

Ascendency analysis

The ascendency indicator was developed to quantify both the growth and development of ecosystems. Describing two attributes of ecosystems, ascendency consists of the total system throughput describing growth, and the average mutual information (AMI) describing how constrained fluxes are as they move from node to node (Fig. 2).

The total system throughput ($T..$) is described above, and a description of the AMI follows here. The degree of constraint of a flux between two nodes is described from its flow weight (T_{ij}), by the proportional weight of all flows entering the sink node in relation to total system flows ($T_j/T..$) and lastly by the proportion T_{ij} takes of all flows leaving i ($T_{ij}/T..$).

Average Mutual Information

The probability that a quantum of material flows along the highly frequented routes is higher compared to a network where all routes transfer the same amount of material. Conversely, the probability that a quantum of material flows along the less frequented routes will be lower compared to a network where all routes transfer the same amount of material. Such a change in probability can be quantified with the help of information theory. Information is defined as the agent which causes a change in probability. Ulanowicz uses the term information to describe "the effects of that which imparts order and pattern to the system."

The most indeterminate, or least constrained, network is one where all compartments are connected with each other and where, in proportion to the compartmental throughput, equal amounts of material flow along the ingoing and outgoing pathways. Quantifying the information which is gained by transferring material along more and less frequented routes thus gives a clue about the unevenness of material flowing along pathways. The change in probability from a situation where a quantum of material flows along an equiprobable pathway (Fig. 2) and along a pathway which is not equiprobable (Fig. 2B) is calculated using conditional probabilities.

Since, from an ecological network point of view, joint and conditional probabilities refer to transfers of material from compartment i to compartment j, the above formula can be rewritten as

$$\text{AMI} = K \sum_{i,j} \left(\frac{T_{ij}}{T..}\right) \log \left(\frac{T_{ij}T..}{T_i.T._j}\right) \tag{23}$$

where the joint probability of a quantum of material ($p(a_i,b_j)$) flowing from species i to species j can be denoted as $T_{ij}/T..$, remembering that the events in an events table are material flows in a system. $T..$ is the total system throughput, or the sum over all combinations of T_{ij}.
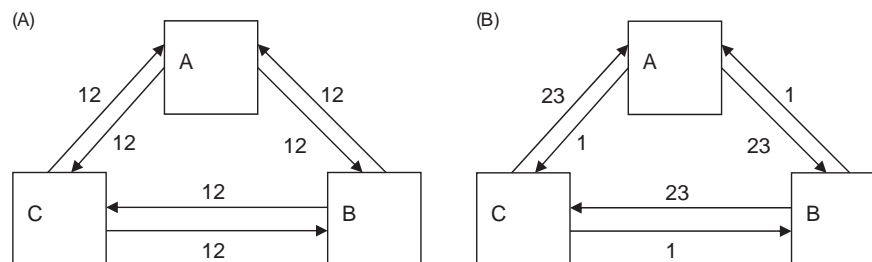

Fig. 2 (A) Hypothetical unconstrained network. Low AMI. (B) Hypothetical constrained network. Higher AMI.

Ascendency

The scalar constant, k, has been retained throughout all calculations. To be able to combine growth and development into one single index, k is substituted by the total system throughput or TST in order to scale the AMI to the size of the system in question. The resulting index is called Ascendency and is denoted by

$$A = \text{TST} \sum_{i,j} \left(\frac{T_{ij}}{T_{..}} \right) \quad \log \quad \left(\frac{T_{ij} T_{..}}{T_{i.} T_{.j}} \right) \tag{24a}$$

or

$$A = \sum_{i,j} T_{ij} \quad \log \quad \left(\frac{T_{ij} T_{..}}{T_{i.} T_{.j}} \right) \tag{24b}$$

Besides indirect mutualism there are a number of influences that can change the ascendency of a system. These influences are thought to not have a favored direction of change, whereas indirect mutualism is believed to drive development toward increased ascendency. Mutualism is furthermore not a result of events elsewhere in the system's hierarchy but can arise at any level. Previously, it was theorized that in the absence of overwhelming external disturbances, the ascendency of a system has a propensity to increase, that is, both activity (TST) and structure (AMI) increase. More recent research (e.g., Goerner *et al.*, 2009; Ulanowicz *et al.*, 2009) has shown that there are limits to the increase in ascendency (see section "Window of Vitality" below).

In theory, ascendency is higher when pathways are less in numbers (more specialization) and more articulated (few pathways transport most of the material). The highest theoretical value of ascendency is achieved when all players in the system have one input and one output only, and are thus joined in one big single loop. This configuration mirrors highest specialization, and in this case AMI = H. This situation cannot be achieved in real systems, due to reasons discussed below under the heading "Overhead" and "Window of Vitality."

Development Capacity

As mentioned above, the limit to development is set by Shannon's diversity index pertaining to the material transfers or flows. MacArthur applied Shannon's diversity index to the material flows in an ecosystem to arrive at a measure for the diversity of flows, H:

$$H = -k \sum_{i,j} \left(\frac{T_{ij}}{T_{..}} \right) \quad \log \quad \left(\frac{T_{ij}}{T_{..}} \right) \tag{25}$$

where k is a scalar constant, and $T_{..}$ is the total system throughput (*TST*), or the sum over all combinations of T_{ij}.

H can, like the AMI, be multiplied by *TST* to scale the diversity of flows to the system in question. TST $\times$ H is called the development capacity, or limit for development, C:

$$C = -\text{TST} \sum_{i,j} \left(\frac{T_{ij}}{T_{..}} \right) \quad \log \quad \left(\frac{T_{ij}}{T_{..}} \right) \tag{26a}$$

or

$$C = -\sum_{i,j} T_{ij} \quad \log \quad \left(\frac{T_{ij}}{T_{..}} \right) \tag{26b}$$

The initial complexity, H, consists of two elements. One is the AMI, describing the information gained by reducing the uncertainty in flow probability. It is an index of the organized part of the system. The other is the residual uncertainty, or H_c (also called conditional diversity). Thus, $H = \text{AMI} + H_c$.

H_c or Overhead

The overhead represents the unorganized, inefficient and indeterminate part of the flow structure and is considered an insurance for the system. Should the system become overly organized (high ascendency), it will also be prone to perturbations. The overhead is split into four components: overhead due to imports, exports, respiration and internal pathways.

The combined overhead is denoted by:

$$H_c = -k \sum_{i,j} \left(\frac{T_{ij}}{T_{..}} \right) \quad \log \quad \left(\frac{T_{ij}^2}{T_{i.} T_{.j}} \right) \tag{27}$$

Scaling H_c to the system by replacing k with by TSTput yields

$$\Phi = -\sum_{i,j} T_{ij} \quad \log \quad \left(\frac{T_{ij}^2}{T_{i.} T_{.j}} \right) \tag{28}$$

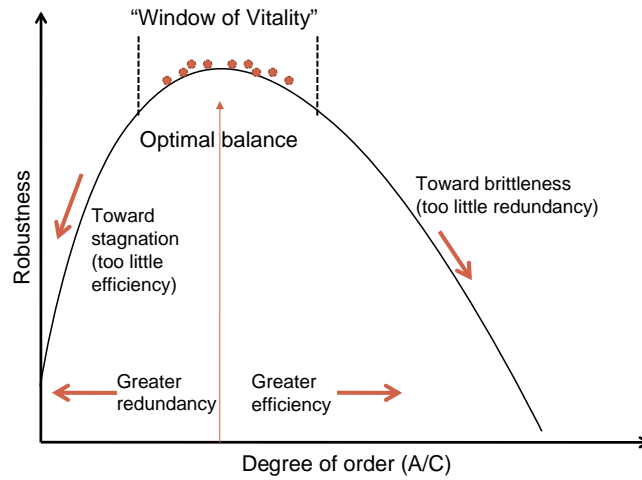The relationship between C, A and Φ so becomes $C = A + \Phi$.

Fig. 3 Robustness as a function of efficiency and resilience. X-axis: $\alpha =$ AMI/H. Y-axis: $-\alpha \log(\alpha)$. Modified from Goerner, S. J., Lietaer, B., and Ulanowicz, R. E. (2009). Quantifying economic sustainability: Implications for free-enterprise theory, policy and practice, *Ecological Economics* **69**, 76–81, with permission.

Similar terms can be derived for the flows that are imports, respiration, and exports.

The formula for the overhead on imports is as follows:

$$\Phi_I = -\sum_{j=1}^{n} T_{0j} \quad \log \left(\frac{T_{0j}^2}{T_{0.}T_{.j}} \right) \tag{29}$$

where imports are assumed to originate from the environment labeled compartment 0.

The overhead on exports is denoted by:

$$\Phi_E = -\sum_{i=1}^{n} T_{i,n+1} \quad \log \left(\frac{T_{i,n+1}^2}{T_{i.}T_{.,n+1}} \right) \tag{30}$$

where exports are assumed to flow into a fictitious compartment $n+1$.

The overhead on dissipation is:

$$\Phi_D = -\sum_{i=1}^{n} T_{i,n+2} \quad \log \left(\frac{T_{i,n+2}^2}{T_{i.}T_{.,n+2}} \right) \tag{31}$$

where respiration is assumed to flow into a fictitious compartment $n+2$.

Redundancy

The fourth part of the overhead is that of internal transfers and represents the extent of pathway redundancy. There are disadvantages to the system in maintaining redundant, or parallel pathways. For once, there can be an increase in dissipations, if transfers occur not only along one most efficient route, but along more than one route. Also, the resource transferred along different parallel pathways might not always end up at the right time at the consumer.

An obvious advantage of parallel pathways is the insurance of having more than one route of transfer in case of disturbances of other routes. Redundancy is denoted by:

$$R = -\sum_{i=1}^{n}\sum_{j=1}^{n} T_{i,j} \quad \log \left(\frac{T_{i,j}^2}{T_{i.}T_{.j}} \right) \tag{32}$$

Window of Vitality

The Window of Vitality describes a trade-off between organization and resilience in ecosystems through a new metric created from the measures of AMI and Overhead. As such it describes the trade-off in a system between its redundancy (high number of pathways with more uniform flow) and its degree of constraint (articulated pathways with more asymmetric flow). This new indicator has first been defined as "fitness for change" (Ulanowicz, 2009, Ulanowicz *et al.*, 2009), consequently as sustainability (Goerner *et al.*, 2009), and then called system robustness (e.g., Mukherjee *et al.*, 2015; Kharrazi *et al.*, 2013). It is derived by multiplying the ratio of A/C (or AMI/H) by the Boltzmann measure of disorder ($-k \log(a)$, Ulanowicz, 2009):

$$Robustness = -\alpha \quad \log \quad (\alpha)$$

where $\alpha = AMI/H$.

Work on empirical ecosystem networks revealed that the robustness of ecosystem peaks at intermediate values of AMI/H, which has been termed the "The Window of Vitality." This window describes an optimum balance between redundancy and efficiency in a network. On either side of the curve, where AMI (efficiency) is high or low relative to H (redundancy), the robustness values are comparatively low. Intermediate constrained networks are therefore thought to be of optimal robustness and sustainability (Ulanowicz, 2009; Ulanowicz et al., 2009; Goerner et al., 2009; **Fig. 3**).

Summary

A practical objective of ecological network analysis in general is to trace material and energy flow–storage through the complex network of system interactions, and has been a fruitful way of holistically investigating ecosystems. In particular, a series of "network properties" such as indirect effects ratio, homogenization, mutualism and ascendency have been observed using this analysis, which consider the role of each entity embedded in a larger system and so tie processes between nodes with their emerging properties describing ecosystem behavior.

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