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Information theoretical analysis of ecological networks†

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Ecological networks are considered from the viewpoint of information theory. Rutledge *et al.*'s model for choice within closed systems is extended to apply to open systems ; and an unbiased version of Ulanowicz's ascendency, a purported index of the development of ecological communities, is given. This information theoretical analysis is also applicable to flow networks arising as models of biological systems, economic systems, social systems, etc.

1. Introduction

The problem of describing how living systems develop is one of the most intriguing issues in all of science. During the past two decades it has become apparent that there are properties shared in common by all systems engaged in the process of development (Glansdorff and Prigogine 1971, Odum 1977). From a strategic point of view it matters little whether one seeks to describe development as it occurs in ontological, ecological, economic, social or political systems—so long as the language of description is sufficiently broad, a general principle could emerge from any of the various disciplines.

An appropriately general language in which to expound the phenomenon of development is that of networks (Bunow and Mikulecky 1982). In ecology, an early attempt at focusing upon a particular property of more developed networks was made by Odum (1953) when he suggested that a multiplicity of parallel pathways between arbitrary pairs of compartments (species or trophic levels) in the network of flows occurring in an ecosystem contributed to greater homeostasis of the entire network. He reasoned that a disturbance along any flow pathway could be compensated for by altered flows in parallel pathways. MacArthur (1955) immediately recognized that Odum was speaking about a particular application of the problem of communication in networks and attempted to invoke information theory to quantify the redundancy inherent in the pathways of communication. MacArthur believed that the entropy of the flow network was a sufficient descriptor of flow redundancy. Unfortunately, the concept of flow redundancy soon became confounded with that of diversity of species ; and over a decade of vigorous, but inconclusive, research ensued on the issue of whether ecosystem species diversity contributed to system homeostasis.

Meanwhile, information indices more useful than entropy in quantifying Odum's argument had become more widely known. Some twenty years after MacArthur had proposed entropy as a descriptor of flow redundancy, Rutledge

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et al. (1976) recast Odum's argument in terms of a more appropriate quantity—the conditional entropy. Conceptually this was quite a refinement of MacArthur's suggestion, except, as Rutledge points out, that the conditional entropy is not always sufficient for ecosystem analysis based upon longer time scales.

Ulanowicz (1979) argued that the complement of the conditional entropy, the average mutual information, more appropriately captured the notion of development in networks over a longer span of time. Later, Ulanowicz (1980) suggested that a scaled variation of the average mutual information synthesized most of Odum's (1969) 24 indicators of mature ecosystems into a single index, which he called the system ascendency. Ulanowicz also attempted to generalize Rutledge's analysis so that it would pertain to open systems. Unfortunately, the information component of Ulanowicz's ascendency had a hidden bias and did not evolve fluently from the body of information theory.

In this work we show how a change in the normalization of the constituent probabilities allows one to derive a revised ascendency from basic concepts in information theory. Furthermore, the new index is more readily extended to non-steady-state networks. The basic forms of the overhead terms (components of the conditional entropy for open systems) remain the same as those defined by Ulanowicz.

2. Ecological networks

We consider ecological networks like the one shown in Fig. 1. Each compartment k is characterized by its throughput T_k of a single given medium such as carbon, nitrogen, mass, energy, etc., and may have several kinds of inputs and outputs as shown in Fig. 2. The inputs are distinguished as to whether they come from the outside world or from other compartments. The outputs entail dissipative flows (respiration, death, etc.), exports useful to other systems, and the flows to other compartments.

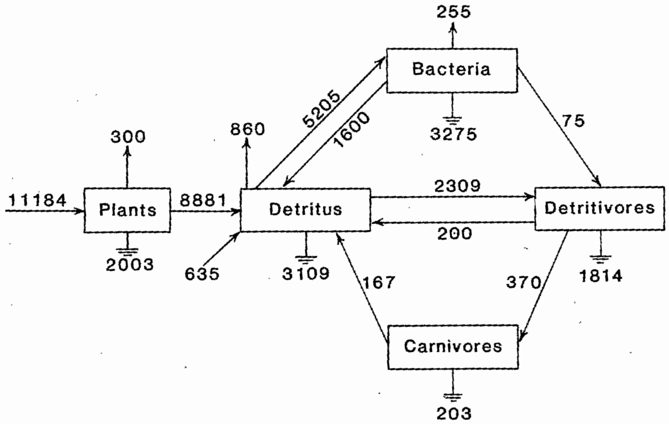

Figure 1. Simple example of an ecosystem flow network. Flows of energy among the five major compartments of the Cone Springs ecosystem are schematically depicted. Annual values for flows are given in k cal/m^2. Ground symbols represent respiration.

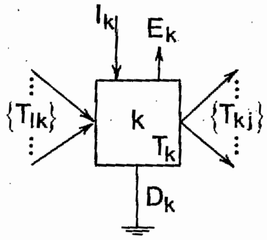

Figure 2. The *k*th compartment of an ecological network.

The symbols for the *k*th compartment are as follows :

T_{kj} : the flow leaving the *k*th compartment and directly contributing to the sustenance of the *j*th compartment ; $T_{kj} \geqslant 0$

D_k : the dissipated flow leaving the *k*th compartment ; $D_k \geqslant 0$

E_k : the useful export leaving the *k*th compartment ; $E_k \geqslant 0$

I_k : the input flow to the *k*th compartment from the outside world ; $I_k \geqslant 0$.

One further defines the throughput of species *k* as

$$T_k = \sum_{j=1}^{n} T_{kj} + D_k + E_k \tag{1}$$

In a system at steady state, such as the one depicted in Fig. 1, T_k also equals

$$\sum_{l=1}^{n} T_{lk} + I_k$$

that is

$$\sum_{j=1}^{n} T_{kj} + D_k + E_k = \sum_{l=1}^{n} T_{lk} + I_k \tag{2}$$

In what follows constraint (2) does not need to be satisfied, and the development will be applicable to non-steady-state configurations.

3. Model for choice within open systems

As shown in Fig. 3, exogenous inputs come from the zeroth compartment ; exports enter compartment $(n+1)$; and dissipation is collected in compartment $(n+2)$. Although one could consolidate input, export and dissipation into one global compartment, they are treated separately to facilitate further extension.

Now time is introduced into the analysis. The time interval for flow from one compartment to another is taken to be θ. New variables are defined as follows :

Q_k : the percentage of the total flow through the ecological network at time t_1 which passes through the *k*th compartment ; $Q_k \geqslant 0 (k = 0, \ldots, n)$, $Q_{n+1} = Q_{n+2} = 0$

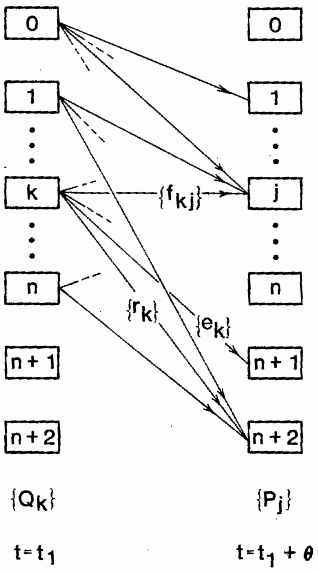

Figure 3. Generic model for choice in open systems.

P_j : the percentage of the total flow through the ecological network at time $t_1+\theta$ which passes through the jth compartment; $P_0=0$, $P_j \geqslant 0 (j=1, \ldots, n+2)$

f_{kj} : the percentage of the total flow through the kth compartment at time t_1 that passes into the jth compartment between time t_1 and $t_1+\theta$; $f_{kj} \geqslant 0$

r_k : the percentage of the flow through the kth compartment which is dissipated; $r_k \geqslant 0$

e_k : the percentage of the flow through the kth compartment which is exported as useful flow; $e_k \geqslant 0$.

The relations between these variables are provided by the equations

$$\left.\begin{aligned} P_j &= \sum_{k=0}^{n} f_{kj} Q_k, \quad (j=1, \ldots, n) \\ P_{n+1} &= \sum_{k=1}^{n} e_k Q_k \\ P_{n+2} &= \sum_{k=1}^{n} r_k Q_k \end{aligned}\right\} \tag{3}$$

where

$$\left.\begin{aligned} \sum_{j=1}^{n} f_{kj} + r_k + e_k = 1 \quad (k=1, \ldots, n) \\ \sum_{j=1}^{n} f_{0j} = 1 \end{aligned}\right\} \tag{4}$$

At steady state the following additional relations hold

$$\left.\begin{aligned} Q_k &= P_k \quad (k=1, \ldots, n) \\ Q_0 &= P_{n+1} + P_{n+2} \end{aligned}\right\} \tag{5}$$

4. Information theoretical discussion of ecological networks

In ecological networks one may identify variables Q_k, f_{kj}, r_k and e_k as follows

$$\left.\begin{aligned} Q_k &= T_k/(T+I) \; (k=1, \ldots, n) \\ Q_0 &= I/(T+I) \end{aligned}\right\} \tag{6}$$

$$\left.\begin{aligned} f_{kj} &= T_{kj}/T_k \quad && (k, j=1, \ldots, n) \\ f_{0j} &= I_j/I && (j=1, \ldots, n) \\ f_{k0} &= 0 && (k=0, \ldots, n) \end{aligned}\right\} \tag{7}$$

$$r_k = D_k/T_k \tag{8}$$

$$e_k = E_k/T_k \tag{9}$$

where

$$T = \sum_{k=1}^{n} T_k \tag{10}$$

$$I = \sum_{k=1}^{n} I_k \tag{11}$$

It is a simple matter to reinterpret the model for choice shown in Fig. 3 as the classical model of a channel illustrated in Fig. 4. Here $A=\{a_k\}$, $k=0, 1, \ldots, n, n+1, n+2$, is the set of input events with probabilities $P(a_k)=Q_k$. $B=\{b_j\}$, $j=0, 1, \ldots, n, n+1, n+2$, is the set of output events with probabilities $P(b_j)=P_j$. $F=\{f_{kj}\}$ is the communication matrix of this channel.

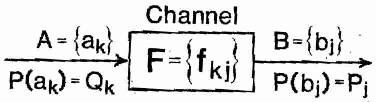

Figure 4. Schematic diagram of a generic channel.

According to the orthodox way of calculating mutual information (e.g., Abramson 1963), one may identify the mutual information contained in the ecological network in the manner shown in Proposition 1. As has been mentioned by Rutledge *et al.* (1976), this quantity represents the average amount of uncertainty resolved by the knowledge of the network structure.

Proposition 1

The information M contained in the ecological network structure is the sum of three terms

$$M = M_{s+\sigma} + M_e + M_r \tag{12}$$

where

$$M_{s+\sigma} = \sum_{k=0}^{n} \sum_{j=1}^{n} f_{kj} Q_k \log \left[f_{kj} \bigg/ \left(\sum_{l=0}^{n} f_{lj} Q_l \right) \right] \tag{13}$$

$$M_e = \sum_{k=1}^{n} e_k Q_k \log \left[e_k \bigg/ \left(\sum_{l=1}^{n} e_l Q_l \right) \right] \tag{14}$$

$$M_r = \sum_{k=1}^{n} r_k Q_k \log \left[r_k \bigg/ \left(\sum_{l=1}^{n} r_l Q_l \right) \right] \tag{15}$$

This is proved in the Appendix.

$M_{s+\sigma}$ captures the amount of information associated with the network flow structure and the pattern of inputs ; M_e, the amount assigned to the pattern of useful exports ; and M_r, the amount contained in the pattern of dissipative flows.

The network information expressed by M_e and M_r is usually lost to the outside world. However, if one considers this network as a subnetwork of a composite system, as in Fig. 5, the information of export M_e becomes a part of the information contained in the composite network flow structure. The information of dissipation M_r is lost in all cases.

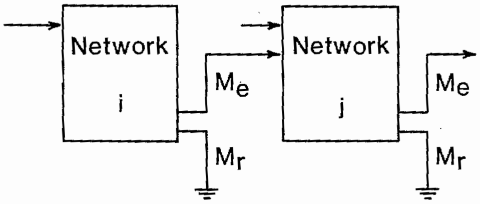

Figure 5. Composite network.

Because M is the mutual information as normally defined, it is always non-negative (Abramson 1963). Although in general one cannot guarantee the non-negativity of an arbitrary part of mutual information, one can prove the non-negativity of $M_{s+\sigma}$, M_e and M_r.

Proposition 2

The three terms of the mutual information in open flow networks are separately non-negative

$$M_{s+\sigma} \geqslant 0 \tag{16}$$

$$M_e \geqslant 0 \tag{17}$$

$$M_r \geqslant 0 \tag{18}$$

This, too, is proved in the Appendix.

Proposition 2 guarantees that each of $M_{\mathrm{s}+\sigma}$, M_{e} and M_{r} may properly be interpreted as information.

$M_{\mathrm{s}+\sigma}$ in Proposition 1 corresponds to the unscaled ascendency in Ulanowicz (1980). Hence, Proposition 1 established the theoretical background for the ascendency and shows how the original version must be revised to agree with the conventions of information theory. Also, to be consistent with the normalization of the P_i and Q_i (see eqn. (6)), the scaling factor for the mutual information should become $T+I$.

For simplicity the ascendency A will be identified with $M_{\mathrm{s}+\sigma}$ in what follows. One can easily verify the following useful relationship among network capacity, network overhead and ascendency.

Proposition 3

The ascendency is the difference between the network capcity and the overhead. The overhead, in turn, consists of three non-negative components associated with the three types of output flows. That is

$$A=C-(E+D+R) \tag{19}$$

where

$$C=-\sum_{k=0}^{n} Q_k \log Q_k \tag{20}$$

$$E=-\sum_{k=1}^{n} e_k Q_k \log Q_k \tag{21}$$

$$D=-\sum_{k=1}^{n} r_k Q_k \log Q_k \tag{22}$$

$$R=-\sum_{k=0}^{n}\sum_{j=0}^{n} f_{kj} Q_k \log\left[f_{kj}Q_k \bigg/ \left(\sum_{l=0}^{n} f_{lj} Q_l\right)\right] \tag{23}$$

Proof of Proposition 3

Equation (19) may be algebraically verified by substitution of definitions (13) and (20)–(23) for the respective terms. Because $0 \leqslant Q_k \leqslant 1$ and r_k and e_k are both non-negative, it follows from inspection of (20)–(22) that C, E and D are non-negative. The non-negativity of R is proved in exactly the same manner as the non-negativity of $M_{\mathrm{s}+\sigma}$ in the Appendix. ■

In Proposition 3, C is the network capacity for development. $E+D+R$ is network overhead, i.e. the portions of the network capacity encumbered by exports (E), dissipation (D) and redundancy of structure (R).

Corollary 1

The ascendency has the upper limit C, i.e.

$$C \geqslant A \geqslant 0 \tag{24}$$

R in (19) corresponds to the index of ecological stability S, in Rutledge *et al.* (1976). The larger S a system has, presumably the more stable it is. After replacing R by S, one can rewrite (19) as

$$S=C-(E+D+A) \tag{25}$$

Then

$$S=[C-(E+D)]-A \tag{26}$$

$$A=[C-(E+D)]-S \tag{27}$$

Thus, development and stability stand in opposition to each other, as seen in (26) and (27).

The particular reasons why ascendency should serve as a reliable index of development in ecological communities are detailed in Ulanowicz (1980, 1981). Briefly, the major attributes of more developed ecosystem networks are a larger number of species, higher degree of cycling within the system, increased efficiency of the components, and greater specialization of the components. Each of these properties is capable of increasing the ascendency of the network. More compartmentalization leads to a higher entropy, thus raising the upper bound on the increase in ascendency (eqn. (24)). The ascendency reaches its upper limit under the ideal conditions when the medium is cycled around a single loop with no losses. Finally, greater specialization is the same as lower redundancy R, which has been shown to detract from the ascendency.

5. Summary

The definitions and propositions presented here should serve to demonstrate the role of information theory in systems ecology. By paying careful attention to definitions Rutledge *et al.*'s model for choice in ecosystems can be extended to open systems and to networks not in balance. Ulanowicz's notion of ascendency can now be strictly identified with accepted variables in information theory. The clear conceptual and mathematical distinction between Ulanowicz's ascendency ($A=M_{s+\sigma}$) and Rutledge's index of stability (S) should provide a starting point for a more enlightened discussion of development and stability than has hitherto been possible.

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Appendix

Proof of Proposition 1

From the definition of mutual information of the channel depicted in Fig. 4

$$\begin{aligned} M &= M(A\,;B) \\ &= H(A)-H(A/B) \\ &= H(B)-H(B/A) \\ &= \sum_{A,\,B} P(a_k, b_j)\log\,[P(b_j/a_k)/P(b_j)] \end{aligned} \tag{A 1}$$

Here

$$\left.\begin{aligned} &P(b_j/a_k)=f_{kj} \quad (k=0,\ldots,n,\quad j=1,\ldots,n)\\ &P(e/a_k)=e_k \quad (k=1,\ldots,n),\quad P(e/\sigma)=0\\ &P(r/a_k)=r_k \quad (k=1,\ldots,n),\quad P(r/\sigma)=0\end{aligned}\right\} \tag{A 2}$$

$$\left.\begin{aligned} P(b_j)&=\sum_{k=0}^{n} f_{kj}Q_k \quad (j=1,\ldots,n)\\ P(e)&=\sum_{k=1}^{n} e_kQ_k\\ P(r)&=\sum_{k=1}^{n} r_kQ_k\end{aligned}\right\} \tag{A 3}$$

$$\left.\begin{aligned} &P(a_k,b_j)=P(b_j/a_k)P(a_k)=f_{kj}Q_k \quad (k=0,\ldots,n,\quad j=1,\ldots,n)\\ &P(a_k,e)=e_kQ_k \quad (k=1,\ldots,n)\\ &P(a_k,r)=r_kQ_k \quad (k=1,\ldots,n)\\ &P(\sigma,e)=P(\sigma,r)=0\end{aligned}\right\} \tag{A 4}$$

where $\sigma=a_0$, $e=b_{n+1}$ and $r=b_{n+2}$.

From (A 1)–(A 4), one can derive (12)–(15).

Proof of Proposition 2

One can easily rewrite $-M_{s+\sigma}$ as follows

$$-M_{s+\sigma}=\left(\sum_{k=0}^{n}\sum_{i=1}^{n} f_{ki}Q_k\right)G \tag{A 5}$$

where

$$G=\sum_{k=0}^{n}\sum_{j=1}^{n}\alpha_{kj}\log\left(\sum_{l=0}^{n} f_{lj}Q_l/f_{kj}\right) \tag{A 6}$$

$$\alpha_{kj}=f_{kj}Q_k\Bigg/\left(\sum_{k=0}^{n}\sum_{i=1}^{n} f_{ki}Q_k\right)\geqslant 0 \tag{A 7}$$

Because the logarithm function is concave, it is possible to derive the following inequality using Jensen's inequality

$$G\leqslant\log\left(\sum_{k=0}^{n}\sum_{j=1}^{n}\alpha_{kj}\sum_{l=0}^{n} f_{lj}Q_l/f_{kj}\right) \tag{A 8}$$

$$=\log\left(\sum_{k=0}^{n} Q_k\right) \tag{A 9}$$

From the definition of Q_k

$$\sum_{k=0}^{n} Q_k = 1$$

Therefore

$$G \leqslant 0 \tag{A 10}$$

Equation (16) follows from (A 5) and (A 10).

Equations (17) and (18) are proved in the same way as (16).

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