2.2.2 INFORMATION THEORY APPLIED TO ECOSYSTEM STRUCTURE[1]

Since biological thermodynamic forces are so obscure, it may be worth exploring how far one may go in describing community behaviour without having to invoke forces. Indeed, it turns out that limiting discussion to fluxes alone allows the application of information theory to network flow structure in a manner which is more satisfying than the *ad hoc* acceptance of species diversity indices. Thus, apart from some arbitrary identification of system compartments, the remainder of this section will be devoted to analysing natural communities as though they consisted exclusively of fluxes.

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[1] By R. E. Ulanowicz, Contribution No. 967 of the University of Maryland, Centre for Environmental and Estuarine Studies.

Section 2.1.2 has already introduced the reader to some current efforts to analyse systems purely on the basis of flows. There it was mentioned that an appropriate scale for a compartment was the total amount of flow passing through it. The sum of the individual throughputs, in turn, defined a community scale factor, the total systems throughput (T). Growth of community scale is generally regarded as an increase in T (e.g. the familiar growth in gross national product).

However, bigger is not necessarily better, and one desires a measure of organization within the community. For the purposes of this discussion organization will be taken to mean the tendency for the community to behave as a coherent whole, as distinct from a mere collection of independent parts. Now for two compartments to act in consort with one another implies that a pathway of communication exists between them. This communication can be achieved by an infinite variety of mechanisms; however, the only interchange visible to an observer who can sense only fluxes will occur along flow pathways. Information can be sent in the form of the magnitude of a steady flux or as a temporal variation in the flow. As in the earlier section on input–output analysis, it will be assumed that the system is at steady state, thereby limiting consideration to steady flows. This assumption is not as restrictive as it may first appear, as choosing an appropriate time interval can cause most dynamic systems to appear to be in quasi steady state.

It is worth mentioning at this point that the pathways of communication and sustenance are perceived to be identical. For species i to communicate with species j implies that i sustains in part the perceptible existence of j (the magnitude of j being defined by its throughput). Attention is now focused on those situations where there is mutual sustenance among compartments. In such circumstances a positive feedback of sustenance occurs wherein the growth of any participating unit will be reinforced by the mutual exchange. If an arbitrary collection of compartmental throughputs is subject to conditions propitious to their growth, those subdivisions engaged in mutual sustenance will grow at a faster rate than the isolated compartments and will emerge as the dominant elements in the community. Such positive feedback phenomena are fundamental to the theory of cybernetics and their application to ecosystems has been emphasized by Margalef (1968) and Odum (1971).

Most of the cited discussions have been directed towards reward loops and attention seems concerned with effects of such feedback upon the individual compartments. But to entertain a holistic view of the system implies that one should search for a means of characterizing the mutual sustenance intrinsic to the entire community. Since the networks of internal fluxes and communication have been assumed identical, it is now appropriate to borrow from information theory to define the average mutual sustenance.

Following Mulholland (1975), the fraction of the total systems throughput pertaining to compartment i will be labelled Q_i. Also, that fraction of species i throughput which flows to directly sustain species j is denoted by f_{ij}. The average mutual sustenance (taken from the average mutual information) is defined as

$$A = K\sum_{j}\sum_{k} f_{kj}Q_k \ln (f_{kj}/[\sum_{i} f_{ij}Q_i]) \tag{59}$$

where K is an appropriate scalar. Now the most appropriate scale for the system has already been assumed to be the total systems throughput. Setting $K = T$ and calling the scaled quantity the ascendancy, it seems probable that during an increase of system size the pattern of flows most likely to emerge would be the one with greatest ascendancy.

It is important to realize that ascendancy cannot increase without bound. One limiting factor is immediately seen to be the external constraints of finite input rates. But input rates alone do not stop ascendancy from increasing, since ever-faster internal cycling of medium (e.g. free energy, mass) could allow ascendancy limitless value. It is immediately obvious, however, that infinitely high internal cycling is proscribed by the second law of thermodynamics. Each pass through a compartment must result in a finite rate of loss of medium. Odum and Pinkerton (1955) contend that near equilibrium, the useful power output of any stage is maximized when the efficiency (defined as the rate of power input to the rate of generation of useful power) is 50 per cent. This is a conservative result, and one has every reason to expect that far-from-equilibrium (e.g. ecological) processes will deliver maximum output at smaller power efficiencies.

Hence maximization of ascendancy is seen to be a compromise between maximizing the scale of the system and achieving the greatest mutual sustenance. Beyond an optimal point, 'attempts' by the system to increase total throughput result in lowered efficiencies and a more than compensating decrease in mutual sustenance. Conversely, for a fixed community of species to increase mutual sustenance by becoming more efficient will decrease T by an even greater proportion.

Now because a community with greatest ascendancy is the one most likely to emerge during growth does not imply that the same configuration will persist. To study the question of persistence it is necessary to consider other components of the total system complexity.

By scaling the familiar Shannon Index by the total throughput, one obtains an expression for the system development capacity, i.e.

$$C = -T\sum_{i} Q_i \ln Q_i. \tag{60}$$

Information theory allows the partitioning of this index into four relevant components:

$$C = A + A_o + S + R \tag{61}$$

where the first of these, the ascendancy, has already been defined.

The second component, A_o, is the uncertainty ascribed to the flows of medium exported from the community, i.e.

$$A_o = -T\sum_i f_{ie}Q_i \ln(Q_i) \qquad (62)$$

where the subscript e refers to the external universe.

The third component, S, defines the uncertainty encumbered by necessary dissipation.

$$S = -T\sum_i r_i Q_i \ln Q_i \qquad (63)$$

where r_i is the fraction of throughput of compartment i that is respired.

The one remaining component, R, is termed the redundancy,

$$R = -T\sum_i\sum_j f_{ij}Q_i \ln(f_{ij}Q_i/\sum_k f_{kj}Q_k) \qquad (64)$$

because it is a measure attached to the redundancy of the flow pathways within the community.

Rewriting Equation (61) as

$$A = C - (A_o + S + R) \qquad (65)$$

one can easily recognize the similarity to the Gibbs or Helmholtz free energies. The development capacity, C, is analogous to the internal energy of a thermodynamic system. Like internal energy, not all of the development capacity is accessible to the system. There will always remain an amount $(A_o + S + R)$ as necessary overhead to *maintain* the system configuration.

The central hypothesis of this section can now be stated: 'A self-organizing community always behaves to optimize its ascendancy subject to hierarchical, environmental, and thermodynamic constraints.'

It is useful to consider how the value of ascendancy might increase in ecosystems through changes in the remaining four state variables. Where helpful, examples of possible mechanisms for the change will be mentioned.

An upper bound on the ascendancy is the development capacity, C. Increase in C allows more possibility for A to rise. Thus, increases in the scale of the system occasioned by increased input fluxes or increasing the partitioning of flow among more species will both augment C. In reality there are limits to how finely flows can be partitioned, since very small populations are more susceptible to chance extinctions. Therefore, availability of resources and environmental perturbations determine that C shall have an upper bound. (What that bound might be is a more complicated issue, since T can be influenced by mutual sustenance.)

Ascendancy is prevented from achieving full development capacity by the overhead inherent in the sum $(A_o + S + R)$. One is tempted at this point to discuss how this sum might be minimized, until it is realized that all the variables are non-conserved (Denbigh, 1975). It is possible to increase ascendancy by increasing the scale of the system, so that the value of the difference between development capacity and overhead can increase, even if overhead is becoming a progressively larger fraction of total development capacity.

Ecosystems do not always develop so as to minimize overhead, in fact the reverse circumstance is probably more common.

If input and output fluxes are completely independent, then minimization of A_o appears a sound strategy for system development. If, however, the given system appears as a compartment in a higher-level system, then exports can become a crucial contribution to the ascendancy of the larger realm (and thereby the continued existence of the smaller community).

In similar manner, if environmental variability is low, the system can develop by reducing redundancy to the point where specialization becomes a prominent feature of the network (e.g. the tropical rain forest). However, such a strategy would be inappropriate under conditions where environmental variation is great. There, network redundancy provides increased freedom for the system to reconfigure itself so as to maintain the level of ascendancy. This is the crux of Odum's (1953) argument that pathway redundancy facilitates system homoeostasis.

The least clearly defined component of the overhead is the dissipation measure, S. The ambiguity stems from the lack of a concrete expression for the optimal efficiency for maximum power production in the far-from-equilibrium realm. Indications are that the optimal efficiency falls monotonically with increasing output, but this notion needs quantitative refinement. The qualitative hypothesis of falling efficiency with increasing power output makes it likely that S will increase during the course of development. The possibility cannot be excluded that under particular conditions the system might develop so as to decrease S, but such conditions represent a (probably small) subset of general circumstances.

No assumption has been made concerning the distribution of the compartments in space. For the sake of simplicity the reader has probably assumed that each compartment represents a species homogeneous in space. But spatial structure and flows are quite important, especially in marine ecosystems. Fluxes have not been constrained to those resulting in biomass transformation, but may also include those associated with biomass transport. Thus, if one is interested in n biological entities distributed over m segments of a spatial domain, there is no conceptual difficulty in treating the generalized flow network among $m \times n$ compartments with the development hypothesis. Maximal ascendancy over both space and species should describe both spatial and trophic structure. Input and output uncertainties (e.g. A_o) are likely to be dominant in marine ecosystems.

The development hypothesis cannot be accepted as valid unless empirical work shows that the macroscopic descriptions it engenders are applicable to a large body of general observations. There are indications that many of the qualitative remarks about ecosystem development (E. P. Odum, 1969; H. T. Odum, 1971) are consistent with the hypothesis (Ulanowicz, 1980), but further investigation is obviously necessary.

Nevertheless, the very possibility of a development criterion based solely on fluxes could have serious implications on the future course of marine ecosystems modelling. Simulation modelling as it is usually practised means that the modeller regards each flow pathway in its turn and chooses a mathematical statement explaining the flow in terms of the contents of various compartments. That is, explanation at the mesoscopic level is usually achieved by assuming that a flow is the consequence of a causative factor, a 'force'. There is no problem with this procedure if one confines the model to a single process (or possibly a few coupled processes). If, however, one combines many such process models into a large community model, the assumption is usually implicit that the network of flows will be the consequence of the combination of separate forces.

The development hypothesis, however, turns matters around. It says that the development criterion resides in the flow structure and is not the consequence of the aggregate forces. One might say that the system develops in such a way as to select for the proper forces to satisfy the community criterion in the same sense that organisms undergo selection. In such circumstances the results of most community simulations are conditional at best.

This is not to imply that simulation modelling at the community level should cease. Rather it is a caution that it should proceed with an eye upon the eventual development of macroscopic principles that can guide the creation of community models. Optimization theory is developing at a satisfying rate, and one can envision an iterative process whereby a simulation model is produced according to the best estimate of aggregate processes, and the simulation of resultant system behaviour is compared against the macroscopic criterion. The model is then modified until an incremental improvement is made in meeting the criterion. Proceeding in this manner, many of the possible alternate configurations of the system should accrue, allowing for at least a probabilistic forecast of the response of the system to perturbation.