An Hypothesis on the Development of Natural Communities†

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A knowledge of the flow structure within a natural community is assumed to be sufficient to describe the behavior of far-from-equilibrium, self-organizing systems. This postulate permits the definition of a non-conservative, macroscopic variable quantifying the ascendency of a natural community. Self-organizing, dissipative systems are hypothesized to develop over time so as to optimize their ascendency. These assumptions appear to be supported by observed trends in ecosystem development. The theory possibly provides a caricature of development phenomena common to ecosystems, organisms, economic communities, evolution, and a host of other self-organizing phenomena.

1. Introduction

When an ecosystem or other natural community is severely disturbed or obliterated, recovery to the "climax" configuration follows an orderly and sometimes repeatable series of states (succession). The "strategy" of ecological succession is believed by some to be a short-term manifestation of the slower process of the evolution of the biosphere (Odum, 1969). When viewed at the level of a single population, or small subset of populations, the intricacies of succession are exceedingly complex, and it seems impossible to formulate a single hypothesis or index relevant to all situations.

Matters are more encouraging, though, when the community undergoing succession is viewed as a whole. Odum (1969), for example, identifies 24 attributes of the total system which can be used to characterize whether a system is in the early stages of development or approaching the climax stage. However, a multitude of sometimes contradictory criteria does not present a coherent picture of the process of development. Needed is a macroscopic

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vision portraying development phenomena in diverse situations as a single, measurable progression.

If a phenomenological description of developing systems is sought, it must either be searched for from within the framework of established phenomenology, or else cast as an acceptable extension to present theory. By an "acceptable extension" is meant that any additional hypothesis must, in the limit, merge smoothly with the accepted results of thermostatics and near-equilibrium thermodynamics. Now, if a smooth transition between old and new theory is required, the implicit possibility remains that clues to formulating any extensions can be found among observable trends in thermodynamics. As a prelude to considering phenomena in the highly irreversible realm of self-organizing systems (e.g. ecosystems), I would like to follow the increasing significance that macroscopic fluxes have towards a phenomenological description of events as a system moves away from equilibrium.

2. A Thermodynamic Trend

Thermodynamic systems are characterized by fluxes and forces. A force (such as a gradient in chemical potential) will cause its conjugate flux (the diffusion of chemical species) to occur. Consider, for example, two quiescent, imiscible liquids with two other mutually-soluble species introduced into one phase. Diffusion will occur in the system until the chemical potentials of each dissolved constituent are equal throughout both phases. From the macroscopic point of view, thermodynamic potentials are necessary and sufficient to describe the equilibrium configuration. Macroscopic fluxes are trivially zero.

Now consider the situation in which the solute potentials are slightly, but arbitrarily, altered at the extremities of the system, and maintained at their new levels. The system will be constrained infinitesimally away from equilibrium. Macroscopic fluxes will be evident; possibly coupling between non-conjugate forces (differences in potentials) and fluxes will occur. The entire system will eventually take on that configuration of fluxes and forces which results in a minimum rate of dissipation throughout the domain of the system (Glansdorff & Prigogine, 1971). Entropy production, in turn, can be expressed as the sum of the products of the forces times their conjugate fluxes. A proper description of the macroscopic stationary state, therefore, requires both fluxes and forces.

Far-from-equilibrium configurations present a number of difficulties—not the least of which is the obscurity of the generalized forces associated with many observed fluxes. To date no generalized force conjugate to an

ecological biomass flow has been identified (Ulanowicz, 1972). When one observes that macroscopic fluxes were unimportant in describing thermostatic situations and gained in relevance as soon as one moved slightly away from equilibrium, one is tempted to extrapolate the descriptive role of fluxes into the highly irreversible domain as becoming entirely sufficient to describe the nature of far-from-equilibrium stationary states. Postulating the descriptive sufficiency of irreversible flows offers a new standpoint from which to construct a theory of dissipative structures.

This assumption may seem excessively radical to some, especially biologists concerned with microscopic and mesoscopic phenomena. But many objections should be tempered by noting that a macroscopic (community) description dominated by flow relations does not imply that forces do not exist or are not important at the level of the subsystem. Nor is there any pretense to providing explanations for phenomena (cf., Drury & Nisbet, 1973; Connell & Slayter, 1977). Rather, the effect here is devoted (as in all of thermodynamics) to quantifying that which is common to general observation. Finally, the assumption is not new. Tisza (1966) points out how the emphasis of early thermodynamicists such as Carnot, Clausius and Kelvin was upon process (i.e. flow) variables. It was not until Gibbs that attention among scientists shifted towards state (equilibrium) variables (see also, Andresen et al., 1977). Thus, the flow hypothesis could be construed as a return to an earlier perspective. More recently, many macroeconomists have implicitly assumed that the salient features of economic community structure can be described by capital flows (Leontief, 1951). Input–output analysis has been applied to ecological networks (Hannon, 1973; Finn, 1976; Levine, 1977; Ulanowicz & Kemp, 1979).

With the discussion focused on fluxes, the description of growth and development may now proceed in a straightforward manner.

3. Growth

Since intracompartmental structure and contents are removed from discussion, there is little ambiguity about how to quantify the constituent compartments (see Hannon, 1973). Limiting the discussion to the flow of a single medium (free energy, mass or currency), one obvious way of describing the scale of a particular compartment is to measure the total flow of medium through that unit. At steady state, compartmental throughput is the sum of either all the inputs to or all the outputs from that subunit.

The scale of the entire system immediately follows as the sum of the individual throughputs, or total system throughput (T). The particular example of the gross national product defining the scale of a nation's

economy is familiar to all. That component of growth associated with an increase in scale is thereby identified as an increase in total system throughput.

4. Development or Organization

Subsequent to an initial phase dominated by an increase in scale, the nature of development shifts towards an increase in organization. The term "organization" immediately begs the question, "For what purpose?" While this is an extremely interesting philosophical issue, it is beyond the scope of this discussion. Suffice it to say that organization is the tendency for the total system to behave in a coherent manner, i.e. as an integral unit, as distinct from a collection of independent parts.

Now for two parts of a system to interact there must be some pathway of communication between them. Communication can occur through a multitude of mechanisms, but to an observer who can perceive only flows, communication is limited to flow pathways. Thus, for component i to communicate with component j also implies that i contributes to (or sustains in part) the discernible size of j (j having been quantified solely by its throughput). If several compartments mutually sustain one another, their growth will be accelerated by the positive feedback effect of mutual sustenance. In any expansion of system size that pattern will dominate which is characterized by the greatest mutual sustenance. This concept of positive feedback is central to the theory of cybernetics, and its importance in ecosystems has been emphasized by Margalef (1968) and Odum (1971).

Communication and sustenance being isomorphic under the flow hypothesis, it becomes possible to borrow from information theory to give mutual sustenance concrete mathematical form. Rutledge et al. (1976) consider an assembly of n compartments in which the ith compartment is characterized by throughput T_i. Thus, each compartment considered separately comprises the fraction $Q_i = T_i/\sum_{j=1}^{n} T_j$ of the total systems throughput. The maximum uncertainty associated with the flows in this structure is identical to the complexity of the system as identified by the Shannon formula

$$C = -K \sum_i Q_i \ln Q_i \qquad (1)$$

where K is an arbitrary scalar.

If, in addition, one determines that the probability of any quantum of flow leaving compartment i directly contributing to the sustenance of j is f_{ij}, then information theory (see Rutledge et al., 1976) describes the average mutual information (and thereby a measure of average mutual sustenance) of the

system as

$$A = K \sum_k \sum_j f_{kj} Q_k \ln \left[f_{kj} \middle/ \left(\sum_i f_{ij} Q_i \right) \right]. \tag{2}$$

The physical meaning of the mutual sustenance is not obvious from the form of equation (2). Perhaps the measure is best described as the coherence of the flow network, i.e. an indicator of the degree to which the flow system differs from either a homogeneous network or a collection of totally independent parts. The measure A can also be interpreted as the average degree of unambiguity with which an arbitrary compartment communicates with any other compartment in the system.

The physical dimensions of the average mutual sustenance are identical to the dimensions of the arbitrary constant K. [The magnitude of information functions depend on the base to which the logarithms are taken (nats, bits, etc.), but physically speaking they are dimensionless.] Most applications of information theory to biology have neglected the importance of the scalar multiplier, and the results are thereby unable to address the difference in scale between any two systems under study (Apter & Wolpert, 1965). Without scaling it might happen, for example, that the Shannon–Wiener index calculated for the flow of carbon through four billion cells of a single human organ would be nearly equal to the same index calculated for the carbon flow through the four billion individuals on earth! Whence, the multiplicative constant is seen to be of paramount importance in defining both the fundamental units and the size of the system being described. In this derivation the most appropriate choice for K is the total system throughput $(T = \sum_{j=1}^{n} T_j)$. Once K has been set equal to T, I choose to call the quantities defined in (1) and (2) the community development capacity and the community ascendency, respectively.

The ascendency measures in one index the two attributes of system size and flow organization, i.e. it is a natural descriptor of the combined processes of growth and development. As we shall see, growth and development of flow systems are sometimes in conflict, and ascendency then serves to define the compromise configuration.

5. A Development Hypothesis

From the introduction to the ascendency, it might be expected that increasing the intensity of the positive feedback loops would cause the value of A to rise. However, other things being equal, greater internalization, increased specialization, or number of compartments also serve to abet the ascendency.

As a simple example it is useful to regard the matrix of carbon flows among several compartments of Lake Findley (Richey et al., 1978) as shown
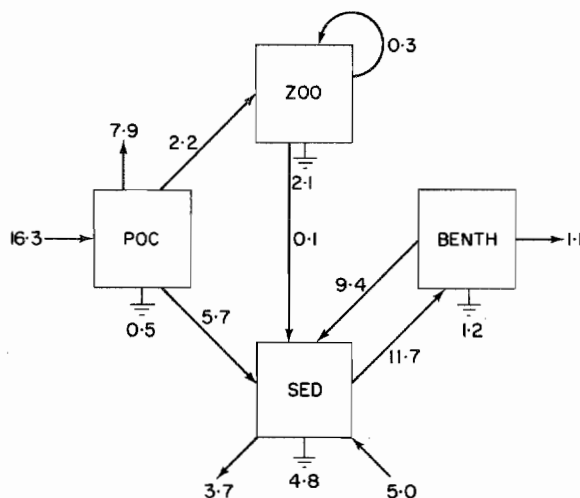
FIG. 1. Carbon flows in Lake Findley (from Richey *et al.*, 1978). All flows in g Carbon m^{-2} year^{-1}; terms include POC (particulate organic carbon as detritus and phytoplankton), ZOO (zooplankton), BENTH (benthic macroinvertebrates), and SED (sediments, macrophytes and periphyton). Ground symbols indicate release of carbon as CO_2. $A = 23\cdot19$, $C = 61\cdot77$, $T = 50\cdot7$ (gC m^{-2} year^{-1}).

in Fig. 1. Three hypothetical amendments to this network will serve to illustrate factors which may increase ascendency.

Greater internalization is taken to mean that some of the exports from the system are redirected towards other internal compartments; or, alternatively, that the export is utilized by a new compartment. The latter circumstance is illustrated in Fig. 2 where the $3\cdot7$ g m^{-1} year^{-1} export is now directed to a new exploiter represented by compartment EX. The total system throughput of the ensemble has increased by only seven percent, whereas the ascendency rises by 25%.

Ascendency is especially sensitive to changes resulting in greater specialization. In Fig. 1 there are two pathways for carbon to flow from the particulate compartment to the sediments—one a direct flow and the other via the zooplankton. If the direct flow were rerouted through the zooplankton in such a way so as to keep T constant (see Fig. 3), the ascendency would climb 32%.

As might be expected, positive feedback loops usually raise the ascendency. Suppose, for example, some mechanism such as resuspension resulted in a feedback flow from the benthos to the particulate phase. Assume further that this feedback was magnified so that the end result was the superposition of a three element loop of magnitude 5 g m^{-2} year^{-1} from
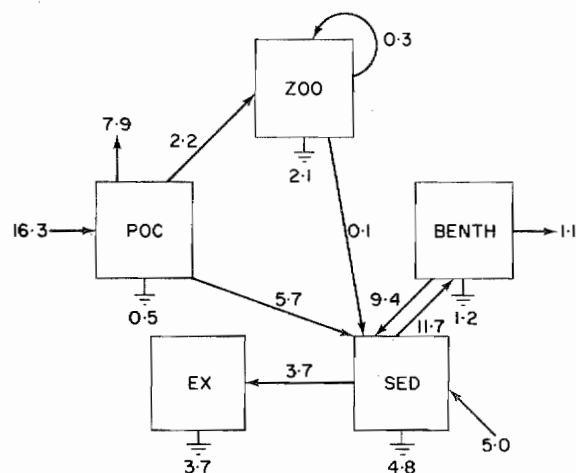
FIG. 2. Same network as in Fig. 1, except export from sediments has been directed into a hypothetical exploiter compartment (EX), i.e. that particular flow has been "internalized". $A = 28 \cdot 93$, $C = 75 \cdot 28$, $T = 54 \cdot 4$ (gC m^{-1} year^{-1}).
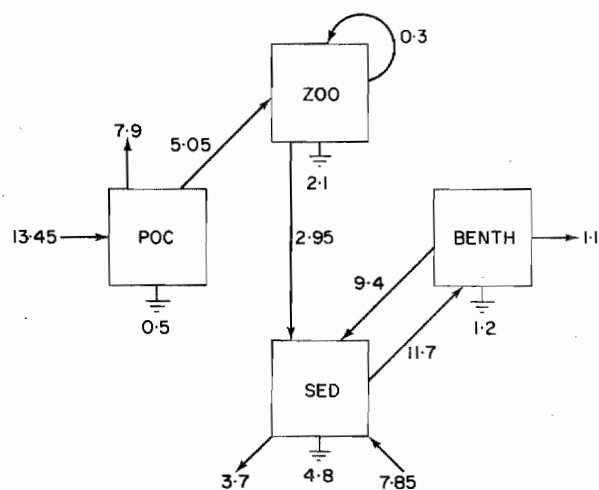
FIG. 3. The direct flow from POC to SED in Fig. 1 has been apportioned to the links POC–ZOO and ZOO–SED. Specialization is thereby increased. $A = 30 \cdot 61$, $C = 65 \cdot 62$, $T = 50 \cdot 7$ (gC m^{-1} year^{-1}).

FIG. 4. A cycle of magnitude 5 gC m^{-2} year^{-1} along the circuit POC–SED–BENTH–POC has been superimposed upon the network in Fig. 1. $A = 33\cdot51$, $C = 79\cdot19$, $T = 65\cdot7$ (gC m^{-2} year^{-1}).

benthos to POC to sediments upon the network in Fig. 1 (see Fig. 4). The result would be to increase T by 30%, but to bolster A by 45%.

One should keep in mind that these sample changes were all hypothetical and that real modifications are likely not to be as simplistic. Furthermore, when more than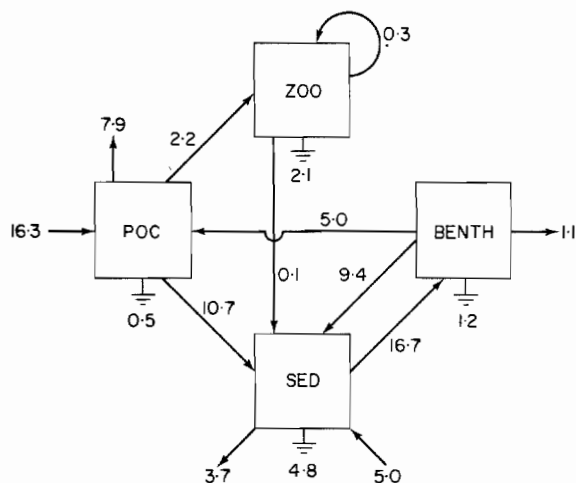 one of the three factors rises simultaneously there is no guarantee that the net result will be an increase in A. [As Odum (1969) remarks, the processes sometimes counteract one another.]

As will be discussed later, Odum (1969) cites empirical evidence that greater internalization, feedback, cycling, specialization and information are all attributes of more developed ecosystems. That the pattern of greatest mutual sustenance should have a competitive advantage over other configurations during system expansion and should also represent in a single measure various attributes observed to characterize developed systems, provides the rationale for the following hypothesis: *A self-organizing community flow network behaves over an adequate interval of time so as to optimize its ascendency subject to hierarchical, thermodynamic and environmental constraints.*

6. The Limits to Growth

Total system throughput is defined in such a way that it can increase with increasing mutual sustenance, even when input fluxes are limited. Medium

could be cycled ever faster, and there seems to be no *a-priori* reason why ascendency should be bounded. As might be expected, however, the limit to A for a given configuration of input fluxes is determined by the Second Law of Thermodynamics. Efficiencies for any process are always less than unity. In reality no compartment can provide its entire throughput as sustenance for other compartments. When one regards the efficiencies of power transfers, thermodynamic restrictions are even more severe.

Odum & Pinkerton (1955) treat the problem of two coupled processes near to equilibrium. They show that the useful power output is maximized when the efficiency (defined as rate of power input to rate of generation of useful power) is 50%. This is a conservative result valid only near-equilibrium, and one has every reason to expect that far-from-equilibrium processes will deliver maximum output at much smaller power efficiencies. (Trophic efficiencies are commonly estimated at 10%.)

Hence, beyond an optimal point, "attempts" by the system to increase T will result in more than compensating decreases in mutual sustenance. Conversely, the "attempts" by a fixed community of species to increase mutual sustenance by becoming more efficient will result in lower T. The optimal configuration of T and mutual sustenance in highly dissipative systems is a subject for further theoretical and empirical thermodynamic inquiry.

Further constraints upon development may be elucidated by quantifying what is meant by systems overhead. It is easy to demonstrate mathematically (McEliece, 1977) that the development capacity will always be greater than or equal to the community ascendency and that both quantities are inherently positive, i.e.

$$C \ge A \ge 0. \tag{3}$$

The difference between C and A (called conditional entropy in information theory) will be termed the overhead, and a few simple considerations will show that overhead can be apportioned into three components.

Let the fraction of throughput T_i which is exported as usable medium be designated by f_{ie} and the fraction dissipated (respired) by r_i, so that $\sum_j f_{ij} = 1 - f_{ie} - r_i$. Then the quantities

$$E = -T \sum_{i=1}^{n} f_{ie} Q_i \ln Q_i \tag{4}$$

and

$$S = -T \sum_{i=1}^{n} r_i Q_i \ln Q_i, \tag{5}$$

which I choose to call the tribute and the dissipation, respectively, will define the portions of the development capacity encumbered by exports and respirations. A little algebra will show that the residual $(C - A - E - S)$ may be written as

$$R = -T \sum_{i=1}^{n} \sum_{j=1}^{n} f_{ij}Q_i \ln\left[f_{ij}Q_i \middle/ \left(\sum_{k=1}^{n} f_{kj}Q_k \right) \right]. \qquad (6)$$

This positive quantity will be called the redundancy (after Rutledge *et al.*, 1976), as it provides a convenient measure of the uncertainty associated with the multiplicity of pathways within the system.

The result of these definitions is that the ascendency may now be written as the difference between capacity and overhead.

$$A = C - (E + S + R). \qquad (7)$$

This relationship among process variables parallels the definitions of the Gibbs and Helmholz free energies in terms of analogous state variables. Just as not all the potential energy or enthalpy of a system is available for doing work, so not all the complexity of a network of flows can appear as coherent structure.

7. Development in Ecosystems

In order to give the foregoing definitions more concrete form and to demonstrate the descriptive power of the hypothesis, it is useful to narrate the development of an ecosystem from a very rudimentary state. Consider, therefore, a biological island which has undergone a severe trauma leaving it depauperate in the number of remaining species.

The immediate response of the community is to recover its "mass" (Golley, 1974) as the more opportunistic of the surviving populations increase their throughputs. T rises abruptly to saturate the available inputs, and what links once existed between surviving species are likely re-established in the immediate recovery process. The other factor in development capacity, the complexity, increases commensurate with the slower rates of new species introduction or behavioral modifications. Development capacity could theoretically increase without limit, even if T were constrained by inputs, simply through the partitioning of flows among progressively smaller compartments. However, environmental perturbations limit how finely throughput may be partitioned, by randomly extinguishing very rare species. Development capacity rises until it is limited by inputs and environmental rigor (see also Robinson & Valentine, 1979).

Contemporaneous with the rise in development capacity is the increase in community ascendency. The difference between the capacity and the overhead should grow in absolute terms. This is not to imply that the overhead is being minimized during the earlier stages of development. It usually increases, and may even increase in a relative sense, so long as the rise in capacity is fast enough to allow for the magnitude of the difference (ascendency) to continue to grow. In pioneer ecosystems, as in pioneer societies, little advantage accrues to conservative behavior.

As discussed, development capacity cannot increase indefinitely, and eventually further growth in ascendency can occur only at the expense of overhead. It behooves us, therefore, to consider how the three terms comprising the requisite overhead may be minimized, and what the consequences of that minimization might be.

Tribute may be reduced by internalization of export flows. An example on our island would be the appearance of a seed-eating insect or mammal to divert a biomass flow away from a migratory bird utilizing the same resource. As long as imports and exports are completely decoupled, minimizing the tribute would always be an advantageous way of promoting ascendency. Should the given community be a compartment of a higher-order community (i.e. a subunit of the next hierarchical level), it may happen that the exports of the subsystem are important elements of the larger system's ascendency. To decrease those flows too much might damage the capability of the larger system to provide necessary imports to maintain the subsystem ascendency; e.g. the migratory bird might import necessary nitrogen and trace elements with his droppings. A more graphic example comes from current world economics, where countries with large oil exports and otherwise scarce internal resources usually realize the disadvantages of cutting back on exports too drastically. There are almost always hierarchical limits on how much ascendency can grow at the expense of tribute.

From an ecological point of view the most interesting tradeoff involves a speculated tendency to maximize ascendency at the expense of redundancy. Suppose, for example, after our island community had undergone its trauma, there existed numerous possible pathways of food transfer from the vegetational canopy to the top carnivores. As new species arrived on the scene, they would likewise add to the choice of pathways and diversity of flows. Development capacity would be driven up by these additions, but most of the increase would occur in the redundancy component. Ascendency is more sensitive to feedbacks and specialization. From among the plethora of pathways, several will consist of chains and loops of higher transfer efficiencies than the rest. If the development hypothesis pertains, flows along these preferred pathways would begin to magnify, driving up the

ascendency through both the increase in throughput occasioned by the higher flow rates as well as by the increase in specialization that occurs as the key outputs grow at the relative expense of those involved in less efficient (in the sense of power transfers) routes. Mutualism and competition are thereby *both* seen as mechanisms which may succor ascendency while eroding the fraction of complexity appearing as redundancy.

It is hardly mysterious, therefore, why observed community diversities might peak during the middle stages of development (Margalef, 1963; Simberloff, 1969). During early development the addition of new species can occur with ease, as constraints upon both ascendency and overhead are weak. With the later saturation of input flows, and the growing probability that large numbers of species in each trophic level will lead to the establishment of patterns of mutual sustenance, those populations participating in efficient mutual sustenance should grow to dominate the flow network at the expense of those components contributing more to network redundancy. While flow diversity (C/T) peaks during this transition, community ascendency, in the absence of major disturbances, should continue to rise monotonically.

Of course, the effect of disturbances cannot be neglected. Apart from limiting the partitioning of flows, as discussed earlier, perturbations probably act to increase the relative amount of redundancy (R/C) in the network. The relative redundancy would then behave as an indicator of the impact that stress is having on the community. It should be high in rigorous environments and lower in more benign, stable circumstances. As all abiotic environments impose some degree of perturbation, there would always remain environmental constraints to the continued increase of ascendency.

A quick digression at this point into the subject of diversity vs. stability of ecosystems is enlightening. Diversity has come almost exclusively to mean diversity of species numbers. The closest correlate in this discussion would be the diversity of species throughputs (the unscaled development capacity, C/T). As May (1973) and Saunders (1968) have suggested, and has been echoed here, a stable environment *allows* a higher degree of diversity to occur. The same stable environment permits ecosystems configurations to exist for longer periods without disruption. To search for a one-on-one causal relationship between diversity and stability is, however, futile.

But the focus upon diversity of species number was a corruption of Odum's (1953) original intention to identify the multiplicity of flow pathways as the network attribute which buffered the response of a system to a perturbation disrupting pathway links. One or more of the relatively unaffected pathways could increase in flow to mitigate the effect of the disturbance. Rutledge *et al.* (1976) suggested that the unscaled redundancy

should offer a measure of the network buffering capacity, but seemed puzzled when (as in the example below) minor stress increased the unscaled redundancy. This response seemed to work against the notion that redundancy could be "expended by the system" as a homeostatic mechanism (see also Atlan, 1974). James Kay (pers. comm.), however, points out that all of the information variables defined are affected by both the number of flows and the evenness of their magnitudes. Disturbances which are not strong enough to decrease the richness of species (and thereby richness of flows) could work towards equalizing the magnitudes of the flows, i.e. to increase redundancy. It is only when richness of flows is degraded by stress that redundancy would decrease, and the concomitant fall of ascendency would then be buffered by the remaining pathways. In both cases, however, a higher redundancy works to diminish the impact of further stress.

Species diversity is likely correlated with flow diversity, which in turn serves as an upper bound on the redundancy. Diversity can thus be viewed as a contributing factor to network homeostasis, but not as its sole cause (Ulanowicz, 1979).

The thermodynamic constraints to the increase of ascendency have already been discussed earlier in this section. Unfortunately, these constraints are in need of quantitative refinement, e.g. what is the functional relationship between efficiency and throughput in the far-from-equilibrium realm?

As a point of contrast with the Prigogine hypothesis, it was mentioned earlier how the minimization of dissipation is not seen to be particularly effective in maximizing ascendency during the early stages of system development. Even after development capacity plateaus, ascendency seems more likely to continue to grow at the expense of redundancy and tribute. Matters might be quite different, however, if input flows are in decline. Flow of medium is then no longer available to maintain ascendency at the expense of redundancy; decreasing the tribute might only have the effect of further decelerating the input rates; and the only option left is to minimize dissipation. Thus, if the inputs to the network continue to fall towards the lower limit for which viability of the system can be maintained, the system will probably enter into a mode of minimizing dissipations. As the system approaches near to equilibrium, the development hypothesis merges with the Prigogine principle.

8. Examples of Developing and Perturbed Ecosystems

Full data on the progression of an ecosystem flow network during succession do not yet appear available. For the time being we must be content

with observed trends in developing ecosystems. Fortunately, many of these have been summarized by Odum (1969) when he listed 24 attributes thought to be indicative of developed ecosystems.

Several of the trends noted by Odum involve greater cycling in more mature systems, e.g. the important role of detritus in nutrient regeneration of mature systems (no. 17). Put in another way, cycling plays an increasingly greater role vis-a-vis inputs and useful exports. The observations that the ratios of standing crop biomass to gross production (no. 2) and biomass supported to unit energy input (no. 3) increase with development; that net community production falls in more advanced systems (no. 4); that total organic matter is high (no. 6), inorganic nutrients are intrabiotic (no. 7), mineral cycles are nearly closed (no. 15), and nutrient conservation is better (no. 21) in older systems are all in accord with the tendency of A (as defined in terms of mass flows) to increase relative to E as the system evolves.

Because development capacity serves as the upper bound on ascendency, increases in complexity such as may occur through greater species variety (no. 8) or biochemical diversity (no. 10) become prerequisites for development. Specialization (no. 12), feedback control (no. 18), internal symbiosis (no. 20), and higher information (no. 24) are all explicit manifestations of greater mutual sustenance.

An initial rise in ascendency will likely occur when a few of the component species engage in mutual sustenance and thereby dominate over less co-operative members. Species equitability (no. 9) will be low to begin with, but should increase as a greater fraction of the species persisting come to engage in mutual sustenance.

Four of Odum's criteria are outside the scope of these macroscopic considerations. Individual organisms exist at the mesoscopic scale, and the development hypothesis expressed on a community level cannot specify behavior of individual populations or organisms. Hence, the size of organisms (no. 13) and a description of their life cycles (no. 14) must be examined in detail. Also, describing change as an idealized succession of stationary states excludes discussion of the transient behavior of the ratio of community production to respiration (no. 1). Fourthly, the foregoing treatise ignores spatial patterns (no. 11) (although it will be suggested below how spatial organization might be examined in the context of flows).

The relationships between the remaining five trends and the development hypothesis are ambiguous. For example, it is not clear what is meant by quality when Odum characterizes the production of early stages by the term "quantity" and that of mature stages by "quality" (no. 19). Possibly he is referring to the informational component E/C. Or he may be thinking of the intrinsic ascendency of the material being exported. Intrinsic ascendency is a

hierarchial concept pertaining to the situation where a compartment is considered separately as a community with its own (intrinsic) ascendency.

Similarly, there is ambiguity as to how Odum views the rate of nutrient exchange between organisms and environment (no. 16). The ascendency as defined here will not be abetted by slow rates of exchange between organisms and environment, yet Odum cites more mature systems as having slower exchange rates with the environment. This conflict can be resolved in one of two ways. Either Odum is referring to the turnover rates for the system, in which case the higher degree of cycling in more self-sustaining systems does increase turnover time; or else he is comparing the state of a mature system with low inputs to the configuration after this system has undergone a large unexpected increase (perturbation) in its input flows.

The latter situation brings out an interesting feature of the acendency. A large increase in T will allow a simpler configuration to have a larger value of A than a more complex system with low exchange rates. This is exactly what occurs during eutrophication. The eventual level of A will probably depend upon the temporal pattern of the influx. If the inputs remain at a high level for a long while, the system would likely develop a pattern of increasing complexity and mutual sustenance. If, however, the input pulses at irregular intervals, A is likely to remain arrested, and any increase in complexity would be characterized by a high degree of redundancy.

Odum interprets stability as the freedom from erratic changes. I have already discussed how higher redundancy might permit the homeostasis of ascendency in a highly developed ecosystem (no. 22). It is difficult, however, to reconcile Odum's observation that developmental stages tend to be linear and mature stages weblike (no. 5) with the results of the development hypothesis. Higher ascendency generally favors linear, chain-like transfers. This tendency may be manifested in real ecosystems by the arrangement of species interactions into "blocks" or subgroups with simple or chain-like transfers between groupings (see also, Margalef, 1968 and May, 1973).

The most problematical of Odum's criteria purports that young ecosystems are associated with high entropy and mature communities with correspondingly lower entropies. Entropy is used loosely in this context, and it would be most convenient to identify the notion with the fraction of the total development potential encumbered by the overhead $(R + S + E)$. Then the earlier remarks on overhead would pertain. During the first stages of development there is little reason to restrain overhead, whereas later limits on the increase of development capacity dictate that overhead will eventually decrease.

The first 15 criteria discussed were important in that they demonstrated the potential unifying power of the development hypothesis. The discussion

of the last five criteria was no less interesting in revealing that by regarding development in terms of a single entity the ambiguities and contradictions inherent in any piecewise view of succession are substantially mitigated.

Not everyone agrees with Odum's views on development in ecosystems. Drury & Nisbet (1973) and Connell & Slayter (1977) criticize the community approach towards succession. Despite the fact that the former authors eschew the notion of emergent properties of communities, none of the alternative mechanisms or models in either paper appears incapable of being reconciled with the phenomenological hypothesis presented here.

Although entire network data on succession are practically non-existent, there have been several efforts to compare the foodwebs of similar systems

TABLE 1

Flow matrix among the components of a juncus tidal creek ecosystem near Crystal River, Florida

	Microphytes	Macrophytes	Detritus	Zooplankton	Benthic Invertebrates	Blacktip Shark	Stingray	Striped Anchovy	Bay Anchovy	Needlefish	Sheepshead killifish
Microphytes			404·0	44·70							0·44
Macrophytes			4163								
Detritus				109·80	2117·90			0·05	0·37		0·79
Zooplankton			73·20					0·09	0·64		
Benthic Inv.			686·90					0·01	1	0·12	0·15
Blacktip Shark			0·50								
Stingray			0·15								
Str. Anchovy			0·03								
Bay Anchovy			0·22							0·63	
Needlefish			0·32								
Sheepshd. killifish			0·65				0·03				
Goldspotted killifish			0·68				0·01				
Gulf killifish			1·32				0·07				
Longnosed killifish			1·06						0·05		
Silverside			3·38				0·51		0·62		
Moharra			1·53						0·02		
Silver Jenny			0·03								
Sheepshead			0·11								
Pinfish			0·41						0·06		
Mullet			16·29			2·51	0·08		0·03		
Gulf Flounder			0·02								
Imports	651·77	6704								1·57	0·02

TABLE 1—*continued*

	Goldspotted killifish	Gulf killifish	Longnosed killifish	Silverside	Moharra	Silver Jenny	Sheepshead	Pinfish	Mullet	Gulf Flounder	Exports	Respirations
Microphytes	0·32						0·16		8·15			194
Macrophytes											219	2322
Detritus	0·71			0·97	0·90	0·02			24·40		567·79	2530·10
Zooplankton	0·22			5·86	3·20	0·05					39·94	31·30
Benthic Inv.	0·61	2·68	5·28	8·59	2·30	0·06	0·16	0·53			427·91	981·60
Blacktip Shark											1·21	0·80
Stingray											0·09	0·46
Str. Anchovy											0·01	0·11
Bay Anchovy		0·50						0·74		0·02	0·74	0·73
Needlefish								0·02			0·32	0·89
Sheepshd. killifish		0·01						0·01			0·14	0·54
Goldspotted killifish		0·09						0·10			0·09	0·89
Gulf killifish											1·50	3·70
Longnosed killifish		0·03									1·27	2·87
Silverside		2·67						0·56		0·02	0·43	7·23
Moharra		0·37						0·01		0·04	1·49	2·94
Silver Jenny											0·04	0·06
Sheepshead											0·09	0·12
Pinfish										0·03	0·38	1·16
Mullet		0·08									2·41	11·15
Gulf Flounder											0·04	0·05
Imports		0·16						0·07				

Each entry represents a flow in mg organic matter m^{-2} day^{-1} from the component designated as a row heading to a recipient as indicated in the column heading. (M. Homer & W. M. Kemp, unpublished data) $T = 15{,}063$; $C = 18{,}452$; $A = 5017$; $R = 4148$; $S = 7421$; $E = 1866$ (mg m^{-2} day^{-1}).

in perturbed and unperturbed states. One reasonably detailed food web analysis carried out by M. Homer and W. M. Kemp (manuscript in preparation) provided estimates for the carbon flows through 21 compartments of two tidal creeks into juncus marshes located in the vicinity of Crystal River, Florida. One marsh served as a control while the second was continually subjected to a 6°C temperature elevation caused by effluent from the Crystal River Nuclear Generating Station. Aggregation in the compartments was not uniform—lower tropic components were highly lumped (macrophytes, detritus, zooplankton, etc.), whereas the finfishes were studied in great detail; but the groupings were consistent between the

two creeks. The network flow matrices (in mg organic matter m^{-2} day^{-1}) are depicted in Tables 1 and 2. The corresponding information variables are presented in the legends.

Noteworthy is the lack of appreciable differences in either the species list or the flow diversity (C/T). But it is evident that dietary habits of the same species are different in the two creeks. That species in the impacted creek are not performing optimally is hinted at by the 20% drop in the total system throughput. As a consequence of the diminished scaling factor, the absolute values of all the information variables are lower in the disturbed system. The changes in the relative proportions of the variable are also quite interesting.

TABLE 2

Flow matrix among the components of a thermally stressed juncus tidal creek ecosystem near Crystal River Florida

	Microphytes	Macrophytes	Detritus	Zooplankton	Benthic Invertebrates	Stingray	Bay Anchovy	Catfish	Needlefish	Sheepshead killifish	Goldspotted killifish
Microphytes			319	39·05						0·12	0·10
Macrophytes			3156								
Detritus				117·15	1485·10		7·74			0·22	0·22
Zooplankton			78·10				13·60				0·07
Benthic Inv.			742·60				2·10	0·17		0·04	0·19
Stingray			0·01								
Bay Anchovy			4·69			0·04			0·24		
Catfish			0·03								
Needlefish			0·06								
Sheepshd. killifish			0·18								
Goldspotted killifish			0·21								
Gulf killifish			0·54								
Longnosed killifish			0·70								
Molly			0·18								
Silverside			0·18								
Moharra			0·16								
Pinfish			0·07								
Spot			0·01								
Black Drum			0·36								
Red Drum			0·07								
Mullet			11·46			0·01			0·06		
Imports	530	5488									

TABLE 2—*continued*

	Gulf killifish	Longnosed killifish	Molly	Silverside	Moharra	Pinfish	Spot	Black Drum	Red Drum	Mullet	Exports	Respirations
Microphytes			0·35							5·73	0·65	165
Macrophytes											166	2166
Detritus				0·06	0·11						616·51	2087·50
Zooplankton				0·33	0·40						32·40	31·30
Benthic Inv.	1·71	3·48		0·49	0·28	0·09	0·07	1·78	0·36	17·19	33·55	681
Stingray												0·04
Bay Anchovy	0·37					0·23					0·75	17·12
Catfish											0·02	0·12
Needlefish											0·01	0·23
Sheepshd. killifish	0·01											0·19
Goldspotted killifish	0·01										0·10	0·26
Gulf killifish	0·01										0·73	1·39
Longnosed killifish	0·17										0·69	1·92
Molly											0·05	0·12
Silverside	0·33										0·05	0·32
Moharra											0·25	0·38
Pinfish											0·09	0·18
Spot											0·02	0·04
Black Drum											0·41	1·01
Red Drum											0·07	0·22
Mullet	0·06										1·32	10·01
Imports						0·02						

Entries are defined as in Fig. 1. $T = 12,033$; $C = 14,575$; $A = 3727$; $R = 3692$; $S = 6145$; $E = 1011$ $(\text{mg m}^{-2} \text{day}^{-1})$.

Consistent with the development hypothesis, the fraction of the development capacity devoted to ascendency has fallen, whereas the fractions encumbered by redundancy and dissipation have both risen. (If the 2% relative changes seem small, it should be remembered that we are dealing with changes in logarithmic variables apportioned over 21 compartments.)

By scaling the information variables and by choosing components of the overall complexity measure which are sensitive to the relations among the compartments, not only are conceptual difficulties with the use of information theory in ecology overcome (see Apter & Wolpert, 1965), but also quantitative comparison of similar ecosystems has been made more discerning.

9. Summary and Generalizations

The essence of the foregoing arguments can be summarized in two statements. The first is a postulate—that flows by themselves provide sufficient description of far-from-equilibrium stationary states. As remarked earlier, this statement will probably sound like a radical simplification to someone interested in a description of events occurring at the level of the sub-system. Certainly, observation at the mesoscopic scale turns up phenomena that are best described in terms of content, morphology and forces. But the aggregation of these explanations does not appear to provide any coherent picture at the community level. If there is any validity to the flow postulate, then it follows that mesoscopic content, form and forces can work to obscure a unified macroscopic description of dissipative processes. Just as Newton eventually arrived at his concept of force by first studying the "fluctions" of momentum, so our focus upon the study of ecosystem flow networks might finally lead to a proper formulation of generalized ecosystem forces.

The second fundamental statement of this paper follows from the flow postulate—that a description of the development of a self-organizing system is possible at the level of the whole community. Some will worry that the development hypothesis has overtones of group selection. Others may say the theory invokes the spectre of teleology. But the body of empirical evidence remains (Glansdorff & Prigogine, 1971) that physical systems composed of mindless, non-living components can develop over the course of time according a single community criterion. There appears to be no logical prohibition to entertaining the possibility that systems composed of living components might behave likewise. Admitting this latter possibility need not brand one as an adherent of any earlier biological theory presently held in disrepute. Holistic though the hypothesis may be, it is, nonetheless, coherent, quantitative and testable.

Although attention has thus far been directed towards development in ecosystems, the development hypothesis is thermodynamic in nature. It should, therefore, find application in the description of a broad spectrum of far-from-equilibrium phenomena. Take, for example, the development of a higher organism beginning with fertilization.

Initial growth occurs predominantly as the multiplication of undifferentiated cells. Calling each cell a compartment, development capacity rises abruptly as both T and cell number increase. Practically all this early capacity consists of dissipation and redundancy. However, as the cell cluster grows, some units experience a slightly different environment from others (e.g. interior vs. exterior) and interior cells can continue to grow rapidly only

through mutual sustenance with those members in closer contact with nutritive fluxes. Ascendency begins to increase, and the pattern of greatest mutual sustenance appears at the expense of flow redundancy. Differences in quantity and nature of throughputs are manifested as morphological changes as specialization proceeds. The increase in growth capacity slows as the rate of cell division wanes. Even after development capacity plateaus and begins to fall, ascendency can continue to increase at the expense of network redundancy. (This seems most apparent in the continuing restructuring of neural networks long after nerve cell division has ceased.) Higher organisms appear to have continuously diminishing ability to replace cells lost to random perturbations (see also Elder, 1979). The consequent decrease in compartment number constrains all the information variables, but the loss of redundancy is critical, as it provides a margin for the increase of ascendency as well as a buffer against continuing disturbance. Redundancy ultimately falls so low that further perturbations take an ever increasing toll upon ascendency. Retrogression of ascendency (senescense) and the eventual collapse of the system toward equilibrium (death) ensues.

It is intriguing to explore the new perspective the flow postulate might provide in the purely physical realm. Paltridge (1975) has employed the principle of minimum entropy production to accurately predict global patterns of temperature and cloud cover. Odum (1971) cites several examples of cybernetic phenomena in physical systems. Every beginning student of fluid mechanics learns that when inertial forces dominate viscous forces, instability of the flow field (turbulence) ensues. It is often not emphasized, however, that the force balance (the field expression of Newton's law) is no longer sufficient to adequately describe the flow field. Quantitative description conventionally shifts to the size spectrum of energy in the flow pattern. But an alternative treatment is possible by regarding the turbulent field as a self-organizing system.

A cybernetic analysis of the flow can be provided by casting an appropriately fine spatial lattice over the region of interest and identifying each spatial cell as a compartment. Flows of kinetic energy through the cells and exchanges of kinetic energy among cells can be expressed in terms of T, Q_i, f_{ij}, etc. If the flow is sufficiently dissipative, the development hypothesis might pertain. A description of the evolution of the flow field in terms of C, A, E, R, and S is conceptually possible.

Compound division of ecosystems into spatial cells as well as biological compartments should provide a network of flows (both spatial flows and biochemical transformations) which is amenable to description using the information variables described here. Biogeographical distributions and migrations might appear as phenomena which serve either to increase the

ascendency of the system, or to provide necessary redundancy in the face of environmental disturbance.

It would appear that the development hypothesis is applicable to self-organizing behavior in economic and social structures, but such identification is best left to experts in those disciplines. I will only mention that pioneer societies resemble embryonic organisms in that the economic ties between individual units are relatively weak. Homestead independence results in a development capacity that consists mainly of redundancy and dissipation. As the society matures, autonomy and egalitarianism tend to be replaced by interdependence, specialization and class structure—all factors in an elevated ascendency. Certainly, knowing the ascendency, redundancy and dissipation values of a nation's economic network gives more insight to the profile of an economy than does reliance on a single scale factor such as the gross national product.

Finally, it would be negligent not to address a few words to the question of whether or not the development hypothesis is applicable to the evolution of the biosphere.

The prevailing opinion in Biology is that the principles of Wallace and Darwin are necessary and sufficient to describe the evolution of species. Some, however, go on to argue that the sufficiency of these laws at the species level renders absurd any effort to formulate evolutionary principles for the community. This subjective view is not self-evident, especially if one's interest is in quantifying the behavior of the whole community. From the macroscopic viewpoint Darwinian principles appear as mechanisms—necessary (perhaps), but insufficient to chart the course of the entire assemblage (Ho & Saunders, 1979).

It would be appealing to hypothesize that communities evolve over geological time so as to optimize their ascendency. But ascendency is defined in terms of flows. It is difficult enough to estimate the flow network of an existing ecosystem. Inferring flow rates from fossil records appears virtually impossible. A flow theory of community evolution does not appear absurd, but rather, improbable to confirm.

This primitive model and its attendant hypotheses possibly provides a caricature of the evolution of the biosphere. Nevertheless, evaluating how appropriate the theory is to such description requires information which shall remain inaccessible. Its application or rejection as an evolutionary principle will likely remain a matter of personal conviction.

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REFERENCES

ANDRESEN, B., BERRY, R. S., NITZAN, A. & SALAMON, P. (1977). *Phys. Rev. A* **15**, 2086.
APTER, M. J. & WOLPERT, L. (1965). *J. theor. Biol.* **8**, 244.
ATLAN, H. (1974). *J. theor. Biol.* **45**, 295.
CONNELL, J. H. & SLAYTER, R. O. (1977). *Amer. Naturalist* **111**, 1119.
DRURY, W. H. & NISBET, I. C. T. (1973). *J. Arnold Arboretum* **54**, 331.
ELDER, D. (1979). *J. theor. Biol.* **81**, 563.
FINN, J. T. (1976). *J. theor. Biol.* **56**, 363.
GLANSDORFF, P. & PRIGOGINE, I. (1971). *Thermodynamic Theory of Structure, Stability and Fluctuations.* London: John Wiley & Sons.
GOLLEY, F. B. (1974). In *Proceedings of the First International Congress of Ecology* (A. J. Cave, Cong. Sec.) pp. 97–102. Wageningen (Netherlands): Centre for Agricultural Publishing and Documentation.
HO, M. W. & SAUNDERS, P. T. (1979). *J. theor. Biol.* **41**, 535.
HANNON, B. (1973). *J. theor. Biol.* **41**, 535.
LEONTIEF, W. (1951). *The Structure of the American Economy 1919–1939*, 2nd edn. New York: Oxford University Press.
LEVINE, S. H. (1977). *J. theor. Biol.* **69**, 345.
MARGALEF, R. (1963). *Am. Nat.* **97**, 357.
MARGALEF, R. (1968). *Perspectives in Ecological Theory.* Chicago: Chicago University Press.
MAY, R. M. (1973). *Stability and Complexity in Model Ecosystems.* Princeton: Princeton University Press.
MCELIECE, R. J. (1977). *The Theory of Information and Coding.* Reading, Massachusetts: Addison-Welsey.
ODUM, E. P. (1953). *Fundamentals of Ecology.* Philadelphia: Saunders.
ODUM, E. P. (1969). *Science* **164**, 262.
ODUM, H. T. (1971). *Environment, Power and Society.* New York: John Wiley and Sons.
ODUM, H. T. & PINKERTON, R. C. (1955). *Am. Scientist* **43**, 331.
PALTRIDGE, G. W. (1975). *Quart. J. Roy. Met. Soc.* **101**, 475.
RICHEY, J. E., WISSMAR, R. C., DEVOL, A. H., LIKENS, G. E., EATON, J. S., WETZEL, R. G., ODUM, W. E., JOHNSON, N. M., LOUCKS, O. L., PRENTKI, R. T. & RICH, P. H. (1978). *Science* **202**, 1183.
ROBINSON, J. V. & VALENTINE, W. D. (1979). *J. theor. Biol.* **81**, 91.
RUTLEDGE, R. W., BASORE, B. L. & MULHOLLAND, R. J. (1976). *J. theor. Biol.* **57**, 355.
SAUNDERS, H. L. (1968). *Amer. Naturalist* **102**, 243.
SIMBERLOFF, D. S. (1969). *Ecology* **50**, 296.
TISZA, L. (1966). *Generalized Thermodynamics.* Cambridge, Mass.: MIT Press.
ULANOWICZ, R. E. (1972). *J. theor. Biol.* **34**, 239.
ULANOWICZ, R. E. (1979). *Oecologia* **40**, 295.
ULANOWICZ, R. E. & KEMP, W. M. (1979). *Am. Nat.* **114**, 871.