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Network Growth and Development: Ascendancy

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We have only recently begun a revolution in ecology . . . [Van Dyne, in *The Ecosystem Concept in Natural Resource Management*, Ch. X p. 333 (1969), Academic Press].

INTRODUCTION

The ecological world, when viewed at the scale of human senses, is a myriad of seemingly random and arbitrary events. We certainly cannot dismiss out of hand the contention that this welter lacks anything akin to an overall organization (Simberloff, 1980). Yet the intuition exists in many, nurtured perhaps by centuries of reflection by artists, poets, and transcendentalist and natural philosophers, that the larger biological realm possesses some degree of coherence, order, or even organization. This issue is emotionally charged and capable of generating heated debate. However, most of the controversy is at best marginally quantitative. As in other chapters of this book, the goal here is to introduce a set of quantitative tools that can be applied to resolving the ongoing disagreement.

It is worth noting that if we existed (like Maxwell's demon) at the molecular scale, the universe would appear extremely chaotic. Uncountable numbers of molecules would streak around, rotate, and otherwise gyrate in a fashion difficult to predict. However, very large collections of these same molecules when observed at the scale of the natural senses often obey deterministic laws (for example, the ideal gas laws). An analogy to this thermodynamic situation of fine-scale chaos but order in the larger domain might be drawn in the ecological realm. But where should one begin?

PROBABILITIES ASSOCIATED WITH DYNAMICS

Probability theory, that branch of mathematics devoted to making quantitative statements on events about which we are uncertain, seems like the most natural starting point. After all, probability theory and statistics are primary tools used in quantitative biology. Similarly, they are the foundations

for statistical mechanics, the attempt to reconcile atomic theory with the phenomenology of thermodynamics.

Well-defined probabilities exist only in relation to well-posed questions. A well-posed question is one for which the outcome is exclusive and the set of possible outcomes is complete. By exclusive is meant an outcome that can occur in only one of the stated options. A complete set of outcomes is simply one that spans the entire gamut of possible outcomes; that is, there is perfect accountability. For example, say that 20 types of organisms constitute the biota of a given ecosystem. An organism is chosen at random. It must belong to at most one of the chosen categories (exclusivity); otherwise, the set of categories needs to be reduced. Furthermore, it must also belong to at least one of the categories (exhaustiveness); otherwise, the set of categories should be expanded. "What is the probability that the chosen species belongs to taxon x " is a well-posed question only when the set of categories (taxa) is both exclusive and complete.

Usually, we apply probabilities to objects at or very near thermodynamic equilibrium, for example, different colored balls in a jar or the faces of a die. But living systems, and ecosystems in particular, are never such static entities. Members of the various taxa are constantly appearing and disappearing and, what is even more interesting, they undergo transformation from one category to another. These circumstances have several consequences for the application of probabilities to ecosystem dynamics.

Almost by definition, if we are concerned with ecological dynamics, the focus is not what is *in* the categories, but rather on what is *entering* or *leaving* a taxon. Thus, the expression $p(a_i)$ might be taken to mean the probability that an organism leaves taxon i at a given instant and $p(b_j)$, that an individual enters taxon j an infinitesimal interval later. Now $p(a_i)$ and $p(b_j)$ are usually not independent of each other. More often than not, a unit leaving one compartment of a set immediately enters another. Such is the case with trophic processes such as herbivory, carnivory, or detritivory. For this reason, it is useful to define a quantity known as the joint probability, $p(a_i, b_j)$, as the probability that an organism leaves i and enters j within some infinitesimally short interval. It should be stressed that the joint probability is not generally equal to the product of the separate probabilities [that is, $p(a_i) \cdot p(b_j)$]. In fact, the degree of this inequality is related to how well "organized" the given dynamics appear.

Like all well-defined probabilities, the joint probability should be complete; that is, any potential transition must proceed from one species in the set to another. Of course, for any given ensemble (ecosystem) of n compartments, not all exchanges originate among or transfer into one of the identified categories. Hence, any analysis must contain at least one compartment to represent the external world, the place from which and toward which these exogenous transfers proceed. For reasons later to become clear, it is useful to identify three such external categories: (1) a category 0 (zero) to serve as the source of all entities entering j , but not originating in one of the n taxa; (2) a category $n + 1$ to represent the destination of all useful things leaving the system; and (3) a category $n + 2$ to receive all units that are lost from the system and of no further use to any other similar system; that is, they are "dissipated" by the originating compartment. Examples of transitions that might occur under this categorization scheme are depicted schematically in Fig. 26.1.

Because $p(a_i)$, $p(b_j)$, and $p(a_i, b_j)$ are each complete, the former probabilities can now be written as marginal sums of the latter:

$$p(a_i) = \sum_{j=0}^{n+2} p(a_i, b_j), \quad (26.1)$$

$$p(b_j) = \sum_{i=0}^{n+2} p(a_i, b_j). \quad (26.2)$$

Also, by ensuring that the joint probabilities are complete, the way is paved for full accountability

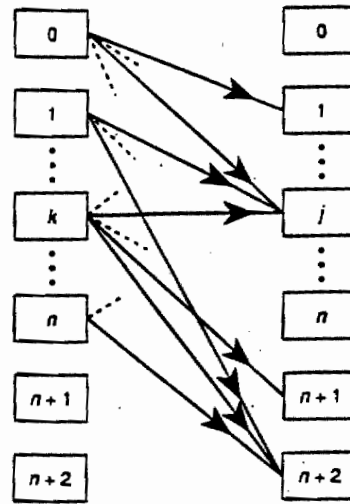


Figure 26.1 Representation of flows among the compartments of a system. Compartment 0 represents the source of all exogenous inputs, $n + 1$ the sink for all usable exports, and $n + 2$ the sink for all dissipations. Boxes on the left represent system nodes at a given time and those on the right depict the same nodes an infinitesimally short time thereafter.

of all transfers regardless of whether or not the organisms (or other appropriate units) that comprise each category are themselves conserved through time.

UNCERTAINTY

Recalling that the pivotal issue addressed in this chapter is whether ecosystems can be considered organized in any sense of the word, it is useful now to consider how to quantify the negative hypothesis—the degree to which an ecosystem is disorganized, or disordered. We are usually very uncertain about the outcome of any event occurring at the “microscopic” level of a disorganized, chaotic, or random assembly of organisms. To be more precise, uncertainty rises in proportion to the number of factors that serve to differentiate the various possible outcomes. Mathematically, this last statement is equivalent to

$$H = -K \sum_{i=1}^m p_i \log p_i, \quad (26.3)$$

where H is the uncertainty attached to the distribution of probability over the m categories enumerated by the index i , and K is a scalar constant.

Equation (26.3) is not as mysterious as it is often portrayed to be, providing we focus on the phrase “number of factors that serve to differentiate” in the statement above. Suppose, for example, that we were challenged to guess an integer chosen from the range 1 to 1024. One straightforward way of targeting the choice would be to ask if the number exceeds 512. If the answer is no, the next query might be if the number exceeds 256. And so on. Using this tactic, we will determine the number after exactly 10 guesses.

Instead of guessing numbers, we might be asked to identify an organism that belongs to one of 1024 possible species that are differentiated by 10 binary choices in a taxonomic key. Again, 10 decisions will identify the organism. The 10 selections may be said to have generated the 1024 categories, each of which may be thought of as a unique combination of the constituent choices in the key. The logarithm of 1024 (the number of “combinations”) to the base 2 is 10 (the number of

decisions). In the case where all final categories are equally populated, the probability of any single category p_i is $1/1024$, so

$$H = -K \sum_{i=1}^{1024} \frac{1}{1024} \log_2 \frac{1}{1024} \quad (26.4a)$$

$$= 10K. \quad (26.4b)$$

In the event that categories are not evenly populated, the combination (26.3) can be thought of as a probability-weighted average of $-K \log p_i$ (or, alternatively, $K \log[1/p_i]$) yielding the average uncertainty.

The numerical results of eq. (26.3) accord well with intuition. If all members are in a single category, then $H = 0$, reflecting no uncertainty. Conversely, uncertainty is maximal if units are uniformly distributed among m categories, and $H = K \log m$. Thus, the range of function (25.3) is

$$K \log m \geq H \geq 0. \quad (26.5)$$

ORGANIZATION

The extent to which a system might be disorganized is quantified by its measured uncertainty. Concerning its outputs there is the amount

$$H(a) = -K \sum_{i=0}^{n+2} p(a_i) \log p(a_i), \quad (26.6)$$

and pertaining to inputs there is the quantity

$$H(b) = -K \sum_{j=0}^{n+2} p(b_j) \log p(b_j). \quad (26.7)$$

Hence, the total uncertainty about the system's dynamics becomes $H(a) + H(b)$. If the inputs and outputs were completely independent of each other, this last sum would exactly measure the disorganization inherent in the dynamic structure.

However, inputs and outputs are not always independent, and the amount by which they are coupled quantifies the coherency of the dynamic structure. If we observe the joint behavior of inputs and outputs over a sufficient interval, it becomes possible to estimate the set of joint probabilities $p(a_i, b_j)$. The uncertainty associated with this set is

$$H(a, b) = -K \sum_{i=0}^{n+2} \sum_{j=0}^{n+2} p(a_i, b_j) \log p(a_i, b_j). \quad (26.8)$$

It can be proved that this joint uncertainty is always less than or equal to the sum of the separate uncertainties, $H(a) + H(b)$. In fact, equality pertains only to the case when inputs and outputs are independent of each other. Under the assumption of independence,

$$p(a_i, b_j) = p(a_i) \cdot p(b_j), \quad (26.9)$$

and substitution of (26.9) into eq. (26.8) along with the completeness requirements,

$$\sum_{i=0}^{n+2} p(a_i) = \sum_{j=0}^{n+2} p(b_j) = 1, \quad (26.10)$$

reveals that, when inputs and outputs are completely independent,

$$H(a, b) = H(a) + H(b). \quad (26.11)$$

More generally, however,

$$H(a) + H(b) > H(a, b), \quad (26.12)$$

and the amount by which the sum of the separate uncertainties exceeds the joint uncertainty is the measure of how coherent or organized the dynamic structure is:

$$A(a; b) = H(a) + H(b) - H(a, b), \quad (26.13)$$

where $A(a; b)$ defines the decrease in uncertainty or the degree of organization inherent in the dynamic structure. Substituting (26.8) into the right side of (26.13) and remembering (26.1) and (26.2) yields

$$A(a; b) = K \sum_{i=0}^{n+2} \sum_{j=0}^{n+2} p(a_i, b_j) \log \left[\frac{p(a_i, b_j)}{p(a_i)p(b_j)} \right]. \quad (26.14)$$

Inspection of (26.14) or (26.13) shows that the order of inputs and outputs in the argument of A is immaterial; that is, $A(a; b) = A(b; a)$.

ORGANIZATION, INFORMATION, AND DEVELOPMENT

Properly speaking, any decrease in uncertainty about or within a system can be defined as "information." As (26.13) reckons a decrease in uncertainty, it describes a quantity called the *average mutual information*. The adjective "average" comes from the averaging technique used in defining the component uncertainties in eq. (26.14), whereas the modifier "mutual" is meant to highlight the fact that A is entirely symmetric with regard to inputs and outputs.

A second and equivalent definition of *information* is given by Tribus and McIrvine (1971) as "anything which gives rise to a change in probability assignment." Thus, if nothing is known a priori about the joint behaviors of the a_i 's and b_j 's, then we are forced to fall back on the assumption of independence; that is, the joint probability is equated to $p(a_i)p(b_j)$. However, after actually empirically measuring the joint probabilities, they become $p(a_i, b_j)$. The information associated with this change in probability assignment is again measured by eq. (26.14).

This second definition of information emphasizes that information theory arises as a natural outgrowth of probability theory. Probability theory by itself is sufficient to analyze static or equilibrium configurations. However, when we attempt to quantify dynamic systems, the probability assignments, by definition, are subject to change. The analysis of any change in probabilities is the domain of information theory. Thus, invoking information theory to study ecosystem dynamics is not the capricious or ad hoc action many ecologists regard it to be. Rather, resorting to information theory is seen to be just as *imperative* to the study of biology as relying on probability theory! This crucial fact has been obscured by the historical accident whereby information theory was originally formulated in terms of communication theory. Once the universal nature of the information concept is more widely appreciated, resistance to the utilization of information theory in ecology should vanish.

The organization of the dynamic structure of an ecosystem has been properly quantified in terms of information variables. It is thus but a small additional step to quantify the notion of development. *Development* is an increase in organization. Any rise in $A(a; b)$ reflects development, and any decrease is a step toward incoherence and chaotic behavior.

The possibility of assigning a number to the heretofore intuitive concept of development is heartening. It allows us to recast the issue of whether ecosystems are organized as a statistical

hypothesis. Kullback (1959) showed how the average mutual information, A , behaves asymptotically like the chi-square function with $(n + 2)^2$ degrees of freedom. Testing whether any observed distribution $p(a_i, b_j)$ reveals dynamical organization to any specified confidence level becomes a matter of rote substitution into tabulated formulas—a typical exercise in statistics.

ESTIMATING TRANSFER PROBABILITIES

Thus far, not much has been said about how to estimate the probabilities $p(a_i)$, $p(b_j)$, and $p(a_i, b_j)$. From eqs. (26.1) and (26.2), it can be seen that it is necessary to estimate only the joint probabilities, because the marginal probabilities are partial sums of these quantities. Usually, we estimate joint probabilities from a matrix of events. That is, the events a_i (a unit leaves compartment i) might identify the rows of the matrix, and the events b_j (a unit enters compartment j), its columns. If the events are reckoned as numbers of organisms, then the observation that one individual of i is eaten by an individual of j would constitute one entry into the (i, j) th position of the events matrix. Calling the cumulative observations x_{ij} and the total number of observations $N = \sum_{i=0}^{n+2} \sum_{j=0}^{n+2} x_{ij}$, the relative frequency of each transfer, x_{ij}/N , becomes the conventional estimator of $p(a_i, b_j)$.

The author is unaware of anyone having calculated the mutual information of ecosystem dynamics from probabilities based on numbers of individuals transferred, although the prospect is intriguing. It is possible that such an exercise might lead to significant insights into the size-frequency distributions (for example, Preston, 1948) commonly observed in nature.

The problem with using numbers of organisms to estimate probabilities is that the disparity in size and makeup of the individuals of various species brings into question the relative significance of each row in the events matrix. To circumvent this issue, ecosystem analysts have taken to choosing a common elemental currency, for example, discrete units (atoms or molecules) of carbon, nitrogen, phosphorus or their compounds, or kilocalories of chemical energy, contained in the organisms being transferred. A second, very significant convenience afforded by this choice is that these currencies are strictly conserved. Whereas individuals appear and disappear, their elemental constituents can be traced intact from compartment to compartment. On the negative side, in the shift from counting organisms to measuring transfers of material among compartments, there is a natural tendency to regard the conveyances of medium as "flows" that are continuous in time. True enough, when the organisms that embody these materials are very small and their transfers very frequent, the transformations do approximate continuous flows. However, we should never lose sight of the fact that ecosystem transfers occur mostly in discrete steps, and to measure the "flow" of, say, carbon from hares to foxes is, in essence, to observe a discontinuous process best treated by probability theory.

With this caveat in mind, attention now focuses on the flows of material from species i to species j . Call such a transfer T_{ij} . The total amount of flow occurring in the system, T , becomes simply the sum of all the individual transfers:

$$T = \sum_{i=0}^{n+2} \sum_{j=0}^{n+2} T_{ij}. \quad (26.15)$$

Among all the activity occurring in the system, the probability of observing an atom of currency going from i to j is estimated by the fraction of the total activity that is comprised by T_{ij} :

$$p(a_i, b_j) \sim \frac{T_{ij}}{T}. \quad (26.16)$$

By (26.1) and (26.2),

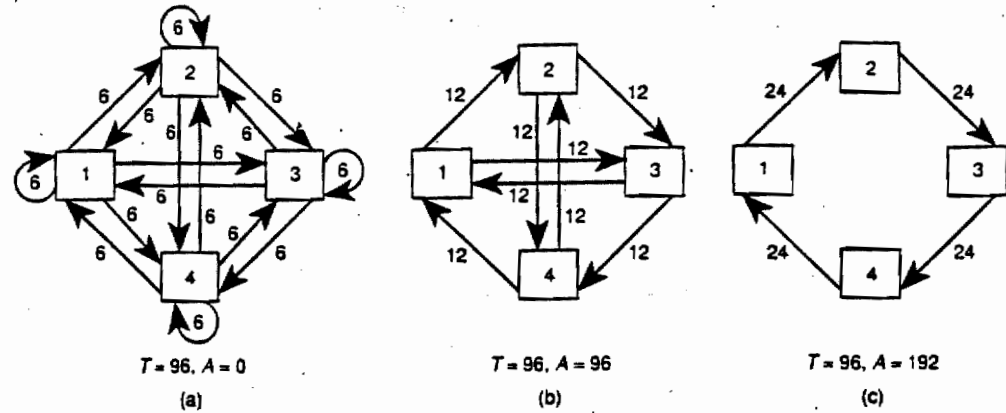


Figure 26.2 Three artificial, closed networks with differing degrees of articulation: (a) the minimally articulated configuration of 96 flow units among four nodes; (b) an intermediate level of articulation; (c) the maximally articulated configuration of flows.

$$p(a_i) \sim \sum_{j=0}^{n+2} \frac{T_{ij}}{T}, \quad (26.17)$$

and

$$p(b_j) \sim \sum_{i=0}^{n+2} \frac{T_{ij}}{T}. \quad (26.18)$$

Thus, substituting expressions (26.16) and (26.17) into (26.14) and simplifying,

$$A = \frac{K}{T} \sum_{j=0}^{n+2} \sum_{i=0}^{n+2} T_{ij} \log \left[\frac{T_{ij} T}{\left(\sum_{r=0}^{n+2} T_{rj} \right) \left(\sum_{s=0}^{n+2} T_{is} \right)} \right]. \quad (26.19)$$

Equation (26.19) can be applied to any well-defined network of ecosystem "flows." It turns out that the measure A quantifies the average degree of articulation inherent in the network. For a network to be well articulated means that, if an atom of conservative substance is flowing through any particular node in the system, it is almost certain to which particular node that atom will next be transferred. By contrast, quanta at any node in a highly unarticulated network can flow almost anywhere during the next transfer. Figure 26.2 shows three networks with different degrees of articulation. In Fig. 26.2a, the network is completely unarticulated and $A = 0$. At the other extreme, the network in Fig. 26.2c is maximally articulated and A equals two units of K . Network 26.2b is intermediate between the two extremes.

SIZE AND GROWTH

When we focus on system dynamics (as opposed to a static distribution), the concept of size literally takes on a new dimension. The "size" of a dynamic system is best captured by the *amount of activity* that is occurring. If this notion sounds strange, recall that the sizes of economic communities are commonly gauged by their aggregate levels of activity, for example, their gross national products

(GNP). An analogous measure for ecosystems has already been defined as T , elsewhere called the *total system throughput* (Hannon, 1973; Finn, 1976).

Growth, in the extensive sense of the word, may be identified with any increase in the size of a system. Hence, system growth can be measured by an increase in T , just as the growth of a national economy is said to be any increase in its GNP.

UNITARY GROWTH AND DEVELOPMENT

The organization, or articulation, of a network is an intensive property of the system. That is, it is independent of system size. The dimensions of A are the same as its scalar constant, K . Usually, K is considered to be fixed by the choice of the base of logarithms used in the calculation. For example, when 2 is chosen as the logarithmic base, one unit of K is called a *bit* (binary digit). When the base e is used, a unit of K is called a *nat*; with base 10, it is termed a *hartley*; and so on.

However, Tribus (1961) suggests that the scalar constant should be used, as its name implies, to scale any intensive system measure. It has just been argued that the appropriate size measure for a flow system is its total system throughput, T . Hence, in setting K equal to T we scale the organization of a dynamic system by its size. The resultant quantity

$$A = \sum_{i=0}^{n+2} \sum_{j=0}^{n+2} T_{ij} \log \left[\frac{T_{ij} T}{\left(\sum_{r=0}^{n+2} T_{rj} \right) \left(\sum_{s=0}^{n+2} T_{is} \right)} \right] \quad (26.20)$$

becomes the product of a factor of size times a measure of organization. This resulting quantity has been termed the system *ascendancy* (Ulanowicz, 1980). It measures the ability of a system to prevail over alternative system configurations. It also measures, in a manner different from exergy (Chapters 22 and 23), the distance of a system from its most chaotic configuration, thermodynamic equilibrium.

To prevail over another configuration requires a propitious combination of size and development. A system that is big but undeveloped is a *Goliath*. One that is highly developed but very small is vulnerable to being extinguished by its less developed but larger neighbors. Both size and organization are required in adequate measures to produce high ascendancy.

Growth is an increase in system size; *development* is an augmentation of its organization. Thus, an increase in system ascendancy is taken to portray the *unitary* process of growth and development. That growth and development are two aspects of a single process is revealed by reference to any dictionary of the English language, where the definitions for the two characteristics can be seen to overlap significantly.

The means are now at hand to assess whether an ecosystem has undergone growth and development. Its underlying networks of carbon and the like or energy flows are estimated at two points in time. Comparing the two associated values of ascendancy will reveal whether or not growth and development have occurred during the interval.

Odum (1969) suggested 24 attributes to characterize more "mature" ecosystems. Ulanowicz (1986a) has shown how increases in most of these characteristics parallel increases in system ascendancy. This is not to imply that all increases in ascendancy are necessarily beneficial to the system or to human society interacting with it. For example, an ecosystem might react to a sudden increase in available resources by rapidly expanding in size (T), at the same time diminishing in organizational status (A/T). If the former increase more than compensates for the latter drop, the product will still rise. Such a situation has been offered as a quantitative description of the process of eutrophication (Ulanowicz, 1986b).

LIMITS TO GROWTH AND DEVELOPMENT

Growth and development, like any natural process, possesses finite limits. The lower limit has already been discussed, that is, when a_i and b_j are completely independent so that $p(a_i, b_j) = p(a_i)p(b_j)$ and $A = 0$. At the other extreme, a_i and b_j are mutually determined, so knowing a_i implies a corresponding b_j for some combination of n unique pairs (i, j) . Under such conditions, $p(a_i, b_j) = p(a_i) = p(b_j)$ for each of those given pairs (i, j) , and $p(a_i, b_j) = 0$ otherwise. Substituting these conditions into eq. (26.14) yields

$$C = -K \sum_{i=0}^{n+2} p(a_i) \log p(a_i), \quad (26.21a)$$

$$C = -K \sum_{j=0}^{n+2} p(b_j) \log p(b_j), \quad (26.21b)$$

where C is the maximum value that A can attain and is therefore called the *development capacity*. Notice that under these extreme circumstances $H(a, b)$, $H(a)$, and $H(b)$ all become identical in value to C . To preserve symmetry, it is best in general to identify C with $H(a, b)$ (Ulanowicz and Norden, 1990). In terms of flow estimators, the capacity (26.21a) is calculated as

$$C = - \sum_{i=0}^{n+2} \sum_{j=0}^{n+2} T_{ij} \log \frac{T_{ij}}{\bar{T}}. \quad (26.22)$$

We expect that

$$C \geq A \geq 0, \quad (26.23)$$

as can be proved algebraically (McEliece, 1977). The nonnegative difference, $C - A$, is termed the system *overhead* and is generated by all real conditions that keep the system ascendancy from reaching its theoretical maximum.

Before considering in more detail the conditions that can contribute to system overhead, it is worthwhile to pause briefly and identify some of the mechanisms that contribute to an increase in ascendancy. In Chapter 4 of Ulanowicz (1986a), it was argued that the principal agent for the rise in ascendancy and the genesis of selection pressure in ecological networks is positive feedback among the members of the community (Wicken, 1984). In those systems that are alive, the ascendancy (and capacity) is dominated by the terms associated with the n members interior to the system.

To understand the nature of the overhead in more detail, we may decompose it algebraically into four separate terms:

$$C - A = I + E + S + R, \quad (26.24)$$

where

$$I = \sum_{j=1}^n T_{0j} \log \left[\frac{T_{0j}^2}{\left(\sum_{k=1}^n T_{0k} \right) \left(\sum_{m=0}^n T_{mj} \right)} \right] \quad (26.25)$$

$$E = - \sum_{i=1}^n T_{i,n+1} \log \left[\frac{T_{i,n+1}^2}{\left(\sum_{k=1}^{n+2} T_{ik} \right) \left(\sum_{m=1}^n T_{m,n+1} \right)} \right] \quad (26.26)$$

$$S = - \sum_{i=1}^n T_{i,n+2} \log \left[\frac{T_{i,n+2}^2}{\left(\sum_{k=1}^{n+2} T_{ik} \right) \left(\sum_{m=1}^n T_{m,n+2} \right)} \right] \quad (26.27)$$

$$R = - \sum_{i,j=1}^n T_{ij} \log \left[\frac{T_{ij}^2}{\left(\sum_{k=1}^{n+2} T_{ik} \right) \left(\sum_{m=0}^n T_{mj} \right)} \right]. \quad (26.28)$$

Notice that I is generated by any multiplicity in the exogenous inputs, while E , S , and R correspond to multiplicities in the exports, dissipations, and internal transfers, respectively. Elsewhere (Ulanowicz, 1980) I have called E the "tribute" to other systems, S the "dissipation," and R the internal "redundancy," that is, the multiplicity of internal pathways connecting any two compartments in the system. (Rutledge, Bassore, and Mulholland, 1976).

When eq. (26.24) is written in the form

$$A = C - (I + E + S + R), \quad (26.29)$$

a verbal narrative for the limits to increasing internal ascendancy (and thereby the overall ascendancy) becomes possible: Any increase in A is occasioned by either an increase in C ; a decrease in one of the terms in the internal overhead, or some combination thereof. C , in turn, is augmented either by an increase in the scaling factor T or by an ever-finer partitioning of flow among an increasing number of nodes (Ulanowicz, 1987). The total system throughput will rise when species are maximizing their power throughput, a nonconservative strategy for survival first advocated by A. J. Lotka and later championed by H. T. Odum (Odum and Pinkerton, 1955). However, the combination of finite input flows and mandatory dissipations at each node serves ultimately to limit the rise of T . The ever-finer partitioning of compartments is likewise limited by the finite availability of resources, which implies that some of the finely partitioned nodes will inevitably become too small to persist in the face of chance environmental perturbations.

It might at first seem counterintuitive that inputs (which are required for sustenance) would contribute to the system overhead. Recall, however, that in developing systems there is a tendency for the magnitude of inputs relative to other system flows to decrease. As Odum (1969) points out, mature systems are predominated by internal activities. As for increasing ascendancy by decreasing the multiplicity of inputs, such overreliance on but few lines of sustenance jeopardizes system maintenance in the face of disruption of those remaining inputs.

Minimizing the tribute by internalizing (recycling) exports is a good way for a system to increase its ascendancy. However, that course of action, too, can have its limits. For if the exports and imports of a given system both happen to be elements in a positive cybernetic loop at some higher hierarchical level, then decreasing exports from the given system might eventually diminish its own sustenance. Such a scenario was played out on the world economic stage with the collapse of the oil cartels in the late 1970s.

Minimizing the dissipation, S , provides an analog to an illustrious principle of irreversible thermodynamics (Prigogine, 1945). However, as long as resources remain abundant, it is unlikely that the system will follow such a course, because A is more readily increased by a growing T and a widening gap between capacity and overhead. Later, however, after limitations on resources become more stringent, minimizing S becomes an appropriate route for increasing A in mature systems. Of course, S is prohibited from ever reaching zero by the second law of thermodynamics.

Finally, decreasing R reflects a more streamlined and efficient network topology. It is a natural consequence of the competition between overlapping cycles of positive feedback. Unfortunately,

more efficient networks also make for more fragile structures. In systems with insufficient R , perturbations at any point in the network are likely to have disastrous consequences on downstream nodes, whereas a modicum of redundant pathways might allow for compensatory flows to downstream nodes via the less affected lines of communication (Odum, 1953). Because real environments always impose some degree of perturbation on a system, continued survival of the system will always require a nonzero level of pathway redundancy to function as "strength in reserve." We anticipate that, over the long term, the amount of redundancy retained by the network will be just sufficient to balance the rigor of the environment. In these terms, the old balance-of-nature precepts now widely rejected by many modern ecologists begin to take on a new dimension and significance.

In summary, there are hierarchical, thermodynamic, environmental, and resource-related constraints acting to retard any increase in internal ascendancy.

A SIMPLE EXAMPLE

An example of an ecological flow network found in numerous other publications is a description (Patten et al., 1976, pp. 572–574) of the energy flows among five functional components of Cone Spring, a small cold-water spring in Iowa. The compartments are depicted, along with their attendant flows (in $\text{kcal m}^{-2} \text{y}^{-1}$), in Fig. 26.3. Arrows not originating in a compartment portray exogenous inputs; those not terminating in a compartment denote endogenous outputs of useful energy to the system's environment; ground symbols represent dissipative flows.

These same transfers may be arrayed in the form of an 8×8 matrix (Table 26.1), where energy flows from row to column designations, for example, $T_{23} = 5205 \text{ kcal m}^{-2} \text{y}^{-1}$ transferred from node 2 to 3. Inputs are arrayed along the 0 row, useful outputs down column 6, and dissipations down column 7. Substituting these T_{ij} values into eqs. (26.15), (26.20), (26.22), and (26.25) through (26.28) yields values for the total system throughput, ascendancy, capacity, and the overhead terms, respectively. These values are listed in Table 26.2 for the Cone Spring model.

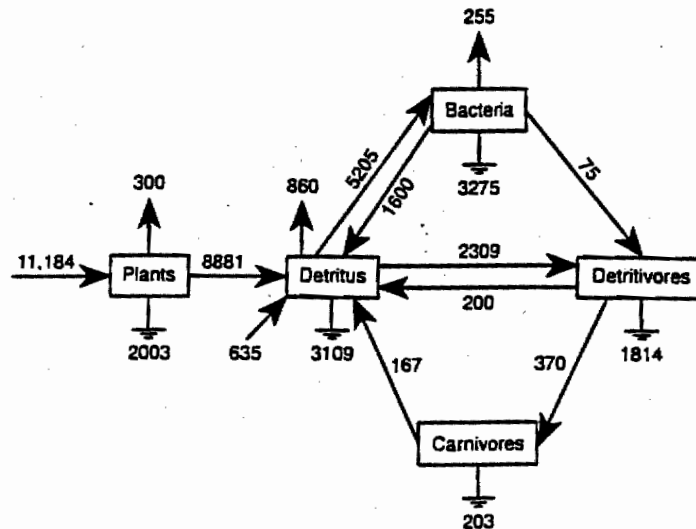


Figure 26.3 Schematic of energy flows ($\text{kcal m}^{-2} \text{y}^{-1}$) among functional components of the Cone Spring ecosystem. Arrows not originating from a box represent inputs from outside the system. Arrows not terminating in a compartment represent exports of usable energy out of the system. Ground symbols represent dissipations.

TABLE 26.1 Flows T_{ij} in the Cone Spring ecosystem model

	0	1	2	3	4	5	6	7
0	0	11,184	635	0	0	0	0	0
1	0	0	8,881	0	0	0	300	2,003
2	0	0	0	5,205	2,309	0	860	3,109
3	0	0	1,600	0	75	0	255	3,275
4	0	0	200	0	0	370	0	1,814
5	0	0	167	0	0	0	0	203
6	0	0	0	0	0	0	0	0
7	0	0	0	0	0	0	0	0

Row i contributes to column j . All values in $\text{kcal m}^{-2} \text{y}^{-1}$.

TABLE 26.2 Calculated values of ascendancy and related variables for the Cone Spring ecosystem model

Total system throughput (T)	42,445
Ascendancy (A)	56,725
Capacity (C)	93,172
Input overhead (I)	6,222
Tribute (E)	7,811
Dissipation (S)	35,274
Redundancy (R)	29,832

Units: total system throughput, $\text{kcal m}^{-2} \text{y}^{-1}$; all others, $\text{kcal-bits m}^{-2} \text{y}^{-1}$.

CONCLUDING REMARKS

The preceding development has been intended to provide a quantitative basis for investigating whether or not ecosystems undergo anything akin to growth and development. The origins and place of the described measures in the domain of probability theory have been stressed in the belief that both sides in any dialogue on the issues involved will accept definitions cast in probabilistic terms. The amount of data necessary to study the behavior of the variables introduced here for realistically modeled systems would be voluminous indeed. Hundreds of ecosystem networks and their time series would have to be examined before any outcome would become apparent. And it would require considerable effort to quantify even one such network of the scope of complexity suggested, for example, in Chapter 20. But the issue, bearing on the nature of supraorganismal organization, ranks today as one of the most philosophically intriguing in all science.

It is exciting to speculate what might happen if the evidence were to favor existence of organized behavior in ecosystems. Would such behavior be reducible to events occurring at the level of the organism or smaller, or is it conceivable that the larger scale phenomena are to a degree autonomous like their living constituent parts appear to be? At first, as embedded parts ourselves, it may seem difficult to imagine how such higher-level autonomy could arise, and even more difficult to concede that we are governed by it. But, somewhere in the feedback structure of complex reticulated relationships between subsidiary units in ecosystems may reside a cybernetic organizing principle capable of being drawn as an appropriate agent behind (semi)autonomous growth and development at the ecosystem level (Ulanowicz, 1986a; Wicken, 1984).

Nothing less than the status of ecology as a science is at stake in this dialogue. If ecosystems are determined by their molecular constituents, then ecology is clearly a corollary discipline to

genetics and molecular biology. If, however, autonomous elements of ecosystems can be clearly identified, then ecology takes on an importance in its own right. Even more to the point, the discovery of autonomous ecosystem behavior would stand as a significant advance in the theory of far-from-equilibrium thermodynamics and catapult ecosystem science into the very forefront of scientific inquiry—which is where it has always belonged!

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