

# An informational synthesis of ecosystem structure and function

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## Abstract

The mechanistic view of ecosystem dynamics, being inherently reversible, seems ill-suited to describe directional behavior, such as ecosystem succession. A more conservative approach, such as one that involves probabilities, seems warranted. Work involving conditional probabilities has led to the development of a systems property called the ascendancy, the increase of which appears to incorporate many of the changes that characterize the successional process. Ascendancy originally was formulated entirely in terms of systems transactions. Hence, it did not address the crux of system dynamics, which is the connection between the stocks of taxa and the trophic flows between these populations. One may, however, expand the definition of system ascendancy in a perfectly natural and consistent way to include compartmental biomasses. The principle of increasing ascendancy, recast in terms of the new definition, provides a whole-system context for hitherto unexplained elements of traditional ecology. For example, the allometric trend during succession towards larger organisms with slower turnover times and the time-honored 'Liebig's law of the minimum' both can be derived from the revised principle. Furthermore, the same derivational techniques provide us with an entirely new criterion for identifying the limiting nutrient linkages within an ecosystem. Such a theoretical 'prediction' might augur the beginnings of a robust theoretical systems ecology. © 1997 Elsevier Science B.V. All rights reserved

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## 1. Introduction

A promising goal of ecosystem science is to seek a quantitative description of the interactions of the various components of a community with each other and with the physical domain in which they are imbedded. One's focus can be prognosticatory, i.e., how to employ a system's current configuration to predict its behavior; or it can be post-dictive, as when one seeks to understand the agencies behind

changes in patterns of system behavior. Often, this last phrase is interpreted as 'to understand the *mechanisms* behind changes in system patterns'. By 'mechanism' is usually understood a relationship between two components that precludes any causal indeterminacy. If *A*, then *B*, without exception. We are concerned, however that the proclivity of most ecologists to search for mechanisms behind every change, to the exclusion of other forms of causality, may not be the most fruitful way to proceed (Rosen, 1991). The mechanisms frequently are elusive, and after one has identified a full set of interacting mechanisms, the prediction capability of the ensuing

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machinery usually is found wanting (Platt et al., 1981). To be sure, relationships which closely approximate mechanisms abound in ecosystems, and certainly much is to be learned by explicating such interactions. However, the fact that one can identify mechanisms in ecosystems (e.g., primary producers respond to light intensity, predators increase in response to prey availability, etc.), is insufficient reason to conclude that system dynamics are comprised entirely of mechanisms.

If one suspects that not all phenomena that comprise ecosystems development are mechanical, how then should one attempt to quantify observed system changes? The natural fallback would be to resort to probabilities. This is hardly a radical move, as probabilities have been a fundamental tool of ecologists since the discipline emerged. But we note that probabilities usually have been regarded by ecologists as being entirely epistemic in nature. That is, probabilities are assumed to convey our *ignorance* of what is happening. The conventional presumption has been that if we could resolve our ignorance, deterministic mathematics then could be invoked. There is a growing trend, however, in physics, philosophy and even biology to regard probabilities more in an ontological light (Depew and Weber, 1994). In this perspective, probabilities refer not only to our ignorance about a situation, but also to an unresolvable *indeterminacy* inherent in the situation itself. What are some of the consequences of this shift in perspective?

Almost every application of probability theory to ecology involves the assumption of stationarity. That is, many elements are assumed to act either independently of each other or in rigid connection over an interval of time so as to yield a probability distribution that does not change. If, however, system elements are *incompletely* coupled (as must be the case if there exists any residual indeterminacy), then system processes are free to act upon each other in ways that change the assignment of probabilities over time.

The most successful way to treat changes in probabilities appears to be contained in information theory. Unfortunately, most readers probably still associate information theory with the study of communications, which was historically where it first evolved. But Tribus and McIrvine (1971) have suggested that the concept of information be generalized

to include 'anything that causes a change in probability assignment'. This definition recasts the role of information theory as the quantitative treatment of changes in probabilities and establishes an organic connection between information theory and probability theory; calculus is to algebra as information theory is to probability theory. The unfortunate history of information theory in ecology, which focusses upon the futile attempt to establish a fixed relationship between the diversity of an ecosystem and its stability to perturbations, has caused many ecologists to eschew information theory. We are suggesting, however, that ecosystem development can be described best in terms of probabilities that interact with and change one another. To exclude information theory from a description of such dynamics would be as otiose as trying to do Newtonian mechanics without calculus.

## 2. Information and ecosystem processes

A major shortcoming of early attempts to apply information theory to ecology (e.g., Woodwell and Smith, 1969) was that the measures used did not quantify information per se. The species diversity, for example, was expressed in terms of the Shannon–Wiener index, calculated using the number or biomass fractions of the various taxa that comprise the system. Hence, the biomass diversity,  $D$ , of a system was estimated as

$$D = -k \sum_i \left( \frac{B_i}{B} \right) \log \left( \frac{B_i}{B} \right), \quad (1)$$

where  $B_i$  is the biomass of taxon  $i$ ,  $B$  is the total biomass of the system ( $B = \sum_i B_i$ ), and  $k$  is a scalar constant.

The fractions  $B_i/B$  in Eq. (1) estimate the stationary probability distribution of biomass within the ecosystem. What one actually calculates from this distribution via the Shannon–Wiener formula (Eq. (1)) is an estimate of the potential *indeterminacy* as to where a particular quantum of biomass might be residing. Actual *information* about the system would have to address the constraints that induce more biomass to be included in certain taxa than in others.

To quantify information about ecosystem behavior, therefore, it becomes necessary to treat *transfers* of biomass among the system compartments. Our attention thus shifts away from biomass stocks and towards trophic flows, which, ironically, was the perspective that MacArthur and Ranch (1955) used when first introducing information measures into ecology.

Instead of Eq. (1), a more appropriate measure of the indeterminacy inherent in a collection of ecosystem transfers would be the *flow diversity*,  $D_f$ , where

$$D_f = -k \sum_{k=1}^m \left( \frac{T_k}{T} \right) \log \left( \frac{T_k}{T} \right), \quad (2)$$

and  $T_k$  is the  $k$ th flow among  $m$  observed flows that sum to  $T$ . One may think of the  $T_k$ s as a collection of  $m$  sticks of various lengths. The sticks may be joined at  $n$  separate nodes in a great number of ways that is characterized by the measure  $D_f$ . But in any given ecosystem the flows are related to one another via biological constraints in a particular pattern. I.e., no longer can the sticks in our analogy come together in arbitrary fashion. They now are constrained relative to each other in a specific way. Rather than referring simply to  $T_k$  as one of  $m$  flows, one may now identify it by its origin and destination. Thus, we refer instead to  $T_{ij}$  as the flow from component  $i$  to  $j$ . The biological constraints also induce changes in probability assignments. Instead of referring to  $T_k/T$  (or equivalently to  $T_{ij}/T$ ) one may now measure a *conditional* probability  $T_{ij}/\sum_q T_{iq}$ , which estimates the probability that a quantum of medium will flow to  $j$ , given that it originated in  $i$ .

Information theory prescribes (Rutledge et al., 1976; Hirata and Ulanowicz, 1984; Ulanowicz and Norden, 1990) that the quantity of information associated with the shift in probability assignments from the joint probabilities,  $T_{ij}/T$ , to the conditional (constrained) probabilities,  $T_{ij}/\sum_q T_{iq}$ , be calculated as the *average mutual information*:

$$I = k \sum_i \sum_j (T_{ij}/T) \log \left( T_{ij} T / \sum_q T_{iq} \sum_r T_{rj} \right). \quad (3)$$

One problem with information measures is that they are inherently dimensionless. That is, the measure  $I$  in Eq. (3) might refer to an ecosystem like the intestinal flora of an insect. It could as well pertain

to the ecosystem of the Serengeti Plain. The magnitude of  $I$  does not reveal the scale of the system being assessed. For this reason, Ulanowicz (1980) followed the suggestion of Tribus and McIrvine (1971) and scaled  $I$  by setting  $k = T$ . The ensuing product,  $TxI$ , he called the network *ascendency*,  $A$ .

The network ascendency thus incorporates aspects of both a system's size and constitutive nature. The factor  $T$  gauges the level of overall system activity; the index  $I$  measures the organization with which exchanges among components are transacted. Increases in system activity,  $T$ , are generally regarded as growth in the economic sense of the word (viz. Gross National Product). A rise in  $I$  signifies that the system is developing further constraints to channel flows along more specific pathways. An increasing  $A$ , therefore, is a quantitative sign that the system in question is growing and developing (Ulanowicz, 1986).

Given the way that ascendency has been defined, it should come as no surprise that many ecological processes that contribute to a higher  $A$  have been identified as factors that contribute to ecological succession (Odum, 1969). For example, a greater richness of species (compartments), more retention of resources within the system, and a tendency towards trophic specialization are the primary trends that Odum identifies with developing ecosystems. All other things being equal, these same system trends augment its network ascendency. Hence, we are led to the phenomenological observation that, in the absence of major perturbations, ecosystems exhibit a propensity to increase their ascendency.

There are at least two interesting conclusions one can draw from the last statement. The first is that the principle defines a preferred direction (increasing ascendency) along which ecosystems usually progress. Newtonian systems do not of themselves yield any directionality. That ecosystems do exhibit succession is evidence favoring non-Newtonian agencies at work (Ulanowicz, 1989, 1990). The second peculiarity is the use of the ambiguous word 'propensity'. This term is invoked to underscore the existence of a degree of causal indeterminacy within the ecosystem. If there is a propensity for  $B$  to follow  $A$  in the system, then after most times that  $A$  has been observed,  $B$  ensues — but not each and every time. On occasions  $C$ ,  $D$  or some other cir-

cumstance might result. In the same vein, it is not being claimed that ecosystems *maximize* or *optimize* their ascendancies (although Ulanowicz (1980) had prematurely suggested this). To invoke variational behavior of this sort would be to force the system into a mechanical strait jacket. Rather, we envision a collection of partially stochastic processes that ratchet against each other in ways that yield an almost desultory rise in overall ascendancy.

### 3. Information and ecosystem dynamics

The calculation of system ascendancy can be extended to apply to systems that are temporally and spatially heterogeneous (Pahl-Wostl, 1992; Pahl-Wostl, 1995). What until now has remained problematical is that the ascendancy has been defined entirely in terms of flows and processes. Biomasses or stocks appear nowhere in its formulation. Of course, at steady-state biomasses become moot, and the effects of stocks are already implicit in Pahl-Wostl's formulation for time-varying systems. But as long as biomass does not appear explicitly in the formula for ascendancy, the index cannot be said truly to address ecosystem *dynamics*. No one yet has succeeded in introducing biomass into the ascendancy in a way that is consistent with the requirements of the underlying probability theory. It is to this task that we now turn.

To recapitulate, information is that which causes a change in probability assignment. There is no requirement, however, that the *a priori* (unconstrained) and the *a posteriori* (constrained) probabilities be estimated using the same types of variables. In fact, if we were to use the biomasses to make *a priori* estimates of interaction strengths (as is done, for example, in chemistry with the law of mass action), we could compare these 'predicted' exchanges with the (*a posteriori*) observed flows to gauge the relationship between biomass and flows, between form and function.

Now, the distribution of biomass can be represented by the quotients,  $B_i/B$ . The same set of numbers can be used to estimate several other probability distributions. For example,  $B_i/B$  also approximates the probability that a quantum of medium is

either entering or leaving compartment  $i$ . (It is easy to cite many reasons why the probabilities of ingress or egress might *not* be proportional to the biomass fractions, but all such reasoning involves interference by factors other than mere biomass.) Hence, the probability that a quantum of currency leaves compartment  $i$  can be taken as  $B_i/B$ , and the probability that a quantum enters compartment  $j$  can be set equal to  $B_j/B$ . If these events were totally independent, then the joint probability that a specific quantum both left  $i$  and entered  $j$  would be  $B_i B_j / B^2$ .

In writing this expression for the joint probability of flow from  $i$  to  $j$ , *minimal* assumptions are made about what makes a quantum flow from donor to recipient. Nothing has been assumed to constrain the exchange other than the magnitudes of the biomasses involved. Hence, this distribution of joint probabilities constitutes the '*a priori*' system configuration required by information theory. The conjugate '*a posteriori*' distribution can be taken as the observed distribution of realized flows. That is,  $T_{ij}/T$  becomes the estimate of the probability that, in a random sample of activity, a direct transfer is being made from  $i$  to  $j$ .

In contrast to the minimum of structural constraints we built into the joint probability,  $B_i B_j / B^2$ , the effects of all actual constraints are implicit in the measured distribution,  $T_{ij}/T$ . These additional constraints are what constitute the relationship between structure and function. They engender a *change in probability assignment* from the former distribution, based on biomasses, to the latter, estimated by flows. The information associated with such change in assignment is measured by the Kullback–Leibler index (Kapur and Kesavan, 1992) as

$$I = k \sum_{i=1}^n \sum_{j=1}^n (T_{ij}/T) \log(T_{ij} B^2 / B_i B_j T). \quad (4)$$

As with the mutual information of flows, we expect  $I$  in Eq. (4) to increase during the course of system development. Furthermore, we also use  $k$  to impart physical dimensions to  $I$ . In principle, one could choose that  $k$  equals either  $T$  or  $B$ . We will use  $T$ , because it is dimensionally more consistent (it cancels with the  $T$  in the denominator of the first probability). More importantly, we discovered by trial and error that when  $A$  was scaled by  $B$ , increas-

ing ascendancy seemed invariably to lead to a static endpoint where all system mass was concentrated in a single, nonliving compartment. We thus define the expanded, or biomass inclusive ascendancy to be

$$A = \sum_{i=1}^n \sum_{j=1}^n T_{ij} \log(T_{ij} B^2 / B_i B_j T). \quad (5)$$

#### 4. Analogies to thermodynamics

There are even deeper reasons for choosing to scale  $I$  by  $T$ . Ascendancy thereby comes to bear formal analogy to variables prominent in the thermodynamics of irreversible processes. For example, if the medium in question happens to be energy, then ascendancy has the dimensions of power ( $\text{m l}^2 \text{ t}^{-3}$ ). Onsager (1931) showed how the dissipation generated by a system of processes always could be written as the sum of the products of each observed flow times its conjugate ‘force’. For example, in a system with multiple processes the flow via thermal conduction is multiplied by the accompanying gradient in the reciprocal of the absolute temperature, the diffusive flux by the negative of its gradient in chemical potential, etc. All such products are summed to yield the overall rate of dissipation. In Eq. (5) the power function,  $A$ , is the sum of products of each observed flow (the  $T_{ij}$ ) times a corresponding logarithmic function. Thus, the logarithmic terms appear homologous to Onsager’s ‘forces’. Popper (1990) has argued, however, that in a world full of nonmechanical causes, ‘forces’ are but a small subset of more general entities that he has called ‘propensities’. Hence, in analogy with Onsager’s scheme, we can identify  $\log(T_{ij} B^2 / B_i B_j T)$  as the *propensity* for flow to occur from  $i$  to  $j$  in the context of the total system (Ulanowicz, 1996). When the separate propensities are each weighted by their conjugate flows and the products then summed, the resulting ascendancy then defines the propensity for the entire system to grow and develop.

For consistency, the expanded ascendancy must reduce to the former ascendancy (Eq. (3)) under limiting conditions. To demonstrate that this is indeed the case, we note that  $A$  in Eq. (5) may be

decomposed algebraically into 3 inherently nonnegative sets of terms:

$$A = \sum_i \sum_j T_{ij} \log \left( \frac{T_{ij} T}{T_i T_j} \right) + \sum_i T_i \log \left( \frac{T_i / T}{B_i / B} \right) + \sum_j T_j \log \left( \frac{T_j / T}{B_j / B} \right), \quad (5')$$

where a dot in place of a subscript implies summation over that index. The first set of terms on the right hand side of Eq. (5') is identical to the earlier definition of the ascendancy in terms of flows alone. Its behavior and modes of decomposition remain unchanged from that described by Ulanowicz and Norden (1990). It is thus reassuring to note that increases in the number of compartments, in the trophic specialization of each compartment, and in the circulation of currency also contribute to increases in the expanded ascendancy.

The reader may notice that the latter two groups of terms in Eq. (5') vanish whenever the proportion of flow through each compartment is the same as its respective fraction of the total biomass. Hence, the expanded ascendancy always equals or exceeds the original value insofar as the compartmental throughputs are disproportionate to their biomasses. Such ‘skewedness’ is hardly arbitrary. It is the consequence of other well-known trends in ecosystem development, as we now show.

#### 5. Developmental trends in structure

The explicit inclusion of the biomass structure into the formula for ascendancy allows one to obtain certain known attributes of developing systems as formal deductions from the principle of increasing ascendancy. To demonstrate this we write the differential of the ascendancy according to the chain rule of differentiation:

$$dA = \sum_i \sum_j \frac{\partial A}{\partial T_{ij}} dT_{ij} + \sum_p \frac{\partial A}{\partial B_p} dB_p. \quad (6)$$

Now, after some calculation and simplification, we find that

$$\frac{\partial A}{\partial B_p} = 2 \left( \frac{T}{B} - \frac{1}{2} \frac{T_p + T_p}{B_p} \right). \quad (7)$$

Eq. (7) means that an increase in  $B_p$  will contribute toward increasing ascendancy whenever the mean throughput rate for compartment  $p$  is less than the overall system throughput rate. I.e., increasing ascendancy implies positive selection for those compartments with slower than average turnover times (Odum, 1969). There is a strong body of empirical evidence and some heuristic geometric arguments that fall under the rubric of 'allometry', which links slower throughput times to larger body sizes (Platt, 1985; Calder, 1985). Hence, increasing ascendancy likewise implies selection for larger body size for some members of the ecosystem.

## 6. Extensions to open and secular systems

Almost all natural ecosystems are open to the transfer of materials with their environments (and all require exogenous sources of energy). Exogenous flows make the definition of probability distributions problematical. Probability distributions are well-defined only if they are complete, i.e., only if they can be normalized so as to sum to unity. With ecosystem flows, exogenous transfers are incorporated into the probability distribution by assuming virtual compartments as the sources and sinks of those exchanges (Hirata and Ulanowicz, 1984). For example, imports to the system are considered to issue from compartment zero, e.g.,  $T_{0i}$  is an exogenous import to species  $i$ . Similarly, useable exports are assumed to enter the fictitious compartment  $n+1$ , and any dissipated flows are directed into  $n+2$ .

The obvious problem with introducing compartmental stocks into this calculus is that no actual biomasses exist for these three virtual compartments. Such difficulty is not insurmountable, however. One slight complication is that in order to cover the general case when the system is not balanced, one must introduce two possible system biomasses. Let  $B_d$  be the system biomass when any flow is being considered from its donor and  $B_r$  be the system biomass when a flow is seen as entering its receptor. Now, the virtual biomasses that we seek will be labelled  $B_0$ ,  $B_{n+1}$  and  $B_{n+2}$  as discussed in the last paragraph. Whence,

$$B_d = B_0 + \sum_{p=1}^n B_p, \quad (8a)$$

and

$$B_r = \sum_{p=1}^n B_p + B_{n+1} + B_{n+2}. \quad (8b)$$

We now define the three virtual biomasses so that each turnover rate is identical to that for the system as a whole:

$$T_{0i}/B_0 = T/B_d, \quad (9a)$$

$$T_{n+1}/B_{n+1} = T/B_r, \quad (9b)$$

and

$$T_{n+2}/B_{n+2} = T/B_r. \quad (9c)$$

Solving Eqs. (8a) and (8b) along with Eqs. (9a)–(9c) for the virtual biomasses yields

$$B_0 = \left( [T_{0i} \sum_{p=1}^n B_p] / [T - T_{0i}] \right), \quad (10a)$$

$$B_{n+1} = \left( [T_{n+1} \sum_{p=1}^n B_p] / [T - T_{n+1} - T_{n+2}] \right), \quad (10b)$$

and

$$B_{n+2} = \left( [T_{n+2} \sum_{p=1}^n B_p] / [T - T_{n+1} - T_{n+2}] \right). \quad (10c)$$

One sees when the system is balanced that  $B_r = B_d = B$ . The ascendancy for open systems then can be written as

$$A = \sum_{i=0}^n \sum_{j=1}^{n+2} T_{ij} \log(T_{ij} B_i B_d / B_i B_j T). \quad (11)$$

In order to write the temporally discrete form of the ascendancy, we must assign values to the flows and biomasses at each discrete interval of time (see Pahl-Wostl, 1992; Pahl-Wostl, 1995). Thus, we denote by  $T_{ijk}$  the flow from  $i$  to  $j$  during time interval  $k$ , and  $B_{ik}$  becomes the biomass in  $i$  during interval  $k$ . The Kullback–Leibler measure of the information inherent in the discrete dynamics then becomes

$$A = \sum_{i,j,k} T_{ijk} \log(T_{ijk} B_{rk} B_{dk} / T B_{ik} B_{jk}). \quad (12)$$

## 7. Development and nutrient limitations

To see how development and nutrient limitations are intimately bound, we choose to reinterpret the

index  $k$  in Eq. (12) so as to refer to any of a suite of chemical constituents comprising the organisms of the ecosystem. That is,  $T_{ijk}$  could also be thought of as representing the flow of constituent  $k$  from compartment  $i$  to compartment  $j$ . For example, one might have data on the concurrent transfers of carbon and nitrogen among the taxa of an ecosystem. Then  $k = 1$  could represent carbon and  $k = 2$ , nitrogen. In Eq. (12) the summation over  $k$  would run from 1 to 2. The ascendancy,  $A$ , would then also quantify the information inherent in the distribution of these two nutrients among the components of the ecosystem.

We wish now to focus upon the sensitivity of the overall index of organization,  $A$ , to changes in chemical constituents among the taxa. To do this we first rewrite the chain rule (Eq. (6)) to include chemical constituents and then look at the analog to Eq. (7), which becomes

$$\frac{\partial A}{\partial B_{pk}} = 2 \left( \frac{T}{B} - \frac{1}{2} \frac{T_{pk} + T_{p,k}}{B_{pk}} \right). \quad (13)$$

That is, Eq. (13) provides the means for us to assess the relative amount that the overall developmental index,  $A$ , would be abetted by an increase of chemical constituent  $k$  in compartment  $p$ .

Looked at another way, for any given taxon,  $p$ , we can compare the relative contributions to whole system development made by increasing each of the chemical constituents in turn. As with Eq. (7), it happens that the system is most sensitive to the constituent in  $p$  with the slowest turnover rate (longest turnover time). It is a rather easy proposition to show that for any particular taxon, the constituent with the slowest turnover is identical to that which is 'presented' to that taxon in least relative proportion.

Eq. (13), then, can be applied to any compartment,  $p$ , of an ecosystem to identify which chemical constituent,  $k$ , is limiting to  $p$  in the sense of Liebig (1840). 'Liebig's law' retains a high profile in ecology. It was derived in what might be called heuristic or ad-hoc fashion, and has come to us almost unchanged over the last century and a half. We now see how Liebig's law appears as a corollary to a more encompassing theory of whole system development.

There are not many ecosystems that have been quantified to an extent that Eq. (13) can be applied to

their constituent nutrient networks. An exception is Chesapeake Bay, for which Baird et al. (1995) have estimated the parallel flows of carbon and nitrogen among the 36 major compartments of the ecosystem in the mesohaline reach of the Bay. To illustrate the use of Eq. (13), we have aggregated the data of Baird et al., that pertain to the planktonic ecosystem according to the scheme suggested by Fasham (1985). The flows of carbon in  $\text{mgm}^{-2}\text{d}^{-1}$  are presented in Fig. 1a, while the corresponding transfers of nitrogen appear in Fig. 1b. For the sake of simplicity, all transfers out of the various members of the planktonic system have been aggregated into a single export out of that box.

The results of Eq. (13) are given in Table 1 in  $\text{d}^{-1}$ . Not unexpectedly, one sees that the contributions to the system ascendancy due to changes in nitrogen stocks is larger than the corresponding contributions by carbon in all six living compartments. (The sensitivities of the non-living dissolved nutrients are identically zero, because the biomasses of all nonliving components were chosen according to Eq. (10) so as to avoid undue bias by large detrital pools.)

Of course, one could have applied Liebig's principle directly to the data on C and N and have come to the identical conclusion that nitrogen is stoichiometrically less abundant to each compartment. Should one wish to know which input of nitrogen is controlling each taxon, however, Liebig's law provides no clue. We are left to assume that if an element is limiting to a compartment, then the source of the largest input of that limiting element should be the controlling flow. In the absence of any guidance to the contrary, this seems like a good assumption.

The theory of ascendancy, however, provides us with further indications as to which flows might be controlling. Thus far, we have used only part of the information on sensitivities provided by Eq. (6). In addition to the sensitivities of ascendancy to stocks, one also may calculate the contributions made to the overall functioning of the system by each individual flow. The counterpart to Eq. (13) in terms of flows works out to be

$$\frac{\partial A}{\partial T_{xyz}} = \log \left( \frac{T_{xyz} B_r B_d}{T \dots B_{xz} B_{yz}} \right). \quad (14)$$

That is, if  $z$  was determined by Eq. (13) to be the element that limits compartment  $y$ , then the source  $x$  of  $z$  to  $y$  that yields the largest value of Eq. (14)

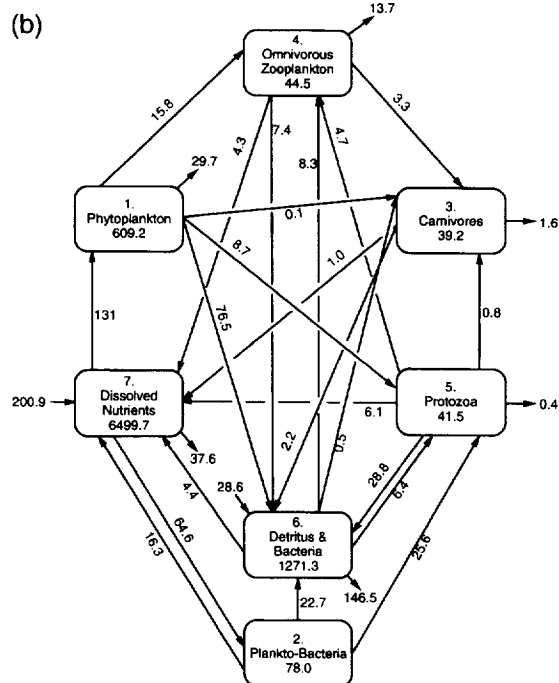
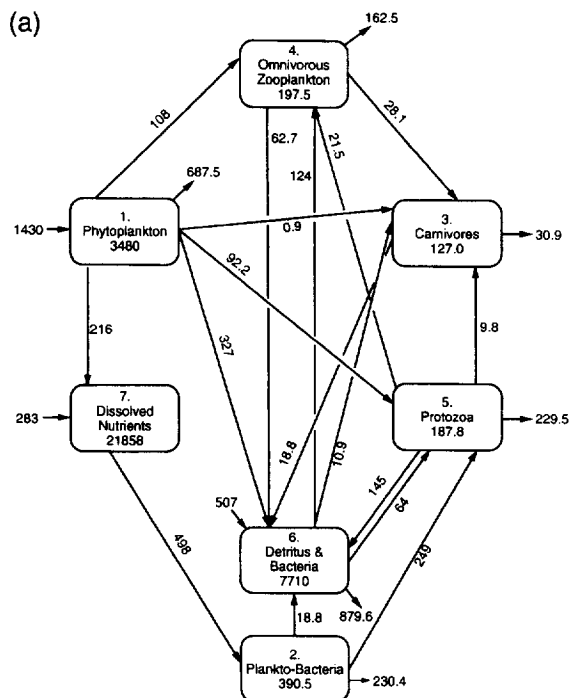


Table 1

Sensitivities of system ascendancy to changes in stocks of C and N in each living compartment (all figures in  $\text{d}^{-1}$ )

Compartment	Carbon	Nitrogen
Phytoplankton	-0.237	0.156
Plankto-bacteria	-1.970	-1.070
Carnivores	-0.196	0.342
Omnivorous zooplankton	-1.980	-0.708
Protozoa	-3.730	-1.380
Detritus and bacteria	0.306	0.324

will identify the controlling flow in the extended sense of Liebig.

Most of the time the controlling source of a limiting element to a compartment is indeed the largest contributor. Such is the case in our simple example for the phytoplankton, plankto-bacteria, carnivores and protozoa. The zooplankton and bacteria, however, are more sensitive to contributions of nitrogen from the protozoa than they are to their largest sources of N, the phytoplankton.

Study of Eq. (14) reveals that the controlling inflow of limiting nutrient depletes its donor pool at the fastest relative rate. For example, one sees in Fig. 1b that the phytoplankton are contributing  $15.8 \text{ mg N m}^{-2} \text{ d}^{-1}$  to the omnivorous zooplankton from a stock of  $609 \text{ mg N m}^{-2}$ . The latter are depleting the stock of the phytoplankton at a rate of 2.6% per diem. The protozoa contribute a lesser amount ( $4.7 \text{ mg N m}^{-2} \text{ d}^{-1}$ ) than do the phytoplankton to the omnivorous zooplankton. That contribution, however, is siphoning the protozoan stocks ( $41.5 \text{ mg N m}^{-2}$ ) at the rate of 11.3% per diem. Ascendancy analysis, therefore, identifies the protozoa as the limiting donor of nitrogen to the omnivorous zooplankton. On hindsight, this conclusion accords well with the sense of Liebig. All other things being

Fig. 1. Annually-averaged flows of (a) carbon and (b) nitrogen among the major components of the planktonic ecosystem of mesohaline Chesapeake Bay. Flows associated with arrows are in  $\text{mg m}^{-2} \text{ d}^{-1}$ . Numbers inside the boxes are in  $\text{mg m}^{-2}$ . Arrows not originating from a box represent imports to the system. Those not terminating in a box depict all transfers out of the plankton. After Baird et al. (1995).



equal, the zooplankton should encounter difficulties extracting N from the protozoa well before they begin to exhaust their larger source of that limiting element from the phytoplankton.

Interestingly enough, when the earlier, flows-only analog to Eq. (14) was used to calculate the sensitivities of the overall ascendancy to changes in individual system flows, the results were *qualitatively* identical to those just described. That is, in case of the phytoplankton, plankto-bacteria, carnivores and protozoa, system ascendancy was most sensitive to changes in the largest nitrogen input in each case. With the zooplankton and bacteria, however, flow ascendancy was more sensitive to nitrogen inputs from the protozoa, rather than from the largest contributor of N, the phytoplankton. It is unclear whether or not this correspondence is accidental. Most likely, further investigations with other systems will uncover instances where the inclusion of biomass makes a qualitative difference. When such discrepancy is discovered, however, heuristics will favor the results from the analysis that includes biomasses. It would have been exceedingly difficult, if not impossible, to convince the reader on the basis of a flow-only analysis that nitrogen from protozoa rather than from phytoplankton is controlling the dynamics of zooplankton and bacteria. Given the familiarity of most ecologists with the Liebig-type analysis, however, an extension of that tradition is likely to appear quite plausible. Of course, it remains to see whether an empirical test of any discrepancy will confirm our intuition.

## 8. Concluding remarks

The concept of the ecosystem as a complicated machine and the directionality exhibited by succession seem highly incompatible. Without speculating further on the nature of any nonmechanical behavior by ecosystems, it would seem judicious to pursue a probabilistic treatment of ecosystem kinetics and dynamics. In following this line of inquiry, one discovers that the interactions of transfer probabilities upon each other is captured quite naturally by an information index, the system ascendancy. Fortunately, the increase of ascendancy is commensurate with several of the trends that characterize ecological succession.

These include more species richness, greater internalization of resources and finer trophic specialization.

Some of the indicators of succession pertain to the contents of ecosystem compartments, e.g., the increases in body size (Odum, 1969). Addressing these trends was difficult using the original ascendancy, predicated as it was solely upon trophic flows. It now appears, however, that biomasses can be incorporated into the definition of ascendancy in a way that is consistent with the requirements of probability theory. Furthermore, the new index reduces to the original ascendancy under limiting conditions. Increases in the biomass-inclusive ascendancy are fostered by increases in the turnover times of some of the living components. Because population turnover times correlate positively in allometric fashion with body size (Calder, 1985), the augmented ascendancy principle now also describes succession in terms of population and organismic parameters: The appearance of populations consisting of larger individuals with slower turnover rates is conducive to a higher system ascendancy.

Further corroboration of increasing ascendancy as a description of natural ecosystem dynamics occurs when one calculates the sensitivities of the ascendancies with respect to component system stocks and flows. Through this exercise one comes to identify the rate-limiting or controlling nutrient as the one which increases the ascendancy most in response to a unit increment in those particular elements. The limiting substances thus defined are identical to those predicted by the application of Liebig's law of the minimum. That is, the principle of increasing ascendancy subsumes Liebig's law in a wholly consistent manner.

In addition, the ascendancy principle appears to predict which of the particular donors of a limiting element should be most important. With such prediction theoretical ecology is beginning to come of age. For the objective of theoretical pursuits is to formulate overarching quantitative maxims that can be resolved in particular situations to prescribe behavior that heretofore would have remained unknown or mysterious. If it could be demonstrated experimentally that the controlling inputs to a population are those to which the system ascendancy is most sensitive, then a new and possibly nonmechanical perspective upon ecosystem dynamics would open to us.

Such confirmation could prompt ecologists to take seriously the non-Newtonian description of the world-at-large.

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## References

- Baird, D., Ulanowicz, R.E. and Boynton, W.R., 1995. Seasonal nitrogen dynamics in Chesapeake Bay: a network approach. *Estuarine Coastal Shelf Sci.*, 41: 137–162.
- Calder, W.A. 1985. Size and metabolism in natural systems. In: ed. R.E. Ulanowicz and T. Platt, *Ecosystem Theory for Biological Oceanography*. Can. Bull. Fish. Aquat. Sci., 213: 65–75.
- Depew, D. and Weber, B.H., 1994. *Darwinism Evolving: Systems Dynamics and the Genealogy of Natural Selection*. MIT Press, Cambridge, MA, 588 pp.
- Fasham, M.J.R. 1985. Flow analysis of materials in the marine euphotic zone. In: ed. R.E. Ulanowicz and T. Platt, *Ecosystem Theory for Biological Oceanography*. Can. Bull. Fish. Aquat. Sci., 213: 139–162.
- Hirata, H. and Ulanowicz, R.E., 1984. Information theoretical analysis of ecological networks. *Int. J. Syst. Sci.*, 15: 261–270.
- Kapur, J.N. and Kesavan, H.K., 1992. *Entropy Optimization Principles with Applications*. Academic Press, Boston.
- Liebig, J.J., 1840. *Chemistry in its Application to Agriculture and Physiology*. Taylor and Walton, London.
- MacArthur, R. and Ranch, D., 1955. Fluctuations of animal populations, and a measure of community stability. *Ecology*, 22: 723–731.
- Odum, E.P., 1969. The strategy of ecosystem development. *Science*, 164: 262–270.
- Onsager, L., 1931. Reciprocal relations in irreversible processes. *Phys. Rev.*, 37: 405–426.
- Pahl-Wostl, C., 1992. Information theoretical analysis of functional temporal and spatial organization in flow networks. *Math. Comput. Modelling*, 16: 35–52.
- Pahl-Wostl, C., 1995. *The Dynamic Nature of Ecosystems: Chaos and Order Entwined*. John Wiley and Sons, Chichester.
- Platt, T. 1985. Structure of the marine ecosystem: its allometric basis. In: ed. R.E. Ulanowicz and T. Platt, *Ecosystem Theory for Biological Oceanography*. Can. Bull. Fish. Aquat. Sci., 213: 55–64.
- Platt, T., Mann, K.H. and Ulanowicz, R.E. 1981. Mathematical models in biological oceanography. In: *Monographs on Oceanographic Methodology*, 7th Ed. UNESCO Press, Paris, p. 157.
- Popper, K.R., 1990. *A World of Propensities*. Thoemmes, Bristol.
- Rosen, R., 1991. *Life Itself: A Comprehensive Inquiry into the Nature, Origin and Foundation of Life*. Columbia University Press, New York, 285 pp.
- Rutledge, R.W., Basore, B.L. and Mulholland, R.J., 1976. Ecological stability: an information theory viewpoint. *J. Theor. Biol.*, 57: 223–254.
- Tribus, M. and McIrvine, E.C., 1971. Energy and information. *Sci. Am.*, 225: 179–188.
- Ulanowicz, R.E., 1980. An hypothesis on the development of natural communities. *J. Theor. Biol.*, 85: 223–245.
- Ulanowicz, R.E., 1986. *Growth and Development: Ecosystem Phenomenology*. Springer-Verlag, New York.
- Ulanowicz, R.E., 1989. A phenomenology of evolving networks. *Syst. Res.*, 6: 209–217.
- Ulanowicz, R.E., 1990. Aristotelean causalities in ecosystem development. *Oikos*, 57: 42–48.
- Ulanowicz, R.E., 1996. The propensities of evolving systems. In: ed. E.L. Khalil and K.E. Boulding, *Social and Natural Complexity*. Cambridge University Press, Cambridge, NY, 217–233.
- Ulanowicz, R.E. and Norden, J., 1990. Symmetrical overhead in flow networks. *Int. J. Syst. Sci.*, 21: 429–437.
- Woodwell, G.M. and Smith, H.H., eds., 1969. *Diversity and Stability in Ecological Systems*, Vol. 22. U.S. Brookhaven Symp. Biol., NY, 264 pp.