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Computational Biology and Chemistry

Computational Biology and Chemistry 27 (2003) 523-530

www.elsevier.com/locate/compbiolchem

Methodological overview

Some steps toward a central theory of ecosystem dynamics

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Received 20 May 2003; received in revised form 22 July 2003; accepted 24 July 2003

Abstract

Ecology is said by many to suffer for want of a central theory, such as Newton's laws of motion provide for classical mechanics or Schroedinger's wave equation provides for quantum physics. From among a plurality of contending laws to govern ecosystem behavior, the principle of increasing ascendency shows some early promise of being able to address the major questions asked of a theory of ecosystems, including, "How do organisms come to be distributed in time and space?, what accounts for the log-normal distribution of species numbers?, and how is the diversity of ecosystems related to their stability, resilience and persistence?" While some progress has been made in applying the concept of ascendency to the first issue, more work is needed to articulate exactly how it relates to the latter two. Accordingly, seven theoretical tasks are suggested that could help to establish these connections and to promote further consideration of the ascendency principle as the kernel of a theory of ecosystems.

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Keywords: Central theory; Ecosystem; Ecology; Ascendancy; Biodiversity; Eutrophication

1. Introduction

Conventional wisdom holds that ecology has no central law or principle like those that characterize the "hard" sciences. Classical mechanics, for example, is built upon the laws of Isaac Newton. In somewhat derivative fashion, electricity and magnetism is constructed around the formulae of Maxwell, while quantum physics derives from Schroedinger's wave equation. More than a century after it first appeared on the scene, ecology today still appears to many to be too diverse and conflicted to be able to coalesce around any one coherent theory.

Despite the consensus regarding the weak status of theoretical ecology, there is no scarcity of candidate laws that have been suggested as governing ecosystem dynamics. Jorgensen (1992), for example, suggests that ecosystems¹ develop so as to maximize their storage of *exergy*, or available thermodynamic work. Schneider and Kay (1994) by contrast believe that ecosystems evolve to degrade exergy gradients as thoroughly as possible. Odum and Pinkerton

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(1955) see ecosystems as unfolding so as always to capture energy at the maximum rate possible. Finally, Ulanowicz (1980, 1997) maintains that ecosystems, during the course of their development, exhibit a propensity to increase their system ascendency. Ascendency is a single index that is the product of two factors, each of which quantifies (see Section 2) a core attribute of networks of trophic exchanges: One factor gauges the extent of system activity, and the second indicates the level of constraint or organization inherent among the trophic exchanges.

The usual progression in science is to *induce* from a multitude of inchoate observations a candidate law, which then achieves a degree of plausibility insofar as one is able to *deduce* from it results that pertain to the universe of particular situations found in that domain and to answer the fundamental questions that define the field of study. An example of this deductive process is how Newton's second law of motion, in the form of vector field equations in the Navier–Stokes format, can be applied along with particular boundary and initial conditions to quantify almost any problem in fluid mechanics. A central principle becomes even more robust when it can be shown to encompass or predict what hitherto had seemed a separate body of phenomenology, or when a previously recognized law suddenly appears as a corollary

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¹ See Appendix A for a lexicon of ecological terms used in the text.

of a more over-arching principle. An example would be the discovery by Oersted that magnetism results from a moving electrical field.

As regards the deductive power of candidate laws pertaining to ecosystems, it now appears that the principle of increasing ascendency is expanding in the range of its applications to various ecosystem behaviors. Ulanowicz and Baird (1999), for example, have demonstrated analytically that Liebig's law of the minimum, familiar to every beginning ecologist, is a corollary of the ascendency hypothesis. Furthermore, ever since May (1973) cast doubts upon the intense efforts during the decade of the 1960s to establish a theoretical connection between ecosystem diversity and any attendant system stability, the worldwide efforts to preserve biodiversity have transpired largely in the absence of any theoretical justification. By way of exception, ascendency theory provides a direct connection between the diversity of ecological processes and system persistence (Ulanowicz, 2000a). In addition, the hottest new issue in Complexity Theory recently has been the re-discovery that the magnitudes of the processes constituting many self-organizing systems are arrayed statistically according to power-laws, rather than exhibiting more well-behaved exponential distributions. Ulanowicz and Wolff (1991) had demonstrated exactly this point more than a decade ago by applying the ascendency measure to a catalog of ecosystem networks.

Finally, Ulanowicz (1999) has shown how the principle of increasing ascendency represents an extension of Newtonian laws (but not the accompanying fundamental assumptions) into the realm of complex, living systems, in much the same way that Schroedinger extended Newton's second law to formulate quantum physics. In brief, the connections between ascendency and the larger corpus of ecosystem studies are growing both in number and in depth. These initial leads open up the possibility that the concept of ascendency (and its related indices) might provide the kernel for a unified, centralized and robust ecosystems theory. Accordingly, in the interest of establishing a foundation for future research in theoretical ecology, it may be worthwhile to seek formal connections between the hypothesis of increasing ascendency and the fundamental questions that are being asked in the pursuit of ecosystem studies.

2. Ascendency theory

Ascendency is a measure derived from networks of trophic interactions. It refers to the combined effects of mutualism occurring among the networks of transfers. In the absence of major destructive influences, mutualism, or strict positive feedback, causes the magnitudes of constituent processes to grow and eventually dominate those of non-participating processes.

To quantify ascendency, one begins by defining T_{ij} as the transfer of some conserved medium (like energy, carbon or

nitrogen) from prey i to predator j. The aggregate extent of system trophic activity then becomes

$$T = \sum_{i, j} T_{ij}.$$

The organization inherent in the system transfers is measured using information theory. In information theory one begins first by assessing an a priori indeterminacy concerning events and then defines information as the amount by which that indeterminacy decreases as the system evolves (additional constraints appear). If one knows, for example, that the amount of biomass in compartment *i* is B_i , and the total biomass of the system is $B = \sum_{i} B_{i}$, then the a priori probability that a quantum being transferred is leaving compartment *i* becomes B_i/B , and that it is entering compartment j, B_j/B . If these two events are considered to be uncoupled, then the joint probability that a flow both leaves *i* and enters *j* becomes the product $B_i B_j / B^2$. Once the flow has occurred, one may assess the a posteriori probability of the same transfer as being T_{ii}/T . According to Boltzmann, the indeterminacy of an event is proportional to the logarithm of the probability of that event. Taking the difference between the a priori and a posteriori indeterminacies and weighting them by the a posteriori probabilities, one arrives at the "Kullback-Leibler" information measure, K (Ulanowicz and Abarca-Arenas, 1997) as:

$$K = k \sum_{i,j} \left(\frac{T_{ij}}{T} \right) \log \left(\frac{T_{ij}B^2}{B_i B_j T} \right).$$

where k is a scalar constant. One may use k to impart dimensions to K. In this instance, if k is set equal to the throughput, T, the result becomes the system ascendency, A,

$$A = \sum_{i,j} T_{ij} \log \left(\frac{T_{ij} B^2}{B_i B_j T} \right).$$

Eugene Odum (1969) cataloged 24 attributes of more mature (better developed) ecosystems. All other things being equal, increases in almost all of Odum's attributes translate into corresponding increases in the ecosystem's ascendency. This correspondence led to the induction of the *ascendency principle*:

In the absence of major perturbations, ecosystems exhibit a propensity to increase in ascendency.

Ascendency readily can be extended into multiple dimensions, such as those pertaining to space, time or chemical species. If the new dimension is partitioned into segments numbered by the index k, then T_{ijk} would represent the flow from taxon i to taxon j within segment k, and B_{ik} would represent the biomass of i present in segment k. The extended ascendency, A_e , would then look like:

$$A_{\rm e} = \sum_{i,j,k} T_{ijk} \log \left(\frac{T_{ijk} B^2}{B_{ik} B_{jk} T} \right),$$

where *T* is now reckoned as T_{ijk} summed over all three indices (Pahl-Wostl, 1995).

It is a straightforward exercise to extend A into even higher dimensions (for example, both space and time), simply by adding the appropriate indices to the T's and B's and then modifying the last equation accordingly.

The foregoing definitions may now be applied to address three major questions commonly posed in ecosystems research:

Question 1. *How do populations of organisms distribute themselves over time and space?*

Usually, this question is approached in the particular, i.e. "Why does species x appear at particular times and in specific places?" It can be approached from an entirely different perspective, however, from the level of the whole system. The higher level information indices, A_{e} , like the original two-dimensional form, were intended to measure coherencies in the added dimensions. For example, if the added dimension is time, temporal periodicities in the biomasses or flows will contribute to the magnitude of $A_{\rm e}$. Similarly, if the third index represents one or more spatial dimensions, then patterns over space will contribute to the value of $A_{\rm e}$. The generic answer to Question 1, therefore, can be stated as, "Populations of organisms tend to distribute themselves over time and space according to patterns that contribute to a higher spatio-temporal ascendency."

Unfortunately, this answer applies only to the whole system when it is considered over the entire domains of time and space. It cannot be used, for example, to predict how much of a certain species will appear at a given time and place. This constraint on prediction is akin to being able to say that the entropy of a particular physical system will increase over time without being able to specify which changes in molecular configurations will bring about that increase. This restriction notwithstanding, if one has data on the distributions of organisms, one can use the ascendency measure to determine the most probable locations of the "bottlenecks" or processes that are limiting system dynamics. Such limiting processes can be identified by comparing the sensitivities of the ascendency to changes in each constituent process. Because the sensitivity of a mathematical function to an infinitesimal change in one of its variables is usually calculated by taking the partial derivative of the function with respect to the variable in question, the process with the highest such derivative should be the one that is exerting the greatest relative control on system dynamics.

Because of its particular form, the mathematical formula for the ascendency is particularly amenable to sensitivity analysis. To be exact, the ascendency is a Euler function, so that taking its partial derivative with respect to some arbitrary process T_{xyz} , yields the amazingly simple result:

$$\frac{\partial A_{\rm e}}{\partial T_{xyz}} = \log\left(\frac{T_{xyz}B^2}{B_{xz}B_{yz}T}\right).$$

Similarly, the sensitivities with respect to the biomass stocks are calculated to be:

$$\frac{\partial A_{\rm e}}{\partial B_{xz}} = 2\left(\frac{T}{B} - \frac{\sum_i T_{ixz} + \sum_j T_{xjz}}{2B_{xz}}\right).$$

This last expression says that the sensitivity of the performance of the whole system (ascendency) to any particular stock varies negatively as the turnover rate of that stock. In other words, that biomass is held longest in storage which exerts the greatest influence upon system behavior. Ulanowicz and Baird (1999) proved how this statement is equivalent to Liebig's "law of minimum proportions", i.e. the nutrient most limiting to growth is the one that is taken up in least proportion. That Liebig's familiar dictum should appear as a deductive corollary of the ascendency principle is the first hint that ascendency might play a central role in describing ecosystem behavior.

To demonstrate the utility of this enticing theoretical result, Ulanowicz and Baird estimated seasonal networks of carbon, nitrogen and phosphorus exchanges in the Chesapeake ecosystem and were indeed able to use the sensitivities of the ascendency to identify which element is most likely to limit the activity of each taxon during each season. They found, as anticipated (Rhyther and Dunstan, 1971; D'Elia, 1988), that nitrogen limits primary production during the summertime. Unexpectedly, however, the analysis revealed that phosphorus plays the controlling role in the activities of bacteria and fish during the same season. Following the same logic they had just applied to the biomass sensitivities, they reasoned that the sensitivities of the ascendency to the various flows should signify which source of the limiting element exerts most control on the receiver (a task notably beyond the scope of Liebig's law). Among their predictions for controlling sources were some that were not the donors of the largest supplies of the limiting element. For example, although the mesozooplankton received most of their limiting element, nitrogen from the phytoplankton, it was the supply of N from the slower pool of microzooplankton that was most critical to mesozooplankton activities. Although this prediction has yet to be tested experimentally, it is encouraging to discover that the ascendency principle is capable of generating falsifiable hypotheses.

Ulanowicz (2000b) examined how when A_e was extended over spatial dimensions, it could be invoked to quantify the movements of populations over a landscape. In particular, he showed how various constraints to movements could be quantified using A_e and how the index could be used to pinpoint migratory bottlenecks. Kikawada (1998) met with limited success in trying to combine Ulanowicz's treatment of spatial migration with simultaneous trophic interactions. Although he was unable to formulate simultaneous migration and trophic interaction, he was able to portray them as sequential activities. Kikawada's difficulty suggests as a research task:

Task 1.1. To study ways of expressing in matrix form simultaneous but distinct activities that vary over a spatial landscape or along a temporal interval.

This is a rather subtle problem that affects how one apportions the magnitudes of activities over a multi-dimensional array. It is related to the problem of how such simultaneous activities can be approximated using cellular automata (Krivov et al., 2003).

Kikawada's progress was also slowed by the lack of a generic algorithm to calculate higher dimensional ascendencies. Whence the need

Task 1.2. To write a generic algorithm that calculates higher dimensional ascendencies from large arrays of data.

This task is more straightforward than the first. Existing subroutines for calculating higher-dimensional ascendencies are cumbersome and exist only in FORTRAN IV code. If one seeks to display various contractions of the ascendency (partial sums over particular indices), one must rewrite sections of the source code to create the desired output. More flexible codes, written either in C++ or Visual Basic (with appropriate graphical user interfaces), are needed to streamline the input–output and give the user greater flexibility in choosing the partial contractions that are to appear in the output.

Question 2. What is behind the frequency distribution of species numbers?

It has long been assumed that species numbers are distributed in log-normal fashion. Robert May (1990), among others, saw the explanation of this phenomenon as one of the major challenges to theoretical ecologists. There is reason, however, to suspect that this issue may have been poorly-posed. Over a decade ago Ulanowicz and Wolff (1991) discovered that the magnitudes of trophic exchanges are distributed more according to Cauchy or power-law functions than in the fashion of more well-behaved negative exponentials. (Although power-law distributions can be normalized, they do not possess the well-defined means or higher moments that attend negative exponentials.) Recently, the relevance of power-law distributions to self-organizing phenomena has been independently rediscovered by the Santa Fe school of complex systems (Watt, 1999) and currently is the object of much popular interest (e.g. Johnson, 2000). As Ulanowicz and Wolff noted, the log-normal distribution lies at the interface between the well-behaved negative exponentials and the power-law family of distributions. Hence, there will always remain some ambiguity as to which side of this divide some actual data sets may fall, for it is always possible to calculate a mean and higher moments for any *finite* data set. That is, it is sometimes not easy to decide whether some data represent a log-normal distribution or whether they might better portray a closely related, but more poorly behaved, power-law formula. To help clarify this ambiguity, it would be helpful

Task 2.1. To revisit the data on species number distributions to see if a clear distinction can be made as to whether they conform better to the log-normal distribution or to some closely related power-law alternative.

A key instrument in Ulanowicz and Wolff's analysis of ecosystem flow magnitudes was the mutual information of the flows (a particular form of the more general Kullback–Leibler information and one of two factors comprising the ascendency). The mutual information of the flows, I_m , can be calculated in terms of the trophic transfers as

$$I_m = k \sum_{ij} \frac{T_{ij}}{T} \log \left(\frac{T_{ij}T}{\sum_m T_{mj} \sum_p T_{ip}} \right).$$

 I_m is a non-negative component of the overall diversity of flows, H (Ulanowicz and Norden, 1990) defined as

$$H = -k \sum_{ij} \frac{T_{ij}}{T} \log\left(\frac{T_{ij}}{T}\right),$$

and the difference, Φ , between this upper bound and I_m turns out to be

$$\Phi = -k \sum_{ij} \frac{T_{ij}}{T} \log \left(\frac{T_{ij}^2}{\sum_m T_{mj} \sum_p T_{ip}} \right).$$

 Φ is related to the effective number of connections per node, c, which can be calculated as

$$c = b^{\Phi/2},$$

where *b* is the base of the logarithms. In particular, Ulanowicz and Wolff discovered that the quantity $(I_m + \Phi/2)$ was the crucial metric for determining whether the flows in a particular system could be best described by a negative exponential distribution or by a power-law decay. Because the product $T \times I_m$ constitutes a part (but not all) of the biomass-inclusive ascendency, one strongly suspects that the principle of increasing ascendency may lie behind the power-law distribution of ecosystem flows, but a formal connection has never been articulated. Thus, it may prove fruitful

Task 2.2. To search for a formal connection between the ascendency principle and the power-law distribution observed among trophic flow magnitudes.

The search would be an algebraic exercise in the manipulation of the above definitions with the goal of establishing an exact functional relationship between the parameters of power-law functions and the value of ascendency.

Question 3. What relationships, if any, exist between the diversity of ecosystems and their homeostasis or persistence?

During the decade of the 1960s ecology was preoccupied with finding a relationship between the stability of an ecosystem and its attendant diversity. Over time this issue devolved into a search for a connection between biodiversity, as measured by the diversity of species numbers or biomasses, i.e.

$$D = -k \sum_{i} \left(\frac{B_i}{B}\right) \log\left(\frac{B_i}{B}\right),$$

and the stability of the predator–prey dynamics as defined by linear stability analysis. Most of these efforts came to a rather abrupt and ignominious end when May (1973) showed how the problem was poorly-posed. That is, how more diverse systems had a greater probability of being unstable in the linear dynamical sense. The ensuing embarrassment among ecologists engendered a widespread and deep skepticism on their part as to the value of information theory in ecology. Unfortunately, this prevailing attitude persists today, as most ecologists would rather not be bothered with reconsidering the possible utilities of newly formulated information-theoretic concepts in ecology. As a consequence of this attitude, popular worldwide efforts to preserve global biodiversity are largely lacking in theoretical support.

This sequence of events was most unfortunate, especially in light of the fact that the emphasis upon diversity of ecological *stocks* represented a diversion from MacArthur's (1955) original application of Shannon's diversity index to trophic *processes*. Rutledge et al. (1976) were able to return to MacArthur's original viewpoint and apply new concepts in information theory that made use of Bayesian or conditional probabilities to networks of ecosystem *flows*. Their work led directly to the formulation of the ascendency and related indicies, as described above (Ulanowicz, 1980). It may prove fruitful, therefore, to revisit the question of ecological stability in the subsequent light of ascendency theory.

In addressing the relationship between ascendency variables and system stability, it is necessary first to distinguish between two types of stability. The first type concerns the internal stability of a system. How likely is it to fly apart spontaneously? How well does it harmonize with the spectrum of predictable variations in its environment? This "type A" stability is rarely considered under most ecological discussions on the subject, but it should be noted that it is related almost tautologically to the information factor in the ascendency: A system with a high internal stability by definition is one with sufficient internal constraints to bind it into a highly organized structure. That is, systems with high mutual information among their flows almost always possess high internal stability.

The information index is, however, only one of two factors in the ascendency-the other being the total system activity, T. Hence, a high ascendency could as well derive from a very high value of T. In fact, the possibility exists for the ascendency to rise because new resources allow an explosion in system activity that overrides a concomitant decrease in the information factor. Ulanowicz (1986) has used this configuration of changes among the factors of the ascendency to give quantitative definition to the process of eutrophication. The definition has already proven helpful in distinguishing true eutrophication from processes that closely resemble it (Almunia et al., 1999). Thus, although it is clear that too much activity can jeopardize internal stability, the reasons (at the system level) why more activity eventually degrades system organization are not well understood. To shed light on this important transition, it would be helpful

Task 3.1. To employ comparative data on similar mesotrophic and eutrophic habitats to see if the degradation of system organization by increased activity can be described using the sensitivities of the system ascendency to the various system components and processes.

Of particular interest is how the various processes of a mesotrophic system fare after enrichment? Following the logic developed under Question 1 above, one might expect those processes and taxa to which the overall system ascendency is most sensitive would be the first to succumb to enrichment. To what extent do existing data bear out this conjecture? If the hypothesis holds, the sensitivities of the ascendency to each process could be used to ordinate the processes into a triage of the vulnerabilities to over-enrichment.

The second type of system stability refers to how the system reacts to novel or unexpected perturbations. Such "type B" stability is the subject of most discussions on the subject by ecologists. As Odum (1953) suggested long ago, a system with many connections between components is less likely to be vulnerable to disruptions among any particular subset of links. Because Φ reveals the degree of connectivity per node, one reasons that some correlation between this measure and the system's ability to adapt to unexpected disturbances should exist. The relationship is decidedly statistical, however. The environment of every system includes at least some disordered, incoherent events (quantifiable in principle by the same information measures that are used to characterize the system itself). The larger the value of Φ in the system, the greater the probability that some of the dysfunctional elements that contribute to Φ can be used by the system in an emergency to counter the effects of the disturbance. That is, ϕ represents a system's "strength in reserve."

It should be noted, however, that Φ is the margin between the system's organization (I_m) and the upper bound on that organization (H). Hence, in an algebraic, as well as a very real sense, Φ depicts the encumbrance on system ascendency. That is why when Φ is scaled by T, the result is called the system "overhead." Overhead represents all those aspects about the system that, under predictable conditions, detract from system organization and performance. Disorganized, stochastic, inefficient and incoherent aspects of a system's activity all contribute to its overhead. In the absence of perturbations, system ascendency tends to increase at the expense of this overhead, and the ultimate result would be a highly organized, tightly constrained, brittle system—one ready to collapse at the next disturbance. In summary, the answer to the question, "What is necessary to have a stable system?" appears to be: Sufficient amounts of two mutually exclusive attributes—system organization and overhead.

Although network investigators have begun to address the sensitivities of the ascendency to various components, no parallel exploration of the sensitivities of the overhead to system components has been initiated. This suggests the need

Task 3.2. To employ available data on the trophic flow networks of perturbed and unperturbed ecosystems to see if there is any correlation between the a priori sensitivities of the overhead to changes in various system components and processes and the a posteriori response of those elements to disturbance.

This would constitute exploration of wholly new territory. It is even difficult to say a priori what the outcome might be. Will any identifiable connection be possible between the sensitive components of the overhead of the relatively undisturbed network and the structure of the system after disturbance? Following LeChatelier's principle, do the components of the overhead inflate or do new ones appear after disturbance to make the system less vulnerable to even further disturbance? A very few pairs of disturbed–undisturbed networks exist for comparison. One is of a tidal marsh gut ecosystem that was subjected to thermal stress (Ulanowicz, 1984), and another now being created is of comparable eutrophic and mesotrophic estuarine ecosystems in the Mondego estuary in Portugal (Patricio et al., submitted to *Estuarine and Coastal Shelf Science*).

Finally, approximately 30 years of cataloging system biodiversities have elapsed since May's work shut down most theoretical speculation on the relationship between biodiversity and stability. The time has come to reconsider

Task 3.3. Can ascendency theory, which is slanted towards flows or processes, say anything about biodiversity, predicated as that notion is upon stocks alone?

Here it is useful to note that the difference between the (biomass-inclusive) system ascendency and the flow ascendency (call this difference Δ_m) can be quantified by sub-traction as

$$\Delta_m = 2 \left\{ T \log \frac{B}{T} - \frac{1}{2} \sum_i \left[\sum_m T_{im} \log \frac{B_i}{\sum_p T_{ip}} + \sum_m T_{mi} \log \frac{B_i}{\sum_p T_{pi}} \right] \right\}.$$

From this expression one notes that the components of Δ_m represent the deviations between the logarithm of the overall system turnover rate and those of its individual components. Experimenting with various distributions of compartmental throughflows, it may prove useful to investigate what corresponding distributions of biomass would yield high ascendencies? What do the diversities of these biomass distributions look like? Can any formal connection be established between biodiversity and Δ_m ? While finding such a link is a long shot, uncovering one would have enormous payoffs for the global effort to preserve diverse biotic ecosystems.

3. Conclusion

It should be apparent that the formal measure of ecosystem ascendency can be linked to various aspects of the most important topical questions in theoretical ecology. The tasks defined above beg the efforts of talented and interested theoreticians.

Acknowledgements

The author was supported in part by the National Science Foundation's Program on Biocomplexity (Contract No. DEB-9981328). He is grateful to Andrzej Konopka for his encouragement to document these research needs and to an anonymous reviewer for some helpful comments.

Appendix A. A lexicon of terms used in the text

Ascendency (or system ascendency): A measure of how well (efficiently) a system is performing. It is based on a quantification of the constraints that serve to channel network flows (by the mutual information inherent in the pattern of system flows (Rutledge et al., 1976)) and is scaled by the total system activity (see below).

Biodiversity: A measure of the diversity of types (taxa) in a biological community. Biodiversity is a function of both the number of types and the evenness with which the tokens are distributed among those types. It is commonly reckoned using the familiar Shannon–Wiener formula for the potential information inherent in a given statistical distribution.

Biomass: The amount of material of biological origin as measured in some appropriate units of mass.

Diversity (of flows or species): A measure of the richness of identifiable types of flows (processes) or species stocks in an ecosystem network. Usually quantified by applying the Shannon–Wiener formula to the distribution of those flows or stocks.

Ecosystem: The combination of a living community of organisms, acting with the non-living elements of their environment as a functional unit.

Eutrophication (eutrophic): The dysfunctional status of a system resulting from too much input of nutrients.

Exergy: The amount of total energy in a system that is available for doing useful work. (The second law of thermodynamics states that not all of the energy possessed by a system can be converted into useful work.)

Extended ascendency: The ascendency expanded to measure coherence and activity over additional dimensions of space and time.

Internal stability: A measure of the internal constraints that hold a system together as a functioning unit.

LeChatelier's principle: Statement about the homeostasis of systems whereby they tend to respond to a an applied perturbation in such a way as to minimize the effects of that disturbance.

Liebig's law: Statement about the nutrient dynamics of a living population whereby the growth of the population is limited by that nutrient which is being supplied in the least proportion.

Mesotrophic: The condition of a system that is being supplied with a moderate amount of nutrients (as opposed to an over-enriched (eutrophic) or impoverished (oligotrophic) system).

Mesozooplankton: Animals in the range of $20-1000 \,\mu\text{m}$ that move with the flow of water.

Microzooplankton: Animals smaller than $20 \,\mu\text{m}$ that travel with prevailing water currents.

Mutualism: The process whereby two or more populations of organisms contribute mutual benefits to each other.

Overhead: That amount of the diversity of flows that does not contribute directly to system performance (as measured by the system's ascendency).

Persistence: The tendency for a system to continue in existence with the same complement of species and flows.

Phenomenology: The description of events in abstraction from their eliciting causes.

Phytoplankton: Microscopic aquatic plants that drift with the water currents.

Power-laws: Statistical distributions that decrease at rates that are inversely proportional to an algebraic power of their independent variable, i.e. they decrease more slowly than negative exponential functions and eventually diverge for large values of the independent variable.

Primary production: The overall rate at which plant material is being produced (carbon is being fixed) in an ecosystem.

Resilience: The rate at which a perturbed system returns to its unperturbed status.

Stability: The capacity for an ecosystem to remain within an arbitrarily-designated, nominal range of behaviors.

Stocks: The number of individuals or the total amount of biomass that constitutes a given population.

Total system activity (a.k.a., total system throughput): The aggregate amount of system activity as reckoned by summing the magnitudes of all system processes in some common units.

Trophic interaction: A feeding interaction. The act of a predator ingesting a prey.

Turnover rate: The overall rate at which a population or the whole system is replacing its stocks (usually reckoned in units of inverse time).

References

- Almunia, J., Basterretxea, G., Aristegui, J., Ulanowicz, R.E., 1999. Benthic–Pelagic switching in a coastal subtropical lagoon. Estuarine, Coastal Shelf Sci. 49, 363–384.
- D'Elia, C.F., 1988. Nitrogen versus phosphorous. In: McCoy, S.E. (Ed.), Chesapeake Bay: Issues, Resources, Status and Management. NOAA Estuary-of-the-Month Seminar No. 5. US Department of Commerce, Washington, DC, pp. 69–87.
- Johnson, G., 2000. First cells, then species, now the web. New York Times, 26 December.
- Jorgensen, S.E., 1992. Integration of Ecosystem Theories: A Pattern. Kluwer Academic Publishers, Dordrecht, 383 pp.
- Kikawada, H., 1998. Applying Network Analysis to Simulated Ecological Landscape Dynamics. Master's Thesis. University of Maryland, College Park, MD.
- Krivov, S., Ulanowicz, R.E., Dahiya, A., 2003. Qunatitative measures of organization for multi-agent systems. BioSystems 69, 39–54.
- MacArthur, R., 1955. Fluctuations of animal populations, and a measure of community stability. Ecology 36, 533–536.
- May, R.M., 1973. Stability and Complexity in Model Ecosystems. Princeton University Press, Princeton, NJ, p. 235.
- May, R.M., 1990. How many species? Phil. Trans. R. Soc. London B 330, 293–304.
- Odum, E.P., 1953. Fundamentals of Ecology. Saunders, Philadelphia, p. 384.
- Odum, E.P., 1969. The strategy of ecosystem development. Science 164, 262–270.
- Odum, H.T., Pinkerton, R.C., 1955. Time's speed regulator: the optimum efficiency for maximum power output in physical and biological systems. Am. Sci. 43, 331–343.
- Pahl-Wostl, C., 1995. The Dynamic Nature of Ecosystems: Chaos and Order Entwined. Wiley, New York, 267 pp.
- Rutledge, R.W., Basorre, B.L., Mulholland, R.J., 1976. Ecological stability: an information theory viewpoint. J. Theor. Biol. 57, 355–371.
- Rhyther, J.H., Dunstan, W.M., 1971. Nitrogen, phosphorous and eutrophication in the coastal marine environment. Science 171, 1008–1013.
- Schneider, E.D., Kay, J.J., 1994. Life as a manifestation of the second law of thermodynamics. Math. Comput. Modell. 19, 25–48.
- Ulanowicz, R.E., 1980. An hypothesis on the development of natural communities. J. Theor. Biol. 85, 223–245.
- Ulanowicz, R.E., 1984. Community measures of marine food networks and their possible applications. In: Fasham, M.J.R. (Ed.), Flows of Energy and Materials in Marine Ecosystems. Plenum Press, London, pp. 23–47.
- Ulanowicz, R.E., 1986. A phenomenological perspective of ecological development. In: Poston, T.M., Purdy, R. (Eds.), Aquatic Toxicology and Environmental Fate, vol. 9. ASTM STP 921. American Society for Testing and Materials, Philadelphia, PA, pp. 73–81.
- Ulanowicz, R.E., 1997. Ecology, the Ascendent Perspective. Columbia University Press, New York, 201 pp.
- Ulanowicz, R.E., 1999. Life after Newton: an ecological metaphysic. BioSystems 50, 127–142.
- Ulanowicz, R.E., 2000a. Toward the measurement of ecological integrity. In: Pimentel, D., Westra, L., Noss, R.F. (Eds.), Ecological Integrity: Integrating Environment, Conservation and Health. Island Press, Washington, DC, pp. 99–113.
- Ulanowicz, R.E., 2000b. Quantifying constraints upon trophic and migratory transfers in spatially heterogeneous ecosystems. In: Sanderson,

J., Harris, L.D. (Eds.), Series in Landscape Ecology: A Top-Down Approach. Lewis Publishers, Boca Raton, pp. 113–142.

- Ulanowicz, R.E., Norden, J.S., 1990. Symmetrical overhead in flow networks. Int. J. Syst. Sci. 1, 429–437.
- Ulanowicz, R.E., Wolff, W.F., 1991. Ecosystem flow networks: loaded dice? Math. Biosci. 103, 45–68.
- Ulanowicz, R.E., Abarca-Arenas, L.G., 1997. An informational synthesis of ecosystem structure and function. Ecol. Model 95, 1–10.
- Ulanowicz, R.E., Baird, D., 1999. Nutrient controls on ecosystem dynamics: the Chesapeake mesohaline community. J. Mar. Sci. 19, 159–172.
- Watt, D.J., 1999. Small Worlds. Princeton University Press, Princeton, NJ, 266 pp.