Symposium: Emerging Science: Transforming the Next Generation
Session: Thermodynamics and Information Theory in Biology Monday,
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Information Theory and Ecology

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Ecology never has nestled comfortably among the traditional sciences. Of course, it is hardly unique in its lack of "hardness" or predictability. Rather, its singular nature has been characterized by Arne Naess (1988) in his writings about "deep ecology" as something that affects one's life and perception of the natural world in a profound way. Others outside of the field have long been aware of ecology's special nature, and see in their own systems of interest inklings of the the ecological dynamic. Thus it is that we encounter contributions on "the ecology of computational systems" (Huberman 1988) or discover institutes devoted to the "ecological study of perception and action" (Gibson 1979.)

Intuition is most valuable and should never be ignored, but the rationalist in most scientists demands a more explicit account of just what makes ecology so different. In my recent book, "Ecology, the Ascendent Perspective" (Columbia University Press 1997), I have endeavored to outline the foundations for an ecological worldview, with emphasis on how the ecological viewpoint differs from the traditional newtonian metaphysic. Time does not permit a full exposition of this particular perspective on ecology, suffice it to mention that it leans heavily on the insights of two philosophers of science, Karl Popper (1990) and Robert Rosen (1985).

Karl Popper is probably best known for his early contributions to logical positivism. Fewer seem to be aware that Popper later came to eschew positivism and concentrate instead on Charles Sanders Pierce's idea that the natural world is open, as regards causality. More particularly, Popper holds that causes can arise by chance at all scales. This sounds, at first, like nonesense to those of us who were steeped in the newtonian tradition that material and efficient (mechanical) causes are the only legitimate concerns of science. In a reductionistic, clockwork world, the occurence of truly chance events at any scale (save at the molecular and quantum netherworlds) seems sure to wreak havoc with traditional interpretations.

Many ecologists, however, have already parted company with the universality so cherished by physicists, and regard the natural world to be organized hierarchically (Allen and Starr 1982). They regard that rules or laws inherently tend to possess diminishing explanatory power at dimensions far removed from the scales at which they were formulated. The obverse of this assumption allows that the influence of chance events at any one scale might not propagate unattenuated into remote domains. As examples of higher-level ordering phenomena Rosen posits how we need to reconsider the utility of Aristotelean formal and final causes that can exert selection pressure upon chance events occurring at smaller scales.

In Popper's open universe, newtonian- like forces are considered to be degenerate members of a more inclusive set of agencies that he terms "propensities." In keeping with the indeterminate nature of Popper's universe, he relates (but doesn't equate) his propensities to conditional probabilities. Whence, a newtonian force will join an antecedent, A, to a consequence, B, with a conditional probability of unity. If A, then B – no exceptions! But this is hardly the situation encountered in many of the "soft" sciences – among them, ecology.

In certain freshwater systems, for example, there may be a propensity for zooplankton of a certain size range to be consumed by a carnivorous aquatic vascular plant of the genus Utricularia (Bladderwort family.) Of course, every time a zooplankton in one of these systems is consumed, it is not by Utricularia. There are significant likelihoods it might also be eaten by a larval fish, by a planktivorous insect, etc. Thus, an investigator might wish to study the mechanics of various forms of predation upon zooplankton, and couple his/her observations with the relative abundances of the predators on these heterotrophs to arrive at probability assignments for the various predators, e.g., $p(B|A), p(B|C), p(B|D), \ldots$, where A might represent Utricularia and C, D, ..., the various other predators of zooplankton, B.

The conventional wisdom would be to assume these various conditional probabilities are independent of one another, and to proceed with some stochastic modelling scheme. But a fundamental attribute of Popper's propensities is that, unlike forces, they never exist in isolation. Propensities always occur in a context, which usually includes other propensities.

The propensity for Utricularia to consume zooplankton, for example, could foster the propensity for periphyton to grow on the incremental Utricularia, which in its turn might reinforce the propensity for zooplankton to graze on the additional periphyton – giving this triad of self- reinforcing propensities an advantage over others in the system (Ulanowicz 1995).

Popper was able to give no quantitative definition for propensities, and simply called for the development of a "calculus of conditional probabilities." I wish to submit that such a calculus already exists: it is called "information theory". For Tribus and McIrvine (1971) have defined information as "anything that causes a change in probability assignment", and conditional probabilities always relate how a marginal probability changes in response to a particular constraint. For example, the probability, $p(B)$, that a zooplankter is eaten changes to $p(B|A)$ when the predator in question is Utricularia, or to $p(B|C)$, when it is fish, etc.

If one knows the magnitudes of trophic exchanges that occur within an ecosystem, it happens that one can employ concepts from information theory to quantify the degree of constraint inherent in the system as a whole. One begins this assessment by quantifying the extent of activity occuring throughout the system as T, the sum of all transfers, $T_{i,j}$, from each prey, i, to every predator, j. The unconstrained, or marginal probability that any given prey, i, is being consumed can then be estimated by the sum of all the outputs from i, $Ti.$, normalized by the total activity, T. According to Boltzmann, the indeterminacy of this event (feeding upon i) is gauged by the formula

$$Hi = -k \log(Ti./T) \tag{1}$$

In like manner, the conditional probability that a specific predator, j, will consume i is estimated by the quotient $(T_{i,j}/T.j)$, and the indeterminacy corresponding to this revised probability becomes

$$Hi|j = -k \log(T_{i,j}/T.j) \tag{2}$$

Usually, the indeterminacy of the unconstrained situation will be decreased by the imposition of a constraint, so that a measure of the effective constraint (information) can be taken as the difference between (1) and (2), or

$$Hi - Hi|j = k \log(T_{i,j}T/Ti.T.j) \tag{3}$$

One calculates the average, or expected constraint at work within the ecosystem, D, by weighting each measure (3) by the joint probability that i and j co- occur, $(T_{i,j}/T)$, and sums over all possible combinations of i and j (Rutledge et al. 1976),

$$D = k \sum_{i,j} (T_{i,j}/T) \log(T_{i,j}T/Ti.T.j) \tag{4}$$

Finally, we impart physical dimensions to this "average mutual constraint" by choosing $k = T$ (Tribus and McIrvine 1971), and rename the result the system ascendency (Ulanowicz 1980), A,

$$A = \sum_{i,j} T_{i,j} \log(T_{i,j}T/Ti.T.j) \tag{5}$$

Whenever ecosystems develop in the absence of major perturbations, they tend to grow richer in number of species (biodiversity), cycle nutrients more tightly, and their predators tend to specialize upon fewer types of prey (Odum 1969). All other things being equal, increases in these same attributes also contribute to larger values of the ascendency of the web of trophic exchanges. Hence, ascendency may serve as an index of an ecosystem's activity level and organizational status.

In ascendency, ecologists now have a tool with which to compare various ecosystems (e.g, Baird and Ulanowicz 1993), quantify the process of eutrophication (Ulanowicz 1986), set the boundaries on ecosystem "health" (Mageau et al. 1995), define what is meant by the intrinsic value of components to the functioning of the entire ecosystem, and even evaluate the performance of a host of more traditional networks, such as computational ensembles (Ulanowicz 1997).

Information theory reveals that the average mutual information is but a single component of the overall system indeterminacy (more commonly, but erroneously called the statistical "entropy"). The functional indeterminacy of an ecosystem may be identified with the diversity of trophic processes and scaled by T to yield what has been called the system capacity, C,

$$C = -\sum_{i,j} (T_{i,j}) \log(T_{i,j}/T) \tag{6}$$

and where $C > /A > /0$. Subtracting (5) from (6) yields a measure of the degree of unconstrained activity, or freedom remaining in the system. This property has been called the system "overhead", V, and is calculated by the formula

$$V = -\sum_{i,j} T_{i,j} \log([T_{i,j}]^2/Ti.T.j) \tag{7}$$

Although most attention in the popular dialogue about the benefits of biodiversity has centered around numbers of species or distributions of populations, I wish to suggest here that C may be a more appropriate index with which to evaluate ecosystem status. One sees from the relationship $C = A + V$ (which follows from information theory) that the system capacity can be parsed into two measures – one that captures how efficiently the system is currently performing, and its complement, which reveals the functional "strength- in- reserve" that the system retains to meet unknown exigencies (Conrad 1983).

Finally, to return to Popper and his notion of propensities, we note how the definition of the ascendency (5) is analogous to what in irreversible thermodynamics is known as a "power function" (James Kay, pers. comm.) A power function for an ensemble of irreversible physical processes is calculated by multiplying the magnitude of the rate of each process times its congugate "force" and summing over all processes in the ensemble. The force is expressed in appropriate units so as to make the product of flow times force have the units of power, as for example, when a mass diffusion flux is multiplied by its accompanying gradient in chemical potential. In eqn. (5) each trophic transfer, $T_{i,j}$, is multiplied by a corresponding logarithmic factor, and the result is summed over the whole system. The logarithmic term is homologous to the "force" in thermodynamical parlance. But Popper exhorted us to think in more general terms, and we are thus prompted to identify the logarthmic factors instead with the "propensities" for their conjugate flows to happen. That is, corresponding to every trophic transfer, $T_{i,j}$, there is a conjugate propensity, $P_{i,j}$ for that flow to happen, where

$$P_{i,j} = \log(T_{i,j}T/Ti.T.j) \tag{8}$$

Not only does information theory yield an explicit formula to quantify Popper's propensities, we also note that by comparing eqn's (5) and (8) one may recognize that the ascendency itself becomes a flow- averaged propensity for the system as a whole. Because Odum's observations suggest that there is an inherent propensity for ascendency to increase in developing systems, the ensuing propensity- of- a- propensity relationship is reminiscent of the second- order process that constitutes Newton's second law. Because our development began with Popper's generalization of force as propensity, it should not be too surprising to learn that the principle of increasing ascendency bears analogy to all three of Newton's laws of motion (Ulanowicz, in prep.)

I conclude, then, by suggesting that information theory, a tool still eschewed by many ecologists, may become the cornerstone to a more robust, coherent and unified theory with which to interpret ecosystems dynamics. Furthermore, it just might be the calculus most helpful in evaluating our broader options in an evolving, open universe.

References:

Allen, T.F.H. and T.B. Starr. 1982. Hierarchy. University of Chicago Press, Chicago. 310p.

Baird, D. and R.E. Ulanowicz. 1993.Comparative study on the trophic structure, cycling and ecosystem properties of four tidal estuaries. Mar. Ecol. Prog. Ser. 99:221-237.

Conrad, M. 1983. Adaptability: The Significance of Variability from Molecule to Ecosystem. Plenum Press, NY. 383p.

Gibson, J.J. 1979. The Ecological Approach to Visual Perception. Houghton Mifflin, Boston. 332p.

Huberman, B.A. 1988. The Ecology of Computation. North- Holland, Amsterdam. 342p.

Mageau, M.T., R., Costanza, and R.E. Ulanowicz. 1995. The development and testing of a quantitative assessemnt of ecosystem health. Ecosyst. Health 1 (4):201-213.

Naess, A. 1988. Deep ecology and ultimate premises. Ecologist 18:128-131.

Odum, E.P. 1969. The strategy of ecosystem development. Science. 164: 262-270.

Popper, K.R. 1990. A World of Propensities. Thoemmes, Bristol. 51p.

Rosen, R. 1985. Information and complexity. pp. 221-233. In: (R.E. Ulanowicz and T. Platt, Eds.). Ecosystem Theory for Biological Oceanography. Canadian Bulletin of Fisheries and Aquatic Sciences 213, Ottawa.

Rutledge, R.W., B.L. Basorre and R.J. Mulholland. 1976. Ecological stability: an information theory viewpoint. J. theor. Biol. 57: 355-371.

Tribus, M. and E.C. McIrvine. 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. A phenomenological perspective of ecological development. pp. 73-81. In: (T.M. Poston and R. Purdy, Eds.). Aquatic Toxicology and Environmental Fate: Ninth Volume, ASTM STP 921. American Society for Testing and Materials, Philadelphia.

Ulanowicz, R.E. 1995. Utricularia's secret: The advantages of positive feedback in oligotrophic environments. Ecol. Model. 79:49-57.

Ulanowicz, R.E. 1997. Ecology, the Ascendent Perspective. Columbia University Press, New York. 201p.

Ulanowicz, R.E. In prep. Life after Newton: An ecological metaphysic. For Biology and Philosophy.

Brief Vita: Robert E. Ulanowicz

Robert E. Ulanowicz is Professor of Theoretical Ecology with the University of Maryland's Chesapeake Biological Laboratory. He is a 1961 graduate of the Baltimore Polytechnic Institute and received a B.E.S. and Ph.D. in Chemical Engineering from the Johns Hopkins University in 1964 and 1968, respectively. He served as Assistant Professor of Chemical Engineering at the Catholic University of America before joining the Chesapeake Biological Laboratory (CBL) in 1970. He is fluent in German, conversational in Ukrainian and has a reading knowledge of Polish and French.

Earlier at CBL, Prof. Ulanowicz pursued research into the estuarine hydrography of Chesapeake Bay and on methods for inverse modeling of ecological systems. His current interests include network analysis of trophic exchanges in ecosystems, information theory as applied to ecological systems, the thermodynamics of living systems, causality in living systems, and modeling subtropical wetland ecosystems.

Dr. Ulanowicz is the author of over 100 scientific articles and has written two books – "Growth and Development: Ecosystems Phenomenology" (Springer- Verlag 1986) and most recently, "Ecology, the Ascendent Perspective (Columbia University Press 1997.)

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