

On quantifying hierarchical connections in ecology

Jeffrey S. Wicken

The Behrend College, Pennsylvania State University, Erie, PA 16563, USA

and

Robert E. Ulanowicz

*The Chesapeake Biological Laboratory, University of Maryland, Solomons,
MD 20688, USA*

Introduction

Natural selection is not just an antecedental accumulator of ecological success. It also has predictive power in the sense that some strategies for surviving and leaving offspring work better than others in the ecological arena. Adaptive strategies involve the effective utilization of resources, which brings thermodynamic considerations to bear on selection.

The idea that selection has a predictive basis in thermodynamics was first explicitly articulated by Lotka (1922), who argued that those organisms would tend to be selected that were most effective in channelling energy flows through themselves and, at the same time, in increasing total flow through their ecosystems. The importance of this conception is that it suggested that natural selection operated hierarchically—on individuals, populations *and* the higher-order flow patterns in which they participated. This theme has been elaborated in recent years by H. T. Odum (1971). Another general trend in developing ecosystems has been toward increased efficiencies, as measured by biomass/throughput ratios (Margalef, 1968) or specific entropy production. Specialization of flow patterns also increases with ecosystem maturation, as measured by reductions of parallel pathways for processing energy (Ulanowicz, 1980). These trends in ecosystem development suggest systems level principles for their explanation.

In a much referenced paper, E. P. Odum (1969) has advanced 24 empirical indices of ecosystem development. These indices can be divided into two general categories. One involves *macroscopic* trends (e.g. toward increased biomass and closure of mineral cycles); the other involves *mesoscopic* shifts in typical adaptive strategies at the level of populations (e.g. from *r* selection to *K* selection). A coherent theory of selection must connect the two trends.

Before indicating the grounds on which we are suggesting this connection be made, let us note that ecology is occasionally criticized as a discipline that settles for less than rigorous scientific explanations (Ghiselin, 1974; Peters, 1976). Ghiselin argues that ecology excessively resorts to functional explanations for selection (i.e. what the

individual strategy contributes to ecosystem operation). In his view, such explanations are teleological, and hence illegitimate in post-Darwinian enlightenment.

We disagree. Neither ecology nor evolutionary theory can do without functional explanations (Wicken, 1987). The sense of the functional-as-teleological criticism, which has been most recently extended to evolutionary theory by O'Grady (1984), reflects a failure to appreciate the *hierarchical* character of ecosystem structure and operation (Allen & Starr, 1982; O'Neill *et al.*, 1986). Dealing properly with the issue of selection in contemporary discourse requires a hierarchical framework which connects the macroscopic and mesoscopic dimensions of ecosystem development (Rosen, 1969). This paper is written with the idea of setting forth such a framework in the currency of thermodynamics. We hope that this attempt to bridge quantitatively the hierarchical levels in ecology will afford some momentum (at least by way of analogy) to efforts by social scientists to elucidate the interplay between the global society and its member states (e.g. Wallerstein, 1974).

The thermodynamic approach, general rationale

Treating ecosystem dynamics thermodynamically allows the 'units of selection' problem to be generalized in a way that does not exclude any level of the organic hierarchy. The most general units of selection in nature are not individuals *per se*, but informed patterns of thermodynamics flow—of which organisms, populations and ecosystems are all examples. Some flow patterns are superior to others in their ability to command resources and are selected on that basis.

The approach also treats the interaction between hierarchical levels as bilateral, such that neither level has causal or ontological priority over the other. This reciprocity provides a basis for understanding the emergence of functional relationships in ecosystems. Ecosystem flow patterns cannot develop, however competitively advantageous they might prove to be, except through individual or group strategies for surviving and leaving offspring. Conversely, the competitive success of higher-order ecosystemic flow patterns imposes selective conditions in the evolution of individual adaptive strategies. Mutualistic interactions, for example, which reduce specific dissipation and increase biomass/throughput ratios at the macroscopic level, are selected for the competitive advantages they afford individuals at the mesoscopic level.

These competitive advantages *occur* because of the thermodynamic constraints under which ecosystems operate. Selective explanations for ecosystemic trends must make contact with both hierarchical levels. Ecosystems are not autonomous energy-transforming units subject exclusively to higher-order laws of resource flow; nor are they 'sums of parts' whose behaviours are reducible to the dynamics of individual competition. A middle ground must be found that treats both individual and system in context of the other. Since organisms and ecosystems are both energy transformers, a reasonable place to search for such connections is with organism strategies for energy allocation. Considerable work in strategies for resource allocation has already been done (e.g. Townsend & Callow, 1981), but it remains to connect these strategies with macroscopic trends.

The macroscopic level

A useful combination of the aforementioned ingredients in the macroscopics of ecosystem development (flux, efficiency and specialization or flow patterns) has been provided by Ulanowicz's (1980) treatment of 'ascendency', derived from Rutledge *et al.*'s (1976)

conception of 'mutual information' in networks and mathematically tightened by Hirata & Ulanowicz (1984). These relationships can be expressed by treating populations as energy-transforming compartments connected by energy flows. We stress here that we are addressing the information immanent in the *structure* of the energy flow network and are not primarily concerned with the cognitive aspects of information that are so prominent in economic discourse (Hirshleifer, 1973; Hirshleifer & Riley, 1979), although the two forms are amenable to a common calculus.

Of course, throughputs begin with inputs. Once in some element or population of a community structure, energy resources have two possible fates: (1) transfer to another compartment within that structure or (2) export to other systems. All flows will additionally be reduced by thermodynamically obligate dissipations. Given these ingredients, the ascendancy of any macroscopic flow pattern can be written as

$$A = \sum_{i=1}^{n+2} \sum_{j=0}^n T_{ji} \log \left(T_{ji} T / \left[\sum_{k=1}^{n+2} T_{jk} \right] \left[\sum_{m=0}^n T_{mi} \right] \right),$$

$$\text{where total flow } T = \sum_{i=0}^n \sum_{j=1}^{n+2} T_{ij}. \tag{1}$$

n represents the number of populations in the system, and the compartments 0, $n + 1$ and $n + 2$ represent *sources* for exogenous inputs and *sinks* for exports and dissipations, respectively.

It appears that systems evolve along pathways of progressively higher system ascendancy. Such observation has the flavour of a 'variational principle', although teleological behaviour is not thereby implied. However, what is inherent in the macroscopic tendency toward higher ascendancies is a non-cognitive scheme whereby the energetic resources are 'valued' by the system in terms other than their availability of thermodynamic quality (Ulanowicz, 1986).

Ascendancy itself is bounded from above by the community development capacity,

$$C = - \sum_{i=1}^{n+2} \sum_{j=0}^n T_{ji} \log \left[\left(\sum_{k=1}^{n+2} T_{jk} \right) / T \right]. \tag{2}$$

The problem is to relate the macroscopic drive toward increasing ascendancy to the selective pressures at the mesoscopic level. To do this requires that the common currency of thermodynamics be applied to the mesoscopic level as well. Suggestions follow.

The mesoscopic level: growth equations

The dynamics of ecological selection are usually treated by elaborations of the Lotka–Volterra equations, which express the effects of resources, competition and mutualistic or predator–prey interactions on systems of populations. The methodological virtues of this approach to treating biological communities as systems, exhibiting systemic responses to perturbations in particular population numbers or particular correlation coefficients, are considerable. But there are well appreciated limitations to the equations as well (e.g. Pimm, 1982), based on certain underlying assumptions required for their solution.

In the Lotka–Volterra formalism, the rate of change of any population dN_i/dt is as follows:

$$dN_i/dt = N_i \left(b_i + \sum_j a_{ij} N_j \right), \tag{3}$$

where the N_i represent numbers of each population, b_i their presumed density-independent birth rates, and various a represent the effects on N_i of each population j in the system. Since prey populations are limited by resources as well as predation (reflected in a negative value for a_{ij} in the above equation), another way of expressing these dynamics is to make explicit reference to carrying capacity, K (MacArthur & Wilson, 1967). For example, for a prey species in a two-population predator-prey system, one can write that,

$$dN_1/dt = N_1 b_1 (K - N_1 - a_{12} N_2) / K. \quad (4)$$

The difficulty with the latter approach is that while the concept of a carrying capacity is useful for setting the general form of population growth, it is difficult to quantify from independent measurements of resources. The difficulty with the Lotka-Volterra approach generally is that it depends on treating the population coefficients as constants, since this is what makes the equations tractable. But this is at best a loose approximation to reality.

Finally, and most importantly, any overall adaptive strategy for survival and reproduction involves some specific strategy of energy uptake and allocation. While the standard growth equations can be parameterized in ways that show the selective consequences of certain kinds of interactions, the terms in these equations reveal nothing of the strategies for energy utilization that are involved in delivering the adaptive pay-offs. In consequence of this, they can say little about the relationship between the strategic trends and the macroscopic trends expressed in ecosystem development. To make the mesoscopic-macroscopic link explicit, a complementary approach is required which deals with the energetic factors involved at the mesoscopic level of selection. In particular, we would like to have the set of n equations describing population growth link with the various flow terms of the macroscopic equations describing ascendancy and community development capacity. The remainder of this article will suggest a procedure for making this connection.

Energy balances and efficiencies

All selectively significant biological processes involve both outputs (new organization) and the inputs required for their generation. The ratio of useful output to total input is the thermodynamic efficiency of a process. Efficiency in biology can have other meanings as well (Callow, 1977). In addition to the efficiencies of energy utilization, there are also the efficiencies of power—measured as the amount of useful output a system can deliver per unit time from a given resource base. The two cannot be jointly optimized (Odum & Pinkerton, 1955). Thermodynamic efficiencies are maximized in reversible processes, where the power of a thermodynamic flow approaches zero. Biological strategies must evidently be geared to achieve those particular balances of thermodynamic and power efficiencies that optimize the conversion of environmental resources into self and seed.

Of prime selective import to any organizational type, and its supporting informational programs, is the conversion of potential energy (I) from the environment into self-maintenance (SM) and the production of progeny organizations (R). All an organism's metabolic processes and behavioural devices subserve the end of organizational success and are selectively justified only by the contributions they make to it (cf. Callow, 1977).

The survival-reproductive efficiency of the organism can be defined as,

$$SRE = (SM + R)/I. \quad (5)$$

The source for *SRE* comes from the various terms in the allotment of ingested energy *I*. These may be crudely classified as follows: (1) behavioural costs (*B*) in energy procurement, predator avoidance and reproduction (including the costs of nurture); (2) metabolic cost (*M*) of growth, biosynthesis, homeostasis and physiological operation; and (3) detritus (*D*), representing the metabolically unused portions of *I*. Thus,

$$SM + R = I - (B + M + D). \quad (6)$$

The adaptive problem is to optimize ($SM + R$).

The variables on the right side of Eqn (6) are interdependent, such that decreasing one tends to increase the others. For example, ingested energy comes in various qualities with different kinds of metabolic accessibility. For a rabbit to reduce its *D* losses by thoroughly degrading cellulose to glucose would require drastic organizational modifications with considerable metabolic costs. Each adaptive strategy carries with it a metabolic strategy, which utilizes some forms of energy and rejects others. Similarly, decreasing the metabolic work of biosynthesis can only be achieved through predatory, symbiotic or parasitic relationships with other organisms that do carry out those biosyntheses—strategies which affect *B* in significant ways. These trade-offs are highly important in establishing the particularities of adaptive strategy, and they also are important to certain ecosystemic trends.

Given the necessity of these various trade-offs, the most straightforward way to maximize ($SM + R$) would simply be to increase *I* and the reproductive rate. In an ecological vacuum, where nutrients were unlimited and predatory pressures absent, this would be precisely the route to success. This is the general strategy of those intensely *r*-selected species which flourish under episodic conditions of plenty. However, in more stable ecosystems, where competition is acute and carrying capacities are approached, this strategy must give way to trade-offs in which the components of ($B + M + D$) are adjusted to give a maximal difference with *I*. These strategies are all developed in the hierarchical context of the individual–population–ecosystem relationship. Preserving and propagating the organizational type is the selective source of all adaptive strategies. But the fact that such strategies are played out in an ecosystemic arena of limited, and limiting, pools of resources imposes certain constraints on the forms they can take.

From the organism-centred perspective, the optimal solution to survival–reproduction under scarce resources would be to reduce ($B + M + D$) to just those proportions required for a direct channel from environment to *R*. This is the strategy of parasitism, and its selective pay-offs have been indicated by a variety of experiments. Biosynthetically diminished microbial mutants have considerable competitive advantages over wild types in suitably reconstituted growth media (Pauling & Zuckerlandl, 1972), as do informationally diminished viral mutants over intact virus in media which do not require infective function (Spiegelman, 1971). Whenever organisms in a given environment are presented with a source of nutrients that they ordinarily make for themselves, survival–reproductive economy selects for divestment of redundant machinery.

While this is the recipe for parasitic devolution rather than for evolution as an ecological phenomenon, the thermodynamic ingredients involving the partitioning of energy flows provides for understanding the latter as well—including its progressive or anagenic dimension. Nature does not provide its fruits *gratis*, in the manner of a laboratory scientist. For the jettisoning of metabolic machinery to be an adaptively successful move in evolution, it must be compensated by appropriate behavioural

modifications which provide for the exploitation of the metabolic labours of other organisms—trading M for B .

Thermodynamic growth equations

The energy balance in Eqn (6) might be regarded as a first law of ecosystem dynamics, analogous to the first law of thermodynamics. However, it contains ingredients from both laws of thermodynamics, because part of the balance includes entropic losses. The competition among alternative patterns of energy flow for resources (natural selection) might then be regarded as a second law of ecosystem dynamics. Investigating the relationships between the various indices of ecological development and these two principles by relating mesoscopic and macroscopic trends requires a formal structure for assessing the effects of energetic trade-offs on population growth. This in turn requires an energy allocation analogue to the Lotka–Volterra equations.

The energy balance equation concerns energetic costs and organizational outputs. But since organization is constantly being produced and degraded, this equation does not deal explicitly in net useful output. For the present purposes, it is useful to treat organisms as devices for making progeny, which, given their own energy expenditures, have the developmental potential for becoming reproductive adult organizations of the same type.

Given a population of N organisms (making no distinction between reproductive adults and progeny), the energy focused per unit time into the potential energy of new organization is $N(\dot{I} - \dot{B} - \dot{M} - \dot{D})$, where the terms inside the parenthesis are the various time rates of energy change averaged over all members of the population. At this crude level of resolution, B contains all the behavioural costs connected with self-production and reproduction. The former include predation and its avoidance, as well as competition for resources. The latter include parental investment in reproduction and nurture as well as progeny investment in their own development to adulthood. Using these relationships, one can write that,

$$dU_i/dt = N(\dot{I}_i - [\dot{B}_i + \dot{M}_i + \dot{D}_i]) - rU_i, \quad (7)$$

where U_i is the total potential energy of the N organisms constituting population i , dU_i/dt is the time rate of change of this potential energy, and r is its average specific rate of disappearance through age, disease or predation.

Since the inputs I_i available to a population will be bounded by limiting environmental resources, this equation has the same general form as the Lotka–Volterra equations. It can, moreover, be rewritten in populational terms that make this connection explicit, by substituting for the total energy U of the population the product uN , where u is the average energy of each organization. Eqn (7) can then be written as,

$$dN_i/dt = N(\dot{I}_i - [\dot{B}_i + \dot{M}_i + \dot{D}_i])/u - r. \quad (8)$$

Again, there are n of these equations for each community structure.

These equations are compatible with the standard logistic equations, but they have very different potential applications. Instead of focusing on the formal parameters contributing to time changes in populational numbers *per se*—such as birth rates, competition and predation—they focus on their energetic sources. Each of the terms in parentheses represents a differential equation of its own, based on the various morphological features of the organisms constituting that population. Each therefore represents a thermodynamic adaptive strategy, which can be used to help interpret macroscopic trends in terms of mesoscopic energy transfers.

The point of this formulation is to quantitatively connect the rates of energy flow and population change to the internal strategies by which organisms deploy energy to survive and reproduce successfully. For given organizational types, variants able to increase the difference between intakes and expenditures will enhance their growth equations and, under selection, eventually become the dominant vehicles for energy transformation. Strategies which can be predicted to evolve under limiting resources are (1) the surrender of biological autonomy through parasitic or symbiotic interactions; (2) the reduction of metabolic work by eliminating the biosyntheses of resources obtainable from other organisms. Such predictions are verified in the movement toward mutualistic interactions in ecosystem development. Finer levels of resolution might be provided by examining populations with regard to patterns of energy utilization among reproductive adults, non-reproductive adults and progeny, but this is well beyond the scope of this contribution.

Connections

Expressing the growth equation in energetic terms allows formulation of adaptive strategies in a way that makes possible specific connections between the dynamics of individual selection and macroscopic ecosystemic trends. Eqn (7) expresses, in effect, a populational pathway of thermodynamic flow. The energetic ingredients in this pathway show the general kinds of adaptive niches a given population opens for the evolution of other populations, and hence an energetic basis for the phenomenon of co-evolution generally. There are two energy outputs in that equation. One is useful output U for that organizational type. The other is detritus D . Both are potential sources of inputs for additional pathways of thermodynamic flow. Such pathways are predicted to ramify over the course of evolution as new strategic vehicles appear and are selected for in terms of energy utilization.

Requirements for competitive success at the mesoscopic level reflect themselves in macroscopic trends. For example, since it is not strategically advantageous for a rabbit to digest most of its cellulose intake, the 'rabbit strategy' opens thermodynamic space for decomposer strategies with different behavioural and metabolic components. The consequence of this chain of relationships is to increase total biomass and decrease specific dissipation. Efficiencies at the upper level are attained by thermodynamic exploitation at the lower level. In general, increasing organization and increasing efficiency parallel each other, since with organization comes the economies of specialization and mutualism. Conversely, the availability of resources at the upper level constrains adaptive strategies at the lower level. The interaction of mesoscopic and macroscopic is bilateral.

The n equations of types (7) and (8) each describe a population's strategy for energy utilization. Thus, the I_i of each equation is identical to the throughput $T_i = \sum_j T_{ij}$ for any compartment in Eqns (1) and (2). The assignment of connections is at least *formally* straightforward. First, there will be entropic dissipation S_i connected with *each term* within the bracketed portions of those equations. So not only will each of the n compartments representing populations have a portion of flow diverted to compartment $n + 2$, but those portions of flow can be further resolved at the mesoscopic, strategic level as parameters which might be subject to optimization. Second, the energy of some populations will be internally routed to other compartments through the food and detritus webs. Finally, some populations P_i will have exports, and have portions of T_i routed to compartment $n + 1$.

The influences of these systems level connections on macroscopic trends can be assessed through optimization modelling by asking how different combinations affect community development capacity and ascendancy—or power and efficiency for that matter. One should be less concerned with macroscopic modelling *per se* than with modelling the mesoscopic–macroscopic connection. It is necessary to consider both the effects of different strategies of energy use on macroscopic trends and the effects of macroscopic conditions (e.g. resource availability) on strategy selection. As an example: elaborate detrital food chains are characteristic of mature ecosystems. Appropriate questions to ask here concern (1) the macroscopic effects of shifting the representation of D_i and U_i in the total food web, and (2) the selective pressures for this shift imposed by changing macroscopic conditions.

The mesoscopic–macroscopic interconnection provides a framework for understanding the possibilities for strategic modification available to a given organizational type—along with the possible pitfalls of overadaptation it might encounter. The terms in the bracketed portions of Eqns (7) and (8) can themselves be written (in principle) as differential equations dependent upon selectively modifiable features—such as size, homeostasis or number of biosynthetic pathways.

It remains to develop a usable thermodynamic, hierarchical theory of selection. One avenue might be to derive Odum's (1969) empirical indices theoretically, using computer optimization techniques (Cheung, 1985) with mesoscopic–macroscopic flow patterns—then to begin to apply the theory predictively to some of the practical problems of ecosystem development in the ways suggested above. This is certainly not an easy task, but it is one well worth undertaking, for it is high time that hierarchy theory in ecology moved beyond just words into the realm of quantitative substance. Besides, reconciling the macroscopic and mesoscopic descriptions of ecology should afford penetrating insights into the nature of the world rivalling those provided by the theories of Darwin and Boltzmann.

References

- Allen, T. F. H. & Starr, T. B. (1982). *Hierarchy*. Chicago: University of Chicago Press.
- Callow, P. (1977). In (A. MacFadyen, Ed.): *Advances in Ecological Research*, vol. 10. London: Academic Press, pp. 1–62.
- Cheung, A. K.-T. (1985). *ECONET: Algorithms for Network Optimization in Ecosystem Analysis*. Technical Report 423, Department of Mathematical Sciences, Johns Hopkins University, Baltimore.
- Ghiselin, M. (1974). *The Economy of Nature and the Evolution of Sex*. Berkeley: University of California Press.
- Hirata, H. & Ulanowicz, R. (1984). *Int. J. Syst. Sci.* **5**, 261–273.
- Hirshleifer, J. (1973). *Am. econ. Rev.* **63**, 31–38.
- Hirshleifer, J. & Riley, J. G. (1979). *J. econ. Lit.* **17**, 1375–1421.
- Lotka, A. J. (1922). *Proc. natl Acad. Sci. USA* **8**, 147–155.
- MacArthur, R. & Wilson, E. O. (1967). *The Theory of Island Biogeography*. Princeton, New Jersey: Princeton University Press.
- Margalef, R. (1968). *Perspectives in Ecological Theory*. Chicago: University of Chicago Press.
- Odum, E. P. (1969). *Science* **164**, 262–270.
- Odum, H. T. (1971). *Environment, Power, and Society*. New York: Wiley & Sons.
- Odum, H. T. & Pinkerton, R. (1955). *Am. Sci.* **63**, 331–343.
- O'Grady, R. (1984). *J. theor. Biol.* **109**, 563–578.
- O'Neill, R. V., DeAngelis, D. L., Waide, J. B. & Allen, T. F. H. (1986). *A Hierarchical Concept of the Ecosystem*. Princeton, New Jersey: Princeton University Press.
- Pauling, L. & Zuckerkandl, E. (1972). In (D. Rolfing & A. Opatin, Eds): *Molecular Evolution: Prebiological and Biological*. New York: Plenum Press, pp. 113–126.

-
- Peters, R. H. (1976). *Am. Nat.* **110**, 1–12.
- Pimm, S. L. (1982). *Food Webs*. London: Chapman & Hall.
- Rosen, R. (1969). In (L. L. Whyte, A. G. Wilson & D. Wilson, Eds): *Hierarchical Structures*. New York: American Elsevier, pp. 179–199.
- Rutledge, R. W., Basorre, B. L. & Mulholland, R. J. (1976). *J. theor. Biol.* **57**, 355–571.
- Townsend, C. R. & Callow, P. (Eds) (1981). *Physiological Ecology: An Evolutionary Approach to Resource Use*. Sunderland: Sinauer Associates.
- Ulanowicz, R. (1980). *J. theor. Biol.* **85**, 223–245.
- Ulanowicz, R. (1986). *Growth and Development: Ecosystems Phenomenology*. New York: Springer-Verlag, 203 pp.
- Wallerstein, I. M. (1974). *The Modern World-System*. New York: Academic Press, 410 pp.
- Wicken, J. (1987). *Evolution, Thermodynamics and Information: Extending the Darwinian Program*. New York: Oxford University Press, 243 pp.