EVOLUTION IN THERMODYNAMIC PERSPECTIVE: AN ECOLOGICAL APPROACH[1]

Bruce H. Weber
Department of Chemistry and Biochemistry
California State University, Fullerton
Fullerton, CA 92634

David J. Depew
Department of Philosophy
California State University, Fullerton
Fullerton, CA 92634

C. Dyke
Department of Philosophy
Temple University
Philadelphia, PA 19122

Stanley N. Salthe
Department of Biology
Brooklyn College
City University of New York
Brooklyn, NY 11210

Eric D. Schneider
Chesapeake Biological Laboratory
University of Maryland
Solomons, MD 20688

Robert E. Ulanowicz
Chesapeake Biological Laboratory
University of Maryland
Solomons, MD 20688

Jeffrey S. Wicken
Behrend College
Pennsylvania State University
Erie, PA 16509

Evolution in Thermodynamic Perspective: An Ecological Approach

ABSTRACT: Recognition that biological systems are stabilized far from equilibrium by self-organizing, informed, autocatalytic cycles and structures that dissipate unusable energy and matter has led to recent attempts to reformulate evolutionary theory. We hold that such insights are consistent with the broad development of the Darwinian Tradition and with the concept of natural selection. Biological systems are selected that are not only more efficient than competitors but also enhance the integrity of the web of energetic relations in which they are embedded. But the expansion of the informational phase space, upon which selection acts, is also guaranteed by the properties of open informational-energetic systems. This provides a directionality and irreversibility to evolutionary processes that are not reflected in current theory.

For this thermodynamically-based program to progress, we believe that biological information should not be treated in isolation from energy flows, and that the ecological perspective must be given descriptive and explanatory primacy. Levels of the ecological hierarchy are relational parts of ecological systems in which there are stable, informed patterns of energy flow and entropic dissipation. Isomorphies between developmental patterns and ecological succession are revealing because they suggest that much of the encoded metabolic information in biological systems is internalized ecological information. The geneological hierarchy, to the extent that its information content reflects internalized ecological information, can therefore be redescribed as an ecological hierarchy.

This thermodynamic approach to evolution frees evolutionary theory from dependence on a crypto-Newtonian language more appropriate to closed equilibrial systems than to biological systems. It grounds biology non-reductively in physical law, and drives a conceptual wedge between functions of artifacts and functions of natural systems. This countenances legitimate use of teleology grounded in natural, teleomatic laws.

KEY WORDS: Nonequilibrium thermodynamics, information, informed patterns of energy flow, ecological hierarchy, geneological hierarchy, succession, development, Darwinian tradition, reductionism, teleology, natural selection

INTRODUCTION

It is universally conceded that biological systems conform to the constraints of the Second Law of Thermodynamics. But most workers have not thought that this, or any other physical law, plays a positive role in explicitly biological reasoning. Recently, however, the notion has gained currency in some quarters that thermodynamical laws do indeed play an informative role in undergirding biological, and especially evolutionary, explanations. This opinion has gained ground in proportion as thermodynamics itself has been expanded to deal with open systems stabilized far from thermodynamic equilibrium. For biological systems at all levels of scale ranging from cellular pathways to ecological systems possess to a high degree the generic properties exhibited by all far-from-equilibrium systems.

In this connection, three highly general propositions have assumed particular importance:

P1: Biological systems are stabilized far from equilibrium by way of self-organizing, autocatalytic structures that serve as pathways for the dissipation of unusable energy and material. Because biological systems are "dissipative structures" in this sense, entropy production and organization are positively correlated (Prigogine, 1980).

P2: Biological systems that dissipate energy more effectively than others will proliferate differentially over competitors, not only because they will utilize resources more effectively than their competitors, but also because they will enhance the integrity and persistence of the web of energetic relations of which they are themselves parts. That natural selection may be conceived as serving this function implies a restatement, rather than a refutation, of the Darwinian tradition (Lotka, 1922, 1925; Wicken, 1987).

P3: Informational complexity, in the form of genetic variation, is subject to the Second Law, which forbids errorless replication for real dissipative systems with finite energy sources. Over time, there is not only an exploration of genetic phase space but an expansion of that phase space. The increase of genetic phase space so guaranteed is an important explanatory factor in phylogeny (Brooks and Wiley, 1986, 1988).

The fact that P1 does not entail P2 and that P2 does not entail P3 suggests that exploration of the relation between evolution and nonequilibrium thermodynamics has not yet resulted in an articulated paradigm and that much foundational work remains to be done. *It is the opinion of the authors of this paper that these inchoate ideas cannot be developed and assessed adequately, or their implications for current evolutionary theory set forth, unless the ecological, and hence energetic, framework in which all such processes are set is given descriptive and explanatory primacy.* We mean this in at least the following three senses:

P4: Just as ecological systems are relational parts of the entire terrestrial biosphere, so all the other levels of what is sometimes called the ecological hierarchy (Eldredge and Salthe, 1984, Eldredge, 1985, Salthe, 1985) are *relational parts* of ecological systems. These include ecosystems, populations, organisms; and, within the economy of the organism itself, cells and biological molecules. All of these are relatively stable, *informed patterns of energetic flow and entropic dissipation, between which selection occurs at various levels.*

P5: Biological systems exhibit diachronic developmental patterns non-trivially analogous to those of ecological systems. The pattern of ecological succession is found as well in the pattern of individual organismic growth.

The point here is not the discredited one that ecological systems are "super-organisms," exhibiting patterns paradigmatically found in developmental biology, but, on the contrary, that developmental patterns are informed patterns of energy flow that have been in-*corp*-orated (literally) by way of information-bearing macromolecules into metabolic pathways.

P6: Much, but not all, encoded information, which enhances autocatalytic processes by increased replicative fidelity, is stored metabolic information and hence [by P5] is internalized ecological information. The genealogical hierarchy that has been distinguished from the ecological hierarchy (Eldredge, Eldredge and Salthe, Salthe) is itself (differently considered) an ecological hierarchy to the extent that its information reflects internalized ecological information. Thus the fact that the branching patterns of phylogeny depend on the Second Law does not by itself imply that this process can be understood either causally or descriptively apart from analyzing energetic pathways.

We put these points forward both as a contribution to theoretical biology and with a view to suggesting that this perspective has important implications for standing issues in the philosophy of evolutionary theory and for the philosophy of biology more generally.

The fact that natural selection may be conceived as differential survival of informed pathways of energy flow does not undermine the core (in Lakatos' [1970] sense) of the Darwinian tradition. Darwinism holds fundamentally that evolutionary change will occur whenever historially conserved variation is accompanied by differential retention (Lewontin, 1974). Selection among differential kinetic pathways in accord with thermodynamical imperatives fully meets these conditions. Thus these ideas are not put forward to "falsify" Darwinism or to render it obsolete in the light of a more general theory. On the contrary, our effort is to update and enrich the Darwinian tradition by reorienting evolutionary science around ecology, thermodynamics and information science in a way that allows us more deeply to understand the underlying dynamics of natural selection, while keeping population genetics as an integral part of the expanded whole. We are thus conservatively attuned to the Darwinian tradition, although we do not retain an expectation of the hegemony of selective processes, but expect that in this richer context it is likely that other evolutionary principles will be recognized as equally important.

What this reorientation does call for is recognition of the fact that the Darwinian tradition, as it has hitherto been articulated, has been encoded within a framework of high-level assumptions about systems dynamics that can be called approximately Newtonian or equilibrial. Taken up by Darwin through Lyell and Malthus, and reflecting the general cultural milieu in which Darwin worked, equilibrial assumptions have been spectacularly successful in organizing several centuries of productive research. Neo-Darwinism is a research tradition that reflects this success. Its fundamental principle, the Hardy-Weinburg Equilibrium Formula, announces its dynamical commitments on its face. It is true that neo-Darwinism reflects a shift from the determinism of Newtonianism, properly so called, to statistical descriptions and "population thinking," on the model, much emulated by Fisher, of statistical mechanics. It nonetheless remains true that the connection between equilibrium thinking and Darwinism is a contingent one; and that further development of the Darwinian tradition may now require loosening the grip of such paradigmatic structures:

P7: Because biological systems are stabilized far from equilibrium they are imper-
spicuously described, and only weakly explained, in a crypto-Newtonian language
appropriate to isolated or closed equilibrium systems.

One measure of progress in the development of any science is its ability
to make close contact with other sciences. In the present case contact is
urged between evolutionary biology and physics and informational science.
It is especially important to point out at the outset, therefore, that

P8: While we take a dim view of the 'autonomy-of-biology' position commonly de-
fended by neo-Darwinians (Mayr, 1982; 1985), the emerging paradigm espoused
here does not seek to "reduce" biology to chemistry and physics.

No science has a permanent, natural, defensible frontier, any more than
the Roman Empire did. Rather, just as the most productive estuaries in
the natural world are those most open to environmental exchanges, so too
the most productive science is that which looks for connection with, and
fertilization from, other disciplines. In the present instance, we seek to
expand biology by judiciously incorporating concepts from the physical
and informational sciences. Far from leading to the reduction of biology to
physics this effort effectively points out what is unique about the biological
world — the stabilization and articulation of energetic pathways by
informational macromolecules, and by the conservation and expansion of
functional information through phylogenetic time. It also changes and
expands the boundaries of physics and chemistry. It is, in short, an
interfield theory (Darden and Maull, 1977) rather than a reduction of one
theory to another.

This cross-fertilization is especially effective in two related areas. It
provides the deep causal principles underlying variation, constraint and
selection, and it allows us to incorporate the emergence of life within the
resultant framework. Darwin would have approved. The inability of the
science of his day to account for the existence of living organizations
vexed him. Reluctantly, he was obliged to take life as a 'given' in order to
move evolutionary thought onto a solid, scientific plane. Now, however,
we can talk about the self-organizing principles that lead to life's emer-
gence in a way that is entirely consonant with the broad Darwinian
schema referred to above.

This perspective has implications, finally, for problems about biological
teleology. The well known tendency of adaptationist explanations in
evolutionary biology to degenerate into illegitimate design-teleology or
"just so stories" represents an acknowledged weakness in current evolu-
tionary theorizing (Gould and Lewontin, 1979). This tendency comes
from viewing natural selection as an alternative means to achieving the
same *kind* of effects as those achieved by design and craft. Like crafts-
manship, natural selection seems on this view to presuppose a picture in
which raw materials are worked up into functional wholes that are them-

selves regarded as assemblages of decomposible and ontologically distinct parts. Among the disadvantages of this assumption is that it sustains the *conceptual* possibility of creationist arguments in a scientific milieu that has overwhelmingly powerful empirical arguments against them. Our view is that:

> P9: When informed patterns of energy flow are treated as units of selection a conceptual wedge is driven between the functions performed by artifacts and the functions performed by natural processes, whose self-organization results in pathways for energy flow and entropic dissipation. This allows us to distinguish legitimate from illegitimate senses of 'teleology', and to ground the former in natural, teleomatic laws.

ECOSYSTEMS PHENOMENOLOGY, ASCENDENCY AND DEVELOPMENT

The focus of ecology is relational. Ecologists concern themselves primarily with the processes that connect species and populations into symbiotic relationships, food chains and other patterns. The fascination of ecologists with homeostatic and mutually adaptational processes so evident among communities of populations has given rise to the view of an ecosystem as a "superorganism" (Cf. Clements and Shelford, 1939, and recently Lovelock, 1979). However, the scorn justly heaped on such notions by biologists and philosophers of science, as well as the tendentious social and political philosophy to which it lent credibility, led to a chastening of ecology. It was eventually reintegrated into the neo-Darwinian Synthesis as a discipline in which ecological systems were construed as the outcome of predator-prey relations governed by the Lotka-Volterra equation and of other dynamics that could be accounted for in terms of competition among individual organisms for scarce resources. Group selection hypotheses were discredited. With these developments, however, the emphasis of early ecologists on the community as a pattern of energy and matter flow was also lost. Attention shifted, under the influence of neo-Darwinian ideas, toward "diversity of population levels" as a surrogate for diversity of flows.

Modern ecosystems phenomenology traces its origins to the students of G. E. Hutchinson, who emphasized the importance of measuring palpable transfers of material and energy among the elements of a living community. Lindeman (1942) sought to portray the influence of the Second Law as a constraint that ordered the "trophic pyramid" inherent in the energy flows occurring in a shallow water lake ecosystem. With his death it fell to Eugene and Howard T. Odum to advocate the measurement of networks of flows occurring in ecosystems. Early among Eugene Odum's (1953) observations was the notion that ecosystem homeostasis could be maintained through the existence of compensatory flow pathways. That is,

if more than one concatenation of transfers linked two arbitrary species in a community, the unexpected disruption of one or some of those pathways might be compensated by augmented flow through those linkages that remained relatively unperturbed.

Eugene Odum took advantage of the flow compensation idea to set forth an entire suite of observations on the development of ecosystems. He listed twenty-four attributes that were correlated with mature communites in the later stages of succession (E. Odum, 1969; Schneider, 1988). These are combinable into five categories. Mature communities tend to possess:

    i. increased energy flow
    ii. greater variety of species
    iii. more narrow trophic specialization by their members
    iv. enhanced amount of cycling
    v. longer retention of media in the system.

At the heart of this ordering process stands the kind of positive feedback inherent in autocatalytic cycling studied by Eugene and Howard Odum (Odum and Odum, 1982; Odum, 1988). In its simplest idealization autocatalytic feedback may be thought to result from a concatenation of positive influences, where one item in the chain catalyzes another. In the ideal cases, the causal links in the loop are the only ones present, and the system appears as a wholly autonomous structure. Of course, real causal loops are always embedded within larger networks of causalities. If one observes only some of the elements of a loop, they will appear to function in a non-autonomous fashion at the behest of the boundary conditions that drive them. However, once the scale of observation is enlarged to include all members of the loop, its overall autonomy then emerges as an attribute of the expanded system as a whole. Seen in this light, the extensive effect of a feedback loop is to enhance the aggregate system activity. Thus an increase in the activity of any element in the loop will propagate to augment the activities of all loop members, including itself.

Seen functionally, the role of autocatalytic feedback is to exert selection pressure upon its own members and to compete with neighboring loops for system resources. Any change in the properties of a loop element that abets its action upon the next member will be rewarded in the next pass. Conversely, changes that diminish autocatalytic activity are self-inhibiting, and the elements in such loops are subject to replacement by newer, more effective components. One can readily imagine, then, a situation wherein all the original members of a loop are replaced in turn, while the loop itself persists beyond the more transitory durations of its components. The same feedback cycle will then have played an active role in influencing what the replacement parts would be.

The overall directional effects of positive autocatalytic feedback loops in networks of flows define the *ascendency* of the system (Ulanowicz,

1986). Ascendency quantifies the total energy transfer in the system and the level of the interconnectiveness among the components of that eco-system. Change in ascendency reflects the effects of positive feedback as an agent in the successive restructurings of the system. Ascendency is measured by dividing the ecosystem into compartments that serve as nodes of the network. Directed graphs are then drawn indicating flows. The mathematical techniques required to estimate ascendency are a combination of Leontieff's input-output analyses with information theory (see Appendix I for a description).

Of course, no system can grow and develop without bounds. Against the inherent tendency of systems networks to become ever more articu-lated stands the vulnerability of such configurations to perturbations. Redundant pathways offer a certain "strength-in-reserve" by virtue of the compensatory rerouting they afford. If a perturbation is entirely new to a community, the system's ability to adapt successfully to it will hinge on the availability of residual, less effective pathways, or even on outright stochastic configurations (Von Foerster, 1960; Atlan, 1974; Conrad, 1983). Losses from the system and the multiplicity of inputs also detract from the rise in ascendency. It is, in fact, never possible to eliminate completely all exogenous transfers. Some of the dissipative losses are in fact necessary to maintain structure at lower levels; and some of the exports to other systems from links in higher-order reward loops. Finally, a system with but a single input is highly vulnerable to disturbance in that source. Hence, that external factors will be the most pronounced factor in a system's fate follows from the very same principle in virtue of which ascendency rewards the increasingly modular stability that we refer to as hierarchical. Each of these influences detracts from the rise in ascendency. These detractors can be quantified in mathematical terms similar in form to those used to measure the ascendency itself. It was, in fact, to quantify such "strength-in-reserve" that Rutledge *et al.* (1976) first correctly applied information theory to flow networks.

Let us look at a number of phenomenological patterns in ecological succession in the light of these principles:

P10: Ecosystems favor species that, in funnelling energy into their own production and reproduction, also increase the total energy flow through the ecosystem.

P11: In succession there is a maximization of energy flow into organizational progaga-tion and a minimization of metabolic costs.

P12: After an initial increase, a monotonic average decrease in the intensity of energy flow (i.e. a weight-specific energy flow) through an open system occurs.

P13: A continual, hyperbolic increase in complicatedness (= size + number of com-ponents + organization) develops.

P14: An increase in internal stability occurs as the rate of development slows down.

P15: There is a corresponding decrease in stability to perturbations.

P10 is a statement of Lotka's power principle (Lotka, 1922, 1925). P11

and P12 together might be thought of as the allocation of a given energy flow to an increasing number of parts insofar as these systems grow. It may also, to some degree, be a consequence of P13 when the decrease mentioned in P12 becomes absolute. P13 is the locus for discourse about macroscopic information and its increase. P12 and P13 are a result of the action of the Lotka/Odum maximum power principle, which is fully realized only in immature stages. P14 could be a consequence of P12 or P13, either separately or together. P11 through P14 reflect the influence of Prigogine's principle of minimum entropy production, which only begins to be realized in these systems during senescence. P14 and P15 together define senescence.

These rules of succession are also applicable to the global ecosphere, which is itself a thermodynamically open system that processes radiant energy from the sun, and exports what is not retained as heat to the sink of space. In a broad sense we note that a decrease in the intensity of energy flow across the surface of the earth has taken place since Hadean times (P12), when the planet was much hotter, was unscreened from the sun, and was subjected to numerous impacts from bodies that would subsequently have burned up in the atmosphere. Meanwhile, an increase in stored information has occurred (P13) — first with the separation of phases in the Hadean period, then with the gradual separation of ores, then with an increase in the diversity of living forms, and finally, just a little while ago, with the increase in the complicatedness of human artifact-mediated production. Whether this process has been, or will be, accompanied by an increase in internal stability and a decrease in stability from external insults (P14—15) remains an open question.

We may also see the same phenomenological rules of succession at work in the development of social systems, presumably among all social animals but in a particularly vivid way in human societies. Cities, for example, are dissipative structures (Dyke, 1988b). They exhibit universal patterns of economic self-organization in which internal complexity, including the peculiar kind of information contained in cultural meanings and other ideological forms, results in progressively more effective ways of directing energetic flow through the system (Odum, 1988). Cities recur and persist as the chief nodal links between the kinship systems out of which they arise and the national and transnational economic systems into which they are (sometimes) linked. The history of their rise, competition as attractors and their eventual, inevitable decline closely parallels the phenomenological rules we have traced.

These phenomenological symmetries between ecosphere dynamics, ecosystem succession and social evolution are striking. *They are, however, far less striking than the fact that the patterns seen in P10—P15 are also observable in, and applicable to, the development of individual organisms* (Zotin, 1972). The first three rules (P10, P11, P12) indicate that the

organism gradually becomes more energetic, while its *specific metabolic energy decreases* over most of its life. The fourth (P13) indicates that our descriptions of an organism's energetic pathways become ever more cumbersome as it develops. The fifth (P14) indicates that an organism's internal tendency to change tends to dwindle with age. Finally, the sixth (P15) rule suggests that, as aging continues, the organism is more and more easily disrupted by fluctuations in its environment. Viewed as a whole, these rules suggest that the stored information curve is a kind of inverse of the energy intensity curve. While the organism is changing most rapidly, it, like the ecosystem, has the greatest specific energy flow through it. On the other hand, increasing complexity results in less flexibility, curtailed metabolic rates and an increased vulnerability to insults. The organism's ability to heal or regenerate as it works on an ever increasing number of homeorhetic problems decreases until a limit is reached and the organism is recycled.

These considerations have suggested to some the old, but recurrent view that the larger systems within which organisms are contained are developmental entities, or "superorganisms," in their own right. This is a misleading way of calling attention to the often-neglected reality of systems above the organismic level, such as the stable feedback cycles between the atmosphere and the biosphere remarked on by proponents of "the Gaia hypothesis," as well as to the fact that organisms are embedded in these larger systems as relational parts. The fact is, however, that organisms are the proximate and proper locus of replicating molecules, and that the greater integrity that we see in organisms, as compared to higher-level ecological units, is not just a matter of our own epistemic perspective, but instead reflects the powerful agency and real effects of the appearance of replicating macromolecules. It is organisms alone, or at most certain informational-sharing symbiotic systems, that have employed informational macromolecules to achieve stable, homeostatic and homeorhetic metabolic pathways, together with reproductive fidelity. For ability to do these things is the very definition of an organism. An organism is an *informed autocatalytic system possessing, in virtue of information stored in macromolecules, an internal organization of kinetic relationships such that it is able to maintain itself by pulling environmental resources into its own production and faithful reproduction and by dissipating unusable energy to appropriate sinks* (Wicken, 1987). Thus in interpreting the observed symmetry between the rules of ecological succession and the patterns of organismic development it is far more informative to speak of organisms as highly integrated, homeorhetic ecosystems than to speak of ecosystems as superorganisms. This view carries with it the suggestion that organisms originated, and continue in part to evolve, by (literally) *incorporating* — storing and deploying in developmental programs — information that, in the first instance, describes patterns of energy flow in more generic kinds

of autocatalytic cycling systems. It also implies that organisms *continue* to be informatively described as autocatalytic systems even after the transformation brought on by replication, with the greater sources of *variation* and internal structure which that entails, and that these facts are still causally relevant to their evolution.

AN ECOLOGICAL APPROACH TO EVOLUTIONARY DYNAMICS

How might these things have occurred — and why? We may push these phenomenological reflections in a causal direction by noting, in the first instance, that the patterns noted in P10—P15 conform to the fundamental propositions of open systems thermodyamics. We can reformulate P10 and P11, for example, in a more *causal* way by asserting that:

> P16: *Natural selection* will favor species that, in funnelling energy into their own production and reproduction, also increase the total flow of energy through their ecosystems;

and that

> P17: *Natural selection* includes (in addition to this flow-expanding principle) an efficiency principle, which promotes a maximization of flow into organizational progagation and a minimization of flow into metabolic costs.

These two principles make opposing contributions to the organization-dissipation relationship. P16 implies a teleomatic drive to expand the energetic economy through evolutionary innovations that multiply kinetic pathways for dissipative flow. P17 leads to specialization and mutualism: In unperturbed ecosystems specific dissipation (per unit of biomass) decreases as the elaboration of mutualistic networks under selection pressure increases biomass/throughput ratios. These principles are yoked together by way of the deeper principles of nonequilibrium thermodynamics. As developed by Prigogine and his school, these state that open systems will dissipate energy as entropy through self-organizing kinetic pathways. These emerge from spontaneous, autocatalytic cycling (P1). Seen in this light Lotka's principles (in the form of P16 and P17) provide an *explanatory* backing for the phenomenology of P10—P15.

This approach implies that natural selection is best conceived within a framework of physical law. Individuals, in the normal sense of organismic units, will not be the paradigmatic units of selection, as they are on the traditional, morphologically-based conception of natural selection, which retains echoes of discourse about craftsmanship and design. Rather, *like ecosystems, individual organisms will be construed as informed patterns of thermodynamic flow*. On this view cells, organisms, populations, and ecosystems will all be units of selection, but it is ecosystems that will

constitute the paradigm case and the matrix within which the others arise. Accordingly, the language in which natural selection is to be conceived, and in which adaptative scenarios are to be couched, is a language of process and pattern rather than of products and entities. In this language what is selected are not parts, in the morphological-artifactual sense, but differential patterns of energy flow. Some flow patterns will necessarily be superior to others in commanding resources, and will be selected on that basis.

The concomitant reconception introduces a dimension of directionality into the notion of fitness. *Those populations are fittest that best enhance the autocatalytic behavior of the reward loops in which they participate.* The effect of such competition is an emergent tendency during the later stages of ecosystem development toward more highly articulated networks of flow, wherein those pathways that foster more efficient transfers flourish at the expense of less effective routes.

Three immediate implications of this reconceptualization are worth noting. First, the competitive success of flow patterns is, at least in part, explained in terms of self-organizing systems dynamics (Csanyi, 1985), rather than being ascribed, as it generally has been by the Darwinian tradition, exclusively to externally imposed forces. It is true that initial and boundary conditions, such as limiting resources, are important factors. But causality is not to be conceived *in the first instance* as a matter of external pressures being exerted on systems that would otherwise remain unchanged.

Second, flow patterns are selected because they contribute to the stability and coherence of the systems of which they are a part. Thus individual interest is contextualized within community dynamics. The nitrogen cycle illustrates this well. Plants take up nitrate from the soil and convert it to amino acids and nucleotides, then to proteins and nucleic acids. Decomposers hydrolyze these polymers, then deaminate the monomers, releasing ammonia. This serves as an energy source for *Nitrosomas* bacteria, which oxidize it to nitrite, which is in turn oxidized by *Nitrobacter* to nitrate. Each microbe is obviously in business for itself, exploiting energy sources for survival and reproduction. But it is the ecosystemic cycle to which they contribute that makes these niches available, and it is their activity within this cycle that sustains the continued self-maintainance of the large flow pattern. In this picture, constraint and selection cannot be conceived apart from each other, or as opposing forces that are somehow balanced off. Rather the fact that the competitive success of higher-order ecosystem flow imposes constraints on lower-order entities is an essential component of the very possibility of isolating units of selection and ascribing adaptations to them. To the theme of selection, as it has emerged thus far within the Darwinian tradition, therefore, we do not propose to add a new theme of constraint. Instead, the theme of constraint makes the

theme of selection coherent and complete for the first time. However, not all traits need be selected. Some can arise through neutral molecular evolution (Kimura, 1983), through endogenous characteristics of genetic regulatory patterns considered as statistical ensembles (Kauffman, 1985; see also Demongeot *et al.*, 1985), or through exploration of the possibilities of developmental alternatives such as neoteny.

Third, in this context units of selection, as they appear in the writings of those who advocate an "expanded synthesis" (Gould, 1982), are necessarily members of an ecological hierarchy. For cells, organisms, populations, ecosystems and regional biota are all phase-separated systems of thermodynamic cycling and flow; and cycling and flow will proceed most efficiently and stably by hierarchical or modular organization (Odum, 1988). Thus, recent calls for an hierarchical expansion of the Darwinian tradition may now be seen to be grounded in the deep structure of evolutionary theory. Recent hierarchical thinking is not called for, as it may have appeared at first, merely because the need has been felt for conceptual models that usefully accomodate new data. Rather hierarchical structure turns out to be a *basic fact* about the biological world.

To these considerations we may add the important consideration that the vexing problem of the origin of life can be productively and suggestively conceptualized within this framework. From the conventional point of view one must begin *either* with proteins *or* with nucleic acids, and then wonder how to get them together into a faithful, functioning self-replicating system, even if we assume that the RNA has catalytic activity. A bootstrapping problem then occurs. As a result the considerable conceptual and explanatory resources of 'hypercycle theory' fail to be fully exploited. *However, within the ecological, thermodynamic context that we have been exploring, hypercycles now can be generalized as autocatalytic cycles of selection and flow within which nucleic acids and proteins are seen to co-evolve, along with energy metabolism, under the imperative of physical laws,* possibly in the phase-separated microspheres (Fox, 1984) or in an amphiphile bilayer vesicle (Morowitz, Heinz and Deamer, 1988) that could provide a proto-organismic setting for the acquisition of genetic information under thermodynamic flows. Accordingly, the chicken-egg problem, which Darwin bracketed long ago by taking living organization as primitive in his scheme, is brought within sight of a solution.

The source of the coevolutionary nexus in the thermodynamic space within which life emerges can readily be shown without getting into equations. Thermodynamic flows require specific mechanisms in order to achieve irreversibility. Those in turn require cycles. For example, a photoreceptor X, excited to X^*, must have some dissipative route back to the ground state to command irreversible energy flow. The emergence of informed dissipative routes is synchronous with the emergence of living organization. Proteins and nucleic acids evolved informationally in this

dissipative setting. Consider the following dissipative route (Figure 1): Protoreceptor X delivers excitation energy to amino acid phosphorylation, indicated by $A \sim P$. The excited monomers then polymerize to poly-peptides PP. If these feed back to catalyze either step leading to their production, as indicated by the arrows in Figure 1, then one has an autocatalytic system capable of pulling energy resources into the pro-pagation of that polypeptide. Such capacities have been demonstrated experimentally (e.g. Fox, 1984). Abiotic polypeptides, operating in phase-separated microspheres, also absorb polynucleotides, and engage them in mutually-stabilizing proto-ribosomal complexes. Since lysine-rich poly-nucleotide complexes have catalytic activities for both amino acid and nucleotide polymerization, one can expand the scheme as indicated in Figure 2. Here, a nucleic acid cycle has been coupled synergistically with the protein cycle. In this diagram T represents nucleic acid template, N nucleotide monomer and $N \sim P$ phosphorylated nucleotide. PP catalyzes the formation both of itself and template T. T provides the template for its own replication and informs the production of the catalytic polypeptide. The system *as a whole* becomes a nucleus for acquiring information through competitions for energy fluxes. The chicken-egg problem is solved in principle, if not in historical particularity, by giving nucleic acid and protein equal ontological status within an information-acquiring dissipative package, thus projecting the ecological/genealogical interaction dynamics back to the origin of life.

The solution to this problem is, moreover, of a piece with an adequate theory of subsequent evolutionary dynamics. We have defined a living thing as an *informed autocatalytic system* that sustains itself by environ-
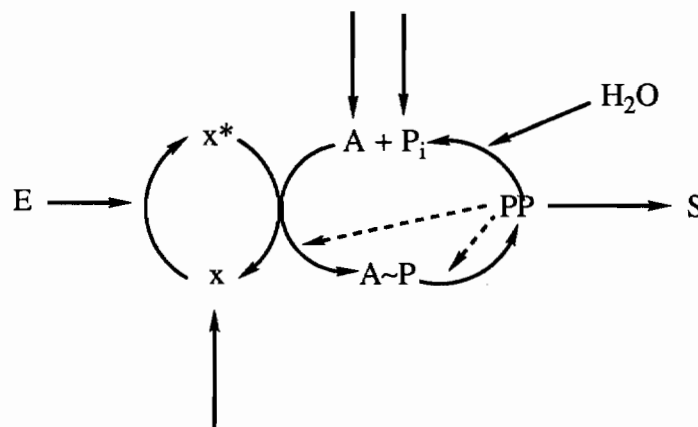

Fig. 1. A hypothetical autocatalytic cycle involving phosphorylation, polymerization, and hydrolysis where polymer PP feeds back positively to either of its precursors.
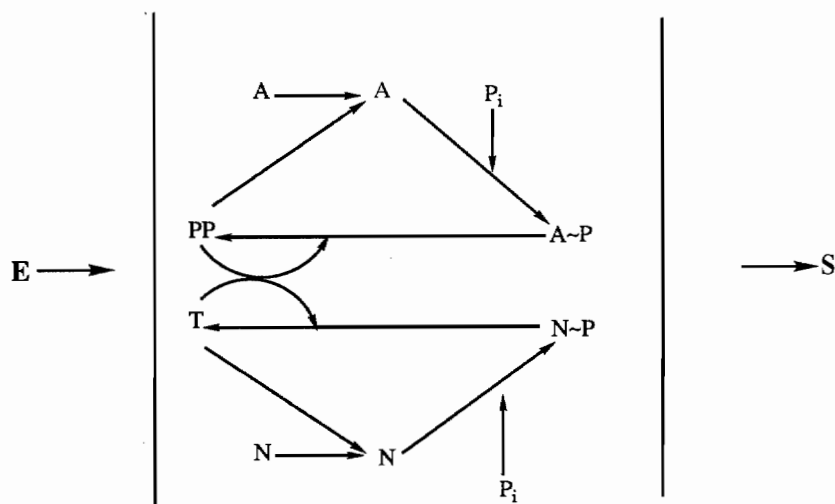
Fig. 2. A minimum 'realistic' autocatalytic cycle in which template T and polypeptide PP work synergistically to pull resources into themselves and degrade energy.

mental energy exchanges and that varies under the drive to configurational randomness. Statistical thermodynamics provides two important principles of randomization that connect life's emergence with its subsequent evolutionary diversification. One is the degradation of free energy to heat. This principle leads, in the first instance, to the 'chemical imperialism' of living matter, by which organisms are able to funnel resources into the perpetuation and propagation of their own organizational types. The other is the drive to configurational disorder, which ensures that new configurations of matter will be delivered into the testing ground of the ecological arena. Mutation and sexual recombination both derive from this entropic drive (Wicken, 1987). Accordingly:

> P18: The principles of variation, constraint and selection that began their operation in life's emergence, and were themselves responsible for that emergence, are also at work in biological evolution.

As successful patterns of dissipation emerge, so too does a tightening of the nucleic acid-protein relationship. With that tightening comes the constraint on variation characteristic of the biological world. The inorganic world thus flows smoothly into the organic world, and genetic information accumulates under thermodynamic selection for stable patterns of entropy production. The internalization by natural selection of informational possibilities stabilizes the energetic (i.e. metabolic) flow patterns, and thus becomes metabolic information. This stabilization defines the boundaries of the organism. But this metabolic information is

in fact selected because it allows organisms to function as relational parts of ecological wholes: It has in part been selected because it stabilizes the network of ecological relationships. Thus, to the extent that it reflects this process, metabolic information is internalized, or, as we have stated previously, incorporated ecological information (P5). As metabolic information accumulates, dissipative flows are guided into new creative channels, which reduce specific entropy production in ever more complex networks through the generation of information space in the form of variational possibilities. The operation of such complex whole systems physically requires the production of yet more variation, or informational possibilities, in a new selective round. This in turn makes possible new ecological pathways and niches. (The idea that the environment shapes the informational content of the genome through feedback interactions between genotype and phenotype has also been explored by Riedel [1977]. This concept does not conflict with the traditional Darwinian insistence that variation is random in relation to selection. The feedback loop runs over the long run. However, if phenomena violating the normal Darwinian rule are confirmed, the view expressed here will be able better to conceptually absorb this than traditional Darwinism.)

ENTROPY, INFORMATION, AND GENEALOGY

The relation between the Second Law and the kinetic phase space represented by metabolic processes is subject to much controversy. No neo-Darwinian has denied that organisms must conform to the dissipative requirements of the Second Law. But when units of selection are thought of as analogous to machines few interesting connections between natural selection and the Second Law appear. By envisioning natural selection as occurring among informed patterns of energy flow, however, this paper makes that connection more perspicuous and tighter. From this perspective there will be deep reasons for expecting that evolution, and phylogenetic branching, will occur, since the Second Law will demand pathways down which entropy can be dissipated. Despite this advantage over neo-Darwinism, however, one might still hold on this view of the matter that the Second Law merely provides the possibility space within which selection at the level of metabolic processes, and evolutionary diversification, are to be construed, and that little if any causal or explanatory force is to be given to the Second Law itself. Alternatively one might hold that there is a non-trivial causal reciprocity between the expansion of information space demanded by the Second Law and the kinetic-metabolic processes that embody and manifest that expansion. If kinetic pathways are means for the dissipation of entropy, we can, on the one hand, say that the fitnesses of these pathways are the proximate *cause* of

diversity, given the background requirements of the Second Law. But it is also informative to say that in *selecting* pathways imperatives of the Second Law explain selection and diversification as a whole. From this largest perspective, the Second Law has causal implications. But at the detailed level the causal accent must be on kinetics.

Might one say that the quantity that increases is not entropy, at least in the energetic sense, but rather information space, and that the Second Law is causally responsible for this quite apart from whatever function is being performed at the energetic level? This view has been vigorously advocated by Brooks and Wiley (1986, 1988), who argue as follows. The concept of entropy can be generalized beyond its original energetic and later statistical senses to an informational definition. This makes the growth of information in genetic systems the expected result of the operation of the Second Law without requiring direct reference to energy flows. Shannon's concepts of transmitter, channel and receiver are extended to biological systems and Gatlin's notions of divergence from maximal informational "entropy" is hierarchically expanded. Unlike Shannon entropies, however, which can be defined formally, the informational entropies being measured here are said to be physically grounded in biological systems (Brooks and Wiley, 1986, 1988; Brooks, Cumming and LeBlond, 1988; Collier, 1986). In Gatlin's work, total information cannot increase over phylogenetic time. In Brooks and Wiley's theory it can. Accordingly, they follow Layzer (1977) in holding that information is the lag between the unlimited expansion of the possibility phase space, H_{max}, and constraints, H_{obs}. This lag, which is seen as the paradigm of entropic processes generally considered, recurs at every level of biological processing. The hierarchical information theory so developed represents a generalized expression of the Boltzmann entropy measure considered as arrays under constraint.

Although Boltzmann entropy measures were originally invoked for energy transformations, Brooks and Wiley view the most general expression of the Second Law as having only a contingent relationship to energy-based processes. They argue that energy transformation in entities in the ecological hierarchy is a *necessary condition* for the expansion of biological information, but that the information passed on is not in itself a measure of energetic processes. On this view, the ever-increasing noise due to errors in replication results from species acting as individuated "information-dissipative" structures, driven by the Second Law. This process is thought to be sufficient to account for diversity. Thus it is thought to be reasonable, indeed necessary, in order to get closure conditions for constructing phylogenies, to ignore input from environmental boundary conditions. Any deviation from the expected informational distributions is then attributed to the action of natural selection, energetically considered, which affects the rate of cladogenesis and prunes the variation so produced. New channels become forever separated, and

"noise" on the overloaded channels is reduced. These concepts are made operational by way of the notion of breakdowns in reproductive "cohesion entropy". This is said to explain, as well as to measure, the informational-entropic bifurcations that now appear as cladogenesis.

This attempt to generalize statistical entropy to informational entropy is based initially on the fact that both formulations use a similar probability theory (Khinchin, 1957). However, we must go back one step and consider the relationship of thermodynamic to statistical entropy. The reason that the Boltzmann microstate/macrostate ensembles are entropically relevant is precisely because of their relevance to the energetics of the systems studied and hence to the amount of work that can be gotten out of such systems. The microstates are energy levels, and the distribution over these levels is constrained by the requirement of the conservation of energy. Not every physical microstate/macrostate distinction that embodies a principle of constraint will yield entropy calculations in the thermodynamic sense; only those that are appropriately connected to energetics will. Entropy is not a measure of every sort of disorder, but only of *energetically relevant* disorder. Disorder in formal, non-physical systems is often lumped into a Shannon "entropy," but what relationship this would have to a true entropy is not clear. This is not meant to deny, however, that a formal analysis of disorder is useful in formal systems — or in physical systems, such as Brooks and Wiley envision, for which the connection to energetics is only a necessary precondition for the existence of the informational arrays. The question rather becomes one of the adequacy and robustness of this formal analysis *for the particular problems of interest.*

The perspective that we have been advocating entails that information remains tied to energy transformation and that encoded metabolic information is a reflection of environmental boundary conditions. Information measures relationships and pathways among such flows. For certain analytical purposes, when tracing phylogenetic patterns, we might concede that it is reasonable to disregard the fact that genealogical information is, to a large extent, encoded ecological and metabolic information. Since cladistic analysis is now generally accepted as the correct way to construct phylogenetic trees, the use of equations from information theory is justified if it improves phylogenetic methods and their applications to biogeography and historical ecology. This does not, however, imply that the relationship between information theory and thermodynamics postulated by Brooks and Wiley (which might be characterized in its putative general form as "infodynamics") has been proven, although it supports the intuition that information and thermodynamics are somehow connected.

What the relationship of information and thermodynamics actually is has been a vexing question. Since the 1940s, information engineers and some general systems theorists have intuited that there is a definite

relationship between thermodynamics and what Shannon called informational "entropy". This intuition was informally extended initially by Crick to macromolecular function and more formally to biological systems in general by Gatlin (1972) and Riedel (1978). More recently, Brooks and Wiley (1986, 1988), Collier (1986), Wicken (1987), and the contributors to Weber, Depew and Smith (1988) have explored the implications of using an enriched thermodynamics of the nonequilibrium sort, fused in some fashion with information theory, to reformulate evolutionary theory. Nonetheless, the nature of the relationship of thermodynamic and statistical concepts of entropy to informational or Shannon entropy remains problematic (see Peacocke, 1983; Denbigh and Denbigh, 1985; Depew and Weber, 1988). It is still unclear whether information represents a generalization of earlier concepts of entropy (Brooks and Wiley, 1986, 1988; Collier, 1986); or is a distinct concept connected to entropy, but not in a linear fashion (Ferracin *et al.*, 1978; Wicken, 1987); or whether information and entropy can only be linked in a metaphorical manner (Stuart, 1985); or whether, finally, present information theory is inadequate for the task of describing information and energy transformations in living systems (Olmsted, 1988).

It might be said that one motive for generalizing entropy to an informational definition that is not so closely tied to energy flow is that thermodynamic entropy is strictly defined only at equilibrium, and that the widely applied minimum entropy-production rule for steady-state systems is only rigorously applicable to isothermal systems near equilibrium and subject to weak energy gradients. Entropy therefore seems to be measurable, and therefore meaningful, only for such a restricted class of systems. It must be acknowledged that those of us who want conservatively to keep entropy tied to energy flows in far from equilibrium systems should keep this point in mind. Those wishing to maintain a connection of entropy to energetics must be willing to explore the likelihood that since living systems are in fact operating far from equilibrium they are, and must be, dissipating entropy, even if no simple measure of it is available. Those with realist preconceptions about scientific theories will have much less trouble with this than those who are wedded to forms of operationalism, where failure to find an adequate measure of some quantity is tantamount to failing to define the concept itself. Concrete measures of information, such as those used to measure ascendency in ecological systems, are, however, closely enough linked to energy flows that they are useful instruments in approximating energy processing information in far from equilibrium systems, such as ecosystems or metabolic processes.

Biological information processing is itself a physical process. Our ability to manipulate information by the physical processes of a computer (Landauer, 1988), which has already led to such powerful suggestions and results, may lead us astray in this connection, for the computer is designed

to transmit and process information *in a particular way*, availing itself of one — but only one — model of physical information transactions. The macromolecular interactions involved in DNA replication, transcription, and translation provide, however, a point of intersection between thermodynamic and informational approaches in which it is clear that the particular physical grounding is not the same as that of a computer. Further, other aspects of metabolism, such as informational processing (integration of non-binary signals rather than receiving a message) by allosteric enzymes and cell receptors, along with the more complex operations of the endocrine and neuronal systems (especially the axonless neurons), need to be explored as unique kinds of biological informational systems. Similarly, developmental programs in DNA appear insufficient fully to provide all the information needed for ontogenesis; metabolic gradients and environmental factors are also important (Stent, 1985). More speculatively, even DNA in contemporary organisms may not be immune to informational transformations due to the action of metabolism, and through metabolism to signals from the extracellular environment, as presented in the concept of "profane genes" (Campbell, 1982, 1985; Campbell and Perkins, 1988). All these phenomena fall within the purview of metabolic information and can be investigated profitably from an ecological perspective. An approach limiting itself to genetic information considered in isolation, on the other hand, will not pick them up.

It must also be borne in mind that every informational component in biological systems acts as both a channel and a receiver. Thus the phylogenetic message cannot be disembedded from its metabolic matrix, both molecular and ecological, except heuristically for analytical purposes (P6). In our view, then, biological information has to be regarded as "interpretive" information: Biological information is information about *function*, rather than about mere signal differentiation. Introducing the concept of functionality into the concept of biological information does not imply that there must be a subjectivity in the "receiver" to "get" the message. Nor does it imply any intentional teleology. It merely reflects the fact that functionality, and the kind of meaning that we ascribe to functions, is a real, objective property of all biological systems. Function appears in a *context* — of metabolic pathways within the cell, of cells in organisms, of organisms in populations, of populations within communities, and so forth. From this perspective, the Second Law is causally relevant, requiring selection among alternative kinetic pathways for energy dissipation and telling us that we are entitled to *expect* that variation and cladogenesis will occur, but telling us also that investigation of why it occurs *in particular patterns in particular cases* requires attention to more particular ecological and metabolic facts.

Ultimately attempts to apply information theory to biological systems require boundary and closure conditions, yet no single stable set of

boundary and closure conditions can be imposed on biological systems without serious distortion. Thus to use informational entropy constant care must be exercised to specify what boundary and closure conditions are assumed, and to recognize corresponding limitations upon interpretation and generalization. Any heuristic closure condition that is imposed will give quantitative expressions that will be interpretable only within the experimental environment defined by the closure heuristics themselves (Dyke, 1988a). That is an inevitable consequence when we cross the barrier that separates the science of complex systems from the science of the simple that has, thus far, provided our culture with its paradigms of successful theorizing. We should expect that new approaches will be needed as we try to account for organized complexity instead of organized simplicity (Newton) or disorganized complexity (Boltzmann), (Serra et al., 1986; Serra and Zanarini, 1986).

REDUCTIONISM, TELEOLOGY AND THE NEWTONIAN PARADIGM

The ecological-energetic perspective presented in this paper informs the philosophical claims made in P7—P9. We hold in the first instance that the far-from-equilibrium character of biological systems allows the Darwinian tradition to be more robustly reformulated by relaxing Newtonian and, more generally, equilibrial background assumptions. Once such a shift in background view has occurred, vexing problems of reduction and teleology may be seen in a new light.

We assume here that successful explanatory theories rest, in part, on highly general, often tacit pictures about the way things are. When such pictures have proven successful in one field they are often transferred to others, and sometimes come to pervade an entire culture, on its cognitive side, forming its peculiar sort of common sense. Following Laudan (1977), we will call such pictures background assumptions. In this light, Darwinism has from its inception been presented and defended in terms of background assumptions associated with Newtonian systems-dynamics. These background assumptions were brought into the study of evolving biological systems by Darwin's encounters with uniformitarian geology and English economics. Darwin's theory can be described, from this perspective, as an attempt to extend Newtonian background assumptions from Lyell's Newtonian or "uniformitarian" geology to biology with a little help from the Malthusian version of Adam Smith's economics, which had already brought the same background assumptions to bear on economic systems.

The entities that enter into a Newtonian system, whatever they may be, are assumed to exhibit inertial motion or rest. Deviation from this state occurs only under the influence of impressed forces. At each instant the

system will tend to restore a dynamic equilbrium between inertial motion and impressed force. What plays the role of inertia in Smith's case is the assumed tendency of each economic agent to maximize command over scarce resources. The laws of supply and demand lead to a constantly threatened, and constantly renewed, dynamic equilibrium by pulling each agent back toward others. By envisioning the environment as a closed Malthusian system characterised by intense competition, Darwin suggested what force could account for the modification of lineages of living things over time. The intrinsic rate of population increase — a property of organisms no less deeply embedded in their natures than is inertial mass in Newtonian entities — is countered by the force of scarcity, an analogue of gravity that every body exerts on every other. To the extent that each competing entity is unconstrained by prior relationships to others, heritable variations will be indefinitely protracted into adaptive changes in lineages that increasingly mirror the demands of a stern environment. In this way Darwin more or less successfully refuted the standing presumption that no natural law could account for the existence of functional organic traits.

Newtonian systems have the following conceptual presuppositions: They are closed, deterministic, reversible and decomposible. They are closed because extrasystemic inputs would dissipate the calculable effect of forces in determining state changes within the system. Malthus's argument about populations illustrates the explanatory role of closure conditions by showing how scarcity, the closure condition of classical economics, can cause economic equilibrium to occur at a point below that where exchanges are correlated with the biological survival of all the entities in the system. Newtonian systems are in addition deterministic: Every state of the system is fully determined by its prior states. Moreover, Newtonian systems are reversible. For the laws governing state changes can be calculated in both direction. Thus every prior or subsequent state of the system is in principle recoverable. There is no inherent arrow of time in a Newtonian system. Finally, reversibility implies decomposibility. A Newtonian system must be atomistic, for if every state change is in principle recoverable every structure in the system must be an aggregate of least units that can be assembled or disassembled by whatever forces are currently operating.

The neo-Darwinian Synthesis retains many of these conceptual proclivities. Sober, for example, has recently provided an analysis of the key concepts of the Synthesis in which a Newtonian concept of force is fused with the notion of equilibrium in the classical thermodynamic sense. According to Sober (1984), the Hardy-Weinberg Equilibrium Formula provides the inertial baseline against which are measured the effects of impinging forces on a system that *would otherwise remain in the same state*. The system will not change its state until it is deflected onto a new

path by the imposition of external forces, such as selection. In this recon-struction equilibrium, and deviation from it, are redefined in statistical terms. For just as in physics classical mechanics gave way to statistical mechanics, so in evolutionary biology neo-Darwinism meant, in part, a shift away from deterministic closure at the phenotypic surface to a two-level statistical reformulation in which gene frequency distributions underlie and cause phenotypic macrostates. (This shift goes back to R. A. Fisher, whose work is based on an explicit analogy between increases in fitness in large interbreeding populations and increases in entropy: Just as entropy is a function of the number of available microstates, so increases in organismic fitness are a function of the genetic variance over a sum of loci [Fisher, 1930].)

This account is and is not Newtonian in the classical sense. It is Newtonian insofar as it is an equilibrium theory, in which state changes are entirely a function of exogenous forces. But it is not Newtonian insofar as it is not based on a picture in which a dynamic equilibrium is achieved by the resolution of competing forces. Rather, 'equilibrium' is defined by zero variance (which for diploid species means the Hardy-Weinberg binomial distribution of genotypes), just as equilibrium is reached in a physical system when the probabilities of its components being in partic-ular microstates are stable. Accordingly, the analogue of inertia is not the Malthusian population parameter, but rather a statistical distribution of gene frequencies, deviation from which indicates the presence of a disturbing force. By defining a biological macrospace in genetical micro-space terms, this statistical reformulation allows for microscopic rever-sibility and macroscropic irreversibility, thus giving a better explanation of our intuitions about the irreversibility of biological phenomena than had the original Darwinism. And, as Robert Rosen has argued (Rosen, 1985), it is in one respect more Newtonian than Newton, for it defines in way Darwin could not the real units or atoms demanded for decomposible systems, namely populations of independently assorting and segregating genes.

Now it is quite possible to imagine systems that are in every way the opposite of Newtonian systems, whether deterministically or statistically considered. The systems that Prigogine calls dissipative structures embody this possibility. Such systems are open, non-deterministic, irreversible and non-decomposible. They are open to extrasystemic inputs of matter and energy, retaining their identities as distinct systems just because of this openness. Dissipative structures maintain a trajectory far from equilibrium as long as appropriate boundary conditions are in place. Indeed, by their own agency they do much to assure that these conditions obtain by drawing resources into themselves and dissipating entropic debt beyond their immediate borders. Dissipative structures are also characterized by tendencies toward spontaneous self-organization and non-deterministic

bifurcation. This occurs because increases in internal entropy production, a cost of maintaining internal structure, are more than compensated for by entropy increases due to energy exchanges between the system and the external environment. Thus internal organization of the system and the entropy production of the system-plus-environment grow together. Accordingly, state changes, or phase transitions, in dissipative structures are not entirely the result of predictable and measurable impressed forces operating against an inertial default drive. Lacking inertial tendencies that counterfactually would reassert themselves when impressed forces are removed, such systems embody a much stronger arrow of time than we have seen in either of the two kinds of equilibrial systems we have recently been considering. Dissipative systems are irreversible, historical entities in a strong sense, and particularly so when the internalization of information in replicating macromolecules provides strong forces for conservation. Finally, because they are composed of complex modules that arise historically and irreversibly across the micro-macro divide, such systems are only partially decomposible. They incorporate their historical trajectories into their very nature.

By shifting the background assumptions of the Darwinian tradition from those of Newtonian or equilibrial systems to those of complex non-equilibrium systems, richer connections between physics and evolutionary biology can be forged, especially by way of the ecological interface between these fields, which gives us deep physical laws on the one hand and biological systems on the other that are clearly energy processing, and therefore entropy producing, entities stabilized far from equilibrium. If, however, one wishes to call such an accomplishment a *reduction* of evolutionary biology to physics, chemistry and information theory, one will have first to revise the received view of what a theoretical reduction is.

As normally understood, the concepts of reduction and reductionism arise within (roughly) positivist conceptions about the philosophy of science. This fact brings with it a bias in favor of studying Newtonian systems as paradigms of mature science. Historically, it was Newtonian physics that first provided a model toward which, some millenial day, other sciences might hope to be "reduced". Formally considered, moreover, covering laws plus initial conditions deductively imply explanations and predictions only on assumptions about system closure that formally mirror the material closure conditions of Newtonian systems. The identity of prediction and explanation rests on Newtonian assumptions about reversibility, just as the deductive nature of prediction and explanation reflects Newtonian determinism. Most important in the present context, however, is the assumption embodied in the received philosophy of science that progress in subsuming a class of phenomena under laws of a higher order of generality will normally be correlated with success in resolving the behavior of wholes into that of smaller and separate parts —

a phenomenon we see vividly in the case of the statistical theory of gases. The explanation of phenomenal laws of gases in terms of the probability distributions of particles is a triumph of reduction in this sense. Reduction, if this is indeed a paradigm of it, implies that productive research strategies will usually or presumptively culminate in both theoretical *and* ontological reduction.

This program can be vividly witnessed in Dawkins' (1976) genic reduction, in which it is colorfully claimed that organisms are merely vehicles for the replication of genes, and that organismic traits are selected in accord with this measure of fitness. In the case, however, of the theory envisioned in this paper, the illumination of evolutionary biology by the laws of thermodynamics actually undergirds a modest holism with respect to entities — none of which will behave according to the specifications for Newtonian systems, any more than the theories that explain that behavior will mirror their formal meta-theoretical counterparts in the philosophy of science. Subsumption of biological phenomena under physical and informational laws leads to explanations in which the spontaneous emergence and behavior of macro-systems are shown to be functions of self-organizing complexity in entities that are relationally constituted as wholes.

Rather, therefore, than refurbish the concept of reduction to accomodate this unexpected divergence between "theory reduction" and "entity reduction" — a divergence that was bound to occur as soon as science began to cross the "complexity barrier" (Rosen, 1985; Dyke, 1988a) — it appears to us to be preferable to speak of the *interanimation* between previously isolated *fields* rather than the reduction of one theory to another (Darden and Maull, 1977).

The methodological implications of this situation should be mentioned here in brief. They are studied in detail in Dyke (1988a). Laws provide not deductive premises, but constraints on the space within which explanatory scenarios are possible, as well as expectations of systems behavior based on very general considerations. Initial and local boundary conditions are then elevated to central importance in a search for "robust theorems" (Levins, 1966) that arise at the intersections of different models as they are brought to bear on particular problems. Laws can be cited as causal only when we ask such general questions as why a given system is a system of some type rather than another.

This perspective has implications for other highly charged issues in the philosophy of biology. One such issue is that of biological teleology.

Traditionally, talk about biological teleology has referred, sometimes ambiguously, to two different things: (1) the functional adaptedness of organisms to environments and of organs to organisms; and (2) the overall direction, and hence alleged directedness, of the evolutionary process toward greater complexity (and/or other directional properties). It can

hardly be denied that the Darwinian tradition has been hostile to (2). It is not nearly so hostile, however, to (1). In recent decades, in fact, philosophers, notably Wright (1973), have analyzed teleological statements roughly as claims to the effect that

X is there because it does Y.

Such claims answer "what for" questions and yield "in order to" answers. Their general form is common to both design arguments and to natural selection arguments. If the former make reference to the intentions of an artificer as the reason an entity has some feature, the latter make reference to the accumulated effects of natural selection as the reason that some trait "is there". There is no reason, therefore, to deny that the latter sorts of arguments are teleological in this sense. Brandon has given the best analysis of this form. According to him (Brandon, 1981), natural selection explanations cite "the effects of past instances of A (or precursers of A) and show how these effects increased the adaptedness of A's possessors (or the possessors of A's precursors) and so led to the evolution of A" (Brandon: 1981: 103).

The problem is that genuine adaptionist accounts can easily be replaced by disguised design arguments. Gould and Lewontin have been highly effective, for example, in pointing out how easily Wilsonian sociobiology slides down this slippery slope into disguised design by retailing "just-so stories" (Gould and Lewontin, 1979). This slide from selectionist reasoning to intentionalist "crypto-teleology" occurs in proportion as the intentional form is treated as paradigmatic, and the natural-selectionist form is regarded as an analogue of it — as Darwin himself clearly treated it. It is for this reason that, the clever work of analytic philosophers aside, teleology is often regarded by biologists as equivalent to the intentional form, and is accordingly either denounced or confessed to in accord with one's proclivities. In the latter case it generates creationism.

One way to break this link, and to drive the wedge between natural selection and design forms of teleological argumentation that Wright's and Brandon's work invites, is to anchor natural selection in natural laws and processes, and so to distance the sort of functional arguments that refer to natural selection from arguments referring to intentional design. However, because many evolutionary theorists have sought to protect the autonomy of biology from physics (Mayr, 1982, 1985, 1988; but see Rosenberg, 1985), and hence are loathe to countenance physical laws as proper premises or principles of their science, it is precisely this sort of assurance that has been lacking from discussions of teleology in evolutionary theory. It is this failure, we believe, that allows creationist arguments, as well as inadequately formulated sociobiological arguments, to retain undeserved places as conceptual possibilities in cultural space.

In discussions of this subject it is customary to distinguish among teleo-

matic (or end-resulting) processes, teleonomic (or end-directed) processes and teleological (or goal seeking) processes (O'Grady, 1984; O'Grady and Brooks, 1988; Mayr, 1988). Our suggestion is that selectionist arguments, whose subjects are *patterns of informed energy flow* (rather than traits or parts that are too closely modelled on artifacts), are grounded in teleomatic laws of nature, especially the Second Law (see also Wicken, 1984). Teleonomic feedback within and between ecological systems, as well as between energy flows and information expansion, arises within this framework. Thus teleonomic processes, occurring within the possibility space of teleomatic requirements for dissipation, provide cycles of cause and effect that fully meet the criteria envisioned by Wright and Brandon for biological teleology. For the objects of selection that result from this reiterated process are *there*, as Wright and Brandon require, just *because* they provide dissipative pathways in an informed system of energy flow.

If natural selectionist arguments were put into this form, and referred to these processes, there would be less occasion for confusing them with disguised design arguments, and hence for refusing to talk about teleology, at least in the sense of the term defended by Wright and Brandon. An advantage of this analysis is that it firmly grounds functional explanations in natural law without undermining genuine functionality. Thus we can have a legitimate place in science for functional explanations complementary to mechanistic explanations. As science shifts its focus of attention from simple to complex systems, the role of functional explanations will, in fact, increase relative to mechanistic explanations, since mechanistic explanations are rooted in simple systems. Explanations based on the concept of patterns of informed energy flow in open systems far from equilibrium are of the teleonomic, and teleological, form because *consequences* (entropy production) are invoked as reasons for the existence of a real unit of selection.

Note, however, that the premisses that generate these arguments also seem to countenance talk about the overall direction of evolution — teleology in sense (2). If kinetic pathways are naturally selected *means* whereby a necessary and inevitable entropic dept is dissipated, are not these pathways there *for the sake of* facilitating dissipation; and must we not say, therefore, that the *function* of the kinetic pathways is to dissipate entropy? But since the laws underlying this process are rooted in very deep, irreversible physical processes, acceptance of this point leads us to expect that there will be an overall pattern to evolution as dissipative pathways complexify in real ecological space. It seems, then, that we cannot talk about local functionality and adaptedness without countenancing larger patterns of evolutionary complexification and directionality. From this perspective, when teleology in sense (1) is conceived in the way just suggested, it seems to countenance certain observations that have traditionally led to teleology in sense (2). To the extent that the Darwinian

tradition has, in its resolute rejection of cosmic design, often run rough-shod over what is physically and biologically sound in those observations, we should welcome an invitation to renew the Darwinian tradition in a direction that promises to explain macroevolutionary phenomena in terms of purely natural processes without inviting regression to cosmic design.

In sum: The shift to nonequilibrium thermodynamic background assumptions as a framework for the further development of the Darwinian tradition leads to the *expectation* of evolution, and so relieves Darwinian explanations of temptations to disguised teleology of the 'design' sort. No longer need Darwinians argue that nature has been able to achieve the same *kind* of effect that an engineer-god could attain by 'using' different means. It is telling that Paley's watchmaker does not disappear in Dawkins' recent account of evolutionary theory (Dawkins, 1986). He merely is said to be 'blind.' From our perspective, however, there is no watchmaker, blind or sighted — for there is no watch. Natural organization is not an artifact, or anything *like* it, but instead a teleonomic, and in a certain sense teleological consequence of the teleomatic action of energy flows.[2]

NOTES

[1] This paper is the result of discussions among the authors and others, which began at the third meeting on the History, Philosophy, and Social Science of Biology held at the Virginia Polytechnic Institute and State University in Blacksburg, Virginia, June 1987.
[2] Some of us have concerns about the ideological and/or theological extrapolations that the reader might be inclined to draw from the issues discussed in this section.

APPENDIX I
Estimating Network Ascendency
Robert E. Ulanowicz

The concept of network ascendency combines the attribute of system size, or level of activity with the relational notion of dynamic organization.

To quantify the level of system activity input-output theory (Leontieff, 1951) employs the *total system throughput*, or aggregate of all the transfers occurring among the system elements. For example, if i and j are two arbitrary members of a collection of n nodes in a directed graph, then the transfer of some particular medium between j and i will be denoted as T_{ji}. The activity level of a specific node i can be gauged either by the sum of inputs to the node,

$$T'_i = \sum_p T_{pi}$$

or by the collection of all flows issuing from i,

$$T_i = \sum_q T_{iq}.$$

($T_i = T'_i$ at steady state.) The activity level of the whole system or total system throughput, T, is equal to the aggregate of the activities at all nodes,

$$T = \sum_i T_i = \sum_i T'_i.$$

Measuring the level of network organization is only slightly more complicated. We begin by defining an organized network as one about which there exists little ambiguity as to where medium at any node will next flow. Ambiguity is associated with uncertainty, and conversely a decrease in uncertainty bespeaks of information. Hence, it is by employing elements from probability and information theories that network organization can be estimated.

Let a_j denote the event, "A quantum of medium leaves node j," and b_i the similar happening, "A quantum of medium enters node i." The probabilities of each of these events actually transpiring are denoted by $p(a_j)$ and $p(b_i)$, respectively. Furthermore, the joint probability that the quantum both leaves j and enters i will be represented by $p(a_j, b_i)$.

The average apriori uncertainty about the sources and sinks of flows is given by the Shannon-Wiener index of uncertainty calculated using the joint probabilities, i.e.,

$$H = -K \sum_{i,j} p(a_j, b_i) \log p(a_j, b_i),$$

where K is an arbitrary scalar constant.

Knowledge about where (on the average) quanta originate and where they end up [the $p(a_j)$ and $p(b_i)$, respectively] decreases this ambiguity, H, by an amount known as the "average mutual information", denoted here by I and calculated as

$$I = K \sum_i \sum_j p(a_j, b_i) \log [p(a_j,b_i)/p(a_j)p(b_i)].$$

One can show (Aczel and Daroczy, 1975) that for any properly defined set of probability distributions

$$H \leqslant I \leqslant 0.$$

Systems that are highly organized, i.e., those wherein knowing the location of a quantum also imparts a reasonable knowledge of whither it will go possess a value of the mutual information, I, that is close to its upper limit, H. That is, most of the ambiguity about which pathway the medium will take has been resolved. Conversely, in systems that are less structured, knowing the location of a given quantum tells almost nothing about where that material is most likely to move and I is insignificantly small. Hence, the mutual information, I, is an appropriate index for network organization.

It remains to estimate I in terms of measured system flows. Toward this end it is helpful first to ask how one would estimate the constitutive probabilities. If T represents that total amount flowing in the system and T'_i is the amount of that flow observed to be entering node i, then $p(b_i)$ can be estimated by the ratio T'_i/T. Similarly, the estimator for $p(a_j)$ will become T_j/T. In like manner, the joint probability $p(a_j, b_i)$ that a quantum will both leave j and enter i can be assigned the value T_{ji}/T. Substituting these estimates into the formula for I yields

$$I = K \sum_i \sum_j (T_{ji}/T) \log (T_{ji}T/T'_j/T_i).$$

There remains the problem of what value to assign to the undefined scalar constant K. Conventional practice is to choose a base for the logarithm and arbitrarily set $K = 1$. But

Trius and McIrvine (1971) argue that K should be chosen so as to impart physical dimensions to the quantity it is scaling. As we have already elected to gauge system "size" using the total system throughput, T, it is both appropriate and consistent to set $K = T$, thereby making the mutual information reflect the size of the system we are observing.

The resulting product of two factors, one representing system size and the other network organization, is called the network ascendency (Ulanowicz, 1980) and is denoted by the letter "A". Knowing the values of all the T_{ji} in the system allows one to assign an actual number to the ascendency according to the formula

$$A = \sum_i \sum_j T_{ji} \log (T_{ji} T / T_j' T_i).$$

Ulanowicz (1986) argues how any increase in A reveals the unitary process of growth and development transpiring in the system, and he shows how one may investigate the limits to growth using certain components of the difference by which A falls short of its upper limit as set by the scaled version of H.

REFERENCES

Aczel, J. and Z. Daroczy: 1975, *On Measures of Information and Their Characterization*, Academic Press, New York.

Atlan, H.: 1974, 'On a Formal Definition of Organization', *Journal of Theoretical Biology* **45**, 295—304.

Brandon, R. N.: 1981, 'Biological Teleology: Questions and Answers', *Studies in the History and Philosophy of Science* **12**, 91—105.

Brooks, D., D. D. Cumming, and P. H. LeBlond: 1988, 'Dollo's Law and the Second Law of Thermodynamics: Analogy or Extension?', in B. H. Weber, D. J. Depew, and J. D. Smith (eds.), *Entropy, Information, and Evolution: New Perspectives on Physical and Biological Evolution*, MIT Press, Cambridge, MA, pp. 189—224.

Brooks, D and E. Wiley: 1986, *Evolution as Entropy: Toward a Unified Theory of Biology*, University of Chicago Press, Chicago.

Brooks, D. and E. Wiley: 1988, *Evolution as Entropy: Toward a Unified Theory of Biology (Second Edition)*, University of Chicago Press, Chicago.

Campbell, J. H.: 1982, 'Autonomy in Evolution', in R. Milkman (ed.), *Perspectives on evolution*, Sinauer, Sunderland, MA, pp. 190—201.

Campbell, J. H.: 1985, 'An Organizational Interpretation of Evolution' in D. J. Depew and B. H. Weber (eds.), *Evolution at a Crossroads: The New Biology and the New Philosophy of Science*, MIT Press, Cambridge, MA, pp. 133—167.

Campbell, J. H. and P. Perkins: 1988, 'Transgenerational effects of drug and hormonal treatments in mammals: a review of observations and ideas', *Progress in Brain Research* **73**, 535—553.

Clements, F. E. and V. E. Shelford: 1939, *Bio-ecology*, John Wiley and Sons, New York.

Collier, J.: 1986, 'Entropy in Evolution', *Biology and Philosophy* **1**, 5—24.

Conrad, M.: 1983, *Adaptability: The Significance of Variability from Molecule to Ecosystem*, Plenum Press, New York.

Csany, V.: 1985, 'Autogenesis: the Evolution of Self-organizing Systems' in J.-P. Aubin, D. Saari, and K. Sigmund (eds.), *Dynamics of Macrosystems*, Springer Verlag, New York.

Darden, L. and N. Maull: 1977, 'Interfield Theories', *Philosophy of Science* **44**, 43—64.

Dawkins, R.: 1976, *The Selfish Gene*, Oxford University Press, Oxford.

Dawkins, R.: 1986, *The Blind Watch Maker*, Norton, New York.

Denbigh, K. G. and J. S. Denbigh: 1985, *Entropy in Relation to Incomplete Knowledge*, Cambridge University Press, Cambridge.

Demongeot, J., E. Goles, and M. Tchuente (eds.): 1985, *Dynamical Systems and Cellular Automata*, Academic Press, New York.

Depew, D. J. and B. H. Weber: 1988, 'Consequences of Nonequilibrium Thermodynamics for Darwinism', in B. H. Weber, D. J. Depew, and J. D. Smith (eds.), *Entropy, Information, and Evolution: New Perspectives on Physical and Biological Evolution*, MIT Press, Cambridge, MA, pp. 317—354.

Dyke, C.: 1988a, *The Evolutionary Dynamics of Complex Systems: A Study in Biosocial Complexity*, Oxford University Press, New York.

Dyke, C.: 1988b, 'Cities as Dissipative Structures', in B. H. Weber, D. J. Depew, and J. D. Smith (eds.), *Entropy, Information, and Evolution: New Perspectives on Physical and Biological Evolution*, MIT Press, Cambridge, MA, pp. 355—367.

Eldredge, N.: 1985, Unfinished Synthesis: *Biological Hierarchies and Modern Evolutionary Thought*, Oxford University Press, New York.

Eldredge, N. and S. N. Salthe: 1984, 'Hierarchy and Evolution', *Oxford Surveys in Evolutionary Biology* **1**, 184—208.

Ferracin, A., E Panichelli, M. Benassi, A. Di Nallo, and C. Steindler: 1978, 'Self-Organizing Ability and Living Systems', *BioSystems* **10**, 307—317.

Fisher, R. A.: 1930, *The Genetical theory of natural selection*, Oxford University Press, Oxford.

Fox, S.: 1984, 'Proteinoid Experiments and Evolutionary Theory', in M.-W. Ho and P. T. Saunders (eds.), *Beyond Neo-Darwinism: An Introduction to the New Evolutionary Paradigm*, Academic Press, London, pp. 15—60.

Gatlin, L.: 1972, *Information Theory and the Living System*, Columbia University Press, New York.

Gould, S. J.: 1982, 'Darwinism and the Expansion of Evolutionary Theory', *Science* **216**, 380—387.

Gould, S. J. and R. C. Lewontin: 1979, 'The Spandrels of San Marco and the Panglossian Paradigm: a Critique of the Adaptationist Programme', *Proceedings of the Royal Society, London, Series B* **205**, 581—598.

Kauffman, S. A.: 1985, 'Self-Organization, Selective Adaptation, and its Limits: a New Pattern of Inference in Evolution and Development', in D. J. Depew and B. H. Weber (eds.), *Evolution at a Crossroads: The New Biology and the New Philosophy of Science*, MIT Press, Cambridge, MA, pp. 169—207.

Khinchin, A. I.: 1957, *Mathematical Foundations of Information Theory*, Dover, New York.

Kimura, M.: 1983, *The Neutral Theory of Molecular Evolution*, Cambridge University Press, Cambridge.

Lakatos, I.: 1970, 'Falsification and the Methodology of Scientific Research Programmes', in I. Lakatos and A. Musgrave (eds.), *Criticism and the Growth of Knowledge*, Cambridge University Press, Cambridge, pp. 91—195.

Landauer, R.: 1988, 'Dissipation and Noise Immunity in Computation and Communication', *Nature* **335**, 779—784.

Laudan, L.: 1977, Progress and Its Problems: *Towards a Theory of Scientific Growth*, University of California Press, Berkeley.

Layzer, D.: 1977, 'Information in Cosmology, Physics and Biology', *Int. J. Quantum Chem.* **12** (suppl. 1), 185—195.

Leontief, W.: 1951, *The Structure of the American Economy, 1919—1939* (Second Edition), Oxford University Press, New York.

Lewontin, R. C.: 1974, *The Genetic Basis of Evolutionary Change*, Columbia University Press, New York.

Lindeman, R. L.: 1942, 'The Trophic-Dynamic Aspect of Ecology', *Ecology* **23**, 399—418.

Lotka, A. J.: 1922, 'Contribution to the Energetics of Evolution', *Proceedings of the National Academy of Science USA* **8**, 148—154.

Lotka, A. J.: 1925, *Elements of Physical Biology*, Williams and Wilkins, Baltimore; reprinted as *Elements of Mathematical Biology*, Dover, New York, 1956.

Lovelock, J. E.: 1979, *Gaia: A New Look at Life on Earth*, Oxford University Press, Oxford.

Mayr, E.: 1982, *The Growth of Biological Thought: Diversity, Evolution and Inheritance*, Harvard University Press, Cambridge, MA.

Mayr, E.: 1985, 'How Biology Differs from the Physical Sciences', in D. J. Depew and B. H. Weber (eds.), *Evolution at a Crossroads: The New Biology and the New Philosophy of Science*, MIT Press, Cambridge, MA.

Mayr, E.: 1988, *Toward a New Philosophy of Biology: Observations of an Evolutionist*, Harvard University Press, Cambridge, MA. pp. 43—63.

Morowitz, H. J., B. Heinz, and D. W. Deamer: 1988, 'The Chemical Logic of a Minimum Protocell', *Origins of Life and Evolution of the Biosphere* **18**, 281—287.

Odum, E.: 1953, *Fundamentals of Ecology*, Saunders, Philadelphia.

Odum, E.: 1969, 'The Strategy of Ecosystem Development', *Science* **164**, 262—270.

Odum, H. T.: 1988, 'Self-Organization, Transformity, and Information', *Science* **242**, 1132—1139.

Odum, H. T. and E. C. Odum: 1982, *Energy Basis for Man and Nature (second edition)*, McGraw-Hill, New York.

O'Grady, R. T.: 1984, 'Evolutionary Theory and Teleology', *Journal of Theoretical Biology* **107**, 563—578.

O'Grady, R. T. and D. R. Brooks: 1988, 'Teleology and Biology', in B. H. Weber, D. J. Depew, and J. D. Smith (eds.), *Entropy, Information, and Evolution: New Perspectives on Physical and Biological Evolution*, MIT Press, Cambridge, MA. pp. 285—316.

Olmsted, J.: 1988, 'Observations on Evolution', in B. H. Weber, D. J. Depew, and J. D. Smith (eds.), *Entropy, Information, and Evolution: New Perspectives on Physical and Biological Evolution*, MIT Press, Cambridge, MA. pp. 243—261.

Peacocke, A. R.: 1983, *An Introduction to the Physical Chemistry of Biological Organization*, Oxford University Press, Oxford.

Prigogine, I.: 1980, *From Being to Becoming: Time and Complexity in the Physical Sciences*, Freeman, San Francisco.

Riedl, R.: 1977, 'A Systems-Analytical Approach to Macro-Evolutionary Phenomena', *Quarterly Review of Biology* **52**, 351—370.

Riedl, R.: 1978, *Order in Living Organisms*, Wiley-Interscience, New York.

Rosen, R.: 1985, 'Organisms as Causal Systems Which Are Not Mechanisms: An Essay into the Nature of Complexity' in R. Rosen (ed.) *Theoretical Biology and Complexity*, Academic Press, Orlando.

Rosenberg, A.: 1985, *The Structure of Biological Science*, Cambridge University Press, Cambridge.

Rutledge, R. W., B. L. Basorre, and R. J. Mulholland: 1976, 'Ecological Stability: An Information Theory Viewpoint', *Journal of Theoretical Biology* **57**, 355—371.

Salthe, S. N.: 1985, *Evolving Hierarchical Systems: Their Structure and Representation*, Columbia University Press, New York.

Schneider, E. D.: 1988, 'Thermodynamics, Ecological Succession, and Natural Selection: A Common Thread', in B. H. Weber, D. J. Depew, and J. D. Smith (eds.), *Entropy, Information, and Evolution: New Perspectives on Physical and Biological Evolution*, MIT Press, Cambridge, MA. pp. 107—138.

Serra, R. and G. Zanarini: 1986, *Tra Ordine e Caos: Auto-Organizzazione e Imprevidibilita nei Sistemi Complessi*, CLUB, Bologna.

Serra, R., G. Zanarini, M. Andretta, and M. Compiani: 1986, *Introduction to the Physics of Complex Systems*, Pergamon Press, Oxford.

Sober, E.: 1984, The Naure of Selection: *Evolutionary Theory in Philosophical Focus*, MIT Press, Cambridge, MA.

Stent, G. S.: 1985, 'Hermeneutics and the Analysis of Complex Biological Systems', in D. J. Depew and B. H. Weber (eds.), *Evolution at a Crossroads: The New Biology and the New Philosophy of Science*, MIT Press, Cambridge, MA. pp. 209—225.

Stuart, C. I. J. M.: 1985, 'Bio-Informational Equivalence', *Journal of Theoretical Biology* **113**, 611—636.

Tribus, M. and E. C. McIrvine: 1971, 'Energy and Information', *Scientific American* **255**, 179—188.

Ulanowicz, R. E.: 1980, 'An Hypothesis on the Development of Natural Communities', *Journal of Theoretical Biology* **85**, 223—245.

Ulanowicz, R. E.: 1986, *Growth and Development: Ecosystems Phenomenology*, Springer-Verlag, New York.

Von Foerster, H.: 1960, 'On Self-Organizing Systems and Their Environments', in M. Yovits and S. Cameron (eds.), *Self-Organizing Systems*, Pergamon Press, New York.

Weber, B. H., D. J. Depew, and J. D. Smith: 1988, *Entropy, Information and Evolution: New Perspectives on Physical and Biological Evolution*, MIT Press, Cambridge, MA.

Wicken, J. S.: 1984, 'The Cosmic Breath: Reflections of the Thermodynamics of Creation', *Zygon* **19**, 487—505.

Wicken, J. S.: 1987, *Evolution, Information, and Thermodynamics: Extending the Darwinian Program*, Oxford University Press, New York.

Wright, L.: 1973, 'Functions', *Philosophical Review* **82**, 139—168.

Zotin, A. I.: 1972, *Thermodynamic Aspects of Developmental Biology*, S. Karger, Basel.