

Entropy and Information in Evolving Biological Systems¹

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ABSTRACT: Integrating concepts of maintenance and of origins is essential to explaining biological diversity. The unified theory of evolution attempts to find a common theme linking production rules inherent in biological systems, explaining the origin of biological order as a manifestation of the flow of energy and the flow of information on various spatial and temporal scales, with the recognition that natural selection is an evolutionarily relevant process. Biological systems persist in space and time by transforming energy from one state to another in a manner that generates structures which allows the system to continue to persist. Two classes of energetic transformations allow this; *heat-generating transformations*, resulting in a net loss of energy from the system, and *conservative transformations*, changing unusable energy into states that can be stored and used subsequently. All conservative transformations in biological systems are coupled with heat-generating transformations; hence, inherent biological production, or genealogical processes, is positively entropic. There is a self-organizing phenomenology common to genealogical phenomena, which imparts an arrow of time to biological systems. Natural selection, which by itself is time-reversible, contributes to the organization of the self-organized genealogical trajectories. The interplay of genealogical (diversity-promoting) and selective (diversity-limiting) processes produces biological order to which the primary contribution is genealogical history. Dynamic changes occurring on times scales shorter than speciation rates are microevolutionary; those occurring on time scales longer than speciation rates are macroevolutionary. Macroevolutionary processes are neither reducible to, nor autonomous from, microevolutionary processes.

KEY WORDS: evolution, entropy, information, hierarchy, ecology, phylogeny, natural selection.

Evolutionary theory is experiencing a period of close scrutiny. Some authors assert that evolutionary theory is essentially complete (e.g. Charlesworth, Lande, and Slatkin, 1982; Stebbins and Ayala, 1981; Buss, 1987), and others argue for a replacement theory that is independent of Darwinian principles. What is needed, however, are approaches that try to integrate traditional principles and research programs with new ideas that can address problems not addressed by current evolutionary theory. This is exemplified by the titles of recent texts and articles that emphasize the need to "expand" (Gould, 1980), "finish" (Eldredge, 1985), "extend" (Wicken, 1987a), or "unify" (Brooks and Wiley, 1988) evolutionary biology. Attempts to find common ground among these various proposals have begun (e.g. articles in Weber, Depew and Smith, 1988). Common to many of these discussions are interests in (1) questions of origin as well as

maintenance in evolutionary explanations and (2) consideration of the relationship between thermodynamics, information theory and evolution.

Physical processes take time to happen. However, many physical phenomena are symmetrical with respect to time reversal. A film showing a reversible process would give no indication whether it was being viewed forwards or backwards. Other physical processes are asymmetrical with respect to time. A film showing such a time-dependent process would differ drastically when shown forward or in reverse. Theories of biological evolution that stem from the neo-Darwinian synthesis share a Newtonian, or time-symmetrical, perspective (Depew and Weber, 1988). Natural selection is a local phenomenon that implies no large scale temporal or spatial structure. A recent text (Luria, Gould, and Singer, 1981: 647) states: "Darwinism is not a theory of intrinsic progress," and goes on to note that adaptations are local only. The gene frequencies of a population are expected to remain constant (given the appropriate assumptions) unless acted upon by natural selection which may shift the population to a new equilibrium if that selection is directional. Cyclic environmental conditions, however, can shift the genetic structure back to its previous equilibrium. Hence, the processes of microevolution postulated by the synthetic theory are in themselves time reversible. For example, suppose one were to view a film showing moths in a forest, and both the moths and the trees appear predominantly light-coloured at first, then become predominantly dark, and then predominantly light again. The observer could tell that directional selection had occurred but could not tell whether the film had been shown in the correct temporal sequence. There are, however, many biological processes, such as reproduction, development (ontogenesis), death, speciation (phylogenesis), and extinction, that are inherently irreversible phenomena. In what follows, we address the question of how time-asymmetric processes are to be explained and integrated into general biological theory.

Time-asymmetric processes can be of very different sorts. Consider, for example, stellar systems and biological systems. The regularity of stages in the "evolution" of different kinds of stars is an example of time-dependent regularity without historical connection. The ontogeny of BO class stars appears to have been similar in every case. The similarity is due only to similar conditions and causes, not to a shared history. This becomes apparent when we realize that BO stars (like the Sun) are formed independently from each other, and do not share a common ancestor that displayed the mass, luminosity and spectral characteristics that characterize BO stars. Rather, BO stars are formed when particular initial conditions in the prestellar stages of star development are realized. Other conditions, such as insufficient mass of prestellar gas, would lead to a star of a different class being formed. In contrast to stellar evolution, biological evolution is dependent not only on initial conditions, but on the interplay

of many unique events specific to the particular history of the evolving biological system. For example, many of the similarities shared by species are the result of common ancestry and not the realization of a repeatable series of events originating from independent, but identical, initial conditions. Thus, such similarities (homologies) are embedded in an inherited, i.e. historical, matrix. In general, unlike many time-dependent physical systems, biological systems retain effects of historical events that are transmitted to them from other, similar predecessors (i.e., ancestral systems). Their time-dependent behavior unfolding into the future is constrained by events that happened in the past, the effects of which they carry with them. In some ways, biological evolution has more in common with the systems studied in cosmology than with stellar ontogeny.

ORIGIN AND MAINTENANCE OF BIOLOGICAL ORDER

Three attributes distinguish living systems from non-living systems: (1) "phrase separation" between the "inside" and the "outside", giving living systems a high degree of autonomy from their environments, (2) replication and reproduction and (3) the internal production of new organized structure (information) through growth or evolution. Living systems are usually adapted to their environments. We could say that living systems typically contain information about their environment. They must at least be able to use available environmental energy to maintain the three attributes listed above. Most living systems, though, go well beyond this minimal requirement and take advantage of their environment to enhance and supplement the processes maintaining these attributes. Although these enhancements, adaptations, are widespread in living systems, we do not regard them as essential to life because the three central attributes can be maintained without—the benefit of differential adaptation to particular environmental circumstances. As long as energy is available under non-equilibrium conditions, as it is virtually everywhere in the biosphere, the essential characteristics of life, phrase separation, replication and reproduction, and the production of structural information, can be maintained.

From the information-theoretic point of view, selection increases the proportion of information in a population that is correlated with its environment (see below). However, two observations argue for the idea that environmental information is neither necessary nor sufficient for the origin and evolution of living systems. First, information changes come from changes in the information systems themselves. Second, the kinds of information change that occur are random with respect to the "needs" of the organism. Thus, there is no direct way for the environment to conjure up adaptive traits. For a trait to be adaptive, it must have been selected in the past. Further, its origin is independent of its selection coefficient in any

particular environment. To argue (as Weber et al., this volume, seem to) that organisms are living systems or that living systems evolve because they have been "informed" by the environments in which they live does not take these points into account. Evolution is quite possible without natural selection and adaptation (see discussion by Endler, 1986).

History strongly influences the form that living organisms take. To understand the influence of history, we must take into account the role of irreversible processes in the origin and maintenance of organisms. In the rest of this section we consider three kinds of irreversible processes. All share a common dependence on the simultaneous internal production of both entropy and order.

The first process is the maintenance and production of biological mass by using available energy and matter. Without continual energy flow, order will dissipate and phase separation with the environment will be lost.

Second, biological systems maintain structural and functional integrity by the storage and transmission of information. Without the accumulation and expression of information, biological systems cannot retain successful patterns of energy flow that enhance their ability to maintain order. The rate of biological processes, such as reproduction, development and microevolution are affected not only by energy available from the environment, but also on internal "production rules" that determine much of the biological forms upon which selection operates. These production rules are determined by information transmitted to the system from ancestral systems. Finally, as a consequence of energy flow, different kinds of entropy are produced at different rates. These differences in the rates of production of different kinds of entropy result in the development of hierarchical structures that demonstrate different kinds of behavior, and affect one another by systems of indirect constraints.

ENERGY FLOW

Lotka (e.g. 1913, 1925) was among the first to discuss biological systems in terms of energy flows and energy partitioning. Biological systems persist by transforming energy from one state to another in a manner that generates organized structures. There are two classes of energetic transformations that can be recognized in biological systems. The first results in a net loss of energy from the system, the loss being measured as heat. Maurer and Brooks (submitted) called these *heat-generating transformations*. The second class of transformation changes unusable energy into states that can be stored and used in subsequent transformations. Maurer and Brooks (submitted) called these *conservative transformations*. All conservative transformations in biological systems are coupled with heat-generating transformations. Lotka (1913) suggested that a system could

delay the time of its inevitable loss of structure by accumulating sufficient bound energy through conservative energetic transformations. Under this view, biological systems slow the rate at which energy stored by conservative transformations is degraded by heat-generating transformations.

Energy flows within biological systems are coupled with the production of entropy. Heat generating transformations generate thermal entropy, which is a measure of the cost of maintaining biological structure. Conservative transformations produce structural entropy (called *information* by Collier, in review), which is a measure of the system's structural complexity. Dissipative structures (Prigogine, 1967, 1980) are non-equilibrium thermodynamic systems in which macroscopic order (structural entropy) is produced by dissipative processes that allow a lower rate of entropy production than if the processes were completely thermal. Because energy stored by conservative transformations degrades at a rate slower than the heat liberated during heat producing transformations, there is a period of time during which the system accumulates structural entropy. This time lag allows the system to isolate processes occurring within the system from those occurring outside the system. Thus, the system can be viewed as maintaining a phase separation between the processes occurring within the system and those occurring without. That is, processes occurring within the system are insulated from fluctuations in processes occurring outside the system that could lead to disorder if carried out within the system. Entropy changes (dS) in such systems can be decomposed into two components, one measuring exchanges between the system and its surroundings ($d_e S$) (changes in the environment) and the other measuring production by processes internal to the system ($d_i S$) (changes in the system). These systems must produce entropy internally ($d_i S > 0$). Or,

$$dS = d_e S + d_i S, d_i S > 0$$

A class of open thermodynamic systems called dissipative structures can arise kinetically when the internal dynamics of the system change the system faster than it can equilibrate with its surroundings. Dissipative structures can also arise physically, when the boundary conditions are such that there is a physical barrier between the system and its surroundings. In each case, a phase separation between the system and its surroundings is formed, allowing the possibility of internal production rules that are not governed directly by fluxes from the environment, but by entropy production within the system. Retained entropy production, such as heat, could establish conditions allowing reactions to occur internally that would be impossible otherwise. The greater the phase separation, or distinction between system and surroundings, the greater the autonomy of the internal production rules. Biological membranes are maintained kinetically and produce a physical phase separation between the living

system and its environment. Hence, biological systems behave as dissipative structures. We will show later that natural selection is expected to occur precisely because of the existence of internal autonomous production rules allowed by this underlying nature of biological systems.

Production rules in biological systems are those processes for which there is an energetic "cost" or "allocation". Following Prigogine and Wiame (1946) and Zotin and co-workers (e.g. Zotin and Zotina, 1978), Brooks and Wiley (1988) denoted such allocations using the symbol ψ , signifying a specific dissipation function. It includes at least two classes of processes: (1) those involved in dissipation from the system, called the *external dissipation function* ($\psi\alpha$) and (2) those involved in dissipation within the system, called the *bound dissipation function* ($\psi\mu$). For biological systems, $\psi\mu$ contains allocations for accumulating biomass ($\psi\mu^b$) and allocations for accumulating genetic diversity ("instructional information" of Brooks and Wiley, 1988) ($\psi\mu^i$).

Maurer and Brooks (submitted) suggested that if all three components of ψ are included in the thermodynamic production term $d_i S$, biological systems exhibiting order must have the following properties: (1) the rules (although not necessarily the details) for both heat-generating and conservative transformations must be encoded in the structure of the system, (2) those production rules must include "information" or "instructions" leading to non-random exchanges between the system and its surroundings, and (3) production by the conservative processes must be positively entropic. Under this view, there is an entropic drive within biological systems resulting from production, which includes processes that result in the accumulation of free energy. The non-random nature of that accumulation according to intrinsic production rules results in the non-random mechanical and chemical gradients within biological systems. The flow of free energy and of structural entropy occur in the same, not different directions.

Frautschi (1988; see also Layzer, 1975; Frautschi, 1982; Landsberg, 1984a, b) recently contrasted two classes of processes that generate entropy. The first is equilibration of temperatures between system and surroundings; for open systems this comes through heat-generating transformations. Biological systems exhibit this kind of entropic behavior through external dissipation processes ($\psi\alpha$). The second is expansion of the phase space of the system, an increase in its number of accessible microstates (possible configurations). System organization increases so long as equilibration (equiprobable distribution of the system over all of its microstates) takes longer than phase space expansion, allowing a lag between the realized entropy and the maximum possible entropy (figure 1). New microstates are formed by the production of new components, either at a given organizational level or through the opening up of new levels. Free energy and structural entropy may accumulate together in

such systems. Cosmological models of the expanding universe discussed by Frautschi (1982) explain the origin of free energy in the universe in this way. In biological systems this is accomplished by conservative transformations. For example, auto-catalytic processes producing monomers make "monomer space" available for chemical evolution. Some monomers have high chemical affinities for each other, and, given sufficient activation energy, will spontaneously clump into oligomers and polymers. A specific set of polymers can correspond to different distributions of monomers, depending on how the clumping occurred. Thus, some monomer microstates correspond to polymer macrostates. Once polymers begin to form, "polymer space" becomes available to the evolving system. Causal interactions between polymers create new levels of organization, and so on. Because new levels create a hierarchy of increasing structural complexity, more and more of the entropy production is invested in complex structure. The allocation of $d_i S$ to $\psi\mu$ should be proportional to entropy increases due to expansion of phase space.

Protocells are additional classes of accessible microstates in the hierarchy of increasing structural complexity. They are more stable and self-organizing than lower-level systems because dissipation products in one part of the system maintain other parts of the system rather than simply being lost into the surroundings. Subsequent evolution in such systems involves progressive binding of functional sub-units into larger functional wholes, accentuating hierarchical organization as a greater percentage of $d_i S$ is allocated within the system, maintaining complex structures. Auto-catalytic and other feedback processes are the source of the cohesion of the entities in biological hierarchies (Collier, 1988). For example, reproduction, like all replication, is auto-catalytic and is the source of cohesion in species. Cell membranes allow for the isolation of cytoplasm and environment that acts to maintain a phase separation between inside and outside allows internal production rules that are relatively autonomous from the external environment. Production itself requires exchanges of matter and energy with the external environment ($d_e S$ and $\psi\alpha$) but the production rules determining the fate of that matter and energy are physically encoded within the system.

INFORMATION

The production rules comprise what we call information. They are ultimately encoded as base pair sequences in DNA (or rarely RNA) and comprise both structural and control genes. Because the most direct manifestations of these production rules are in ontogenies, Waddington (1966) referred to them as "instructions." Like computer programs, they are a kind of information. Replication and reproduction transmit semi-

conserved copies of the production rules in addition to making products structured according to the rules (within the confines, of course, of natural laws and particular external circumstances). From this point of view, living systems are "informed autocatalytic systems" (Wicken, 1987a; Brooks and Wiley, 1988). Although the processes of information transmission and transformation are dependent on energetic processes of the sort described in the last section for the production of new structures and the maintenance of existing structures, the fidelity of these processes allows us to consider the information "budget" separately from the energy "budget." Just as matter and radiation become partially decoupled (and distinct kinds) in the early development of the universe, so biological energy and biological information probably became partially decoupled early in the development of life. For this reason, it has been useful to develop information theoretic analogues of the expanding phase space process (Brooks, Leblond, and Cumming, 1984; Brooks, Cumming, and Leblond, 1988).

Information depending on the state of a physical system is called *bound information* (Brillouin, 1962). It is information in the sense that the physical system has a determinate form (examples of systems containing bound information are DNA strands, the states of a computer memory, and the macrostructure in a turbulent flow). Measurements are able to read this information and we can use them to produce a representation of the system. Bound information is a measure of the causal power of a physical system in the sense of its maximal ability to make a distinction between, or a difference in, systems with which it interacts (Collier, in press). Collier suggested that bound information has two manifestations, *intropy*, the complement of entropy, and *enformation*, which is structural in nature and which guides, or directs, the flow of available energy. Both are required for causal activity. Although the two are interconvertible, they are distinguished in particular cases by their relative roles. Loosely, enformation is the static component or the organization of a system while intropy results from the system not having fully "relaxed" (i.e., gone to equilibrium). All stability, however, is a matter of degree, and no real systems are ever fully relaxed. The distinction between intropy and enformation is more a matter of convenience than anything else. Both are forms of information. Any attempt to draw a fundamental distinction between structural information (enformation) and entropy related to concepts of order (intropy) is purely artificial.

Genetic information is bound information, but also serves as a code for information transmission. Thus it has characteristics usually associated with physical entropy as well as characteristics usually associated with communications theory (Shannon and Weaver, 1949). These two approaches to information have been seen by some to be incompatible (cf. Wicken, 1987b). In the case of DNA, however, both seem to apply; chemistry and representation come together head-on. We call such configurations arrays.

Arrays have both entropic and representational characteristics (Collier, 1986). They are composed of relatively stable elements that can combine freely under moderate constraint. The elements are nucleotides and an example of a moderate constraint is nucleotide complementarity. These characteristics are rather like the letters of the alphabet although they are not necessarily constrained to combinations in one physical dimension.

A set of elements and the arrays they can form constitute a physical information system. For example, the physical information system of most humans is based on an array found on 48 strands of DNA. Cohesion creates new higher level elements that can form their own arrays. Triplets code for amino acids. Genes code for enzymes and structural proteins. Leaders, operators, promoters and CAPs regulate and/or promote the transcription of DNA while post-transcriptional editing by other enzymes converts immature mRNA into mature mRNA that can be used for translation. Cohesion at this level is an emergent property of the constraints placed on DNA variation. There are, of course, many other levels of cohesion that place constraints on lower levels of organization. Given the finite size of an information system at any given time, for any higher level we can determine the possible variants at lower levels given the constraints resulting from the cohesion that produces the higher level of organization. This defines the degeneracy of the level in the same way as the various possible microstates of any other physical system determine the degeneracy of its macrostates. Since variations (due, for example, to mutation and recombination) are random relative to the constraints at the higher level, the degeneracy determines an entropy for the information at the higher level.

The definition of the informational entropies of higher level arrays is exactly analogous to the statistical definition of entropy in statistical mechanics. The configurational information in an array is best regarded as enformation when it is considered as a cohesive structure. If viewed as a temporary arrangement of somewhat limited stability, it is best regarded as intropy. It would be foolish to insist that it must be one or the other. Stability is a matter of degree, and it is well known that DNA is both relatively stable and subject to change that produced significant variations in base pair sequences. Given the arbitrary nature of the distinction between enformation and intropy, there is no good reason to assume that array entropy is fundamentally different from thermodynamic entropy.

This distinction between informational macrostates and microstates gives us a physically based informational entropy determined entirely by conditions within the information system itself. The usefulness of this entropy measure results from the relative autonomy of the informational budget from the energy budget. Without this autonomy, the entropies involved in the information system would be so small as to be overwhelmed by the energies' entropies. (We can see this relative autonomy

when we consider that the energetic entropies of two DNA sequences will be quite similar while their information "content" of base pair sequences can be quite different.) Standard techniques for determining information values use probabilities or combinatorics. These methods are not very useful for estimating the information contents of physical systems since they presume a state space of hypothetical alternatives that are not accessible for physical examination. If, however, we think of causal processes as computations, with the initial state the input, the laws of nature the program, and the final state the output, we can use algorithmic information theory (Kolmogorov, 1968; Chaitin, 1975) to represent the information content of states in terms of the causal power required to produce them (Collier, in review).

Algorithmic information theory, conveniently, yields the same information values as the more common probabilistic and combinatorial approaches, except for a small additive factor for computational overhead. The algorithmic information content $I(X)$ of an object X is the size (in bits) of the shortest self-delimiting program that computes X . This is the computational complexity of X . In physical terms, this is the causal power required to produce X from fundamental components. The entropy of a macrostate M , whether an array or other physical state, is the indeterminacy of its microstate m given M . This is just the conditional information $I(m/M)$ of m given M , which is defined as the length of the shortest program required to compute m given $I(M)$. In this case $I(m/M) = I(m) - I(M)$. Because causal processes involving only properties of M cannot compute states with information greater than $I(M)$, m is random with respect to M to the extent that it is underdetermined by $I(M)$, i.e., to degree $I(m/M)$, the entropy of M . The emergence of macrostates then, creates entropy, except in the trivial case in which the macrostate has only one possible microstate. (For further details, see Collier, 1986; Collier, in review; Brooks, Cumming and LeBlond, 1988; Brooks and Wiley, 1988; Smith, 1988).

For a given level in a physical information hierarchy, the difference between the entropy maximum (H_{\max}) and the actual entropy (H_{obs}) measures the organization of the system at that level (figure 1). This difference is $I(M)$, the macroscopic information (Layzer, 1975). It is also a measure of constraint, representing possible variation that has been historically excluded. H_{obs} is a measure of the internal entropy ($\psi\mu$, the bound dissipation), and also represents the realized diversity in the information system (figure 2).

The dynamic we describe has three major elements: (1) H_{obs} is an increasing function of time, as mandated by the Second Law of Thermodynamics; (2) H_{obs} is a concave function of time, as historical constraints retard the rate of entropy increases; and (3) the difference between H_{\max} and H_{obs} is an increasing function of time, proportional to the growth of

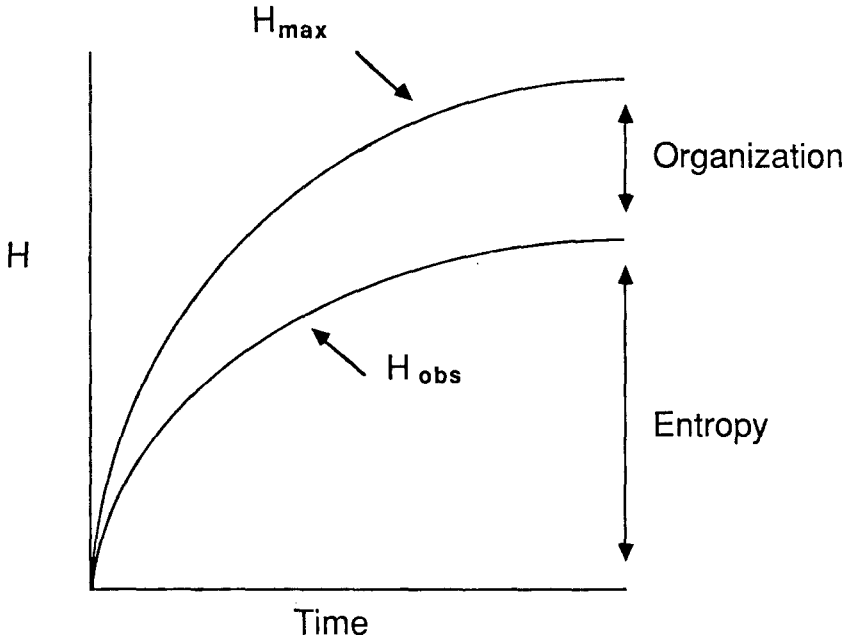


Fig. 1. The relationship between increasing entropy maximum (H_{\max}) and the observed entropy (H_{obs}) of a physical system over time. The difference is proportional to organization while the value of H_{obs} is a measure of the entropy of the system.

organization in the system (Brooks and Wiley, 1988). Smith (1988) has shown mathematically that a general class of models, the so-called “partitioned Lebesgue spaces with automorphism,” has these properties. This class of models includes stationary Markov chains.

The informational budget of living systems shows many of the same properties as the energy budget. The same fundamental properties apply, those of non-equilibrium systems obeying the second law of thermodynamics. For examples of applications of these principles to the information budget, see Chapters 3 and 4 of Brooks and Wiley (1988).

SCALING OF ENTROPY PRODUCTION

Entropy is produced at different rates in a biological system because energy stored by conservative transformations is degraded at different rates. Thus, biological systems develop organized structures that exist on different spatial and temporal scales (Maurer and Brooks, submitted). At the lowest organizational level, the shortest time intervals, and the smallest spatial scales, the greatest relative contribution to ψ will be $\psi\alpha$. Hence, macroscopic manifestations of $\psi\alpha$ will predominate our observations. For

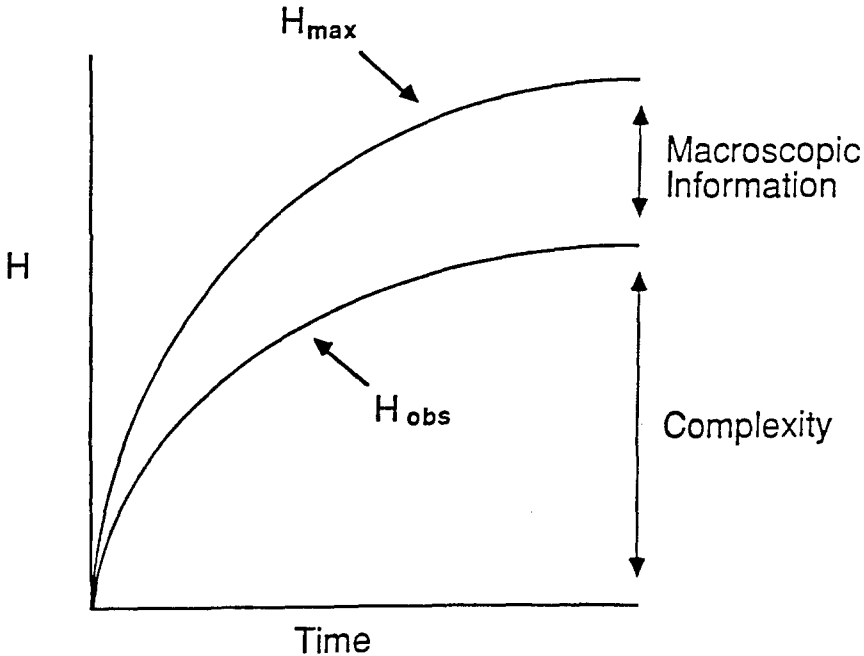


Fig. 2. The relationship between macroscopic information and complexity of a physical information system.

example, if we examine cellular or sub-cellular structure over short time intervals, processes such as metabolism dominate. Most of the readily observable entropy production is dissipated into metabolic heat loss, and the biological systems will appear to behave as classical dissipative structures. At more intermediate levels of organization, space or time, $\psi\mu^b$ predominates. Most entropy production at this scale is dissipated into biomass accumulation and maintenance. And on the largest and longest scales, $\psi\mu^i$ predominates, and the patterns relevant to biological explanations pertain mostly to the accumulation and maintenance of genetic diversity. Figure 3 depicts a heuristic view of the relationship between energy allocations into the three components of ψ and temporal scaling.

Perhaps the most important aspect of scaling is the implication that there is no objective level of organization, time interval, or spatial interval for biological evolution. This arises from the same sorts of considerations that blur the distinction between enformation and intropy. Evolutionary processes operate on all levels and at all scales. The macroscopic manifestations of evolutionary principles differ depending on the level one chooses for observation and study. As a result, we would envision robust evolutionary explanations to be formulated somewhat like explanations using Analysis of Variance (ANOVA), in which the relative contributions of a variety of influences to the total variance are assessed.

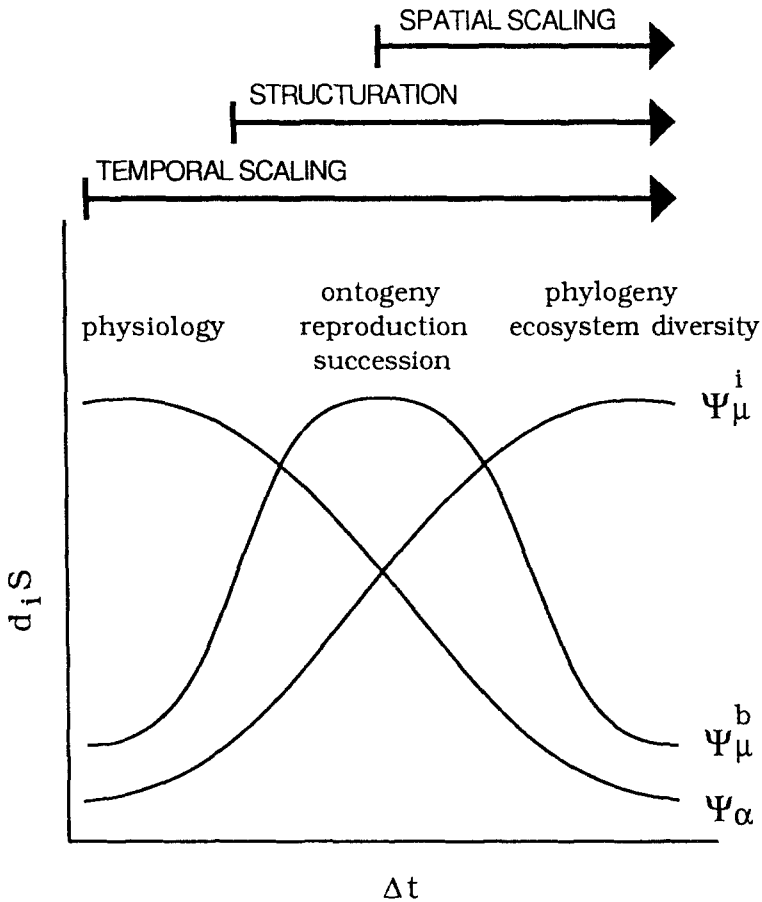


Fig. 3. Temporal scaling of major production components in living systems, and their macroscopic manifestations. The axes are entropy production, $d_i S$, and time intervals (Δt). $\psi\alpha$ refers to external dissipation, $\psi\mu^b$ to biomass accumulation, and $\psi\mu^i$ to genetic diversity accumulation. All processes contribute at all time intervals, but to different degrees for each Δt . This is represented heuristically by the curves accompanying $\psi\alpha$, $\psi\mu^b$, and $\psi\mu^i$.

ORIGIN OF THE ECOLOGICAL HIERARCHY

Environmental and genealogical phenomena are intimately connected in biology. Pre-biotic environmental conditions established the boundary (characterized by Salthe, 1985, as pre-biotic ecology) within which life could originate. Conversely, genealogical processes that characterize life and evolution are autonomous enough from environmental conditions to be capable of overrunning available required resources and of changing the environment substantially. The longer life exists on the planet, the

more it shapes the environment. Today, much of the environment consists of the products of genealogical processes. Eldredge and Salthe (1984), Salthe (1985), and Eldredge (1985, 1986) have suggested two forms of hierarchically-organized behavior in biology. The realm of *interactors* is the *ecological hierarchy*, and encompasses exchanges of matter and energy between system and environment ($d_i S$ and $\psi\alpha$). The realm of *replicators* is the *genealogical hierarchy*, resulting from production processes ($\psi\mu$).

The two hierarchies, as we construe them, are not ontologically equivalent. To use a sports metaphor, the ecological hierarchy explains the dimensions of the playing field, while the genealogical hierarchy gives the rules of the game being played. Many different games can be played on a given field, but only one at a time. Biological systems obey rules of self-organization carried genealogically (historically) and played out within environmentally defined boundaries. The self-organizing rules of the game by which living systems evolve can produce changes in the dimensions of the playing field. To extend the metaphor, the game may redefine the boundaries of the playing field, and is not necessarily constrained by them. For example, the evolution of photosynthetic prokaryotes resulted in increased oxygen content in the atmosphere. This increase, produced by the organisms themselves, established the initial conditions that later led to the evolution of oxidative phosphorylation and changed the distribution of anaerobic organisms, limiting them to relatively rare environments.

Thus, while the exchange of energy and matter with the environment is essential to biological functioning, the irreversible behavior and the increasing complexity characteristic of biological evolution is not an unaided consequence of environmental forces. The creation and maintenance of biological systems requires environmental resources but does not require that the information in biological systems originates in the environment (although some of it may). Biological systems have intrinsic capacities to create hierarchically organized structures so long as they have an adequate source of matter and energy. The environment is not inherently organized as the ecological hierarchy; its organization into an ecological hierarchy is largely a consequence of organization intrinsic to the genealogical hierarchy. Species do not fill empty niches, they create their own niches. At the same time, the environment provides an important constraining influence on biology, and the (self-generated) ecological hierarchy plays an important feedback role in evolution (see next section). The ecological hierarchy is the means by which two different genealogies, or two different generations in one genealogy, can causally influence one another.

If the entropic behavior of a system affects its surroundings, then it is possible for the system to play a role in structuring its environment. Heuristically, for biological systems

$$d_i S = \psi = \psi\alpha + \psi\mu^b + \psi\mu^i$$

This production term corresponds to the products of the genealogical hierarchy. These products exist by exploiting "entropy gradients" in the surroundings, which we view as the ecological hierarchy, and associate with $d_e S$. These gradients, and thus the ecological hierarchy, are determined partly by abiotic factors and partly by biotic factors. $\psi\alpha$ determines how the abiotic portion of the ecological hierarchy can be structured by products of the genealogical hierarchy. In this way part of the production term, $d_i S$, can influence the exchange term, $d_e S$. $\psi\mu^b$ and $\psi\mu^i$ determine the portions of the ecological hierarchy that are products of the genealogical hierarchy. The relationship between the two hierarchies based on the above view is shown schematically in figure 4.

Ecosystems have long been considered energy-exchange systems (Lotka, 1925; Lindeman, 1942; Emig, 1985; Maurer, 1987). Lindeman (1942) suggested that production in ecosystems involved both "dissipation" (loss) and "growth" (biomass accumulation). Over very short time periods ecosystems behave like dissipative structures and can be treated essentially as steady-state phenomena. For example, Levins (1975) suggested that over long time periods, the macroscopic state of an ecosystem was proportional to the ratio of dissipation: growth. A value of unity corresponds to a steady-state ecosystem, with some (theoretical) probability of

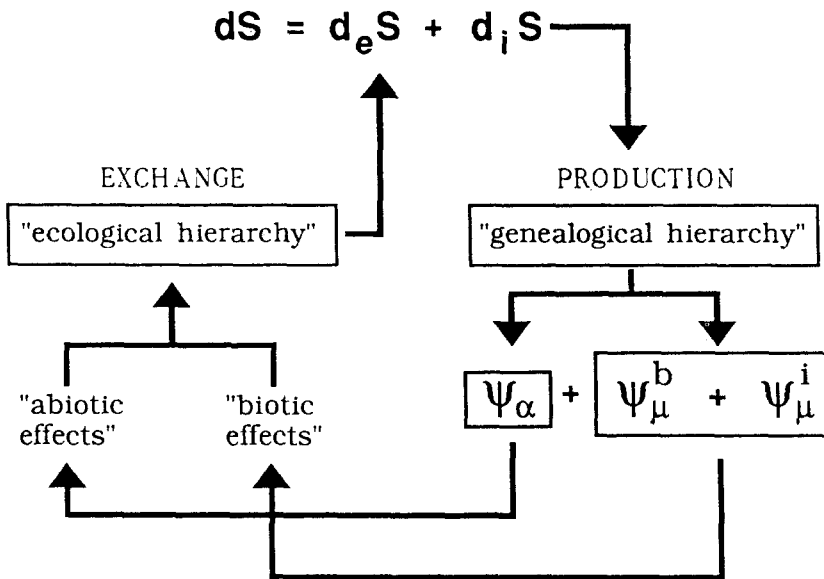


Fig. 4. The conceptual relationship between the genealogical hierarchy (biological production) and the ecological hierarchy (environment/biological systems exchanges) in terms of entropic behavior of open systems. The degree to which the genealogical processes shape the ecological hierarchy is the extent to which organisms have changed the environment of earth during evolution.

extinctions for particular members. Values higher than unity indicated senescent ecosystems, with an increased probability of extinctions; values lower than unity indicated a growing ecosystem, with decreased probabilities of extinction.

ORIGIN OF ENVIRONMENTAL NATURAL SELECTION

Over long time intervals we expect macroscopic information (I), or organization, to grow (figure 1). We therefore expect increasing values of the Function Q , where

$$Q = 1 - (H_{\text{obs}}/H_{\text{max}}) = I/H_{\text{max}}$$

Landsberg (1984b) termed Q *macroscopic order*. It is also known as *redundancy* (Gatlin, 1972). The redundancy concept also figures in communications theory views of information (Shannon and Weaver, 1949). In that formulation, however, the definition of redundancy relies on the interpretation of a message by the source. If we use the assumptions of Collier (1986) about physical information systems, then the redundancy concepts are the same. For this to be so, the message, the source of transmission, and the receiver of the message must be parts of the same system. We believe that this underlies at least some attempts to use information theory to help with studies of communication in animal behavior (Hailman, 1977). If this dynamic in biological systems results from intrinsic (genealogical) rather than extrinsic (environmental) factors, we should expect the products of reproduction and ontogeny to show high degrees of structural and functional organization that is buffered from changes in the environment. Organisms, populations and local communities are not simply the products of their environments. Rather, they are primarily products of their histories and these histories are predictors of their "performance" in any particular local community. The sum of these histories could provide predictors of community structure.

In information theory, correlation is the same as mutual, or shared, information. Adaptations (i.e., adaptive traits, not the process of adaptation) certainly involve a correlation between organism and environment, so we can say that adaptations involve mutual information between an organism and its environment.

One might consider the argument that the information in the environment is being passed to the biological system (Weber *et al.*, this volume). We might entertain the possibility that biological organization is structured by the environment. If so, then the mutual information shared by the biological system and its environment should be heavily weighted such that most components of the biological information are correlated with the current environment. At the time scale represented by species and higher

taxa (i.e., the phylogenetic time scale), we would expect to see more convergence between attributes than homologies. The only shared homologies not correlated with proximal environmental conditions would be old adaptations that are being phased out by selection. The biological system is nothing but a reflection of its current environment plus some transient, now irrelevant, adaptations to past environments. Selection, in this view, orders the system. However, we do not observe such character distributions. Convergence is certainly present, and even common, but convergence is not so prevalent as to frustrate our attempts to reconstruct the phylogenetic histories of lineages in spite of the fact that environmental trends tend to be cyclic (cf., Wiley, 1981).

This point of view might be relevant in non-living systems with no intrinsic information arrays, but it is not plausible for biological systems where information is inherited from the previous generation because this point of view suggests that maximum "adaptation" can occur only when there is no phase separation between the biological system and its environment. But, such a separation is necessary if natural selection is to occur (Endler, 1986: 4, point c.).

We believe that the amount of intrinsic information in a biological system is much greater than the amount of mutual information shared between the system and its environment. We see no mechanism for the environment to "inform" biological systems in a manner that permits the environment to structure the system directly, much less in a manner that would allow information to flow from the environment to the system. Rather, we see environmental selection much the same as more "orthodox" Darwinians (cf. Endler, 1986). Reproduction may result in more organisms needing a particular environmental resource than is available in the environment. If heritable fitness differences exist between individuals in the population, then the trait composition of the population will change in a manner predictable if one understands the environmental parameters affecting fitness. Since inheritance is essential and since new mutations or new recombinations are independent of the needs of the organism in a given environment, natural selection is a process involving environmental effects under conditions established by genealogically driven self-organization. Selection does not introduce genealogical organization, it reduces excess genealogical production through its effects on differential reproduction. In doing so, it may reinforce or add to ecological organization by increasing the mutual information between a population of organisms and the environment in which they live.

Genealogical processes determine constraints on the manner in which and the degree to which populations respond to environmental influences (construed as both biotic and abiotic influences). We believe that history is a better predictor of characters than environment. This can be shown by a simple thought experiment. Suppose we were to pick, at random, any

organism from a known tide pool. Then we would pick, again at random, a crab from an unknown place somewhere in the world. If we then asked for a list of predicted morphological, behavioral, and ecological characteristics of the unknown organism from the known habitat (the tide pool) and of the known crab from an unknown habitat, we would expect more of the predictions for the known crab to be correct. Knowing that we are dealing with a crab imparts more evolutionary and ecological information than the most detailed description of the tide pool. In terms of research programs in evolutionary biology, this means that all evolutionary explanations, including those for ecological traits and interactions, must include explicit reference to genealogical sequences (phylogenies) that must extent back to the origin of the relevant traits (see e.g. Lauder, 1981, 1982). Further, we predict that phylogeny is an excellent indicator of ecological traits, those traits that should be better predicted by external influences. This is apparent for many traits when we plot them on phylogenetic trees and see that they characterize entire clades of organisms rather than appearing repeatedly as convergences at the beck and call of selection regimes.

The relative importance of genealogical factors compared to environmental factors can also be demonstrated when we consider photosynthesis. There is abundant solar energy falling on the earth's surface. Only a small portion is actually captured. Solar radiation has a high thermodynamic grade, but it is fairly simple from a configurations point of view. Its information content is almost certainly low. Photocenters, the reception points that capture the energy in photons, are relatively complex from a configurations point of view, and certainly Photosystem I or a coupled Photosystem I + II are highly complex. If we compare the complexity of the environmental factor, solar radiation, with the complexity of its correlated organic adaptation, a photosystem, there would be little disagreement that the adaptation would win hands down. This is exactly the opposite of what would happen if biological information always originates in the environment before being incorporated into living systems. We admit that photosystems evolved in a more complex environment in which solar radiation was not the only relevant factor. Perhaps competition for resources and space with nonphotosynthetic organisms contributed to the eventual selection of the original photosystem. *We, of course, see this as interaction of the genealogical hierarchy with itself via the environmental hierarchy. The complexity of biological phenomena comes from within.*

ORDERLY DIVERSIFICATION OF BIOLOGICAL FORM

The dynamics of information in genealogy determines a "phase space" that is filled to the extent that different possible genetic combinations are realized. It grows entropically in proportion to the accumulation of

novelties arising through changes in genetic systems. Reproduction and recombination tend to fill that space. That the phase space is only partially filled tells us that there are constraints on entropy increases, either inherent constraints, such as those arising from the "rules" of the genetic system (such as those discussed by Lima-de-Faria, 1983) or extrinsic forces. These constraints are analogous to economic constraints on the free market economy — in this case they are factors that distort the free exchange of genes rather than commodities. But this does not describe the particulars of the constraints. What is needed is an inventory of "assembly rules" for different levels of organization in biological systems, analogous to the set of assembly rules provided by chemical kinetics for physico-chemical systems.

Goodwin (1985 and references therein) outlined an approach to theoretical biology called "structuralism". Goodwin proposed that there is a dichotomy between contingencies, which he associated with phylogeny, and regularities, constraints, or order in biological systems, which he associated with "generative principles" derived from field theories of morphogenesis. The generative process that underlies all of biology is thought to determine discrete "morphological stability domains" (Goodwin, 1985: 117) that will occur regardless of ancestry or environment. Evolution is "intelligible only in relation to the logic of the creative process." (Goodwin, 1985: 118). Structuralism of this form attempts to reduce biological explanations to the kinds of explanations usually associated with physics and chemistry. Such explanations tend to be deterministic and time-independent with respect to the expectations of natural laws. Hence, the structuralist approach views species as natural kinds rather than individuals. In a similar vein, Goodwin (1982) suggested that the only rational taxonomy would be a periodic table of morphogenetic fields, rather than a phylogenetic hierarchy of species.

Waddington (1966: 109) considered morphogenetic fields to be "something that is extended in the time dimension." He viewed what we would term developmental phase space as an epigenetic landscape characterized by "chreodes" or developmental trajectories. A chreod for Waddington consisted of a "region in a multi-dimensional configuration space. The region is extended along the time dimension and along the three axes of space, and also includes a number of other dimensions. Such a region has a chreodic character when there is a hyperspace within it, extended in the time dimension, which acts as an 'attractor' with respect to the neighboring vector fields." We believe that many biological processes which are characterized by regularities, constraints and order are also inherently historical, i.e. time-dependent, in nature. Among these are ontogeny, reproduction, and speciation. Unlike Goodwin, we do not see a dichotomy between historical effects and regularities in biology—historical effects are part of the regularities. Nor do we see a conflict between historical

explanations and physical law, since in physics and chemistry time-dependent phenomena are explained by reference to thermodynamics and statistical mechanics.

There is a second view of the relationship between ontogeny and phylogeny that is relevant to this discussion. To some, ontogeny and phylogeny are parts of the time-dependent nature of biology, but differ markedly as processes. Ontogeny is viewed as predictable and irreversible, a dynamic macroscopic process that smooths out perturbations resulting in a high degree of predictability in the outcome. Phylogeny, to the contrary, is unpredictable and involves only the relatively passive accumulation of genetic diversity resulting from the interplay of ontogenies and environmental changes (Salthe, 1985; Wicken, 1987a). On this view, phylogeny could be viewed as an epiphenomenon having no dynamic behavior or regularities. We believe that the concept of temporal scaling provides a common ground for reconciling these apparent differences in perspective. In our view ontogeny and phylogeny are both products of the genealogical hierarchy and have similar dynamics (see empirical examples in Brooks and Wiley, 1988), differing primarily in their temporal and spatial scaling. Ontogeny involves *cell division and differentiation* and operates at the level of individual organisms (unicellular or multicellular) over relatively short time scales. Phylogeny involves the *reproduction and genetic change* and operates at the level of the individual species (unicellular or multicellular) over long time scales. Both processes involve (1) irreversibility, (2) a mixture of historical constraints that provide predictability and indeterminism that provides individuation, and (3) spontaneous growth, although the tokens of growth are different. Both are dynamic and their units are subject to selection processes.

The bulk of constraints on entropy increases in evolution originate in the genealogical flow of information, transmitted through reproduction. History acts as a "force" (i.e. constraint) keeping biological systems from occupying all possible genetic configurations. Two major manifestations of biological production rules that evolved long ago are membranes and organelles. Membranes increase the phase separation between system and surroundings (as discussed earlier), sequestering energy and allowing new production rules. The more membranes, the more times energy can be used before it is lost from the system (i.e. the greater the entropy production). Organelles (whether derived endosymbiotically or via membrane elaboration) provide new production rules, but organelles are allowed only if enough energy to maintain their structure can be sequestered. Membranes restrict the influx of matter and energy, but need both to be accessed. There is probably an "upper bound" on structural complexity, given that the structure must permit enough influx to "pay for itself" energetically. Other evolutionary trade-offs are also implied: (1) there will be increasing autonomy of internal production rules, leading to increasing

amounts of endogenous organization, but this will be offset by a restriction of options and loss of flexibility in the face of environmental changes; (2) the endogenous organization will provide historical continuity and inherent constraints on evolutionary change, but change will occur because production rules are entropic; (3) increasing variation will increase the kinds of energy-using systems in the biosphere, but not all will survive because of the organization of the biosphere, leading to an expectation that environmental selection will be an important component of evolution; and (4) the elaboration of membranes and organelles will allow the emergence of multicellular organisms as hierarchically organized systems, but this will be offset by a loss of evolutionary independence for the component subsystems.

EMPIRICAL ANALYSIS OF BIOLOGICAL SYSTEMS

Empirical research following this approach to evolutionary explanations has been called historical structuralism (Brooks and O'Grady, 1986; Brooks and Wiley, 1988). By documenting the historical origins of traits, either functional or structural, workers in this new research program hope to find, among other things, the origins of "key innovations" that arose once historically and served as major constraints on subsequent evolutionary diversification, and to find recurring themes in biological evolution implicating structuralist regularities in the evolutionary process (Lauder, 1981, 1982). Phylogenetic systematics (Hennig, 1966; Wiley, 1981), vicariance biogeography (reviewed in Wiley, 1988), historical ecology (Brooks, 1985), and the phylogenetic study of heterochrony (Fink, 1982) are research programs in historical structuralism. A recent case study (Wake and Larsen, 1987) emphasizes the connections between this approach to evolutionary explanations and more traditional approaches.

The success of incorporating data that explicitly include phylogenetic, and therefore historical, information into evolutionary ecological explanations is apparent from many recent studies on the nature of biological communities (Ricklefs, 1987). As an example, consider the reoccurring debate in ecology regarding the role of competition in determining the number, kinds, and densities of species in a community. Inclusion of phylogenetic information has significantly increased knowledge regarding the process. It has long been suspected that species that are closely related are more likely to share common resources and hence compete (e.g., MacArthur, 1958, 1972; Root, 1967). This conclusion has received considerable support from the observation that congeneric species tend to be found together in ecological communities less often than expected by a process of randomly combining groups from a pool of all possible species that have access to a community (Bowers and Brown, 1982). The proper

context of the role of competition has been elucidated by recent studies that have attempted to apply historical information. Initially, it was thought that species interacted together over time to evolve adaptations to each other that allowed their coexistence (e.g., Schoener, 1974; Roughgarden, 1979; Slatkin, 1980). However, the observation that species rarely occur together in the same community frequently enough in space and time to allow such adaptations to evolve has cast serious doubts on this position (Maurer, 1985; Graham, 1986). Inclusion of phylogenetic information in analyses of multispecies systems can identify patterns of historical associations among species, and hence the necessity of ecological explanations for observed relations among species (Diamond, 1986; Roughgarden *et al.*, 1988). In fact, it has been suggested that ecological communities can be arrayed in a periodic table of sorts that describes the likelihood of historical and ecological explanations for observed patterns of association (Schoener, 1986). An important component of this table is the characteristics that organisms exhibit. These characteristics are the outcomes of past evolutionary history.

CONCLUSIONS

As we stated in the introduction, we believe that there are common conceptual bonds among the views expressed by a group of heterodox evolutionary biologists. Our goals in this paper were twofold: first, document the connections among these views and second, present them to a broader group of evolutionary biologists. In a real sense, this is a request that the agenda of acceptable research programs in mainstream evolutionary biology be enlarged, in the spirit of Futuyma (1988).

Our proposal for an expanded agenda is based on trying to find a common *conceptual* theme to link various research efforts. The theme that we have chosen is the use of energy in maintaining and transforming ordered states of matter. Using information and entropy concepts associated with discussions of energy use, as an accounting system, we have been able to document a common phenomenology for a number of processes occurring on different levels of organization in biological systems (Brooks and Wiley, 1988). Processes relevant to evolution are either generative (originating or diversifying) in their effects, or conservative (maintaining or selective) in their effects. The interplay of diversity-promoting and diversity-limiting processes through time produces historically-constrained order. Many processes affect biological systems, at all levels of organization and at all times, but their effects are often manifested on different time scales. Changes occurring on times scales shorter than speciation rates will appear as microevolutionary patterns; those occurring on time scales longer than speciation rates will appear as

macroevolutionary patterns. In this sense, macroevolutionary processes are neither reducible to, nor autonomous from, microevolutionary processes.

We are optimistic that a unified conceptual framework for evolutionary biology can be distilled from various attempts to “expand”, “extend”, or “finish” the job begun by Darwin. We also believe that the speed with which such a unification occurs will be proportional to the degree of cooperation among evolutionary biologists, each having particular strengths and particular biases.

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