

SEARCHING FOR A GENERAL THEORY OF BIOLOGICAL EVOLUTION

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Abstract. One approach to finding a unified theory of biology stems from perceptions that (1) the direction of time and history are important aspects of biological systems, (2) biological systems are highly non-linear, (3) biological systems are far from equilibrium, and that the historically-constrained nonequilibrium behavior of biological systems produces (4) hierarchical organization and (5) steady states that may act as local equilibria to such an extent that natural selection is expected to play an important role in explaining much of their short-term (micro-) evolutionary behavior. Internal production rules in biological systems require outside energy but are also highly insensitive to the conditions of the external environment from which the energy comes. This leads to the production of historically constrained, spontaneously stable, complex structure. Because the production rules are physically encoded in the structure of the system, biological systems are physical information systems, and their expected behavior over time follows a general entropic dynamic. The autonomy of the production rules leads to an explanation for the reality of natural selection that does not rely on analogy with human economic theory. The historical nature of the elements of diversity at any given time leads to an expectation that the details of responses to external evolutionary forces (such as natural selection, competition, geological changes) will be highly individualized. Hence, evolutionary regularities will tend to be highly generalized (macroevolutionary) or statistical in nature. **KEYWORDS:** evolution, entropy, hierarchical organization, production rules, intropy, enformation.

I. Introduction.

One of the oldest and dearest biological concepts is the "balance of nature". Whether speaking in terms of genetic configurations, ecological interactions, or patterns of energy use within ecosystems, biologists tend to expect biological systems to exist in states of balanced equilibrium with their surroundings. Much of the mathematical development of evolutionary theory has been based on assumptions of equilibrium conditions, and this has led to many valuable insights. However, we think that "equilibrium thinking" leaves several key elements of the existence, behavior, and evolution of biological systems unexplained, and this is the

reason we believe we have not yet achieved a general theory of biological evolution. To understand why this is so, it is important to state some of the general attributes of all equilibrium systems.

First, explanations of dynamic systems distinguish "forces", which act on the system, and "flows", which signify the way in which the system responds to the forces. In equilibrium systems, the distinction between forces and flows is so marked that we can equate them with "cause" and "effect" or "environment" and "system", respectively. Second, any system that is in equilibrium with its surroundings is assumed to be "at rest" or inactive with respect to the interplay of forces and flows. Hence, any changes in the surroundings will cause changes in the system. Finally, the properties of the system itself play no role in determining the equilibrium state; that state is determined by environmental conditions (the forces impinging on the system). Thus, the system is expected to assume the same equilibrium state for any given environmental configuration, regardless of the temporal sequence in which that environmental configuration arises. If the environment changes from state "A" to state "B", then back to state "A", an equilibrium system will return to the state from which it began. Many components of biological systems appear to behave in this manner. However, there are important aspects of biological systems that violate these assumptions, ranging from metabolic reactions to cell division and ontogeny, to reproduction and death, and finally to speciation and extinction.

Clearly, biological systems are not equilibrium systems so they must be investigated within a nonequilibrium context. There are at least two general classes of nonequilibrium systems. In the "close to equilibrium" class, the system is comprised of a large number of sub-units, or "cells", each of which is assumed to exist at (or extremely close to) equilibrium. If the system is large enough, however, it may encompass an environmental gradient in which individual groups of cells are in equilibrium with different environmental conditions and thus there is no overall equilibrium state for the system. In this idealization then, the assumption of local equilibrium replaces the assumption of global equilibrium. Nevertheless, the suppositions that "forces" are properties of the environment, "flows" are properties of the system, and system states are reversible through time, still holds for close to equilibrium cases.

In "far from equilibrium" idealizations, there is no assumption of local equilibrium on any scale. Rather, it is assumed that the system will adopt local "steady states", defined as the most efficient functional states possible given particular combinations of environmental *and* system properties at any given time. This is analogous to saying that mechanical systems follow the line of least resistance. There is no assumption that forces and flows are distinct from one another: both can be properties of the environment *and* of the system. Systems for which forces and flows can be considered distinct are also called "linear" systems; consequently, far from equilibrium systems are called "non-linear". Because the system's properties may act in part as "forces" determining the "flow", there is no reason to assume that the system will respond to the same environmental conditions in the same way at different times. Thus, the history of the system plays a role in determining the response to environmental forces, eliminating the assumption of temporal reversibility. We think biological systems are far from equilibrium systems. To show this more clearly, and to understand why we think this is important, we will consider evidence that (1) the direction of time ("time's arrow") and history are important aspects of biological systems, (2) biological systems are highly non-linear, and (3) biological systems are far from equilibrium. The historically-constrained nonequilibrium behavior of biological systems, in turn, produces (4) hierarchical organization and (5) steady states that may act as such strong local equilibria that natural selection is expected to play an important role in explaining much of their short-term (micro-)evolutionary behavior.

II. On the Ubiquitous Nature of Time.

Time, by definition, is directional. Some physical processes are tied to the directional nature of time, others are not. For example, if you leave a pan of hot water on a table in a cold room, the water will eventually cool to room temperature. However, the reverse process, a pan of cold water spontaneously becoming warmer, never occurs. The flow of heat between the water and the surrounding air thus incorporates a directional component into the processes involved in heat transfer. Such processes are often referred to as time-dependent, temporally asymmetrical or irreversible. Now consider the bonds forming among the water molecules in our hypothetical pan of water. Although the system as a whole maintains its functional integrity, the bonds which confer such a particular nature upon "water" are constantly breaking and reforming. Any two molecules may be joined at one moment in time and separated at another, and this continues indefinitely with no general trend towards molecules being "bonded" or being "free". The ebb and flow of bond formation is an example of a time-independent, temporally symmetrical or reversible process.

Just as physical processes can be assigned to one of the two preceding temporal categories, so biological processes show evidence of the differential influences of time. For example, suppose you were shown a film of light colored moths fluttering about in a forest of predominantly light colored trees changing to darker versions of the same moth fluttering about in a forest of darker colored trees. Since you could identify the moths as different colored morphs of the same species, and could identify an independent environmental variable correlated with the change in color

morphs, you could postulate that natural selection had occurred but you could not tell whether the film had been shown forwards or backwards. Hence, natural selection, like the formation of bonds between water molecules, is reversible through time. In contrast to this, there are many biological processes, such as reproduction, development (ontogenesis), death, speciation (phylogenesis), and extinction, that are inherently irreversible phenomena. Evolutionary change is therefore the result of a complex interaction among both reversible and irreversible biological processes.

There are many kinds of temporally asymmetrical processes. Consider the differences between the evolution of stars and the evolution of biological systems inhabiting the planets surrounding those stars. The "evolution" of different kinds of stars incorporates time-dependent regularity without historical connections. For example, the ontogeny of "BO" stars appears to have been the same for every member of that star class; however these parallels are due only to similar initial conditions and causes, not to a shared history. In other words, all BO stars are formed independently from one another, and none of them share a common ancestor that displayed the mass, luminosity and spectral characteristics that define a BO star. Rather, this star type is formed when particular initial conditions in the prestellar developmental stage are realized. Other conditions, such as insufficient mass of prestellar gas, would lead to the formation of a different class of star. In contrast to stellar evolution, biological evolution is dependent upon both initial conditions and the interplay of events unique 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. Such similarities (homologies) are embedded within an inherited (i.e., historical) matrix. In general, unlike time-dependent physical systems, biological systems retain many of the effects of history as these events accumulate and are transmitted from ancestor to descendants. The unfolding of a biological system's time-dependent behavior is thus constrained by the amount of historical baggage it is carrying into the future.

III. On the Ubiquitous Nature of Entropy.

Three attributes distinguish living systems from non-living systems: (1) "phase separation" between the "inside" and the "outside", (2) replication/reproduction and (3) substantial autonomy from their environments. Irreversible processes play key roles in the origin and maintenance of these attributes. First, biological systems must maintain themselves by using available free energy. Without continual energy flow, order will dissipate as a consequence of the second law of thermodynamics. Second, biological systems maintain structural and functional integrity (order) by the storage and transmission of information. Without the accumulation and expression of information, biological systems cannot harness the energy flow that enhances their ability to maintain order. Information, in turn, is encoded and interpreted within a set of internal "production rules" 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. This results in the development of hierarchical structures expressing diverse behaviors, and affecting one another by systems of indirect constraints.

Lotka (1913, 1925) was among the first 20th century authors to discuss biological systems in terms of energy flows and energy partitioning. He recognized that living systems persist in space and time by transforming energy from one state to another in a manner that generates organized structure. There are two classes of such energy transformations. The first class, referred to as *heat-generating transformations*, involves a net loss of energy, measured as heat, from the system. The second class, *conservative transformations*, involves changing free energy into states that can be stored and utilized in subsequent transformations (Brooks, Collier, Maurer, Smith and Wiley, 1989). Although all conservative transformations in biological systems are coupled with heat-generating transformations, the reverse is not necessarily true; therefore, there is a heavy cost to maintaining structure. Lotka (1913) suggested that the inevitable structural decay which must accompany such costs could be delayed by the system's accumulation of bound energy. According to this view then, the interplay between energy flow and partitioning in biological systems acts only to slow the rate at which energy stored by conservative transformations is degraded by heat-generating processes.

IV. The Terminology.

Energy flows within biological systems are coupled with the production of "entropy". Unfortunately this word carries with it the weight of a very formidable history. However, this discussion need not be so intimidating if the following five points are remembered: (1) Heat generating transformations produce *thermal entropy, a measure of the tendency of the system to move towards disorganization*; (2) Conservative transformations produce *structural entropy, a measure of the tendency of the system to move towards structural complexity*; (3) *Dissipative structures* (Prigogine, 1967, 1980) are systems in which structural entropy is produced by dissipative processes that allow a higher rate of structural entropy production than if the processes were completely thermal (heat generating); (4) 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 processes occurring within the system to be isolated from processes occurring outside the system ("phase separation"). Consequently, fluctuations in processes occurring outside the system, that could lead to disorder, are prohibited from disrupting the internal structure of the system; and (5) the formation of a phase separation between the system and its surroundings allows the evolution of *internal production rules* that are not governed directly by fluxes from the environment, but rather by entropy production within the system. In general, then, dissipative structures can arise kinetically when the internal dynamics of the system change the system faster than it can equilibrate with its surroundings. They can also arise physically, when the boundary conditions are such that there is a physical barrier between

the system and its surroundings. *The greater the phase separation, or distinction between system and surroundings, the greater the autonomy of the internal production rules.* For example, cell membranes are maintained kinetically and produce a physical phase separation between the living system and its environment. Hence, biological systems behave as dissipative structures, at least in some aspects.

V. The Equations.

Entropy changes (dS) in such systems can be subdivided into two components, one measuring exchanges between the system and its surroundings ($d_e S$) (observed as changes in the environment) and the other measuring production by irreversible processes internal to the system ($d_i S$) (observed as changes in the system). Exchanges between biological systems and their surroundings are accompanied by a great deal of waste; hence, $d_e S$ is very large compared to $d_i S$. However, if biological systems are to maintain their structural integrity, they must produce entropy internally ($d_i S > 0$). Or:

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

Therefore, it is $d_i S$ that is important in considerations of biological evolution.

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. ψ includes at least two classes of processes: (1) those involved in dissipation from the system, called the *external dissipation function* (ψ_a , or thermal entropy) and (2) those involved in dissipation within the system, called the *bound dissipation function* (ψ_b , or structural entropy). In biological systems, ψ_b can be further subdivided into allocations for accumulating biomass (ψ_b^b) and allocations for accumulating genetic diversity (ψ_b^i). Brooks and Wiley (1988) suggested that all three components of the biological production term ψ should be included in the thermodynamic production term $d_i S$, shown heuristically as:

$$d_i S = \psi_a + \psi_b^b + \psi_b^i$$

Biological systems must therefore 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 bound energy. Since the non-random nature of this accumulation results in the production of 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.

VI. The Diagram: The Far-From-Equilibrium Shape of Biological Evolution.

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 (ψ_a). The second is expansion of the phase space occupied by 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 increase in realized entropy (H_{obs} or "complexity") and the increase in maximum possible entropy (H_{max}) (Fig. 1; for biological applications see Ulanowicz, 1980; Brooks, LeBlond and Cumming, 1984; Brooks, Cumming and LeBlond, 1988; Smith, 1988). In other words, so long as the phase space expands faster than the system can fill it up, conservative processes will be an allowed class of entropy-producing phenomena. In cosmology, this argument is used to explain the spontaneous and irreversible formation of stars, solar systems, galaxies and other organized structures, in which gravity slows down the entropic expansion of matter in the universe to such an extent that organized structures can emerge even though entropy is increasing. In biological systems, mutations act to expand the genetic phase space (Layzer, 1978, 1980), while genetic and genealogical bonds linking all organisms play an analogous role to gravity (Brooks and Wiley, 1988). Notice that this is merely a more sophisticated version of our early observation that 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.

The increase in the number of accessible microstates is accomplished 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. 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 will spontaneously clump into dimers and polymers. Once polymers begin to form, "polymer space" becomes available to the evolving system. At this level, polymers are "macrostates" and monomer and dimer distributions are the "microstates". Causal interactions among polymers create new levels of organization in which polymer distributions are the microstates and new levels of organization are macrostates, and so on. Because new levels create a hierarchy of increasing structural intricacy (= complexity + organization), and more and

more of the entropy production is invested in structure, the allocation of $d_e S$ to ψ_a should be proportional to entropy increases due to expansion of phase space.

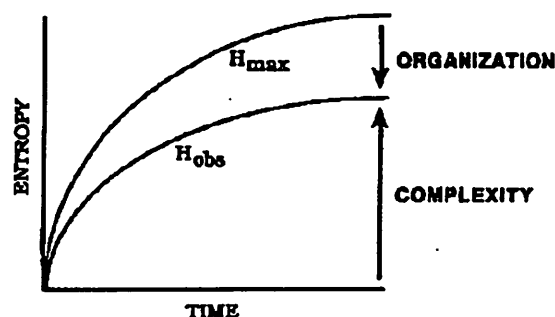


Figure 1. The relationship between an increasing entropy maximum (H_{max}) and the observed entropy (H_{obs}) of a physical system over time. The value of H_{obs} is a measure of the realized entropy (or complexity) of the system, which is expected to increase over time in accordance with the second law of thermodynamics (denoted by the upward pointing arrow). The difference between H_{max} and H_{obs} is proportional to the organization (or structure) within the system. In biological evolution, this difference is expected to increase as a result of the historical accumulation of constraints that retard the increase in realized entropy (denoted by the downward pointing arrow). Notice that realized entropy = complexity. This is immediately counterintuitive; surely organization = complexity? Consider the following two situations (1) an alien creature standing on the bridge of the *Enterprise* and (2) the alien creature transported, on the widest possible beam, into space; its molecules scattered across the universe. In the first situation the creature is obviously an organized biological system, in the second the organization is minimal, to say the least. Now, which situation is more difficult to describe mathematically, the position of molecules within the creature's organized body (structure) or the position of those molecules spread throughout the galaxy?

The difference between the entropy maximum (H_{max}) and the actual entropy (H_{obs}) is proportional to the organization of the system at that level (fig. 1). This difference has also been referred to as the macroscopic information of the system (Layzer, 1975). According to this perspective, H_{max} represents the total information capacity and H_{obs} represents the information content of a physical information system. The difference between total information capacity and information content is proportional to the constraints placed on the information system (see also Brillouin, 1962; Gatlin, 1972; Brooks, LeBlond and Cumming, 1984; Collier, 1987; Brooks, Cumming and LeBlond, 1988; Smith, 1988; Brooks, Collier, Maurer, Smith and Wiley, 1989). Overall, then, H_{obs} (Fig. 1) is a measure of the realized entropy as manifested by the complexity (the information diversity) of the system. The difference between H_{max} and H_{obs} (Fig. 1) is a measure of the internal entropy (ψ_a , the bound dissipation) manifested

in the structural organization (the macroscopic information, or the constraints) of the biological system. From this we can see that biological information is the carrier of constraints on the system, and constraints, in turn, include possible variation that has been historically excluded (Fig. 2).

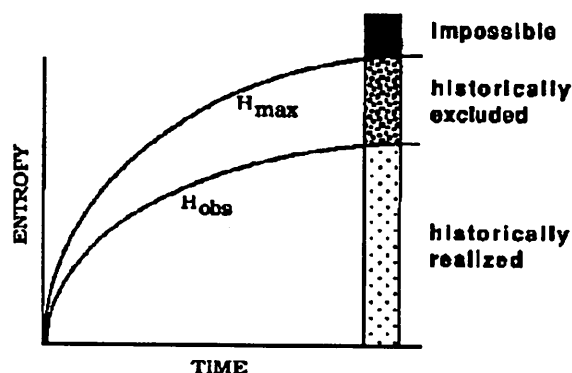


Figure 2. The relationship between total information capacity (H_{max}) and information content (H_{obs}) of an array of physical systems comprising a number of evolutionary lineages. Historically realized diversity is measured by H_{obs} . Historical exclusion of the expression of certain kinds of information is proportional to $H_{max} - H_{obs}$. The area above H_{max} represents impossible combinations at any given time.

In summary, the following three conditions form the boundary rules within which the evolution of biological systems operates: (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 organization in the system (Brooks and Wiley, 1988). Hence, biological systems are far from equilibrium systems and their historical constraints are responsible at least in part for their far from equilibrium status.

VII. The Nature of Information.

Discovering that biological information is the carrier of constraints on the system moves us a step closer towards formulating a more complete theory of evolution. The next step requires that we investigate just what is meant by the term "information". Information theory has been developed from two perspectives, "communications theory" and "physical measurement theory". These perspectives overlap in their belief that

information is (1) anything transmitted from a "source" through a "channel" to a "receiver" and (2) an abstraction rather than a material part of any system.

In classical communications theory, the amount of information sent from a source is calculated using a statistical entropy function. Errors in transmission can result from poor encoding at the source or from noise in the channel. The meaningful information is that subset of the information transmitted which is actually recorded by the receiver. All of the processes affecting the transmission and reception of the information thus decrease the entropy of the message from its maximal state at the source. Since physical entropies are expected to increase as a result of work done on the system, either information transmission is not a physical process, or the communications theory view of entropy is a non-physical one.

Physical measurement theory has provided a second formalism for information. Brillouin (1962) distinguished between "free information" which is an abstraction involved in descriptive exercises, and "bound information", which refers to material properties of systems (but stops short of stating that information per se can be a material part of a system). Bound information is determined with respect to the complexions (microstates) of the physical system. Hence, bound information is also calculated using a statistical entropy function, but, contrary to communications theory, is expected to exist only in systems for which there is a non-arbitrary microstate/macrosate distinction [i.e., $I(M) = f(M_m)$]. Bound information is defined as:

$$I = H_{max} - H$$

where H_{max} corresponds to the totally relaxed state of the system (generally estimated by a randomization of the observed components of the system at hand). Brillouin defined "I" as negentropy, which is converted into bound information by measurement (measuring devices are thus receivers), so negentropy = information. Information has a physical basis, but is not a material part of the system (however, it does point to material regularities that require explanation).

Biological systems require a modification of these views about information. For one thing, biological information has both communications and physico-chemical functions. And for biological evolution, we need an account of the growth of information through time, rather than of a distillation of information from an initial pool of all possibilities. Biological evolution as a negentropic phenomenon makes sense if all genetic possibilities were present at the beginning of life, and we have simply seen a distillation and reduction in those possibilities, resulting in the diversity we see. However, biologists do not think that evolution works that way - they believe that evolution results in the growth of information and complexity through time. So, what we need is an account of biological information that is physically realistic, that is intrinsic to the system rather than to measuring devices (i.e., it is material rather than abstract), and that can grow over time as a result of spontaneous (entropic) processes. For this, we refer to work done by Collier (1987) and Smith (1988).

VIII. Is There a Physical Basis for Biological Information?

Intrinsic information is related to concepts of the "causal capacity" of a system, or its ability to impose distinctions on its surroundings (including measuring devices). Hence, the emphasis is on how the system produces effects on measuring devices and not on how the measuring devices affect the system. Physical information systems (those having intrinsic information) occur as arrays, or multi-dimensional messages, in which microstate and macrostate distinctions are distinguished non-arbitrarily (Collier, 1987; see also Brooks, Collier, Maurer, Smith, and Wiley, 1989). Collier (1987) stated that in order for the biological view of information (Brooks and Wiley, 1986, 1988) to be related to physical concepts there must be: (a) an energetic "cost" in producing and maintaining biological information, (b) a physical (material) basis for the information, and (c) a real (i.e., non-arbitrary) macrostate/microstate distinction. His formalism for addressing these conditions is below:

Energy coming into a system can have two fates; either it can be dissipated from the system as a result of work done within the system [ψ_u of $d_i S$, *intropy* (internal entropy, or the entropy produced within the system as required by nonequilibrium thermodynamics), or heat-generating processes], or it can be converted into structure within the system [ψ_u of $d_i S$, *enformation* (encoded information in the system), or conservative processes]. Since all conservative processes within biological systems are coupled with heat-generating processes, there is a demonstrable energetic cost associated with the production and maintenance of biological information. Intropy and enformation are interconvertible (e.g., energy brought in from outside can be converted into structure, say glycogen, and that structure can be converted into heat). Intropy is converted into enformation by cohesive properties of the system. Cohesion is thus analogous to inertia, which provides inherent resistance to change. Cohesive properties, which can range from molecular affinities to cell-cell adhesion to genetic compatibility, mate recognition, and genealogy, also provide resistance to fluctuations from lower levels, and this is a key to (a) the microstate/macrostate distinction, (b) the origin of natural selection, and (c) the emergence of hierarchical structure in biological systems.

Under Collier's view, microstate/macrostate distinctions are determined by part/whole associations. For example, a protein coding unit might be considered a macrostate, while all the actual sequences that code for that protein would constitute the microstates. Or, one could consider a locus to be a macrostate, and all sequences that correspond to the locus to be microstates. Extending the reasoning further, phenotypes could be macrostates, and all genotypes corresponding to a given phenotype could be microstates. What makes all this tricky is that the encoded information is also the carrier of the cohesive properties, so production of biological information involves the production of variation *and* constraints *at the same time*, and this alone ensures that genealogy will be a combination of continuity and change. Thus, genealogical processes alone are necessary and sufficient for evolution to occur (Brooks and Wiley, 1986, 1988). This is not a non-Darwinian position, because it does not rule out a *significant* role for natural selection; however, it does call into question its *exact* role.

IX. The Origin of Natural Selection.

The basis for the theory of natural selection was Darwin's intuition that the production of offspring overruns the production of necessary resources. This limitation leads to a "struggle for existence" in which only the "fittest" survive, fitness being defined by an individual's ability to compete for limited resources, and measured by reproductive success. Over the past century various researchers have documented the intraspecific differences in survivability and reproduction vital to the concept of natural selection. However, the evolutionary interpretation of these results has traditionally been set within an equilibrium context. A population is expected to reach a genetic (and hence informational) equilibrium with respect to its environment, and to remain there as long as the environment remains constant. Subsequent to this, any environmental change creates a new equilibrium point, towards which the population moves (adapts). How can the existence of this equilibrium process be reconciled with a far from equilibrium theory of evolution? In order to answer this, we must investigate where natural selection comes from in the first place; that is, what conditions are necessary for natural selection to occur?

From our perspective, the key to answering these questions and to deriving Darwin's intuition lies in understanding the conditions that allow a surplus of organisms to be produced in the first place. In order for such "population overruns" to occur, the "rules" governing production of offspring must be independent of, or at least highly insensitive to, the environmental resources relevant to the offspring. Otherwise, the number of organisms produced would conform to an equilibrium number determined by the fluctuating availability of resources. In addition, if intraspecific competition is a major driving force in evolution, then conspecific offspring must display overlapping requirements and abilities. Overall then, if a large number of similar organisms are to be produced, the system's internal production rules must be insensitive to environmental fluctuations (autonomous), extremely redundant (conservative) and have a high replication rate.

Only far from equilibrium systems are characterized by autonomous production rules and by a high degree of self-organization that is manifested, in part, by the maintenance of organized structure. In other words, the tendency towards increasing organization is inherent in the system, not caused by the environment. Naturally occurring populations of highly similar (redundant) organisms existing as cohesive wholes are one class of steady state outcomes in far from equilibrium population dynamics. Such populations might be expected to exist over short temporal scales during which the portion of the genealogical flow determined by the origin and spread of new information within the system will be much less than the flow determined by environmental forces. Or, in other words, populations function within boundaries defined both by history and by the environment, and during the time periods that the historical effects are essentially constant, population changes will be due to environmental changes. During these phases, populations could be treated as local equilibria (or close to equilibria) cells making up the nonequilibrium systems called species. Hence, standard population biological treatments, with their assumptions of equilibrium and constant (i.e., negligible)

historical effects, will be useful in explaining this component of biological functioning. However, the stability of a population (i.e., the ability to persist through time and over space) will be proportional to its ordering due to the effects of historical processes transmitted via reproduction. This will determine the ways in which and the extent to which the population can respond to environmental changes. Natural selection thus emerges as a steady state process embedded within long-term genealogical transformations in the far from equilibrium view of evolution.

We can symbolize this idea as follows. Macroscopic information (I), or organization, increases over long time intervals (Fig. 1); therefore, we expect to see an increase in the value of the function Q , the *macroscopic order* (Landsberg, 1984b) or *redundancy* (Gatlin, 1972) of the system:

$$Q = 1 - \left(\frac{H_{obs}}{H_{max}} \right) = \frac{I}{H_{max}}$$

The portion of biological information that is the carrier of evolutionary constraints can be depicted as $H_{max} - H_{obs}$. Since this also describes macroscopic information ($I = H_{max} - H_{obs}$), biological information must be a form of physical macroscopic information. In other words, the increase in redundancy (i.e., the production of highly similar offspring) through time is accompanied by an increase in biological information in the system. Some of this information is shared between biological systems and their environment. If the environment is the source of evolutionary macroscopic organization, then the percentage of biological information that is shared with the environment should be relatively high. This presents us with a paradoxical view of natural selection because, if the overlap is high, then the "fit" between biological systems and their environment is almost perfect; therefore, the rate of evolutionary change will be either negligible or stochastic with respect to the environment. This paradox can only be resolved by postulating that the percentage of biological information that is shared with the environment is, in fact, low. When this happens, the number of organisms requiring a particular environmental resource will exceed the availability of that resource; some organisms that are otherwise functional will not survive to reproduce or will not reproduce to the same extent as others. Thus, *in order for selection to be an important evolutionary force, it must operate under conditions established by genealogically driven self-organization, which, in turn, produce constraints on the degree to which and the way in which organisms and populations can respond to natural selection.*

The dependence of natural selection on organization generated by genealogical processes re-emphasizes two general features of production in biological systems. First, the general production dynamic is one in which actual diversity increases at a slower rate than maximum possible diversity. This means that there is a high degree of redundancy in the products of genealogical processes (Fig. 3).

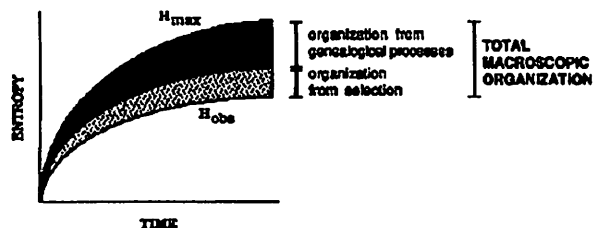


Figure 3. The total amount of macroscopic organization ($H_{max} - H_{obs}$) in biological diversity is a function of the organizing influences of genealogical processes plus the organizing influences of environmental, or selection, processes. These influences complement each other because their effects are to limit the increase in the entropic accumulation of diversity (H_{obs}) over time.

Working within this framework, selection increases redundancy and further contributes to the increase in the macroscopic ordering of the system in two ways. Natural selection, which arises from the *insensitivity* of the production rules to the environment, increases organization by eliminating outliers. It is the result of an interaction between genealogical and ecological processes. Sexual selection, by contrast, arises when there is a high degree of *sensitivity* between the products of genealogy. Since it is the result of interactions purely within the genealogical realm, this form of selection increases organization by intensifying connections. Consequently, we would expect sexual selection to strengthen genealogical ties (homology), whereas we would expect natural selection to result in convergent and parallel evolution.

Second, although production requires influxes of matter and energy from the environment, the rules governing the fate of that matter and energy are not found in the environment but in the organisms themselves. Production rules are thus relatively autonomous from the environment, making it more likely that excess organisms will be produced. The primary way to enhance the autonomy of the production rules is to increase the historical burden of constraint, so that over time the final products can be explained better by reference to their ancestry than to their current environments. In other words, so long as the genealogical portion of the difference between H_{max} and H_{obs} is larger than the selection component, history will be a better predictor of characters than environment. The current database in historical ecology (Brooks, 1985; Brooks and Wiley, 1986, 1988; Brooks and McLennan, 1991) supports this contention. 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) extending back to the origin of the relevant traits (see Brooks and McLennan, 1991, in press and references therein). However, because it is reasonable to believe that there will be species and clades for which the selection component of the difference between H_{max} and H_{obs} will be greater than the genealogical component, we may find that not all groups will be equally amenable to historical ecological research.

In summary then, information and order are inherent properties of biological systems, produced by a set of "rules" that are autonomous from, and relatively insensitive to, the environment. These rules are responsible for the production of surplus, redundant organisms and this, in turn, sets the stage for the appearance of differential survival and reproductive success (selection). The interaction between selection and the internal properties of the system establishes a feedback loop through which genealogical processes constrain the manner in which and the degree to which populations can respond to both biotic and abiotic environmental influences.

X. What Is The Information Theoretic Role Of Natural Selection?

Most attempts to relate information theory to biological systems have assumed that the genetic system is the *source*, that reproduction and ontogeny are the *channel*, and that the environment is the *receiver*. We feel that the environment cannot be a receiver, in a physical sense, because it does not measure or interpret the message; it only sorts through and eliminates part of it. Therefore, the environment plays the role of a *converter* rather than a receiver. It is a form of noise in the channel, or a filter. Using Collier's formalism, we can say that the environment converts some information (biomass or ψ_a) into entropy (dissipated energy or ψ_e), so both the growth of the information system and the elimination of information by intrinsic or extrinsic processes in biological systems are entropic phenomena. This, in combination with our proposal that natural selection emerges as a result of genealogical autonomy, begs the question, what is acting as the receiver, if not the environment?

Since Darwinism, like most physical theories, is a theory of external causality, the receiver has always been construed as a part of the surroundings, i. e., a localization in space. While it is true that biological systems are localized in space, it is also true that they are localized in time as well. This temporal component of biological systems plays a critical role in evolution because all *temporally-dependent* (spontaneously irreversible) processes in biology are *spatially-independent*. We therefore propose that the receiver is not a place, but a time. The source is the genetic system at any given t_0 , the channel is reproduction and ontogeny, and the receiver is the genetic system at any given $t_{1..n}$. If the source precedes the receiver in time, the source can produce the system (or at least encode it), and the system can later become the source itself. This temporal sequence conforms to the requirement that the source, as the initiating condition, be "outside" of the receiver.

Concepts were originally borrowed from economic theory to support, by analogy, the "reality" of natural selection. We believe that the ideas discussed in this paper will allow us to move beyond analogy to an explanation for the origin and operation of natural selection that is embedded within a biological and physical, and hence evolutionary, framework.

XI. The Two Biological Hierarchies.

Hierarchical structure, from the genealogical relationships of individuals and species to the behavioral relationships of complex social systems, has played an important role in biological evolution. The importance of that role was underlined by Salthe (1985) when he concluded that hierarchies provide stability, reinforce boundaries between system and surrounding, allow increasing amounts of complexity, and provide a way in which causation and control can be tied together. He suggested that hierarchical structure can be decomposed into sets of "triads", comprising (1) upper-level (causal or initiating) and (2) lower-level (control or boundary) elements impinging on (3) a focal level, from which emerges a particular level of structure/organization. Complex hierarchical systems are thus combinations of triadic units linked together.

Environmental and genealogical phenomena provide a good starting point for the investigation of hierarchical interactions because they are intimately connected in biology. Pre-biotic environmental conditions established the boundary (characterized by Salthe, 1985 as a pre-biotic ecology) within which life could originate. Conversely, genealogical processes that characterize life are autonomous enough from environmental conditions to be capable of overrunning available resources and of changing the environment substantially. The longer life exists on this planet, the more it shapes the environment. Today, much of the environment consists of the products of genealogical processes. Thus it is no surprise that it is difficult to disentangle "environmental effects" from "genetic [genealogical] effects" in evolutionary studies. Eldredge and Salthe (1984), Salthe (1985), and Eldredge (1985, 1986) have suggested that two forms of hierarchically-organized behavior exist in biology. The *ecological hierarchy* encompasses exchanges of matter and energy between the system and the environment ($d_e S$ and ψ_a). It is the realm of energy use patterns, or of biological *interactors*. The *genealogical hierarchy* results from production processes (ψ_a^b and ψ_a^c). It is the realm of energy allocation patterns, or of biological *replicators*.

Brooks and Wiley (1988), following Salthe (1985) and Eldredge (1985), suggested that evolution results from the nonlinear interaction of two biological hierarchies, each possessing unique characteristics ("rules") in addition to the properties arising from their interaction. The ecological hierarchy is an economic system, manifested by patterns of energy flow in ecosystems. It is also the hierarchy of biological classes, such as trophic levels or ecological associations. By contrast, the genealogical hierarchy is an information-flow system, manifested by patterns of ancestral relationships among all living organisms. It is the hierarchy of individuals. The relationship between the two hierarchies can be illustrated with the following sports metaphor: the ecological hierarchy establishes the dimensions of the playing field, while the genealogical hierarchy establishes the rules of the game being played. In other words, biological systems obey rules of self-organization transmitted 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 may be subsequently constrained by these self-imposed changes. For example, the evolution of photosynthetic prokaryotes from

anaerobic ancestors resulted in increased oxygen content in the atmosphere. This increase, in turn, ultimately altered the diversity 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 intricacy characteristic of biological evolution is not an unaided consequence of environmental forces. Biological systems have intrinsic capacities to create hierarchically organized structures. Therefore, the creation and maintenance of biological systems requires environmental resources, but does not require that the information in those systems originates in the environment. The environment is not inherently organized as an ecological hierarchy. The existence of an ecological hierarchy is largely a consequence of organization intrinsic to the genealogical hierarchy.

The relationship between the two hierarchies based on this perspective is shown schematically in Figure 4. The genealogical hierarchy is composed of the products of two entropic processes as depicted heuristically by the familiar equation:

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

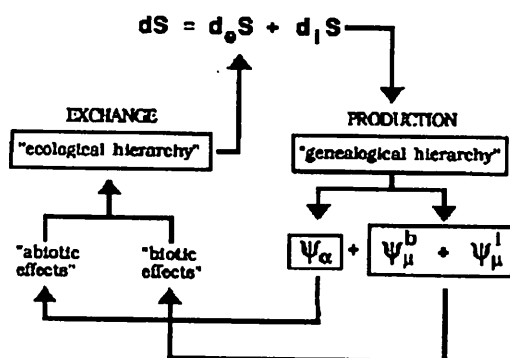


Figure 4. The conceptual relationship between the genealogical hierarchy (biological production) and the ecological hierarchy (environment/biological systems exchanges) in terms of entropic behavior of open systems. The degree to which the genealogical processes shape the ecological hierarchy is the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

Recall that ψ_α is a form of thermal entropy, and that ψ_μ or structural entropy, is subdivided into allocations for accumulating biomass (ψ_μ^b) and allocations for accumulating genetic diversity (ψ_μ^i). As Lotka proposed more than 70 years ago, conservative processes are involved in the

production and maintenance of the structure of the genealogical hierarchy, while the products of thermal processes are a disorganizing influence on this structure.

The products of the genealogical hierarchy are maintained through time by the exploitation of "entropy gradients" in the surroundings, which we view as the ecological hierarchy, and associate with the exchange term $d_e S$. These gradients, and thus the ecological hierarchy, are, in turn, determined by the interactions between abiotic factors and biotic factors. Interestingly, the abiotic portion of the ecological hierarchy can be structured in part by the ψ_α component of the genealogical hierarchy. For example, from an energetic perspective, metabolic processes are involved in the degradation of high grade energy sources into lower grade forms of energy, including heat. Both the capture of incoming solar energy by biological systems, and the mass re-radiation of heat by these organisms affect the thermal profile of this planet. Additionally, the production of oxygen as a byproduct of photosynthesis or carbon dioxide as a byproduct of aerobic metabolism affect the composition of our planet's atmosphere. So, the thermal entropy portion of the production term, $d_i S$, can influence the exchange term, $d_e S$. The biotic portion of the ecological hierarchy is subject to the influences of the structural entropy portion of the genealogical hierarchy (ψ_μ^b and ψ_μ^i). Because of this, species do not fill empty niches, they create their own niches (Fig. 5). So, the amount of available "niche space" is not a fixed function of the environment, but rather is dependent upon the evolution (appearance) of new species, and the interactions between those species and the environment. For example, the evolution of grasses produces potential "herbivore niche space" which, when occupied by herbivores, produces potential "carnivore niche space" and so on. The structuring of trophic levels in the ecological hierarchy is therefore the direct result of the biological production of the genealogical hierarchy, which, in turn, is a direct result of the entropic accumulation of diversity.

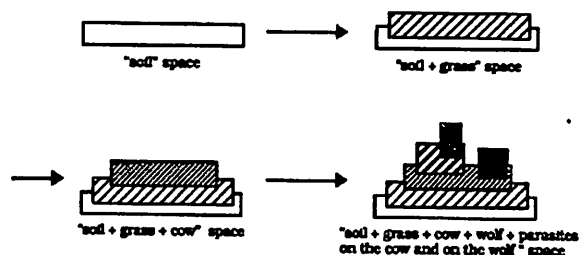


Figure 5. Niches are not fixed in space and time, they are a function of evolutionary change. This hypothetical example traces the expansion of potential niche space as a result of the appearance of different organisms and of the interactions between those organisms and their environment. (From Brooks and McLennan, 1991)

The environment provides an important constraining influence on biology, and the (self-generated) ecological hierarchy plays an important feedback role in evolution. The ecological hierarchy is the means by which two different genealogies, or two different generations in one genealogy, can causally influence one another. We believe this is the reason historical ecology is important to the development of evolutionary theory in general. The conservative nature of ecological diversification uncovered so far by historical ecological methods implies that adaptive processes act as constraints rather than as driving forces in evolution. This further begs the question of just what is the driving force. The unified theory suggests that the driving force is in the genealogical hierarchy, manifested by the entropic accumulation of diversity organized in part by the constraints of history and in part by the constraints of adaptation. Since genealogy constrains the way in which organisms respond to their environment, and the environment acts as a filter through which the products of genealogical processes must pass, evolutionary explanations which do not incorporate information from both these hierarchies are inherently incomplete.

XII. Scaling of Entropy Production: The Source of Hierarchical Organization.

Entropy in its different manifestations is produced at different rates in biological systems 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 (Brooks and Wiley, 1988; Maurer and Brooks, submitted: Fig. 6). Because of this, the parts of the evolutionary play that we can see will change depending upon the dimensions of the window through which we view it. At the lowest organizational level, the shortest time intervals, and the smallest spatial scales, the greatest relative contribution to ψ will be ψ_α (external dissipation or thermal entropy). Hence, macroscopic manifestations of ψ_α will predominate our observations in such frames of reference. For example, if we examine cellular or sub-cellular structure over short time intervals, processes such as metabolism and respiration dominate explanations of observed structure. Most 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, the effects of ψ_μ^b are predominant. Most entropy production at this scale is dissipated into biomass accumulation and maintenance. Finally, on the largest and longest scales, ψ_μ^i predominates, and the patterns relevant to biological explanations are formed mainly by the accumulation and maintenance of genetic diversity.

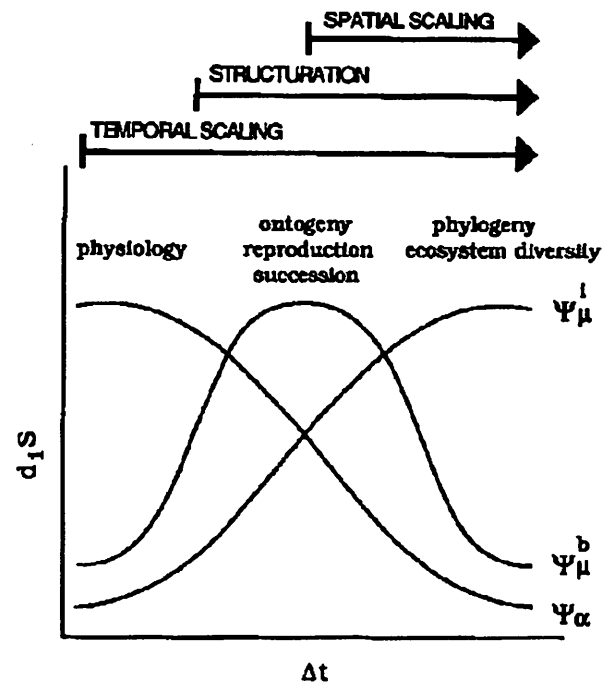


Figure 6. Temporal scaling of major production components in living systems, and their macroscopic manifestations. The axes are entropy production, dS , and time intervals (Δt). ψ_α refers to external dissipation (waste), ψ_μ^b to biomass accumulation, and ψ_μ^i to genetic diversity accumulation. All processes contribute at all time intervals, but to different degrees for each Δt . This is represented heuristically by the curves accompanying ψ_α , ψ_μ^b and ψ_μ^i .

There are numerous ways in which the effects of temporal and spatial scaling shape our evolutionary perspective. The designation of plesiomorphic or apomorphic status to character states in phylogenetic systematic studies is a relative, not absolute, statement. All characters begin as evolutionary novelties (autapomorphies) in a new species. If the species undergoes another speciation event before the character changes again, the character becomes a synapomorphy uniting the descendant sister species. If the speciation continues in this lineage while the character remains unchanged, the character will come to be considered plesiomorphic for the group (Fig. 7). This reemphasizes the basic phylogenetic assertion that only synapomorphies (homologous similarities on an intermediate temporal scale) are useful for reconstructing phylogenetic relationships. Differences on a small temporal scale (autapomorphies) or homologous similarities on a large temporal scale (plesiomorphies) do not contain information useful to this reconstruction. In a similar vein, the difference between convergent and divergent adaptation is also dependent

upon the temporal scale of the investigation. All *convergent* adaptation is the accumulation of parallel independent episodes of *divergent* adaptation between sister species (Fig.8).

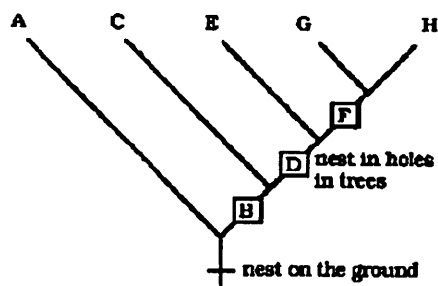


Figure 7. The plesiomorphic or apomorphic status of a character is relative to the temporal scale of the investigation. There has been an evolutionary change from nesting on the ground to nesting in trees in this hypothetical clade of birds. Nesting in tree holes is an autapomorphy for species D, a synapomorphy for species D+E+F and a plesiomorphy for species D+E+F+G+H.

Perhaps the most important aspect of scaling considerations is the implication that *there is no objective level of organization, time interval, or spatial interval for biological evolution*. This is the reason Brooks and Wiley (1988) referred to their theory as a relativistic one. A variety of evolutionary processes operate on all levels and at all scales; however, they do not all play equally important roles at all levels. Therefore, the macroscopic manifestations of evolutionary principles will differ depending on the window of observation. Microevolutionary processes, although important, are not the sole forces of evolution. They simply dominate evolution on the moderate temporal and spatial scales which are the most easily accessible windows of study for organisms with our biological and career life span constraints.

This can be extended to include the organizing influences of entropic production on biological systems. It appears that the way the phase space expands in biological systems leads to hierarchical organization of entropy flow through the system and to hierarchical structuring, with all its attendant properties, of the system. Since potential phase space and realized phase space are not the same (i. e., the phase space expands faster than the system can fill it up) organization (biological structure) accumulates, and this, in turn, creates new levels in a hierarchy of increasing structural intricacy. For a given hierarchical level, then, the difference between the entropy maximum (H_{max}) and the actual entropy (H_{obs}) is proportional to the organization of the system at that level (see Fig. 3). Based on this, we view biological evolution as the complicated end product of the interplay between the creative force of entropic increase (macroevolutionary process) and constraints on that increase (both macro- and microevolutionary processes). In other words, the entropic accumulation

of organization and complexity drives evolutionary change, while the constraining influences of history and selection limit the potential scope of that change, providing its unique shape.

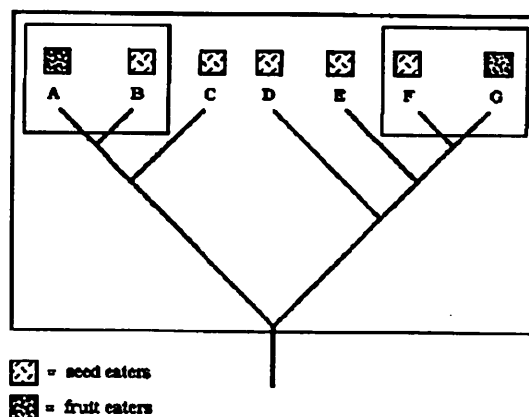


Figure 8. Identification of convergent and divergent adaptation is dependent upon the temporal scale of the investigation. The change from eating seeds to eating fruit represents independent cases of divergent evolution between sister species A+B and sister species F+G. The temporal scale must be increased to include all the members of this clade before the convergent evolution of fruit eating in species A and G can be identified. (From Brooks and McLennan, 1991)

We would like to close with the observations of Wiley and Brooks (1987: 374) about the utility of the theoretical framework outlined above:

We believe that our theory reconciles a number of issues. It connects biology with physico-chemical laws without reducing biology to atomistic physics. It integrates directionality, developmental constraints, and historical constraints in biology without sacrificing selection theory. It integrates the thermodynamic "why" with the kinetic "how" without fostering (sic) an artificial dichotomy between the two. Finally, it provides an empirically tractable set of systems behaving according to one class of nonequilibrium phenomenology.

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