ENERGY FLOW AND ENTROPY PRODUCTION IN BIOLOGICAL SYSTEMS

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Abstract. Biological systems persist because they process energy and accumulate excesses that are usable in growth and maintenance. There are two general types of energy transformations that occur in biological systems. Heat generating transformations result in lost energy. Conservative energy transformations produce energy that can be stored and used later to do work. Different types of entropy can be associated with each of these types of energetic processes. Heat generating energy transformations occur when energy and entropy flow in opposite directions. Conservative energy transformations are characterized by entropy and energy flowing in the same direction. Thus the system has conflicting tendencies: heat generating processes move it towards unstructured states and conservative processes move it towards complex structured states. Both tendencies increase the entropy of the system. These ideas are examined from the viewpoint of energy flow through organisms and populations of organisms. As entropy and energy flow through such systems at different rates, structure accumulates at any given biological level, and that structure is constrained by energy and entropy flows at other levels of organization. Rate gradients in entropy production lead to different types of constraint systems governing hierarchically related entities and to the generation of historical constraints at any given level of organization.

I. Introduction.

Much has been said about how biological systems are able to maintain their organization in the face of the second law of thermodynamics. Most of these formulations, however, have not explicitly considered the constraining role that accumulated genetic information exerts on energy flows. The realization that such constraint exists requires that the relatively simple concept of entropy inherent in classical thermodynamics be extended to include the complexity inherent in biological systems. Such a reexamination of concepts of entropy lead Brooks and Wiley (1988) to postulate that certain kinds of entropy that act as descriptors of complexity should increase through time. Here, we attempt to examine how Brooks and Wiley's (1988) concept of entropy production might be coupled with the flow of energy in biological systems. We believe that this is necessary before their ideas can be placed in a more empirically testable framework. Brooks and Wiley did not explicitly deal with energy flow in their conceptualization of entropy production, but recently, Brooks et al. (1989) explicitly considered the role of energy flow in the Brooks-Wiley model. Our purpose in this manuscript is to pursue some of the initial ideas of Brooks et al. (1989) in greater detail.

Biological systems are systems which persist by transforming energy from one state to the next in a manner which generates structures that allow the system to persist for a finite period of time. There are two classes of energetic transformations that can be recognized in biological systems. The first type of transformation results in a net loss of useful energy in the system, the lost energy being measured as heat. We call these types of transformations heat generating transformations. The second type of energy transformation, however, changes low quality energy into a state that can be stored and used by the system in subsequent transformations. We call these types of transformations conservative transformations. Any time a conservative transformation occurs, it is always coupled with a heat generating transformation. Only biological systems that accumulate an excess of useful energy persist. Essentially, a biological system slows the rate at which energy stored by the conservative transformations is degraded by the heat generating transformations.

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This change in rates allows for a finite period of time that useful energy remains stored, and hence allows the generation of biological structures.

These ideas regarding the energetics of biological systems have been around for a number of years, being first discussed by Lotka (1913, 1925). Yet there has been little progress in integrating them with the mainstream of biological thought. This may be partly due to the fact that most biologists do not need to be concerned about energetics explicitly to study their systems. Yet without eventually describing biological phenomena in terms of energy transformations, the advances in biology that have profound implications for the organization of the physical world cannot be integrated into descriptions of the natural world that arise in other sciences, especially physics (Lazlo 1987, Brooks &Wiley 1988).

In the following paper we suggest that it is necessary to make the distinction between the two types of energy transformations described above before it is possible to understand how energy processing and storage by biological systems allow them to maintain their structure. We first show that a useful way to make a distinction between the two types of energy transformations can be derived from the concept of entropy production discussed by Brooks and Wiley (1988). Based on the concept of entropy partitioning, we show how it is possible to describe biological systems in terms of how they partition entropy production. Finally, we show how the partitioning of entropy production leads to hierarchical structures in biological systems. By partitioning entropy along energetic pathways that differ in the rate of energy flows, biological systems constrain the structure of faster pathways by the historically determined configurations of energy flows in slower pathways.

II. Energy and Entropy in Biological Systems.

Since energy is used in biological systems to change the distribution of matter in the system, it is useful to define how energy flows are related to the state of the system. One way to do this is to relate changes in entropy with energy flows. If entropy, however defined, is a description of the complexity of the system in terms of both the total number of states in which the system can exist and the probabilities of the system existing in each different state, then relating entropy changes and energy changes allows a description of the role of energy in changing the state of the system. Changes in entropy (dS) for open systems, such as living systems, are decomposed into two terms. One of these terms (d_eS) represents changes in entropy due to exchanges between the system and its surroundings; the other term (d_iS) represents changes in entropy due to production by irreversible processes operating within the system (see, e.g., Prigogine 1980). Such systems operate spontaneously when "entropy production", represented by d_iS is positive:

$$dS = d_eS + d_iS, \quad d_iS > 0 \qquad (1)$$

Prigogine and Wiame (1946) equated d_iS only with heat generating processes, denoted by a specific dissipation function, ψ. So long as there are any heat generating processes within the system, the second law of thermodynamics is satisfied. Subsequent discussions of the connection between biological systems and thermodynamics have dealt with conservative processes as if they were due strictly to exchanges (d_eS) between the system and its surroundings (i.e., that they are caused strictly by fluxes from the environment that bring characteristic order into the system). If this is true, there is no necessity that conservative processes show entropy increases (or indeed any lawlike behavior). In fact, the accumulation of free energy within biological systems has indicated to many that entropy actually decreased in biological systems. This was in accord with classical beliefs that entropy is an increasing function of time and is inversely related to the order of the system.

Zotina and Zotin (1982) considered d_eS to represent the *source* of energy and matter for biological systems, whereas d_iS represents the *fate* of that energy and matter. In their formulation, ψ has two components: ψ_α, the *external dissipation function*, which represents energy transformations that result in energy lost to the system, and ψ_μ, the *bound dissipation function*, which represents energy that is transformed and retained within the system, eventually to be lost or used again. Brooks and Wiley (1988) equated ψ_α with what we have called heat generating energy transformations (e.g., physiological losses), and decomposed ψ_μ into ψ_μ^b, representing entropy production resulting from energy used in accumulation and maintenance of biomass, and ψ_μ^i, representing entropy production resulting from energy used in accumulation and maintenance of genetic and epigenetic information. Entropy production by heat generating processes can be measured as heat lost from the system; entropy production by conservative processes is manifested in the accumulation and maintenance of molecular structure. This being the case, both heat generating and conservative processes must be included in the thermodynamic production term d_iS.

We postulate that biological systems exhibiting order must have the following properties: (1) the rules for both heat generating and conservative processes must be encoded in the structure of the system; (2) these production rules must include "information" or "instructions" leading to non random exchanges between the system and its surroundings; and (3) production by conservative processes must be positively entropic. Under such a view, the thermodynamic drive in biological systems stems from energy flows being constrained by the production inherent in genetic and epigenetic information. The nonrandom nature of this accumulation according to intrinsic production rules results in the nonrandom mechanical and chemical gradients seen in biological systems. The flow of energy and the increase of bound entropy in the form of biological structure are directly, rather than inversely, proportional.

Frautschi (1988) has recently discussed two models or idealizations for entropy production in physical systems. In one idealization, entropy is produced as a result of equilibrating temperatures between the system and its surroundings. In biological systems, heat generating transformations are manifestations of this kind of behavior. In the second idealization, entropy is produced as a result of structural changes that result when the system is changed on time scales shorter than its normal equilibration time. This means that if the phase space in which a system is extended is expanding faster that the system can distribute itself equiprobably among the new states allowed by the expanding phase space, the structural rearrangements that occur will produce entropy, but may also correspond to structural states that are ordered. Landsberg (1984a,b) demonstrated that any system exhibiting spontaneous growth will exhibit this second type of entropy production. The general dynamic for this second idealization is one in which (1) both the phase space expansion (S_{max}) and entropy production (S) are increasing functions of time and (2) S is a concave function of time. Thus, the difference between S_{max} and S must increase with time. The degree of structural organization that emerges is proportional to that difference.

From the forgoing discussion, it is possible to relate the type of entropy production (or dissipation) and the nature of energy flows within biological systems. Recall that entropy dissipated into waste products tends to move the system towards a set of many, simple, equiprobable states, and thus increases the overall entropy of the system. On the other hand, entropy dissipated into biomass and genetic information moves the system towards a small set of structurally complex states, so again, the overall entropy of the system increases. Therefore, entropy dissipation into waste must occur as energy flows in the opposite direction of the dissipation. That is, as energy is lost from a system, the system moves towards a set of many equiprobable states. Thus, entropy dissipation into waste is a consequence of heat generating energy transformations. In addition, entropy dissipation into biological structure occurs in the same direction as the accompanying energy flow. That is, as energy enters the system, some of it is used to increase the structural complexity of the system. Thus, entropy dissipation into structure is the consequence of conservative energy transformations. Notice, that because heat generating transformations always accompany conservative transformations, entropy dissipation into waste always occurs when entropy is dissipated into structure.

Notice that this view of the relationship between energy and entropy in a biological system creates conflicting tendencies in the system. On the one hand, entropy increases due to heat generating transformations move the system towards increasing number of unstructured states. On the other hand, entropy increases due to conservative energy transformations tend to move the system towards increasing structural complexity. Persistence of a biological system then depends on the rates of energy fluxes: if conservative energetic transformations accumulate sufficient bound energy, then the system can delay the time of its inevitable loss of structure due to heat generating energetic transformations (Lotka 1913).

III. Energy, Entropy, and Structure in Biological Systems.

How might these ideas on the relationship between energy transformations and entropy changes be used to describe biological systems? We illustrate such a description by considering the energy flows experienced by an individual organism. Here, we assume we are dealing with multicellular, sexual organisms, but the extension of these ideas to simpler organisms should be straightforward.

Organisms are typified by their ability to use external energy to maintain themselves. This is illustrated in Fig. 1 as an energy flow from a source, E, denoted by an energy storage symbol using Odum's (1983) energy symbols. Organisms have two types of cells: (1) somatic cells (denoted by Q_1 in Fig. 1), which form the bulk of the organism and are involved in organismal structure and maintenance, and (2) germ cells (denoted by Q_2 in Fig. 1), which preserve information about the structure of the organism and transmit it to future generations. Energy entering the organism is accompanied by an increase in the entropy of the energy source, d_eS.

Energy that enters an organism does so in certain states that existed prior to the entry into the organism. Organisms are structured so that these states are broken down and reassembled into new states that are compatible with the system. For example, in metabolism of carbohydrates, complex carbohydrates are broken down by digestive enzymes into glucose and other simple sugars. These then cross intestinal cellular membranes and are eventually reassembled in storage organs again as complex carbohydrates. Thus, organismal structure includes "filtering" mechanisms that transform entering energy from one complex state external to the organism to a complex state within the organism. As discussed above, these transformations involve both conservative transformations, which increase the structural complexity of the organism, and heat generating transformations. This is depicted in Fig. 1 by a filter symbol that requires the input of energy stored in somatic cells, and is accompanied by a dissipation of entropy into waste. This increase in the waste entropy is the cost of obtaining energy at less than perfect efficiency, and is denoted by ψ_{α}^{c}. Note that it flows in the opposite direction of energy spent on filtering incoming energy.

Organisms store energy in somatic cells through a variety of means, including cell division and growth. A myriad of biochemical pathways exist to accomplish energy storage, and are many redundant. For example, energy stored in diverse biochemical products such as proteins, fats, or carbohydrates is liberated using common catabolic pathways. Storage of energy in these various biochemical structures requires the expenditure of energy. Thus, a second type of waste entropy generated by organisms is attributable to the costs of storage. The lost energy flows as heat and waste products from somatic cells to the outside of the organism, and is accompanied by another dissipation of entropy into waste, denoted by ψ^s_α in Fig. 1.

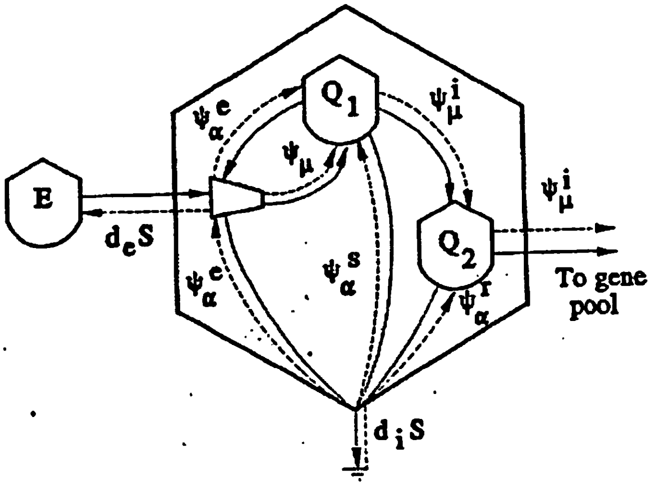

Figure 1 - Routes of energy and entropy flow in an organism. E is an environmental source of energy. Q_1 is biomass storage in somatic cells, and Q_2 is biomass storage in germ cells. Solid lines denote energy flows and broken lines denote entropy flows. The symbol at the bottom of the figure consisting of three parallel lines of different lengths denotes energy lost to the system as a result of heat generating transformations.

A final dissipation of waste entropy occurs as somatic cells are involved in the generation, maintenance, and perpetuation of germ cells. Much of the energy that flows from the soma to germ cells is eventually lost in maintenance. Note that the depiction of the relationship between somatic and germ cells in Fig. 1 makes no assumptions about the timing of germ cell determination during development (Buss 1987), and thus need not be constrained by conventional ideas regarding the separation of germ and somatic lines. The accompanying entropy dissipation is denoted as ψ^r_α in Fig. 1.

Although there are many energy flows that are involved in heat generating transformations, some are also involved in conservative transformations. It is these energy flows that are responsible for the generation of organismal structure, and hence are accompanied by increases in the structural complexity of the organism. The major source of organismal structure is from energy entering from the outside of the organism. This dissipation of entropy into organismal complexity is denoted by ψ_μ in Fig. 1. This dissipation is directed at somatic cells, following the flow of incoming energy. Since germ cells originate from somatic cells and are dependent on them for maintenance energy, a portion of the entropy dissipated into somatic cells is dissipated further into germ cells, specifically, into gametes. This is indicated as the dissipation term ψ^b_μ by Brooks and Wiley (1988). It is this accumulation of complexity in somatic cells that must balance the tendency towards loss of structure due to heat generating energy transformations if the organism is to persist for a finite time period. Another important consequence of the slower rate of entropy dissipation into gametes is evident when it is realized that the ultimate fate of the gametes is to leave the organism. This flow of energy and structural information out of the organism results in the maintenance of higher levels of biological organization. These higher levels of biological organization have analogous energy and entropy flows to organisms, but derive their energy and structural entropy from that generated at lower levels (Fig. 2). The rates of entropy dissipation are consequently slower at high levels than at the organismal level.

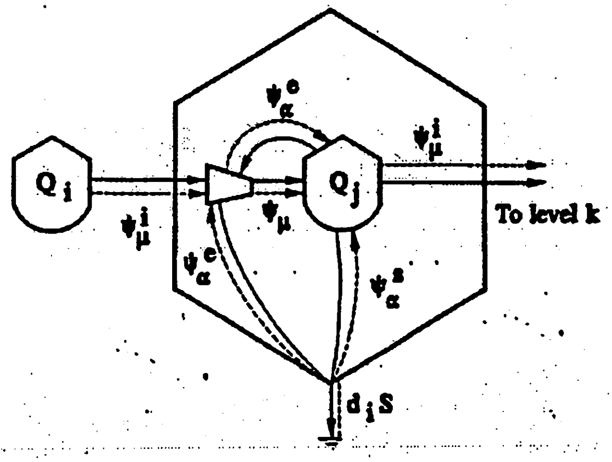

Figure 2 - Generalized supraorganismal systems indicating energy and entropy flows from storages at lower levels (Q_i) to storages at higher levels (Q_j). Note that there may be more than one storage involved in Q_i, although for simplicity only one is shown.

This transfer of energy and structural entropy from lower levels in the biological hierarchy to higher levels can be illustrated by considering the relationship between organisms and the next level, the population. Energy and entropy enter the population from the organism initially as gametes. The flow of gametes into the population is also filtered by a number of population level processes such as mate recognition systems, gametic compatibility, etc. The result of this filtering is that as gametes unite to form new organisms, the structure of the information that left the organismal level is changed at the population level.

As new organisms are added to the population the structural complexity of the population changes. At the population level, there are again two types of entropy changes. First, entropy is dissipated into wastes. This includes heat-generating energy transformations that are required to unite gametes, ψ_{α}^{c}, and those that occur to allow maintenance of a stable population, ψ_{α}^{e}, such as death and emigration. Second, entropy is dissipated into structure (ψ_{μ}). Some of this entropy is tied up in changes in the number of organisms (population dynamics; represented by $\psi_{\mu}^{b} = \psi_{\mu} - \psi_{\mu}^{e}$) and some is tied up in changes in the gene pool. Since the population exists longer than any individual organism, the rates of entropy dissipation into population level structures must be slower than the rates of entropy dissipation into organism level structures.

IV. The Nature of Hierarchical Constraints.

The slower rates of entropy production in higher level biological structures allow them to constrain the characteristics of lower level structures. At the same time, since higher level structures derive their energy and structural entropy from lower level structures, they are also constrained by the nature of these structures. Salthe (1985) has differentiated between these types of constraint. His model of biological organization postulates that all biological structures are determined by the interactions of focal level entities and both lower level and upper level constraints.

The relationship between upper level constraints and lower level constraints can be illustrated by the relationship between organisms and populations described above. We have shown that the population derives its structural entropy through conservative energy transformations within and among organisms. The collection of organisms that comprise the population provide the characteristics upon which population level processes, such as natural selection, assortative mating, population regulation, etc., operate. The results of these processes are the selective propagation of kinds of organisms. The cumulative result of this selective propagation is that organisms with certain combinations of characteristics cannot exist, hence, the properties of organisms are constrained by the history of selective propagation due to the characteristics of the population.

Notice that the characteristics of a level influence the future characteristics of that level by the constraints it imparts to both upper and lower level entities. Hence, the properties at any given level are constrained by the past history of properties at that level as they have constrained both lower and upper level entities. Thus, the origin of historical constraint at any level is ultimately due to the differences of the rates of entropy production between that level and adjacent levels.

V. Discussion and Conclusions.

As levels of decreasing rate are considered (i.e., higher levels in a biological hierarchy), it is possible to associate their properties with types of entropy production that occur at different rates (Brooks et al. 1989). Thus, in low level systems such as organisms, processes such as metabolism and respiration dominate in determining the observed structure. Hence, most of entropy production in organisms is dissipated into waste. At higher levels, such as species, the accumulation of genetic diversity dominate in determining the observed structure. Hence, biological systems at different hierarchical levels can be recognized as being dominated by different kinds of entropy dissipation. Such differences in rates should show up in comparisons of the amount of variance in properties of systems at different hierarchical levels. Recently, for example, Nagy and Abst (1991) showed that body size explained 91% of the variance in field metabolic rates among a number of bird species, while phylogeny explained a much smaller amount. Thus, the amount of energy used by a bird is related much more to its body size than to its genetic makeup relative to other birds. On the other hand, Maurer (1991) calculated variance components for body size and phylogeny using average population densities of 380 species of North American birds. He found that phylogeny explained 41% of the variability in population density among species, while body size explained only 2%. Population density is a property of a system that exists at a larger spatial and temporal scale than an organism. Hence, these data suggest that phylogeny contributes more to the properties of larger scale systems than it does to smaller scale systems (Brooks and Wiley 1988, Brooks et al. 1989).

It is also important to note that biological systems at any given level often participate in several different kinds of constraint systems (Eldredge 1985, Salthe 1985). For example, organisms are reservoirs of genetic information, and hence participate in a system of constraints that has been called the genealogical hierarchy (Eldredge 1985, Salthe 1985). The ecological hierarchy, or interactor hierarchy, is the realm of exchange components (d_eS) in biological systems. Brooks and Wiley (1988) have suggested that the relationship between these two constraint systems can be related to the partitioning of entropy in the biological system being considered. This relationship is consistent with our assertion earlier that the processes responsible for determining exchange requirements stem from genealogical production. Thus, the two hierarchies are complementary but not ontologically equivalent in the same way that entropy exchange and production are. Just as d_iS is the only term constrained to show entropy increases over time, only genealogical production must show lawlike regularities. We would expect ecological patterns and processes that show lawlike behavior to have a genealogical component. The exchange of matter and energy by a biological system with its surroundings is essential to biological production, but the rules governing these exchanges, and hence the ultimate fate of matter and energy in the system, are embodied within the system and derived causally through reproduction. Generally, most physically definable biological systems (e.g., organisms, populations/demes, species) are complex enough so that they have different properties that make them part of different constraint systems. Biological systems that are difficult to define physically, such as ecosystems and communities, are also difficult to assign to more than one system of constraints.

Biological order is a direct consequence of the flow of energy through biological systems. It is created because there are a class of energy transformations that increase the complexity and hence structural entropy of biological systems for a finite period of time in the face of loss of structure due to heat generating transformations. Because certain types of entropy dissipation into structure occur at different rates, this allows different levels of biological order to be maintained, with higher levels changing at slower rates than lower levels. These rate gradients in entropy production lead to different constraint systems of hierarchically related entities as well as generation of historical constraints at any given level of organization.

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