

Entropy in Evolution

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ABSTRACT

Daniel R. Brooks and E. O. Wiley have proposed a theory of evolution in which fitness is merely a rate determining factor. Evolution is driven by non-equilibrium processes which increase the entropy and information content of species together. Evolution can occur without environmental selection, since increased complexity and organization result from the likely "capture" at the species level of random variations produced at the chemical level. Speciation can occur as the result of variation within the species which decreases the probability of sharing genetic information. Critics of the Brooks-Wiley theory argue that they have abused terminology from information theory and thermodynamics. In this paper I review the essentials of the theory, and give an account of hierarchical physical information systems within which the theory can be interpreted. I then show how the major conceptual objections can be answered.

Keywords: Entropy, evolution, information, thermodynamics

Daniel R. Brooks and E. O. Wiley (Wiley and Brooks, 1982; Brooks and Wiley, 1984; Brooks, 1983; Brooks and Wiley, 1986) have proposed a theory of evolution based on non-equilibrium thermodynamics and information theory. According to their theory, the dynamics of evolution derive from historically constrained increases in the information and entropy of a system of imperfectly reproducing organisms. Natural selection is merely rate-determining, and is best viewed as an extrinsic factor affecting evolutionary dynamics. The contrast between the Brooks-Wiley theory and selectionist theories is established most clearly by their result that evolution is possible even without environmental or sexual selection as they are usually understood. Neo-Darwinism and the Brooks-Wiley theory complement each other. They are both extensions of a yet to be completed systems theory which treats environment, biological entities, and their interactions using common principles (see Stegmüller (1976) on the notion of an extension of a theory). The Brooks-Wiley theory contradicts contemporary neo-Darwinism only to the extent that neo-Darwinism is held to be a complete theory of evolution.

The Brooks-Wiley theory has been criticized (Lovtrup, 1983; Bookstein, 1983; Wicken, 1983) for abusing terminology from thermodynamics and information theory and for not accurately describing the phenomena. Responses to the criticisms (Wiley and Brooks, 1983; Brooks and Wiley, 1985) indicate that they are based on misunderstandings of the intent and limits of the theory. As they state, Brooks and Wiley deviate from traditional thermodynamics and information theory. A clear statement of the relation of the terminology they use to traditional terminology is needed. In this paper I first state the essentials of the Brooks-Wiley theory, and then describe the classical views of information and entropy from communications theory and measurement theory, showing how they are inadequate for the Brooks-Wiley theory. Next, I outline a more general approach to information theory which underlies the Brooks-Wiley theory. I then list and reply to the major objections. My interpretation and replies are largely informed by Brooks and Wiley's own. My purpose is to bring out the underlying coherence of their views. In the process I will note several areas which I believe require more work.

1. The Brooks-Wiley Proposal

Brooks and Wiley (Wiley and Brooks, 1982; Brooks and Wiley, 1986) start with the perhaps obvious fact that organisms are self-organizing dissipative structures which persist at the expense of environmental free energy. (See Prigogine (1961), Nicolis and Prigogine (1977) and Janstch (1981) for discussions of non-equilibrium systems and dissipative structures.) This suggests that entropy is important for understanding the dynamics of evolution. A second obvious fact that Wiley and Brooks consider is that biological reproduction requires the physical transmission of information from an organism to its progeny. The intuitive (if somewhat vague) relation of information to entropy (Shannon and Weaver, 1949; Brillouin, 1962; Gatlin, 1972) also suggests that the dynamics of evolution involve

entropy. Last, the evolutionary requirement of imperfect replication implies the introduction of disorder, which further suggests entropy change.

Although notions such as temperature and free energy have no obvious correlates in evolutionary biology, it is possible to use the organizational and probabilistic aspects of entropy and information to introduce a notion of biological entropy. This is not necessarily the same as thermodynamic entropy, and the exact relation is open to question. Wiley and Brooks (1982) argue that for problems of evolution (as contrasted with problems of the origins of life) we can ignore contributions to entropy due to energy, since free energy is in abundant supply. The organization which allows organisms to use the available energy is more important than the availability of energy. This suggests that species and organisms are best understood in terms of their information content (Wicken 1983; 1984). According to Brooks and Wiley, evolutionary changes in information content have two sources: increases in species organization and decreases in species cohesiveness. Both of these processes correspond to an increase in the entropy of the information in the system.

Brooks and Wiley make two independent distinctions between types of biological information. The first is the distinction between stored (or expressed) and potential information. Stored information is information which is expressed at some time in either the organism's structure or functioning. The idea is that stored information determines the organism's phenotype, and is involved in the organism's interactions with its environment. Potential information is information which is present but not expressed, such as the information in recessive alleles, or the information which defines possible developmental pathways which are never triggered. According to Brooks and Wiley, the stored information of species is consistent among all members of the species, whereas potential information varies from member to member. I think this way of putting the distinction for the case of species is incorrect for two reasons: first, species show extreme variation between members, and, second, it is useful for technical reasons to define stored information as a variety of potential information. I will modify the distinction below to accommodate these two problems.

The second distinction is between canalized (or regulatory) and non-canalized (or structural) information. Canalized information is responsible for the control of development and genetically determined behavioral traits. The canalized information of a species determines the interactions of its members, providing it with a functional unity (Wiley and Brooks, 1982; Brooks and Wiley, 1986). It seems, therefore, to determine the individuating characteristics of species. Stored canalized information is therefore a central concept of the Brooks-Wiley theory of evolution. I find two problems with the notion which are of some theoretical interest, though they need cause no immediate trouble. The interest of the problems involves their impact on the relation of the Brooks-Wiley theory to biochemical theory and to selectionist theories of evolution.

Although canalized and non-canalized information are supposed to be mutually exclusive, it is not clear that regulatory and structural information are entirely distinct (Bookstein (1983) hints at this problem), since form can determine function. Structural information is supposed to determine the "building blocks" which canalized information directs into more complex functional structures, which can presumably themselves form the basis for even more complex structures. At bottom, however, are the structural units of amino acids and nucleic acids, and their initial physical relations. It seems that canalized information must ultimately be based on structure. The two distinctions, between structural and regulatory information and between canalized and non-canalized information, do not quite line up. The distinction between canalized and non-canalized information is essentially functional, and may cut across structural distinctions. Since the genetic and species levels are distinct (see section 4 below), it is not impossible that the same unit of information could be structural at one level, and regulatory at another. The exact relation between structural and regulatory information requires further investigation. This problem need not cause immediate difficulty, however, since in many cases the intent of the distinctions is clear enough for the purposes of analyzing biological information. The difficulties become more acute, however, for even a mildly reductionist program.

A second difficulty arises from the distinction between internal and external factors in evolution. Inasmuch as some stored canalized information determines behavior, which at least *prima facie* involves environmental characteristics which are nominally extrinsic to the organism, it seems that some external factors are involved in the distinction between canalized and non-canalized information. An analogous problem exists for canalized information regulating development whose expression depends on environmental factors. Even some potential canalized information must be referred to the environment, since the canalization is defined in terms of its determination of behavior. This problem can be avoided by defining canalization in terms of determination of possible phenotypes, but this blurs the distinction between stored and potential canalized information. Since it is only stored canalized information which determines the identity of a species, this problem is not insignificant. Normally, development and behavior will occur under quite regular conditions for a given species, and deviations can be accounted for as abnormal. The problem takes on greater importance, however, in debates about whether environmental factors are really extrinsic.

Biological information is subject to two sorts of variation producing new information. First, potential information can be converted into stored information, creating new expressions in the individual or new stable structures in a species, perhaps yielding a new species. The second sort of new information is produced by alterations to the genetic structure resulting in new information of one of the four possible types. Both types of new information add new possibilities, in the first case

for development and environmental interaction, and in the second case, since it may involve the creation of potential information, for future expression as well.

There are two entropies important in biological systems, the entropy of information and the entropy of cohesion. The information of a system in a particular state is the difference between the maximum possible entropy of the state and its actual entropy. The entropy of information is the amount of information required, given the information of the state, to determine its microstructure. In other words, the entropy of information represents the residual uncertainty about the physical system after the ordering effect of the information contained in the biological system is subtracted. Stated still differently, the entropy of information is a measure of the indifference of the system to random fluctuation, or of its ability to withstand random fluctuations, i.e., its stability. This phenomenon is known in communications theory as redundancy (Shannon and Weaver, 1949: 56). Any ordered disturbance impinging on the system which has an information content greater than the entropy of information must of necessity disrupt the system.

Species can be more or less cohesive depending on the degree to which their diverse members' genetic material is mixed in reproduction (panmixis) (Wiley and Brooks, 1982). This is determined in two ways: (1) the interbreeding of members of diverse epiphenotypes, and (2) the interbreeding of members of diverse demes. In some species viral transmission of genetic material may be significant. The entropy of cohesion is a measure of the disorder of the biological entity resulting from the segregation of its parts. In the case of species, this is due to difficulties in sharing genetic material between diverse members (Wiley and Brooks, 1983; Brooks and Wiley, 1986).

Evolution, then, results from the joint effect of increases in the entropy of information and the entropy of cohesion. Brooks and Wiley have demonstrated that various forms of speciation events are compatible with this thesis (Wiley and Brooks, 1982; Brooks and Wiley, 1986). They do not make the relationship between the two entropies entirely clear. At equilibrium (constant entropy within the system) the two are inversely coupled: a decrease in cohesion entropy results in greater variation within a species, producing a higher entropy of information. This may at first seem counter-intuitive, since the species has not lost (or gained) any genetic information. The genetic information determines the maximal entropy, not the information content of the species, which depends on how that information is organized. Organization is a source of redundancy, reducing the total amount of genetic information expressed. Since the ontogeny of an organism determines its stored information and ontogeny is determined by the history of the organism and its ancestors, past events are the source of the organizational information of the species. Brooks and Wiley argue that ontogeny is also entropic, and that individual development can also be understood using the non-equilibrium model (Brooks and Wiley, 1986: Chapter 3). The genetic information varies subject to historical

constraints, which allows the entropies of cohesion and information to increase simultaneously. Although the stored information of the species and each of its members is parasitic on the genetic information, being negentropic with respect to that information, increases in stored information are entropic, due to changes in the information system. I will clarify this statement in the next three sections.

2. Evolution and Classical Theories of Information

The chief conceptual difficulty underlying the Brooks-Wiley approach is the relation of the concepts they use to standard concepts in thermodynamics and information theory. As I have already pointed out, they do not use the classic thermodynamic conception of entropy. This does not mean that their entropy is not physical, as I will show presently. The classical conception of entropy must be broadened to include physical information systems. Another problem is their use of "information". This is a difficult concept in any case; there is even fundamental disagreement among the primary authors in the field. I will consider the views of Shannon and Weaver (1949) as representative of the communications theory school, and those of Brillouin (1962) as representative of the measurement theory school. The problem of interpreting Brooks and Wiley will shed some light on a fundamental disagreement between these two schools.

The basic assumption of communications theory is that there is a code with fixed characteristics in which messages of arbitrary length can be constructed. Each distinct type of element of the code has a probability determined by the total number of elements and the constraints on the ways it can be concatenated with other elements. The information content of a token of code (in bits) is the absolute value of the base two logarithm of the probability of its type:

$$[1] \quad I = -k \ln(1/p), \text{ where } k \text{ is the base 2 logarithm of } e$$

The information content of a message is the sum of the information contributed by its component tokens reduced by the constraints on the likelihood of particular combinations, and is a measure of the unlikelihood of the message. (For details, see Shannon and Weaver, 1949.) This is a purely syntactic definition: there is no implication that a message will be more meaningful or more valuable if it contains more information. Codes are abstract information systems. The information content of a message puts an upper limit on its semantic content, but does not determine it.

Shannon and Weaver (1949: 49-51) define the entropy of a message as equal to its information content. The rationale behind this definition is that the most informative messages of a given length are the ones which are most random *a priori*. If all of the code units are equiprobable (no constraints on combination) the

information content of a message is maximal. Any variation from equiprobability creates redundancy which reduces the total information content of the message.

Brillouin (1962: 161) has pointed out that Shannon's definition of entropy allows entropy to decrease in irreversible processes, and cannot, therefore, be identical to physical entropy. Perhaps the simplest example of this is noise which destroys information, thereby decreasing the entropy of a message. Shannon and Weaver (1949: 57-58, 93) prove that transducers can irreversibly reduce entropy. Brillouin argues that the sign of Shannon-Weaver entropy must be reversed to represent physical entropy. He contrasts "free information", which is abstract and has no particular relation to physical properties, with "bound information", which can be interpreted physically in terms of the complexions (microstates) of a physical system (1962: 152-153). Bound information is a special case of free information. Bound information can be converted into negative entropy (negentropy), and vice versa. Put somewhat differently, entropy measures the lack of information about the actual state of the system (Brillouin, 1962: 160). The concept has its origins in measurement theory. Measurements convert negentropy (equivalent to physical order in many simple cases) into bound information. Brillouin is somewhat vague about whether the two are identical.

Neither the Shannon-Weaver nor the Brillouin theories of information are adequate for the Brooks-Wiley theory. Shannon-Weaver information gives an account of the internal entropy of a code, but the entropy is not physically realistic. Bound information avoids this problem, but it gives no representation of the internal entropy of a code. These failures indicate that neither theory is sufficiently general. This might also be inferred from the fact that they clash, despite their individual intuitive appeal. There are several characteristics of information in the Brooks-Wiley theory which account for the failure of the classic theories. Unlike Shannon and Weaver, Wiley and Brooks require that the code can be expanded through random variation, and that message lengths as well as structure are determined by the code. Unlike Brillouin, for whom the information content of a system is determined solely by the current state of the system ("boundary conditions model"), Wiley and Brooks insist that the information content is historically determined ("initial conditions model"). Furthermore, neither theory can account for the physical expression of both stored and potential information. A generalized information theory will have to accommodate these possibilities.

3. Physical Information Systems

Gatlin (1972: 49) calls the Shannon-Weaver information "potential information", since it is a measure of the capacity to carry real information. She measures the stored information so that it equals the product of the redundancy and the maximal information content, noting that it should be negentropic. (I should note that her definition of redundancy (1972: 39, 69) is incomplete, since it considers only monadic and diadic contributions to redundancy.) Her notion is

similar to the stored information of Brooks and Wiley. Their potential information, however, is quite different, since it is a) constrained by the actual probabilities of combination, b) defined as not being stored, and c) physically present.

A physical information system is a system containing stored information whose properties depend only on properties internal to the system. Stored information is like Shannon-Weaver information, except that like bound information it is physically real. It exists whenever there are relatively stable structures which can combine lawfully. These structures are the elements of the information system. The stored information of an element cannot be greater than its bound information (or else either lawfulness or the second law of thermodynamics would be violated), but the actual value is determined by its likelihood of combination with the other elements. The information content of a physical combination of elements (an "array") is the sum of the contributions of the individual elements. For example, the nucleic acids have a structure which contains a certain amount of bound information (they are not just random collections of atoms), and can interact in regular ways with other nucleic acids (as a consequence, but not the only one, of their physical structure). The stored information of a given nucleic acid sequence is determined by the *a priori* probability of that sequence relative to all the permitted nucleic acid sequences with the same molecules. The bound information, which will be greater, is determined by the probability of the sequence relative to all the random collections of the same molecules. (Nucleic acids, of course, have regular interactions with other structures, so the restriction of the information system to just nucleic acid sequences is questionable. We can justify singling out these sequences because of their special role in ontogeny and reproduction.) The lawful (regular) interactions of elements of an information system determine a set of (probabilistic) laws of combination, which we can call the constraints of the information system (see Shannon and Weaver (1949: 38) for a simple example of constraints). Irregular interactions, either among elements of the information system or with external structures, represent noise to the information system.

The elements of an information system, since they are relatively stable, have fixed bound information. It is therefore possible to ignore their bound information in considering entropy variations. The elements are the "atoms" of the system, while the arrays are the states. The stored information of an array is a measure of its unlikelihood given the information system. The entropy (*sensu* Brillouin) of this unlikelihood equals the entropy of the physical structure of the array (see Holzmüller (1984: 92-94) for an account of the entropy of "biomolecules") minus the entropy of the information system constraints. This value is negative, indicating that the stored information of an array is negentropic. Its absolute value is the product of the redundancy of the information system and the Shannon-Weaver entropy. This is just Gatlin's stored information. Array entropy so calculated reflects more realistically what can be done with an information system than the

Shannon-Weaver entropy. In particular, random alterations to an array make it difficult to recover the array.

This definition of array entropy is inadequate, since it is defined in terms of properties not in the system, namely the entropies of the constraints and the structure constituting the array. The entropy of a system is usually defined in terms of the likelihood of a given macrostate. Two microstates are equivalent macrostates if they have same effect at the macro level (ignoring statistical irregularities). If we assume that all states must be defined internally to the system, the above analysis of arrays does not allow any non-trivial macrostates; each macrostate has just one microstate. This forces a definition of entropy in terms of elements not in the system, or else a "cooked" definition, like Shannon-Weaver entropy. A satisfactory definition of array entropy must be given entirely in terms of the defining physical properties of the information system elements. Such a definition can be given by distinguishing between actual and possible array states.

By assumption, the elements of the system are relatively stable and combine lawfully to form arrays. Possible maximal arrays of elements are the microstates. The macrostates are the actual array states. The microstates of an array are the possible maximal arrays of which it is a part. The information and entropy of a macrostate are defined in the usual way in terms of probabilities of microstates. In abstract information systems this definition degenerates, since arrays can be arbitrarily large. In realistic information systems, though, there is an upper limit on possible array size (though it might be somewhat vague). In organisms the maximum array size is restricted largely by the lengths of the chromosomes. In species it is restricted to the maximum number of characteristics of a member. (There must be such a maximum, since the amount of genetic information is finite.) The array information is a form of bound information, but also has an entropy defined only in terms of the information system characteristics. The external entropy of the null array is the entropy of the constraints on the information system. The external entropy of a maximal array is the base line from which the internal entropy can be measured. It can be called the entropy of the information system. The size of the information system is the difference between these two entropies:

$$[2] \quad \text{Size} = H(\text{constraints}) - H(\text{system}).$$

The external entropy of an array is the internal entropy plus the entropy of the information system, equal to the entropy of the constraints minus the array information:

$$[3] \quad H(\text{external}) = H(\text{internal}) + H(\text{system}) = H(\text{constraints}) - I.$$

The internal entropy of information systems is an extension of the classical statistical entropy of thermodynamic systems. It treats information systems as

closed with respect to information but open to matter and energy, whereas mechanical systems are closed if they allow energy to flow in and out of the system, but not matter (Wicken, 1983). The internal entropy of an array is determined by the physically possible ways it could be realized, just as the entropy of a thermodynamic state is determined by its possible microstates. The internal entropy is no less physical than the thermodynamic entropy, unlike the sequence or configurational entropy of Shannon-Weaver information. Array information is a special case of message information, just as bound information is a special case of free information. In this sense it is not anthropomorphic to speak of a biological code or a chemical message.

4. Information and Entropy in Hierarchies

Codes can be hierarchical. Units concatenated out of elements of a lower level can form natural elements of a higher level. An example is the hierarchy of characters, words and sentences. Sequences of characters terminating with a special character, like a space, comma or period, form possible words. Sequences of words terminated by a period or other sentence terminator form possible sentences. Not all possible words are words, nor are all possible sentences sentences. Otherwise the hierarchy would be trivial. Words are distinguished from non-words by having a meaning or grammatical function, and sentences are distinguished from non-sentences by being grammatical. Because these properties of words and sentences are useful, words and sentences tend to outnumber other character strings. Some non-words and non-sentences are present in the language, however, which are potentially words or sentences, since they would be so if they fell into common use.

Brillouin (1962: 55) points out that a more efficient code for English would exploit the fact that not all potential words are words by encoding words so as to permit fewer non-words. The information required per character could be reduced by a factor of more than two, yet the same amount of information could be conveyed by the same number of characters. An even larger reduction could be achieved by eliminating potential sentences, and even more, no doubt, by eliminating unverifiable sentences. This would not only make language learning difficult, but would also reduce the likelihood of change in the language.

Using Brooks-Wiley terminology, the distinguished set of higher level messages contain the stored information of the information system, while the variants contain the potential information. The stored information is what distinguishes a system from other systems. In physical information systems the basis of the individuation must be some physical property.

There are at least four levels in the hierarchy of biological information. The lowest level is chemical, containing, among other things, DNA, RNA and proteins. The elements are nucleic acids, amino acids and the like. The arrays are macromolecules. At the next level, genetic information is stored in the macromolecules, but not all macromolecules are involved in storing genetic information. Some are involved only in "housekeeping" activities which maintain the chemical system. Others might do nothing. These two groups make up the potential information at the genetic level.

The next clear-cut level is the phenotype. The genetic information determines its characteristics. Not all genetic information is expressed. A recessive allele in a heterozygous individual is an example. The expressed genetic information is the stored information at this level. The potential information is the unexpressed genetic information.

According to Brooks and Wiley, the species level stored information is the set of characters common to all members of the species. This is not quite right, since all members of a species might share some character just by accident. A species is individuated by being closed under the possibility of successful interbreeding. The stored information of the species, then, is the set of characteristics required to allow closure under the possibility of successful interbreeding. All other characteristics which are expressed are part of the potential information of the species.

Although the information content of the lower levels is irrelevant to defining the properties of the information system at the higher levels, there is a clear sense in which the higher level information depends on the information at the lower levels: if the lower level information did not exist, neither would the higher level information. The possibility of the higher level information system depends on the maintenance of the stability of the lower level. Variations at the higher level are created by changes at lower levels. The physical processes which maintain the information system can occur at a low level, and as long as they yield relative stability at the higher level, they can largely be ignored. One important constraint, however, is that all higher level processes must be physically compatible with the lower level processes they depend on. In particular, any entropy and information produced at the higher level must be equal to or less than the entropy and information produced at the lower level (viewed externally).

5. Evolving Information Systems

Landsberg (1984) has shown that the disorder of a system, which he defines as the entropy divided by the system's maximum possible entropy, decreases as the system increases the number of its microstates as long as the entropy increases less quickly than the maximal entropy. One example he gives from measurement theory shows that information can both increase entropy and decrease disorder if the

additional information is that there are more states. Brooks and Wiley (1986) give examples of increases in free information which increase entropy. Brooks, Leblond and Cumming (1984) have constructed a computer model which shows how this might occur in biological evolution. The relationship between measurement theory and physical information theory suggests that the creation of new information through the addition of elements to a physical information system can increase the internal entropy of an array.

It is fairly easy to demonstrate this. New information can come either from a new element incorporated into an array, or from new constraints on the array elements. By assumption, the constraints are a consequence of the physical properties of the elements, so the latter case could occur only through replacement of one array element by another. This is equivalent to the deletion of an element and the addition of a new one. The addition of a new element to an array can occur either through the addition of an element already in the information system, or through the addition of an element new to the information system. The former case involves a reduction of entropy, and can occur regularly only if this entropy loss is compensated by increases elsewhere in the system. The latter case involves an entropy increase unless the new element is constrained to occur at only one location in the array, in which case the entropy remains constant. The entropy increase arises from the possibility of the new element substituting for others in the permitted possible maximal arrays. Deletion is the inverse case of addition. Replacement will increase both entropy and information if the deleted element remains in the system, the added element is new to the system, and the added element has greater information content than the old. In summary, addition increases both entropy and information if a new type of element is added to the system, replacement increases both if the replaced element is of a type which remains in the system, the replacement is of a new type, and the replacement contributes more information to the array than the replaced element. Deletion can never increase both entropy and information. Information new to the system is just noise which becomes incorporated into the system. Information and entropy both increase due to the incorporation of this noise.

Stored information at a given level must satisfy more constraints at that level than the potential information, so it seems that potential information should increase faster than stored information, yet we observe that variation with a species is lower than this might lead us to expect. The answer is to be found in reproduction. In order to understand this phenomenon, we must distinguish between absolute and distributed information (Brillouin, 1962: 265-266). Information can be redundant in two different ways (Gatlin, 1972: 70). Redundancy can result from constraints on the combination of elements, called structural redundancy, or else from the repetition of combinations, called repetitive redundancy. Both are similar in that they protect the system from error due to noise. Absolute information is a measure of structural redundancy. It can be distributed repetitively among a number of identical arrays. The distributed

information is the absolute information content multiplied by the degree of repetitive redundancy. Reproduction increases the repetitive redundancy.

Stored information at the species level has a high repetitive redundancy, since it must be duplicated throughout the species. A deletion of stored information through variation in a species member (interference by noise) would interfere with successful breeding, thereby eliminating the variants from the species. Such variants might be able to reproduce, in which case a new species would appear. (This non-selectionist theory of speciation explains how the "hopeful monsters" required by some evolutionists to explain complex features could make their appearance. The present theory allows such features as accidental consequences of speciation events which have no adaptational dynamic.) The degradation of stored information at the species level results, then, either in the casting off of the information entirely, or else in a speciation event. If the degradation is too fast, the species disappears. In order to avoid this, the reproduction rate must be higher than the production rate of variants to the stored information. Furthermore, potential information at the species level is unnecessary for reproduction, so it can degrade without destroying the species. Consequently, stored information will tend to be preserved, while variation will be maintained at a more or less constant level.

This effect at the species level has ramifications for the lower levels as well. Genetic potential information cannot contribute to reproduction, therefore it will tend to be in equilibrium with mutations. Likewise for potential chemical information (except inasmuch as it is required for maintenance of the information system). Stored chemical and genetic information will tend to be preserved to the extent that they contribute to stored information at the species level, whether in previously existing species or in species produced by new variation. Species act as filters which preserve some information and cast off other information. By far the larger number of variations will be cast off, due to the fairly stringent constraints on stored information. The production and maintenance of species feeds on the production of information at lower levels; only that which is reproduced survives. Species are informational dissipative structures, since they preserve themselves by storing information repetitively and produce themselves by capturing variant information produced at lower levels, increasing their internal entropy. In the process they cast off information which does not contribute to these processes.

High repetitive redundancy is inherently unstable, since more individual arrays are likely to vary. The species is protected by high redundancy, but is also more susceptible to variation. Most individual stored information variations will be cast off, but some will reproduce. The more repetition, the more likely this is. High repetitive redundancy of stored information, therefore, tends to produce speciation.

Cohesion can be explained fairly easily using the notions of potential information and repetitive redundancy. When cohesion is high, there is little tendency for sub-species to form which have a high degree of internal repetitive

redundancy of potential information. This becomes more likely as cohesion is lost, since characteristics peculiar to a sub-species are less likely to be propagated through the species. The higher repetitive redundancy of the potential information makes it more likely that a loss of stored information can be replaced by the redundant potential information in the sub-species, resulting in speciation. This is particularly obvious in the case in which characteristics are the cause of the lack of cohesion, since the very characteristics which make it more difficult for the sub-species to interbreed with the rest of the population are exactly those which make it more likely that loss of stored information can be replaced by potential information. Loss of stored information is not even required in these cases; the potential information can be converted directly into stored information if it becomes a prerequisite for breeding. Although cohesion increases the stored information entropy of the species by tending to equalize the probability of its microstates, it is itself entropic since it tends to produce isolated sub-systems. The two are balanced at constant entropy, but can increase together when stored information is added to.

To summarize, increasing information adds new components to the system, which both raises the entropy of the system constraints, and lowers the entropy of the information system. This allows both the information and the internal entropy to increase. This may seem paradoxical, and directly contradicts the views of many authors (Schrodinger, 1945; Gatlin, 1972; Holzmuller, 1984). They have either made the error of taking Shannon and Weaver entropy to be physically entropic (Gatlin), or have implicitly assumed that external entropy is what is required for understanding biological systems (Schrodinger and Holzmuller). As I have shown, the Shannon and Weaver definition of entropy is unphysical, allowing irreversible processes to decrease entropy. Bound information explicitly ignores coding, which is fundamental to biological processes such as reproduction and ontogeny. Some authors (Holzmuller, and perhaps Gatlin) have made the dual error of confusing biologically realized information with abstract information and also assuming that abstract information is bound information.

Although it is true that life processes are negentropic as viewed externally, viewed internally the significant processes of ontogeny and evolution are entropy producing despite producing information. This is possible because species capture the small proportion of random variations which can reproduce regularly and cast off the rest. Species create and maintain themselves on the information produced by lower levels of biological functioning.

6. Objections and Responses

Bookstein (1983), in a vitriolic attack, complains that Brooks and Wiley abuse the terminology they use - "information", "entropy", "equilibrium" and "thermodynamics" (for replies see Brooks and Wiley, 1985). His first complaint is

that they mix notions of information from communications theory and measurement theory. As I have already pointed out, neither of these theories is adequate for dealing with biological systems. The measurement theory definition of information Bookstein prefers ignores the necessity of accounting for the coding of information in biology and the transmission of information from one biological entity to another (on the necessity, see Wicken (1983)). Communications theory is also inadequate because it does not give a satisfactory account of entropy. Brooks and Wiley use a more general theory of information than either of the classic theories. They do not abuse terminology. If they are guilty of anything, it is of not adequately explicating their terminology. I hope I have gone some way in making up for this deficiency.

Bookstein's next complaint is that Brooks and Wiley confuse the levels of species and organism. He objects that this is a difference between type and individual, but in so doing he begs the question against Brooks and Wiley's assumption that species are individuals (Ghiselin, 1974; Hull, 1976, 1980; Brooks and Wiley, 1984). He does not appreciate that biology is hierarchical, and that the levels are natural, based on the stability of components from the lower levels. Consequently, he demands a definition of information which is not relative to level. This demand is unreasonable, since the processes involved in information transmission within a given level are only loosely coupled to those at other levels, and the relationship between adjacent levels is one of stored to potential information. Furthermore, one need not refer to individuals except to account for repetitive redundancy. Although the concept of cohesion entropy, for full explication, requires the treatment of sub-species as individuals, there is nothing in the explanation of speciation which forces species to be treated as individuals. Ironically for the species-as-types position, it is the uniqueness of the type which makes this ambiguity possible. If Bookstein's criticism is correct, it is irrelevant.

Bookstein's complaint that the species level and individual level distinction is incoherent because of intermediate possibilities such as slime molds and insect castes makes the error of assuming that levels are distinguished *a priori* rather than on the basis of empirically determined information systems. There is no reason why there could not be intermediate levels of organization between species and individuals; in fact it is likely. Nonetheless, the species and individual levels are the most obvious ones, and are the first to require analysis.

Bookstein objects to the concept of cohesion, arguing that assortative mating within a species shows order, not disorder; therefore Brooks and Wiley have the sign of cohesion wrong. He argues that it requires more information to specify a member of a panmictic species than a member of a less cohesive species. This is, of course, true. But it is quite irrelevant. Species cohesion is a property of species, not of organisms. The information required to describe a panmictic species is low: we need merely specify the stored and potential information systems, and the fact that

it is panmictic. To specify a non-panmictic species, we must specify the information systems and also detail how the species deviates from panmixis. Panmictic species are therefore more ordered, and Wiley and Brooks have the sign correct.

Finally, Bookstein complains that Brooks and Wiley have entropy confused, since entropy and information are opposite in sign. Here he demonstrates his misunderstanding of Wiley and Brooks and his failure to appreciate the limitations of the classic definitions of information with respect to biology, a failure which is demonstrated in the second half of his paper, in which he compares biological systems with mechanical systems which have no internal characteristics allowing reproduction.

Lovtrup (1983) makes many of the same criticisms as Bookstein (for replies see Wiley and Brooks, 1983). He holds that loss of information is characteristic of evolution, which is true of the whole species and environment, but misleading about the information economy of species. He complains that levels of organization are involved in biological systems, but that this cannot be dealt with using classical information theory. This is true, but Brooks and Wiley introduce the concepts of stored and potential information to allow hierarchical organization. Admittedly, they do not make the relations clear.

Lovtrup complains that energetic entropy increase alone is not equivalent to evolution, whereas a literal reading of Wiley and Brooks (1982) evolution equation implies it is. This is true, although energetic entropy increase is a necessary factor for evolution. Brooks and Wiley (1986) seem to have backed off on this. His charge that the units of entropy are incompatible with units of information and cohesion is unfounded, however. Brillouin (1962: 3) shows how the units can be made compatible.

One of Lovtrup's criticisms shows a surprising lapse of biological acumen: He objects to Brooks and Wiley's discussion of conspecifics which can mate successfully on the grounds that "by definition the members of a species can mate successfully", so the "can" is redundant. One wonders if he has ever seen a great dane and a chihuahua. Although the closure of reproduction individuates a species, not all members of a species must be able to successfully interbreed.

Wicken (1983), while generally supporting the Brooks-Wiley view, makes several astute criticisms, which can nonetheless be met (for replies see Brooks and Wiley, 1985). Wicken raises the same cohesion issue as Lovtrup and Bookstein, which Brooks and Wiley answer directly in their reply, and I answer more generally above. The nature of cohesion cannot be properly understood without understanding the relation between stored and potential information, which Wicken does not discuss.

Wicken's treatment of Brooks and Wiley falls down most seriously in failing to understand their use of "information". Distinguishing "thermodynamic" entropy from "sequence" entropy (the latter corresponds Shannon and Weaver entropy), he points out accurately that sequence entropy does not have the properties of physical entropy, and that evolution can be (misleadingly) described as negentropic with respect to thermodynamic entropy. He argues that Brooks and Wiley have used the sequence entropy in their theory. Given a choice between sequence information and physical information, Brooks and Wiley information is certainly closer to sequence information, but as Brooks and Wiley (1985) point out, Wicken ignores the role of initial conditions (historical constraints) which distinguish their stored information from sequence information. As I have shown in the previous section, it is possible to give an account of information which satisfies the requirements of the Brooks-Wiley theory and is also "thermodynamically" entropic.

Wicken (1984) argues that dissipative structures persist by "feeding" on the negentropy of their surroundings, but that Brooks and Wiley have developed a theory which depends only on internal factors, which he finds puzzling, and tries to trace to errors in their use of equations from non-equilibrium thermodynamics. This is a misrepresentation of their views, since they assume that species are maintained by thermodynamic non-equilibrium processes, and then proceed to study how these structures evolve. Wicken has a point that there is something to be understood about the relation of species to their environment. This is a commonplace observation, however. What is really remarkable is that so much of the evolution of species can be understood without looking at the details of environmental interchanges. There is a clear sense in which species are informationally at least strongly analogous to dissipative structures in thermodynamics.

7. Evolution and Physics

I have argued that Brooks and Wiley are correct in viewing their entropy as compatible with thermodynamic entropy. I have also shown that criticisms of their theory stem largely from a failure to appreciate the nature of stored information, which appears only in systems which are historically constrained and contain information systems. A species is determined by its stored information, which has properties which explain evolution and speciation as entropic processes. The concept of stored information also explains how information systems can be built out of progressively lower level systems to form biological hierarchies. This suggests that there is no essential difference between biological systems and physical and chemical systems. In this sense my presentation of the Brooks-Wiley theory is reductionist. There is a further question which might be asked concerning evolution, however, before the question of reduction can be settled: Is evolution a thermodynamic process?

Given the compatibility of biological and thermodynamic entropy, the answer to this question may be affirmative. Against this is the problem that there is no obvious correlate to heat or free energy in biological information systems. The lack of a correlate of heat is not necessarily a problem. Electricity, a very high grade of energy, must be degraded before it shows signs of heat. We can, however, calculate a temperature for electromagnetic radiation in terms of the temperature of heat with which it is in equilibrium. This procedure is obviously impossible in the case of biological information, since equilibrium with heat would destroy the non-equilibrium conditions required to maintain the information. Mechanical energy is perhaps a better analogy, since it too is destroyed if it is in equilibrium with heat. We can measure the equivalent heat content of mechanical energy by measuring the amount of heat given off as its free energy decays. This changes the mechanical energy, of course, but does show the equivalence. Similarly, we could allow biological information to decay, and measure the heat given off. The value would be very small, but there is no reason to believe that it would be zero. The energy requirements of the kidney have been shown to include the amount required to create the information to sort molecules from the blood. Presumably there is also an energy requirement for sorting information structures. The values involved should be calculated, so the energy requirements for storing biological information can be determined.

A generalized theory of evolution will include not only internal informational processing and external constraints, but will also describe the interaction between the two in information theoretic terms. The hierarchy of organization extends not only downwards towards molecules, atoms, and perhaps further, but also upwards to populations, ecosystems and worlds. The circumstances vary according to the organization of the level. The same principles apply throughout.

APPENDIX A Simplified Example

Consider the following sequence of DNA bases:

ATGGTTGGGTCCGTTGCATTTGCCAAAAAGT

The sequence has 30 members. The free information of this sequence, assuming that there are no restrictions on combinations of the four elements A, C, G, and T, is

[A1] $30k\ln(1/p)$, where $p = 1/4$

The value is 60 bits, in standard information units. If we assume that the sequence above is a random aggregate of bases, this is also the value of the bound information.

There are 6 A's, 5 C's, 9 G's and 10 T's in the above sequence. If we assume that its length is fixed by physical or historical constraints, like a chromosome, and that the bases in the sequence are the only ones available to the information system, the number of possible arrays is:

$$[A2] \quad \frac{N!}{N(A)!N(C)!N(G)!N(T)!} = \frac{30!}{6!5!9!10!}$$

which is about 2.3×10^{10} , giving a stored information of about 51 bits for the complete sequence. The difference is due to the fact that the constrained information disallows variation in the number of each base type present. Each appearance of a particular base type decreases the probability of its appearance elsewhere in the sequence. No such constraint applies to the free information.

The bound information of the sequence includes both the information of the constraints and the stored information. The bound information of the constraints is therefore about 9 bits. This value can be ignored in calculations of the stored information. The entropy of the constraints is 51 bits plus any residual entropy of the physical system not included in the entropy of the information system (e.g., due to chemical structures maintaining the system). This is the upper limit of the information system. The lower limit is just the residual entropy. The internal entropy of the array is zero, since it is maximal.

If we consider the chemical information system made up of nucleic acids, amino acids, lipids, and the like, the internal entropy of the array in this system will be non-zero, since it is no longer maximal. The stored information in the chromosome is only part of the total chemical information.

Going in the opposite direction, we might suppose that only the first three codons (ATTGTTGGG) code genetic information, and that the rest of the DNA is non-functional, being only potential genetic information. The internal entropy of the stored genetic information at the chromosomal level is about 38 bits. The stored information is therefore about 13 bits. This can be verified by calculating the probability of each additional unit in the sequence, multiplying them to get the probability of the sequence, and using equation [A1], replacing 30 with 1.

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