A Downward Slope to Greater Diversity

Two phylogeneticists argue that increasing species diversity is an inevitable consequence, not a violation, of the second law of thermodynamics

History indicates that life on earth has followed a progressive, if somewhat uneven, increase in complexity and diversity. And throughout its history there has been a readily demonstrable hierarchy of form, a phylogenetic pattern that is cogent evidence of the fact of evolution. One problem biologists have faced is the apparent contradiction by evolution of the second law of thermodynamics. Systems should decay through time, giving less, not more, order.

One legitimate response to this challenge is that life on earth is an open system with respect to energy and therefore the process of evolution sidesteps the law's demand for increasing disorder with time. A different, and currently contentious, response comes from Edward Wiley and Daniel Brooks, at the Universities of Kansas and British Columbia, respectively. In a paper entitled "Victims of history—a nonequilibrium approach to evolution"* they argue that evolution and the appearance of a hierarchy of life is not only compatible with the second law of thermodynamics but is also an inevitable outcome of the inescapable increase in entropy in the system.

Brooks and Wiley offer their theory as an alternative to neo-Darwinism—no small claim. Neo-Darwinism, they say, is based principally on population genetics, which is a field largely concerned with reversible phenomena and thus employs equilibrium equations. "Equilibrium equations cannot predict the historical hierarchy we see," says Brooks.

Responses to the proposal have been mixed and often quite strong. Some consider the theory to be a brilliant insight that will advance evolutionary biology immeasurably. Others vehemently reject it as an ill-founded attack on neo-Darwinism. Curiously, yet others regard it as nothing but neo-Darwinism translated into incomprehensible form. Still others contend that Brooks and Wiley's use of nonequilibrium thermodynamics is untenable in this context.

The application of nonequilibrium thermodynamics to living systems is still relatively new and controversial. Ilya Prigogine of the University of Texas, who pioneered much of this field, heard Brooks talk about his and Wiley's theory at a seminar earlier this year. "I see how you can do this with molecules," he told Brooks, "but I don't see how you can do it with species. I don't understand the extrapolation." If nonequilibrium thermodynamics *can* be applied to species then the theory might prove to be rather intriguing. A sector of opinion is taking this wait-and-see position.

Prigogine developed nonequilibrium thermodynamics, the thermodynamics of irreversible systems, because he felt that the conceptual framework for physics was inadequate for describing biological systems. He produced the following summary equation to account for entropy production by dissipative systems

$$dS = d_eS + d_iS$$

where dS represents the change in the thermodynamic structure of the system, d_eS the entropy flow of energy in the system, and d_iS the entropy flow of irreversible processes in the system. Brooks and Wiley's task was to see how this might be applied to species.

For evolution to be described by nonequilibrium thermodynamics its constituent parts must be closed or partly closed and must involve irreversible processes. Brooks and Wiley considered three aspects of populations and species in their work: information, which directs species growth and ontogeny (embryological development); cohesion, which results from mating bonds between individuals in a species; and energy flow. As energy is essentially unlimited as far as biological systems are concerned, it does not provide for closure. "In speciation," conclude Brooks and Wiley, "the currency of evolution must be information and cohesion."

Individuals can readily be shown to be closed systems as far as information is concerned, because they do not receive extrinsic genetic instructions. The genetic program, which drives ontogeny, provides the intrinsic constraints characteristic of closed systems.

What of species? "Species cannot be completely closed systems," argue Brooks and Wiley, because "if they were they would be cut off from an outside energy source and life would be impossible. Species cannot be totally open systems because, if 'they' were, there would only be one of 'them.' Thus we may regard species as partly closed systems simply from the observation that there is more than one species."

Another demonstration of closure is the elucidation of self-organizing or anamorphic (complexity generating) properties of the system. "If the system is partly closed, transformational and noncyclic, then each transformation will be historically unique. . . . " This applies to evolution, say Brooks and Wiley, because organisms, which are the components of species, exhibit ontogenies that are transformational and noncylic. Moreover, empirical data show that species may be hierarchically related to each other, sharing some common characters while possessing others that indicate their historical uniqueness. "If evolution were cyclic we would expect no hierarchy of taxa and characters or we would expect a different hierarchy for every set of characters we analyzed."

Intrinsic constraints on evolutionary change and the generation of a hierarchy of historical relationships are the key features of Brooks and Wiley's theory. They describe population genetics as the core of neo-Darwinism and suggest that, by contrast, it is compatible with equilibrium thermodynamics. "This framework does not address the possibility of intrinsic constraints or of irreversible processes in a system. Thus, a unique hierarchy of entities is not predicted by equilibrium thermodynamics." Brooks and Wiley also suggest that equilibrium thermodynamics does not address the possibility of new ordered states. It does not explain speciation.

Many evolutionary biologists, of current and earlier times, have stressed the importance of historical and architectural constraints on evolution. Brooks and Wiley acknowledge this and point out that these biologists have strayed into nonequilibrium thermodynamics without being aware of it.

Once Brooks and Wiley had satisfied themselves that species could be treated as entities in a nonequilibrium system they formulated an equation for evolution, guided by Prigogine's summary equation

$$E = \frac{dS_i + dS_c + dS_e}{dt}$$

where E represents evolution, dS_i stands for the change in entropy levels of information, dS_c for changes in entropy levels for cohesion, and dS_e for changes in

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Systematic Zoology **31**, 1 (1982).

entropy levels of energy. The ($dS_i + dS_c$) term, Brooks and Wiley concluded, is equivalent to Prigogine's term for entropy flow of irreversible processes, d_iS.

"The difference in the equations appears to result from our interest in the origin of diversity, whereas Prigogine and his colleagues have seemed more concerned with the origin of life from abiotic material," explain Brooks and Wiley. With energy assumed as a nonlimiting component, the equation reduces to

$$E = (dS_i + dS_c)/dt$$

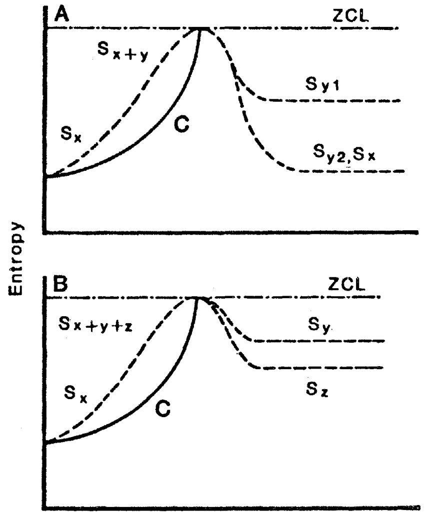
Borrowing notation from the late British embryologist Conrad Waddington, Brooks and Wiley label information as being of two types: canalized information, which is responsible for the sequence of ontogenetic events; and noncanalized information, which directs the production of material used in ontogeny and metabolism in general. Canalized information can be equated with regulatory elements in the genome while noncanalized information represents structural genes. The origin of diversity is suggested to rest principally on alteration of canalized information, a proposition that accords with the view of many evolutionary biologists.

Not every individual is identical, even in its canalized information. The source of this variation might be the expression in some individuals of canalized information quiescent in others. Or it could arise as evolutionary novelties from any one of many different modes of genetic modification. The greater the variation there is within a species, the more complex and disordered it may be said to be.

Cohesion, the subject of the second term in the equation, describes the potential for reproduction between members of the species. If there are no barriers—either genetic, behavioral, or geographical—to reproduction between members of a species, then there is a high degree of cohesion and the species is said to be simple and organized. As barriers arise, the species becomes more disorganized with respect to cohesion.

As information increases in a species, there is a consequent increase in complexity and a higher entropy state, at least initially. This may give rise simply to polymorphism within the population or to geographic variation. With sufficient rise in complexity, cohesion will break down and speciation follows.

The point at which speciation occurs depends in large measure on the geographic distribution of the species. A species which is split into, say, two geographically isolated populations is already disorganized to a considerable extent in terms of cohesion. Speciation in this case would require less change in information than is necessary for speciation in a geographically coherent species. These are known as allopatric and sympatric speciation, respectively. Midway between these two extremes is the case in which two major population concentrations of a species are united by a narrow population bridge. Speciation in this case is termed parapatric.



Dynamics of speciation

As genetic variation accumulates in a species, x, entropy states of cohesion (solid line) and information (dashed line) rise and meet at the zero cohesion line, ZCL. *At this point new species form. In (A) the ancestral species persists; in (B) the ancestral species becomes extinct and two new species remain.*

"This pattern of the relative ease of speciation—allopatric followed by parapatric followed by sympatric—has been intuitively recognized for a very long time," says Brooks. "What we have done is provide a causal explanation."

Although Brooks and Wiley envision intrinsic factors as providing the principal thrust for evolutionary change, extrinsic factors play a part, as the effect of geographic distribution on ease of speciation clearly demonstrates. "Every species lives in the context of its environment," they write, "and this environment provides an additional series of constraints which may speed up or slow down the evolutionary process."

Natural selection, a central feature of neo-Darwinism, is allowed for in Brooks and Wiley's theory, but only as a minor influence. "It can affect survivorship," says Brooks. "It can weed out some of the complexity and so slow down the information decay that results in speciation. It may have a stabilizing effect, but it does not promote speciation. It is not a creative force as many people have suggested."

Competition, another important feature of neo-Darwinism, is again relegated to a minor role in Brooks and Wiley's theory. "We haven't thrown out natural selection and competition," explains Brooks. "They are real, but they are not important in explaining the hierarchy that is surely central to understanding evolution."

What Brooks and Wiley have presented so far in their theory are heuristic formulations, not mathematical proofs. "It remains to be seen whether our work can be mathematically linked with Prigogine's," says Wiley. Meanwhile, they propose ways to move their proposals to a quantitative plane. This involves a marriage between developmental biology and phylogenetics, a particular form of analysis of species' relatedness.

This quantitative analysis requires a yet to be realized ability to measure changes in information and cohesion that are reflected in a species' evolutionary change. As phylogeneticists themselves, Brooks and Wiley are confident that a sufficiently rigorous analysis of relevant characters among groups of related species is possible and that this can be equated with change in entropy states. They are also optimistic that, through the application of information theory, changes in the developmental program may be quantitatively correlated with their morphological effects. From this should flow an assessment of the entropy changes involved in speciation.

"We may postulate a theoretical amount of added information above which . . . speciation will occur," they write. "We would suggest that the threshold values differ between species and, that while we may examine the history of exceeding thresholds by studying the results of history, we cannot predict the future of evolution."

Brooks and Wiley's theory declares species to be "victims of the historical burden they inherit." This being so, they argue, "there should be a correlation between the history of a species and the historical order observed in the characters that organisms exhibit. We observe parts of this order when we observe the ontogeny of individual organisms. We discover this order when we perform phylogenetic analysis and find that such analyses give us a minimum entropy description of the historical course of character evolution." In other words, ontogeny and phylogeny are linked through nonequilibrium evolution—that is, if Brooks and Wiley are right.

—Roger Lewin