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Non-Equilibrium Thermodynamics:

An Alternate Evolutionary Hypothesis

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An alternate evolutionary hypothesis is discussed: non-equilibrium thermodynamics. It is argued that evolution is an axiomatic consequence of organismic information obeying the second law of thermodynamics and is only secondarily connected to natural selection. As entropy increases, the information within a biological system becomes more complex or variable. This informational complexity is shaped or organized through historical, developmental, and environmental (natural selection) constraints. Biological organisms diversify or speciate at bifurcation points as the information within the system becomes too complex and disorganized. These speciation events are entirely stimulated by intrinsic informational disorganization and shaped by the extrinsic environment (in terms of natural selection). Essentially, the entropic drive to randomness underlies the phenomenon of both variation and speciation and is therefore, the ultimate cause of evolution.

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1 Introduction

Although evolution through natural selection has been vastly accepted in the scientific community as a fundamental law of biology, it has been criticized for being an incomplete interpretation of evolutionary processes. Natural selection can not account for 1) the irreversibility of evolution, 2) the complexity-generating or anamorphic tendency of biological systems, and 3) the self-organizing behaviour exhibited by all biological life forms (Wicken, 1979). Consequently, in an attempt to explain these three evolutionary trends, various scientists have strived to make a connection between physical laws and biological systems (Pike, 1929; Blum, 1935).

To elucidate the existence of complex, organized systems and the rules that govern them, an alternative view of biological evolution has been proposed. This unique, but controversial, evolutionary scenario suggests that the 'driving force' behind biological evolution originates in the physical principle of thermodynamics and that natural selection is a microscopic process only secondarily connected. More specifically, proponents of a thermodynamic evolutionary theory consider the ultimate, macroscopic cause of biological evolution to be an axiomatic consequence of organismic ‘information’ obeying the second law of thermodynamics in a non-equilibrium fashion (Wicken, 1979; Wiley and Brooks, 1982). This paper provides an integration and summary of the literature on non-equilibrium thermodynamics and its relationship to evolutionary processes.

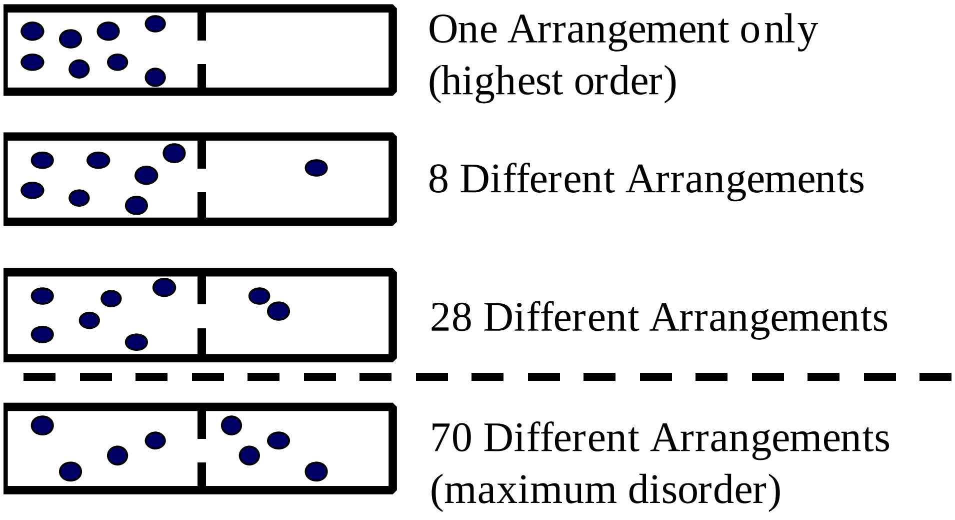
2 Non-Equilibrium Thermodynamics: How It Works

2.1 The 2nd Law

The second law of thermodynamics asserts that if a spontaneous reaction occurs, the reaction moves towards an irreversible state of equilibrium and in the process, becomes increasingly random or disordered. It is this increasing disorder or *entropy* of a system that forces a spontaneous reaction to persist; but, once a system attains maximum entropy or equilibrium, the spontaneous reaction ceases to continue. For example, if a glass of hot liquid is placed in a colder room a flow of heat is spontaneously produced from the cup to the room until it is minimised (or the entropy is maximised) at which point the temperatures are the same (a state of equilibrium) and all flows stop. But, why do spontaneous reactions always move towards ever increasing entropy and ultimately equilibrium?

To solve the equilibrium paradigm of the second law, Ludwig Boltzmann, one of the great theorists of classical thermodynamics, contrived a simple, yet ingenious, thought experiment. Suppose you have a box, bisected down the centre by an imaginary line, and eight distinguishable molecules (Figure 1). How many ways are there to arrange the molecules on the left and right side of the partition?

Figure 1 Boltzmann's thought experiment demonstrating the probability of disorder. (From Capra, 1996 p. 187)



First, all the molecules can be arranged on one side of the box in only one way (highly organized). However, there are eight possible different arrangements if seven molecules are placed on the left side of the box and one molecule is placed on the right. This example illustrates how the number of possible arrangements increases as the differences between the left and right sides of the box becomes smaller, until eventually, the left and right sides equalize (equilibrium) and the number of possible arrangements reaches seventy (highly disorganized) (Capra, 1996). In other words, the entropy of a system is always increasing because it is more probable that a system will be disordered than ordered.

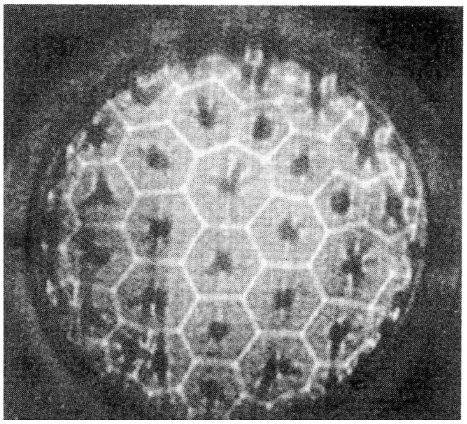
Boltzmann referred to all the possible arrangements of a system as ‘complexions’ and equated them with the concept of order (Capra, 1996). Basically, the more complexions within a system, the further that system is from being ordered. But, this connection between increasing disorder and complexity contradicts the essence of biological organisms; the living world is characterized by increasing order and complexity. As a result, biological systems must be functioning at a state far from equilibrium. This observation has lead to the development of non-equilibrium thermodynamics (Wicken, 1979; Brooks and Wiley, 1982)

2.2 Non-equilibrium Thermodynamics

2.2.1 Dissipation and Self-Organization

How are biological organisms able to self-organize and maintain their life processes far from equilibrium? The answer to this essential question is found in the theory of ‘dissipative structures’ (Capra, 1996). Dissipative structures are open systems, they need a continual input of free energy from the environment in order to maintain the capacity to do ‘work’. It is this continual flux of energy, into and out of a dissipative structure, which leads towards self-organization and ultimately the ability to function at a state of non-equilibrium. A famous example of a self-organizing, dissipative structure is the spontaneous organization of water due to convection (Figure 2).

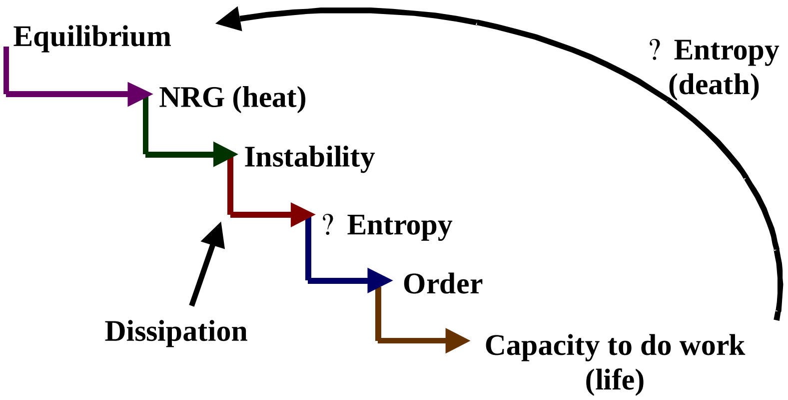
Figure 2: The spontaneous organization of water due to convection: once convection begins and the dissipative structure forms a pattern of hexagonal Bénard cells appear. (From Capra, 1996 p. 87)



If you take a thin layer of water, at uniform temperature, and start heating it from the bottom, a strange ordered structure begins to appear. As the temperature between the bottom and top of the water reaches a critical level, the water begins to move away from an equilibrium state and an instability within the system develops. At this point, convection commences and the dissipative structure forms. As heat is transferred through the liquid, a patterned hexagonal or 'honey combed' shape emerges (Bénard cells) and the capacity to do 'work' is realized (life). But, as soon as the energy source (heat) is taken away, the ordered pattern disappears and the water returns to an equilibrium state (death).

Just like the convection of water, biological organisms are also self-organizing dissipative structures, they take in and give off energy from the environment in order sustain life processes and in doing so function at a state of non-equilibrium (Figure 3). Although biological organisms maintain a state far from equilibrium they are still controlled by the second law of thermodynamics. Like all physiochemical systems, biological systems are always increasing their entropy or complexity due to the overwhelming drive towards equilibrium. But, unlike physiochemical systems, biological systems possess 'information' that permits them to self-replicate and continuously amplify their complexity and organization through time (Brooks and Wiley, 1986).

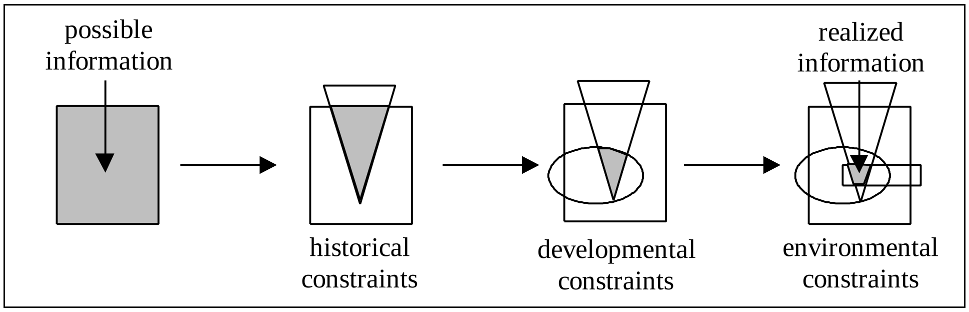
Figure 3 A flow diagram depicting the emergence of a dissipative structure from an equilibrium state.



2.2.2 *Biological Information*

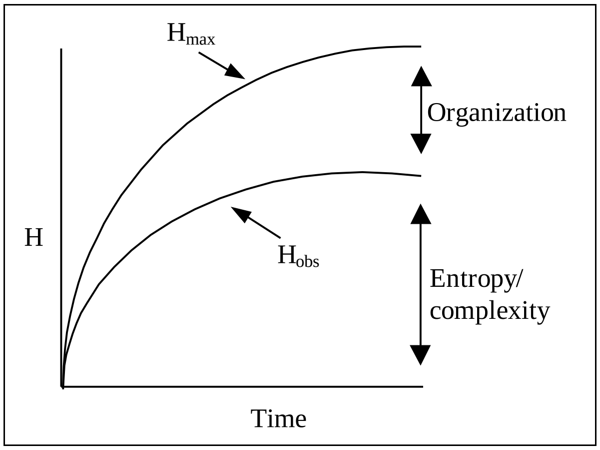
All biological systems contain information in the form of DNA (except for viruses which contain RNA). It is this information that the second law operates on in order to generate biological complexity (variety) and order (Wiley and Brooks, 1982; Brooks and Wiley, 1986). In this sense, biological information can be expressed in terms of an entropic phenomenon; the more information contained within a system, the more entropy that system possesses (i.e., the system is more complex) (Brooks and Cummings, 1984; Brooks and Wiley, 1986). But, if biological evolution is defined by ever increasing complexity through time, how do biological systems remain organized?

Figure 4 A diagrammatic representation of the sequence of constraints operating on information. (Redrawn and modified from Brooks and O'Grady, 1986)



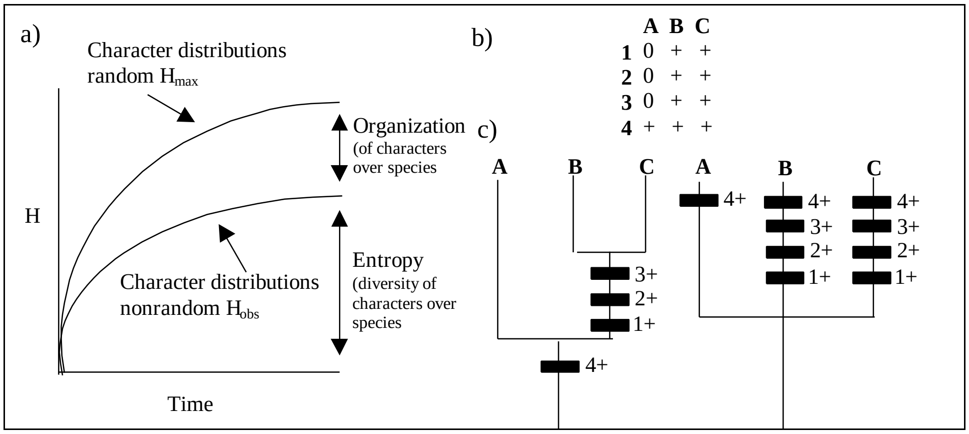
The secrete to biological organization is informational constraints. Biological systems are constrained by there history, development, and environment (Brooks and Wiley, 1986; Brooks et al. 1988; Wiley, 1988) and because of these constraints the number of possible informational arrangements or variations within a population are dramatically decreased (Figure 4). It is the presence of informational constraints which cause biological systems to function at an entropic state (H_{obs}) far less than maximum (H_{max}) (Figure 4).

Figure 5: The relationship between an increasing entropy maximum (Hmax) and the observed entropy (Hobs) of a physical information system over time. The difference is organization while the value of Hobs is a measure of the entropy/complexity of the system. (Redrawn and modifies from Brooks and Wiley, 1986 p.40)



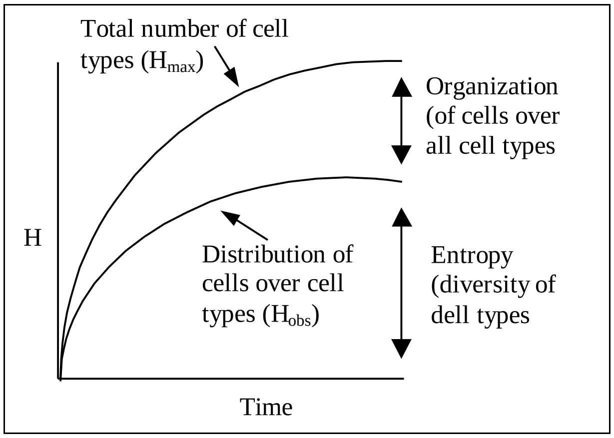
The most important and influential informational constraint is an organism's phylogenetic history because all biological organisms form and evolve from pre-existing, ancestral, life forms (Brooks and Wiley, 1986). This historical constraint is evident when looking at the character distribution on a phylogenetic tree (Figure 6). If biological organisms were not historical slaves, character distribution would be random, maximum entropy would be realized, and biological systems would succumb to equilibrium. What is observed on a phylogenetic tree is a non-random character distribution. This character arrangement causes the observed entropy of the system to be less than maximum and allows biological organisms to become more complex and organized through time.

Figure 6: . *a)*, graph showing the expected relationship between random and actual character distribution over lineages in a clade. *b)*, a character matrix for three species comprising a strictly monophyletic group. *c)*, distribution of character under historical constraints. *Bottom right*, distribution of characters under the assumption that there are no historical constraints. (Redrawn and modifies from Brooks and Wiley, 1986 p.46)



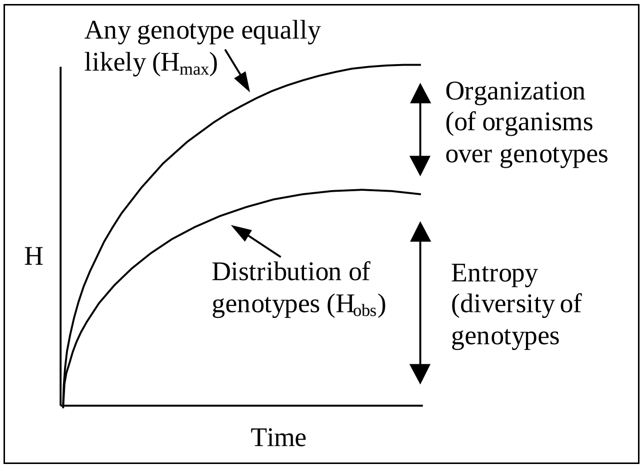
The second most significant informational constraint is an organism's development or ontogeny, which is still ultimately controlled by its history (Brooks and Wiley, 1986; Wiley, 1988). Developmental constraints are easily established by looking at the process of cellular differentiation (Figure 7). Basically, the total number of cell types in an organism increases at a slower rate than the number of cells per cell type; this causes a non-random distribution of cells over cell types. Because the observed distribution of cells is non-random the system functions at an entropic state far less than maximum and the developing organism becomes more complex and organized through time.

Figure 7: The relationship, during growth and development of an organism, between the total number of cell types (H_{max}) and the observed distribution of cells over cell types (H_{obs}) the organization represents the ontogenetic constraints and history of the pattern of development. The entropy represents the complexity of the organism. (From Brooks and Wiley, 1986 p. 44)



The third, and final, informational constraint governing biological organisms is the environment in terms of natural selection (Brooks and Wiley, 1986). If natural selection did not play an intricate role in biological evolution, we would expect all genotypes in a population to be equally likely and we would observe an increase in phenotypes with every evolutionary novelty (Figure 8). But, natural selection, coupled with an organism's historical and developmental limitations, cause the observed distribution of genotypes within a population to be less than maximum. This genotypic lag ultimately forces biological systems to become more complex and organized through time.

Figure 8: The relationship, among an array of organisms, between the diversity of possible genotypes and the observed distribution of organisms over genotypes. If the array is riding the upper line (H_{max}) , then any genotype is as likely as the others. But, not all genotypes are equally likely, therefore, the observed distribution of genotypes is non random (H_{obs}) and the array of organisms become organized. (From Brooks and Wiley, 1986 p. 45)



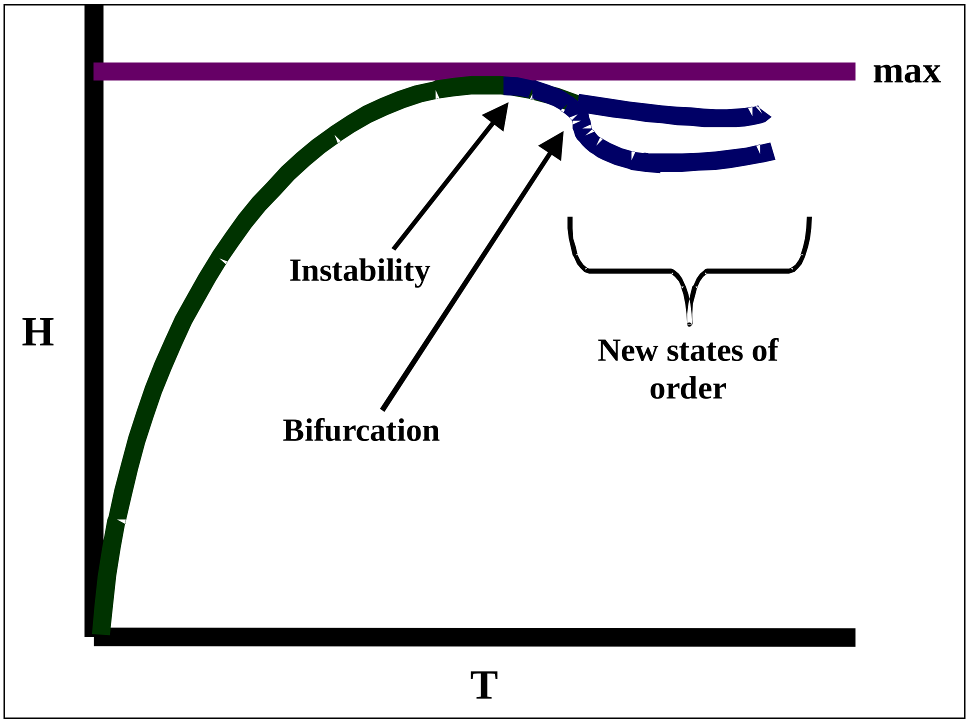
Non-equilibrium thermodynamics describes biological organisms as dissipative systems, continuously ascending the information entropy curve because of intrinsically generated complexity (O'Grady, 1982). But, because this informational complexity is constrained by its history, development, and environment, biological systems are able to organize through time. So, if biological organisms are able to maintain such a stable state of organization, how do they diversify? In other words, how does the second law of thermodynamics explain speciation and extinction?

2.2.3 Speciation and Extinction

From a non-equilibrium thermodynamic perspective, speciation or extinction results when a species' information system becomes disorganized or too complex (to many variants) (Brooks and Wiley, 1982; Wiley and Brooks, 1986). This disorganization is a consequence of the addition of new information (mutations etc.) into the system, a process that naturally occurs as entropy increases. More specifically, speciation or extinction transpires when a species is no longer able to re-organize their information. But, what causes such highly organized systems to become disjointed?

The solution to informational disorganization is found in non-linear dynamics. Non-linear systems are characterized by self-reinforcing feedback loops (Capra, 1996). A feedback loop is a circular sequence of causally united elements in which an initial cause is able to propagate around the links of the loop, so that each element has an effect on the next. Ultimately, feedback loops are able to amplify even the smallest amount of new information into an uncontrolled chaos. It is this chaotic behaviour that can spontaneously lead to the sudden emergence of new states of order.

Figure 9 A diagrammatic representation of an informational bifurcation. As the information within the system becomes to complex, the system is no longer able to remain organized and becomes unstable. This instability within the system stimulates a bifurcation event that leads to new states of order because both descendant branches have less entropy than the ancestral branch.



New states of order are created at informational bifurcations (Figure 9). These bifurcation points are entirely stimulated by intrinsic mechanisms (informational entropy) and are highly unpredictable, irreversible, and extremely sensitive to change (Wicken, 1983, 1986,1988; Capra, 1996). At each bifurcation point the system is given two choices, the branch taken or its mirror image. The system 'chooses' a branch (or becomes extinct) based on the current extrinsic conditions by means of natural selection. Therefore, after a branch has been selected the system cannot subsequently jump to its mirror image.

After the bifurcation event, the system spontaneously begins to re-organize. Re-organization occurs because each descendant branch that was produced by the bifurcation has less entropy or information than its ancestral branch. This loss in entropy does not break the second law of thermodynamics because both descendant branches have a combined entropy equal to or higher than the ancestral branch (Wiley and Brooks, 1982). In this way, biological systems evolve to form a bifurcation tree of hierarchical relationships.

2.3 A Review

Non-equilibrium thermodynamics is a special case of the second law of thermodynamics that is used to explain the existence of self-replicating dissipative structures. It describes how biological systems become more complex and organized through time as the result of, not at the expense of, increasing entropy. More specifically, non-equilibrium thermodynamics applies the concept of entropy to the formation of informational complexity and describes how it is shaped or organized by historical, developmental, and environmental constraints. Furthermore, non-equilibrium thermodynamics describes how biological systems diversify at bifurcation points if the information becomes disorganized; these bifurcation events are ultimately stimulated by intrinsic informational disorganization and shaped by the extrinsic environment (in terms of natural selection).

3 Non-Equilibrium Thermodynamics: It Makes Sense!

Proponents of non-equilibrium thermodynamics view natural selection as a secondary cause of evolution. In other words, natural selection only tells us 'how' evolution occurs, not 'why' it occurs (Wicken, 1980, 1985). To understand 'why' evolution takes place, non-equilibrium theorists have tried to reduce evolution to a general physical law: the second law of thermodynamics. But, does this alternate scenario of evolution make sense?

Biological systems exist as an intricate part of the universe; because of this, it seems reasonable to conclude that evolution, like all natural processes, rests ultimately on physical laws. All physical laws, with one exception, fail to differentiate between the two directions of time. The one exception is the second law of thermodynamics, which asserts that all physical processes generate entropy. Therefore, it seems logical that evolution, which more than any other natural phenomenon distinguishes between the direction of the past and the direction of the future, could ultimately derive its 'arrow' from the second law (Layzer, 1987).

Making this reasonable connection of asymmetry between biological processes and the second law of thermodynamics permits the non-equilibrium hypothesis to attach the concept of entropy to evolution. More specifically, we are able to analyze the addition of information into biological systems as an entropic phenomenon. Consequently, non-equilibrium thermodynamics is able to provide us with the rationality to explain why biological systems become more complex and organized through time, two significant characteristics of evolution natural selection fails to account for.

Darwin recognized that it was the generation of complexity or variation in biological systems that permitted evolution to transpire (Darwin, 1859). In other words, entropy is what produces the variability or complexity that natural selection 'selects'. In this sense, natural selection can be viewed, not as the fundamental law of biology, but as an auxiliary law that acts to constrain (organize) the possible variants produced by the second law of thermodynamics.

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