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Kahn Liberal Arts Institute Working Paper

# TRANSCENDENTAL THERMODYNAMICS

Richard E. Morel  
George Fleck

*Created in conjunction with the Kahn Liberal Arts Institute project Liquid Worlds (January, 2010)*



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**Abstract:**

Thermodynamics is often viewed as a narrow, introspective discipline, trapped by its origins in the 18th and 19th centuries. By dramatic contrast, we show that the Fourth Law of Thermodynamics provides explanations and interpretations of all natural events, extending across artificial boundaries of traditional academic disciplines. The Fourth Law of Thermodynamics states that far-from-equilibrium systems increase entropy at the maximum rate available to them. This broadly inclusive paradigm applies to systems from molecules, to organisms, to the biosphere. The Fourth Law is the Law of Evolution. All systems that communicate with their environment exhibit self-organization and self-optimization, enabling the emergence and the evolution of life as a sustained optimization of entropy increase.

**Keywords:** amoeba, biodiversity, butterfly, conservation, dissipative, earthworm, ecosystem, economics, energy, entropy, environment, equilibrium, evolution, fourth law, interdisciplinary, metabolism, organize, sustainability, system, thermodynamics, termite, yeast.

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# Transcendental Thermodynamics

Richard E. Morel and George Fleck

## Introduction

Michael Faraday (1791-1867) chose the topic “The Chemical History of a Candle” for a series of six demonstration lectures, which he delivered at the Royal Academy of Great Britain during the Christmas holidays 1859-1860. He opened his first lecture with the assertion: “There is not a law under which any part of this universe is governed which does not come into play and is touched upon in these phenomena. There is no better, there is no more open door by which you can enter into the study of natural philosophy than by considering the physical phenomena of a candle.”<sup>1</sup> We follow Faraday’s lead as we introduce the subjects of self-organization and self-optimization by looking at a familiar candle flame in a new light, in the context of the Fourth Law of Thermodynamics.<sup>2</sup>

The dynamic, self-generated organization of a flame is amazingly reproducible if the flame is burning in surroundings whose attributes are consistent with the stability range of the flame. If you blow hard enough, you can blow the flame out... but if you blow gently, the flame may be extinguished and then reignite, spontaneously reestablishing its organized structure. Humans have long marveled at this remarkable self-organization, using phrases such as “living fire” to describe flames. Faraday elaborated on the self-optimization of flames: “I cannot imagine a more beautiful example than the condition of adjustment under which a candle makes one part subserve to the other to the very end of its action. A combustible thing like that, burning away gradually, never being intruded upon by the flame, is a very beautiful sight; especially when you come to learn what a vigorous thing flame is—what power it has of destroying the wax itself when it gets hold of it, and of disturbing its proper form if it comes only too near.”

Earlier, in 1783, Antoine Laurent Lavoisier (1743-1794) and Pierre-Simon, marquis de Laplace (1749-1827) had conducted calorimetric experiments in which they compared the heat produced by a living guinea pig with heat produced by a burning candle. They concluded that animal respiration is combustion. A candle flame became their metaphor for animal metabolism. Faraday concluded his sixth Christmas lecture by amplifying the metaphor: “Thus, you see the analogy between respiration and combustion is rendered still more beautiful and striking.” For us, the self-sustaining candle flame is a faithful metaphor for self-organizing systems, a metaphor for dissipative structures, and a metaphor for the application of the Fourth Law of Thermodynamics to self-optimization in a wide range of systems.

It was in the spirit of the scientific revolution, of which Lavoisier, Laplace, and Faraday were central figures, that transcendentalist Ralph Waldo Emerson (1803–1882) wrote in the introduction to his 1836 essay *Nature*: “All science has one aim, namely, to find a theory of nature.” And 92 pages later, he concluded with “So shall we come to look at the world with new eyes.”<sup>3</sup> In our paper, we look at both the microscopic world and the macroscopic world with new eyes, with a 21<sup>st</sup>-century thermodynamic transcendent vision.

## Self-Organizing Systems

Nature is insistent and consistent in creating organized forms and structures.

Self-organization pervades the entire material world. Chemistry is the study of self-organized systems of nuclei and electrons. In the absence of external forces, a collection of electrons and nuclei spontaneously organizes itself into spherically symmetrical atoms with predictable structures and properties. In favorable environments, these atoms spontaneously organize themselves into molecules. Not every conceivable geometrical arrangement of atoms occurs; bonding patterns reveal nature’s insistence on order, regularity, and functional form, and on nature’s predilection for atomic and molecular symmetry. The molecules, under appropriate circumstances, spontaneously organize themselves into liquids, crystals, or other orderly condensed states of matter.

Although chemists may take personal credit for their syntheses of compounds, a chemist’s actual role in directing chemical change is to provide an environment in which self-organization will occur. In many cases, a chemist needs to be creative in arranging conditions that minimize impediments to formation of a desired compound, and that maximize impediments to undesired “side reactions.” In routine syntheses and routine crystallizations, self-organization may seem ordinary and expected. Although neither mysterious nor miraculous to seasoned chemists, such phenomena often amaze the uninitiated. These phenomena are the ways of our world and of our universe.

A collection that contains only one oxygen nucleus, two hydrogen nuclei, and ten electrons spontaneously organizes itself into a dynamic system called a water molecule. The H–O internuclear distance in gaseous water is reliably 0.96 Å, and the H–O–H angle formed by the three nuclei is reliably 104.5°. The symmetry of the electron distribution is the same as the symmetry of the arrangement of nuclei. A water molecule is really a very complex system, a challenge to characterize but far from chaotic. It consistently and reliably self-organizes itself without external intervention. An isolated water molecule is the same as every other isolated water molecule, with the same internal structure, the same properties, and the same chemical reactivity.

Many compounds contain just carbon nuclei, hydrogen nuclei, and electrons. In each of these hydrocarbons, the collection of nuclei and electrons self-organizes into individual molecules with consistent and reliable symmetries, internuclear distances, and “bond angles.” A playful sculptor could fashion many hypothetical models of the hydrocarbon methane, CH<sub>4</sub>, but the methane of nature spontaneously organizes itself only into molecules with tetrahedral symmetry and equal distances between pairs of hydrogen and carbon nuclei.

So it is with every chemical compound. Because every molecule of a particular compound is organized in the same way, chemistry has the predictive capability that permits analysis of substances, synthesis of new compounds, and elucidation of a vast array of chemical reactions. It should come as no surprise that systems composed of self-organized atoms and molecules should themselves self-organize. We shall examine some of these systems, and comment on transcendent implications of their self-organization.

## Dissipative Systems

A flame is a self-organized system that facilitates controlled oxidation. A living organism is also a self-organized system that facilitates controlled oxidation. Flame and organism alike organize to create entropy faster than their immediate surroundings would create it without their presence. Systems that increase the rate of entropy production are called *dissipative systems*. Every living system is a dissipative system.

The Fourth Law of Thermodynamics is a macroscopic rationalization for the ordered structure of a candle flame. A candle flame is a three-dimensional dissipative structure involving coupled flows of energy and matter. In a more complex manner, a living organism is a dissipative structure that efficiently and consistently maintains the rate at which entropy is produced by its metabolism. Unlike a burning candle, a living organism preserves its identity and integrity as it constantly manages the chemical turnover and repair of its components.

It may seem a long leap in dissipation from Faraday's candle flame to a living system. It may seem a longer leap in self-organization from an atom to a living organism. So, instead of giant steps, let us examine a series of "simple" self-organized, dissipative systems that illustrate how common (and often overlooked) phenomena can be incorporated into a Fourth Law worldview in which systems are constantly and consistently optimizing their capability to produce entropy. In Emerson's words, we shall "look at the world with new eyes."

We begin at the breakfast table. The thermal relaxation of an initially hot cup of coffee can be described simply as heat flow from a system whose interior structure is ignored. Treated only as an uncomplicated process, the cooling of a cup of coffee can be investigated by measuring temperature at a single point in the system as a function of time. This straightforward experiment, with thermometer readings recorded at a series of times, masks significant dynamic aspects of the interior of the cup of coffee.

Cooling of a cup of coffee is more complicated and much more interesting. Meteorologist Vincent Joseph Schaefer noted: "When a cup is filled to the brim with black coffee (instant or otherwise) which is close to boiling and is viewed with good illumination, the first thing noticed is that the surface of the steaming coffee displays an irregular cellular pattern. The cells, in polygonal array, show cross sections of approximately 1 to 3 cm and appear to consist of dusty white areas outlined by narrow dark lines. These visible cells mark areas of rising columns of hot water, and the dark lines mark the region where the spreading, slightly cooled liquid is descending into the body of the coffee to form what are called Bénard cells."<sup>4</sup> You cannot see the *heat* flow, but you can observe the effect of that flow. From the viewpoint of an observer, the surface patterns are visual messages that reveal otherwise invisible internal fluid circulation.

Physicist Jearl Walker described<sup>5</sup> dissipative phenomena when cool cream is added slowly to hot coffee. Simultaneous thermal gradients and concentration gradients are immediately established and made visible; flows of both heat and matter occur and interact. Although you cannot see the *heat* flow, you can observe the effect of coupled flows by watching spiraling patterns of cream within the coffee. The cream makes the flows seeable, as well as contributing to the flows.

Each pattern of swirls is created by complex superpositions of simultaneous thermal and material flows. The qualitative features of the patterns are predictable, but the precise geometrical form of the swirls depends on initial conditions in ways that resist prediction. Some observers might describe the coffee-cream system as *chaotic*, because the patterns created are so dependent on subtle details of initial conditions. Other

observers might describe the coffee-cream system as an example of a self-organized dissipative structure that increases the rate of entropy production. This is a dynamic structure that stirs the liquid and increases the rate of attainment of thermal equilibrium between the initially hot interior and the cooler surface. It is also a structure that mixes cream and coffee, thereby increasing the rate of attainment of uniform composition. In both cases, the structure increases the rate of entropy production in the system. Jearl Walker suggested that experiments in a coffee cup can serve as models for large-scale atmospheric vortex motion, including the motion that occurs in dust devils, tornadoes, firestorms, and hurricanes. Each of these meteorological phenomena is a dissipative structure.

The self-organization phenomena described by Vincent Schaefer and by Jearl Walker are examples of Stefan flow, named for the Austrian mathematical physicist and poet Jožef Stefan (1835–1893), who investigated dynamics of many multi-species systems. Stefan flow occurs when chemical species are transported in a fluid because of concentration changes at an interface. Such processes as evaporation, condensation, chemical reaction, adsorption, and absorption can induce Stefan flow. Stefan flow occurs in a wide variety of seemingly unrelated systems, creating dissipative structures and increasing the rate of entropy creation.

Surface chemist Irving Langmuir (1881-1957; Nobel laureate 1932) conducted experiments at Lake George, New York, during the years 1928 and 1929. He reported formation of parallel streaks (windrows) on the lake surface in the direction of a prevailing wind. “[T]he water between two adjacent streaks forms a pair of vortices: The water on the right-hand side of the vertical plane halfway between the streaks has a clockwise rotation (right helix), that on the left a counter clockwise rotation (left helix).”<sup>6</sup> Formation of this pattern of helices requires both a steady wind and a temperature gradient near the water surface. He had become intrigued by this phenomenon after observing windrows of drifting seaweed in the Sargasso Sea in 1927. This Langmuir circulation—a wind-driven helical circulation in an ocean or in a lake—continues to generate interest among theorists interested in spontaneous pattern formation, as well as engineers in the field of fluid mechanics. Langmuir circulation is an aspect of the complex way in which thermal imbalances in the waters and the atmospheres of the Earth result in stirrings of ocean currents and in weather patterns. These flows in oceans, lakes, and ponds result in transport of biological organisms, bubbles, suspended solids, and dissolved substances.

Theodore von Kármán (Szöllöskislaki Kármán Tódor, 1881-1963, Hungarian physicist who emigrated to the United States in 1930 to be director of the Guggenheim Aeronautical Laboratory at the California Institute of Technology, and who in 1944 was cofounder of the CalTech Jet Propulsion Laboratory) described “cloud streets” formed in the atmosphere. Warm air rises on one side, the air cools, water vapor condenses to form a cloud, and the air sinks on the other side. These convection “rolls” can line up next to each other, creating lines (streets) of clouds, and repeating patterns of swirling vortices.

## **Living Systems**

Cells are the fundamental organized functional units of living systems, just as atoms and molecules are the ordered units of chemistry. Only in the last hundred years, have scientists succeeded in elucidating any molecular reaction mechanisms within living cells. Progress in biochemical research has taken advantage of the fact that many molecules of metabolic importance within living systems have properties that can be studied outside living systems—studied in glass beakers and flasks. Each enzyme molecule is a biological catalyst, a protein that increases the rate of a chemical reaction. The mode of catalysis can often be investigated quantitatively by extracting enzyme molecules from dead cells, and then adding those enzyme

molecules to a laboratory-prepared reaction mixture. Insofar as the enzyme demonstrates the same catalytic role *in vitro* as *in vivo*, such experiments can give insight into metabolism in a living system.

It is an open question whether a “complete” chemical description of separated components of a cell could yield understanding of the salient properties of that island of life. Such a description would involve vast numbers of individual chemical reactions and molecular interactions in each cell. Such a description would be enormously complicated, necessarily three-dimensional, and constantly changing. Molecular biology is nowhere near such a description. A transcendent first principle is needed to interpret the complexity of even the simplest living system. The Fourth Law is a parsimonious enabling principle that guides both the specialized researcher and the interested layperson in appreciating *why* islands of life occur, *why* they persist, and *why* they evolve. Whereas each non-living dissipative structure can be described as a tune with only one note (*maximization*), living dissipative structures are entropic symphonies at the cellular level and beyond. These symphonies are composed with the grand theme of *optimization*.

With organized cells and cellular complexity come enormous opportunities for systems to move transactions at rates unseen in non-living systems. From a thermodynamic perspective, cells are dissipative systems that combine *form* (structured matter) and *function* (energy transactions) in ways that optimize the production of entropy. The structurally simplest living cells are prokaryotic cells, cells without a nucleus. We shall look first at a selection of prokaryotic organisms as open systems.

Prokaryotic cyanobacteria were among the first successful life forms. The fossil record reveals evidence of cyanobacteria in 3.5 billion-year-old rocks of Western Australia. Cyanobacteria live today in a vast range of habitats, including fresh water and seawater, damp soil, and even deserts. These “simple” organisms are open systems that can capture energy from sunlight and use that energy to reduce nitrogen and carbon, and to produce molecular oxygen. This photosynthetic capability of transducing radiant energy into metabolically available chemical compounds is essential for sustaining life.

## Photosynthesis

Harvesting incident light by a cyanobacterium occurs within the cell in structures called thylakoid membranes. A thylakoid membrane contains colored molecules that absorb visible and near-infrared light. These colored molecules, often called antenna pigments, include carotenoids, chlorophylls, and phycobilins. Light absorption occurs when a single molecule interacts with a single photon of light. The photon—a package of energy—activates the molecule to a high electronic energy level. Decrease in entropy accompanies this absorption of radiant energy. Dutch biophysicist Louis Nico Marie Duysens was one of the first scientists to investigate this fundamental aspect of the thermodynamics of photosynthesis.<sup>7</sup> Following the lead of Duysens, biophysicists during the 1960s investigated and wrote about the continuous influx of “negative entropy” from the Sun into photosynthetic systems.<sup>8</sup> With a continually replenished supply of negative entropy, a photosynthetic system proceeds to support life via a host of processes that individually and collectively optimize entropy production.

In the thylakoid membranes of cyanobacteria, antenna pigments bond chemically to (or closely associate with) clusters of specialized reactive molecules, including proteins and carbohydrates. Absorption of light by a pigment molecule initiates a cascade of energy-transfer and electron-transfer processes, facilitated by specific enzyme catalysts that accomplish two critical chemical tasks: nicotinamide adenine dinucleotide phosphate (NADP<sup>+</sup>) is reduced, and adenosine diphosphate (ADP) reacts with phosphate to generate adenosine triphosphate (ATP).<sup>9</sup>

In a salient economic analogy, it is often said that living organisms use ATP as their primary energy currency, facilitating their entropic transactions. The  $\text{ATP} \rightarrow \text{ADP}$  conversion is implicated in multi-step, enzyme-catalyzed syntheses of most molecules that comprise living systems. The reverse  $\text{ADP} \rightarrow \text{ATP}$  conversion is essential for the many different chemical reactions that result in utilization of nutrients and in utilization of energy-storage reserves by living organisms. Among the many chemical products of cyanobacterial photosynthesis and subsequent metabolism are carbohydrates and nitrogenous compounds, leading to many examples of nutritional symbiosis where non-photosynthetic bacteria (as well as multicellular organisms) utilize these compounds, released into their immediate environment by bacteria, as a primary energy source.<sup>10</sup> Nutrients can also be exchanged when a cyanobacterium cell is engulfed and chemically digested (phagocytosed) by another organism.

The individual prokaryotic cells and the community of symbiotic cells are open systems that have self-organized. These islands of life use energy captured from the sun to fuel metabolism, thereby increasing entropy at the optimum rates available to them. This transduction is in precise agreement with the predictions of the Fourth Law.

### **Growth of a Bacterial Colony**

Prokaryotic bacteria have been enormously successful in colonizing and exploiting ecological niches. Their spreading out and diversifying, in conformity with the Fourth Law, is a consequence of the ability of each individual cell to reproduce by binary fission, by splitting into two replicate cells. Unless there is mutation during the fission, the replicate cells are genetically identical. Growth of a bacterial colony is the result of successive fissions of many cells.

The first step in fission is duplication of the macromolecular deoxyribonucleic acid (DNA) that contains the cell's chemically coded genetic information. The cell elongates, and the duplicate DNA strands move to opposite ends of the cell. In the midsection, the cell membrane grows inwards, splitting the cell into two daughter cells. Each cell is an independent organism with its own DNA.

The classical description of bacterial growth involves three phases. When a population of bacteria is introduced into a high-nutrient environment, there is a period of slow growth of the population combined with high rates of biosynthesis within individual cells: additional molecules of the enzymes necessary for rapid utilization of the nutrients are synthesized. Growth in the second phase is exponential. During the exponential phase, nutrients are metabolized and entropy is produced at the optimal rate consistent with increasing the population of viable cells. The final phase of growth is a stationary phase, caused by nutrient depletion. The cells reduce their metabolic activity and consume nonessential cellular proteins. The stationary phase is a transition from rapid growth to a stress-response state, with increased expression of particular genes that are involved in repair, antioxidant metabolism, and nutrient transport. The Fourth Law predicts that a cell, when it finds itself in the new environment, will spontaneously self-organize to be able to create entropy as rapidly as possible. The Fourth Law predicts that a cell that has transformed itself into an efficient processor of nutrients will produce progeny as rapidly as possible to increase the overall rate of entropy production. The Fourth Law predicts that a colony of cells, confronted with depleted nutrients, will spontaneously reorganize its metabolic patterns in ways that preserve the colony as an optimizer of entropy production for as long as possible.

The growth of the marine bacterium *Pseudomonas natriegens* has been studied in the laboratory.<sup>11</sup> In its exponential growth phase, observed in the experimental environment, the number of *P. natriegens* cells doubled every 9.8 minutes. If this growth rate were sustained, then a single cell would have more than a million progeny after twenty doubling times (3.3 hours). This exponential growth cannot be sustained if most

of the cells are being crowded, surrounded by other cells that are competing for the same nutrient supply. The impediment to continued population growth is the unavailability of sufficient nutrients for individual cells. The Fourth Law predicts the genesis of controls on nutrient consumption, controls that preserve the overall entropic system when the resource geometry of the environment is incompatible with population increase.

During exponential population growth, most daughter cells will be exact genetic copies. However, because of the vast number of created new cells, there will be some mistakes. Genetic changes in bacterial genomes may come from random spontaneous mutation during replication. Another source of genetic changes is “stress-directed mutation,” where genes involved in a particular growth-limiting process have an increased mutation rate.<sup>12</sup> Whatever the source of new genetic diversity, the Fourth Law predicts that the community will seize every opportunity to optimize entropy production by appropriate selection of survivor cells.

The community of prokaryotes has already shown, in one of the most dramatic events in geologic history, that it could seize opportunities to optimize entropy production. This epic event, which defines the boundary between the Cretaceous and Tertiary periods, was the greatest mass extinction of living species for which we have evidence. The “age of dinosaurs” came to a sudden end. It has been estimated<sup>13</sup> that “up to 95 percent of marine species and 85 percent of those on land went extinct.” Prokaryotes not only survived the cataclysm, but they may have “played a leading role in the extinctions.” In ways that are still being investigated by geochemists and biologists, bacteria and other prokaryotes were performers in a Fourth Law drama. They organized themselves to occupy abandoned ecological niches and to create new niches.

## Lac Operon System

Consider the short-term (homeostatic) and the long-term (evolutionary) dissipative and systemic entrenchment (the “entropic sense”) of the lac operon system in the prokaryotic bacterium *Escherichia coli*. The system has a cosmic elegance, demonstrating optimized entropy production in this unicellular organism. The cellular architecture of *E. coli* is ensconced genetically with the ability to maintain homeostasis in a changing environment. Over evolutionary time, this organism has developed the ability to cope both with the Fourth Law requirement that entropy production be optimized, and with the ecological reality of variable external glucose resources.

In *E. coli*, a segment of DNA that codes for the lactose dissipative system is incorporated into the genome of the bacterium. This segment—the lac operon—contains adjacent operator and regulatory genes. The lac operon is a back-up system that allows for survival of its possessor when a preferred resource becomes scarce or absent. In this case, the preferred resource is glucose. Two of the enzymes in the code—permease and  $\beta$ -galactosidase—are directly involved in the transport and catabolism of lactose, a dimeric sugar composed of the simple sugars glucose and galactose. Permease is a membrane protein that actively transports lactose into the cell;  $\beta$ -galactosidase hydrolyzes lactose into its glucose and galactose components.

The glycolytic cycle is a series of metabolic reactions that break down glucose to produce pyruvic acid or lactic acid, releasing energy for the cell in the form of adenosine triphosphate (ATP). When glucose is present in its environment, *E. coli* turns down the lactose system to a very low level of activity, even if lactose is present. The system seizes the most expeditious route for maximizing the entropy-making capacity of the cell. The Fourth Law predicts that glucose will be the metabolite of choice in a glucose-rich environment when the availability of these two nutrients fluctuates. In this environment, moving free glucose

into the glycolytic cycle is the most efficient means of extracting energy from the surroundings and increasing entropy.

Metabolizing glucose is the most expeditious route to optimizing entropy increases, consistent with the cell's overall potential and consistent with survival of the *E. coli* strain over evolutionary time. Turning on "reserve systems" would be the equivalent of "not saving for a rainy day." The Fourth Law exactly predicts using the best first option, and holding a second choice in reserve. Glucose can move directly into the glycolytic pathway. Alternatively, lactose must be hydrolyzed into glucose and galactose, and then the galactose must be metabolically restructured into glucose. However, if glucose becomes depleted and lactose is present, the bacterium quickly turns on the lactose system and thereby maintains optimized entropy production under new conditions of availability.

Depletion of glucose in the universe of a bacterial cell is as catastrophic to the bacterium as is an asteroid's collision with the Earth to our planet. However, the *E. coli* genetic system has incorporated genetic codes that provide a "micro-pre-diversification" that has been set by the Fourth Law.

Micro-pre-diversification is a most interesting consideration. Even after massive extinctions on Earth, a huge proportion of established genetic and entropic capacity remained in surviving species. Just as the lactose system provides for survival, life after major extinctions built on life's remaining and memorized entropic capacity. Life diversified toward refashioning a maximized entropic dynamic. In this entropically evolved and managed lac operon system, an "ace up the sleeve" exists. A repressor protein, bound to the operon of the DNA segment that codes for the enzymes, detaches when lactose binds to it. Two genes that code for the enzymes that process lactose—permease and  $\beta$ -galactosidase—are then switched on. They are transcribed and translated.

Permease accelerates the movement of lactose across the cell's plasma membrane to its dissipative partner,  $\beta$ -galactosidase, which cleaves lactose into glucose and galactose. Glucose is then free to move into the glycolytic cycle. The galactose can be converted to glucose by four enzyme-catalyzed reactions that represent yet another closely allied dissipative system. In *E. coli*, the lac dissipative system is poised to seize specific opportunities to create entropy, as the availability of nutrients oscillates. The Fourth Law predicts that the lac operon system would act as a biologically adaptive system, an entropic alternative to glucose metabolism.

If entropy production is to be maximized, then why don't both systems operate simultaneously when both glucose and lactose are available? Presumably, the lac operon system arose in environments where glucose and lactose were at times both abundant. At other times, one or the other became depleted. Consuming both glucose and lactose simultaneously when both were present in abundance might leave behind only very low levels of lactose when glucose levels were depleted. *E. coli* cells that consumed low entropy resources without control would give way, over time, to *E. coli* cells that more effectively managed their entropic repertoire. Since the lac operon system did not evolve in an ecological vacuum, the Fourth Law requires that *E. coli* contain this survival strategy in its entropic memory.

The Fourth Law predicts controls on consumption, controls that preserve the overall entropic system in the broad context of a surrounding, living universe that contains competing entropic systems. A living *E. coli* cell is a dissipative system composed of coordinated and managed dissipative capacities that greatly enhance and maintain a consistent level entropy production. Each *E. coli* cell contains a pliable, regulatable database (a genome) that allows it to adjust to changing opportunities for processing low-entropy matter. These adjustments are directed at maintaining a maximum flow of entropy within the context of a homeostatically balanced organism and its evolutionary experience with its surroundings. The rate of entropy production in

this real world tends to remain at a maximum, consistent with the organism's evolutionary experience and with competitive interplay.

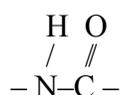
## Biocatalysis

A prokaryotic cell contains water, many different kinds of low-molecular-weight molecules, and many different kinds of high-molecular-weight macromolecules. Among the low-molecular-weight molecules are carboxylic acids, nitrogenous bases, sugars, vitamins, lipids, steroids, and phosphate esters. Among the macromolecules are carbohydrates, proteins, and nucleic acids.

If an investigator were to prepare a sterile mixture by stirring together (in an ordinary glass laboratory flask) chemically pure samples of the known low-molecular-weight cell components with water, in the naturally-occurring proportions, the result would certainly not be a living system. It would not be a solution, because several of the compounds are only sparingly soluble in water. After a few initial chemical interactions, and maybe some bubbling, the result would be a *stranded system*, a mixture unlikely to undergo spontaneously all its potential reactions within the lifetime of the investigator. A charitable observer might call the mixture an unseemly mess, but an accurate description would probably have a barnyard flavor.

That artificial system would be stranded because of several impediments. For life-like chemical reactions to occur, the *scale* must be close to the size of a cell, not the scale of laboratory glassware. There must be intricate *organization* at the molecular level. There must be *compartmentalization*, including membranes and a demarcation structure that separates (but does not isolate) the system from its surroundings. There must be both aqueous (water-like) regions and non-aqueous (fat-like) regions, separate yet contiguous. Critically important, there must be a full complement of *biocatalysts* to regulate rates of specific chemical reactions. Spatial organization of these biocatalysts is undoubtedly essential.

Most biocatalysts are enzymes, protein molecules that are linear polymers of amino acids, folded into functional geometries. Twenty different amino acids are found in proteins, each amino acid molecule containing at least one amino group ( $-\text{NH}_2$ ) and at least one carboxylic acid group ( $-\text{COOH}$ ). The usual chemical linkage between two amino acids is an amide bond



formed between the amino group of one amino acid and the carboxyl group of the other amino acid. (A water molecule is released when the amide bond is formed.) The small enzyme *4-oxalocrotonate tautomerase* is a linear polymer of 62 amino acids.<sup>14</sup> Some larger enzymes contain more than 2,500 amino acids. The catalytic properties of an enzyme molecule depend on the particular amino acids, the sequence in which they are joined together, and the three-dimensional folding geometry of the resulting polymer chain. In many cases, only a half dozen amino acids comprise the catalytic region (the *active site*) of the enzyme.

Enzymes function in a living cell to increase entropy production. Many chemists were surprised to learn that the “instantaneous reaction”



(half-life about 5 seconds) is not fast enough to satisfy the requirements of human respiration. *Homo sapiens* has an enzyme (carbonic anhydrase) to increase that reaction rate.<sup>15</sup> At the extreme opposite of the reaction-

rate spectrum, the extraordinarily slow hydrolysis of the phosphomonoester dianion has a half-life of  $1.1 \times 10^{12}$  years, a hundred times longer than the lifetime of the universe; enzymatic catalysis permits this reaction to proceed with a half-life of milliseconds.<sup>16</sup> In *H. sapiens*, there is an enzyme for essentially every chemical reaction needed for our metabolism. For most reactions, the enzyme is specific for that reaction alone. Without enzymes, cells would be stranded chemical systems, unable to execute even minimal biochemistry. With the full complement of enzymes, cells have the metabolic capability to increase entropy at rates fast enough for the cells to be alive, to function, and to survive.

## Eukaryotic Cells

Prokaryotic cells are spatially organized, often with metabolic functions localized in identifiable regions (microcompartments) of a cell. Eukaryotic cells have enclosed compartments (organelles), including vacuoles, the endoplasmic reticulum, the Golgi bodies, and especially the nucleus. The cell nucleus, visible with a light microscope, is a distinctive characteristic of eukaryotes. With the advent of organelles, eukaryotic cells opened a window to further dimensions of entropic layering. Each organelle is an island of life *within* an island of life. By compartmentalizing metabolic processes, each eukaryotic cell opened new avenues for exploring and exploiting its own sustained far-from-equilibrium universe. Eukaryotic cells finessed the need to rely on rates of diffusion for internal transport and distribution of vital goods and services. A single eukaryotic cell can be large, and compartmentalization allows transport of materials through a greater surface area. Transport can occur in ways unavailable to its prokaryotic companions in the biosphere.

In asexual replication, the nucleus of a eukaryotic cell copies its DNA and creates two identical daughter nuclei. Then a fission process occurs, similar to prokaryotic cell division. The cell is split, with each daughter cell containing its own nucleus and about half of the organelles and other contents of the original cell.

It may have taken a billion years for living cells to discover and implement the practical strategy of encapsulating their genetic information—their chemically encoded entropic memory—within a nucleus. We have noted that prokaryotic cyanobacteria were living at least 3.5 billion years ago. Chemicals found in crude oils from Australian shales are believed to be derived from the sterols of eukaryotes that lived 2.7 billion years ago.<sup>17</sup> Other evidence suggests that eukaryotes appeared between 1.6 and 2.1 billion years ago.<sup>18</sup> There is much speculation and much controversy about *how* the transition (or multiple transitions) from prokaryotes to eukaryotes occurred. Because eukaryotes are so effective in optimizing entropy production, the Fourth Law tells us *why* eukaryotes emerged. Once eukaryotes emerged, they thrived. The biotic world has never been the same since.

Among the unicellular eukaryotic organisms are yeasts, algae, protozoa, amoebae, and paramecia. Microbiologists have classified some of these organisms as plant-like or animal-like. Such classification has always been controversial. Regardless of taxonomic categories, it is clear that unicellular eukaryotes are extraordinarily numerous, prolific and diverse, that they possess enormous capability to adapt and evolve, and that they illustrate the Fourth Law imperative to spread out as individuals, as species, and as strains of species. By spreading out to occupy ecological niches, unicellular eukaryotes consistently and persistently optimize entropy production. We shall look at a selection of eukaryotic cells.

**Yeasts.** Our first example is the yeast *Saccharomyces cerevisiae*. *S. cerevisiae* is one of the earliest domesticated organisms. Archaeologists have found early grinding stones and baking chambers for yeasted bread in Egypt, as well as drawings of 4,000-year-old bakeries and breweries. Chemical evidence enables fermented beverages to be traced back as far as 7,000 B.C.E. in China.<sup>19</sup> Cell biologists have used *S.*

*cerevisiae* as a model organism; this species may be the most thoroughly studied eukaryotic microorganism in the laboratories of biochemists and biologists.

*S. cerevisiae* cells use simple sugars such as glucose and fructose and disaccharides such as sucrose and maltose as their primary energy sources. The temperature for their optimum metabolism is 30 °C. They survive freezing under certain conditions, and are quiescent between 0 °C and 10 °C. The cells become stressed and fail to divide properly above 37 °C; they seldom survive above 50 °C.

Yeasts are omnipresent. Wild-type strains of yeasts can be isolated from sources rich in sugar, such as plant sap, or fleshy grapes, apples, or peaches. Genetic studies of domesticated *S. cerevisiae* suggest a Mesopotamia-based origin of most wine strains. It appears that *S. cerevisiae* followed human migrations and the accompanying vine migrations. There is evidence<sup>20</sup> that *S. cerevisiae* does not live in nature at all, but can be found only in environments such as wineries. The geographical distribution of contemporary strains suggests local domestication.<sup>21</sup>

Human beings were (and continue to be) part of the domestication system. Yeasts convert sugars to ethanol; they also consume ethanol. Without encouragement from humans, wild yeasts do not accumulate much ethanol as a stored resource. With human intervention in the selection of yeast strains, *S. cerevisiae* has directed its metabolism toward production of ethanol and developed the ability to live in environments approaching 20 percent ethanol. Because ethanol is toxic to many microorganisms, this ability may help *S. cerevisiae* defend sugar resources against competitors.<sup>22</sup> Humans have recognized and exploited the preservative value of ethanol since prehistory.<sup>23</sup> In recent years, humans have intervened again to develop microorganisms to convert cellulosic carbohydrates to automobile fuel. Research continues in wineries and associated research laboratories to improve *S. cerevisia* strains for production of beverages. In each of these examples, a system has organized itself to optimize entropy production. Optimization has required preservation of the integrity of *S. cerevisiae* strains. The definition of optimization has been under partial control of humans who were part of the relevant systems, humans who intended to benefit from the products of optimized yeast metabolism.

**Amoeba proteus.** This unicellular eukaryote is named after the Greek sea-god Proteus. Both *Amoeba proteus* and Proteus are renowned for changing shape. In his *Odyssey*, Homer relates how the mythological Proteus took the forms of a lion, a serpent, a leopard, and a pig. We shall describe how a single *A. proteus* cell changes shape as it optimizes entropy production.

A flexible cell membrane surrounds the cell contents. This membrane is composed of fats, proteins, and polymeric sugars, with phosphate bonded at many sites on the fats, proteins, and sugars. An oversimplified description is that the boundary membrane is a lipid bilayer, reminiscent of the spherical micelles that spontaneously form when detergent-type molecules are mixed with water. The membrane can change shape, surround a solid particle, and capture the particle. The membrane opens, engulfs the particle, and then quickly reseals. Within the cell, the ingested particle is digested, together with portions of the disrupted cell membrane, by enzymes. This behavior is called phagocytosis. When an *A. proteus* cell detects food, it transforms its three-dimensional conformation to envelope its prey. The transformation tactics differ, depending on the type of prey. The range of materials captured by *A. proteus* is broad, including bacteria, other amoeba, and even small crystalline mineral particles. Any ingested material that is not digested is released extracellularly, a process known as exocytosis.

An *A. proteus* cell uses shape transformations to move through its environment.<sup>24</sup> As kitchen chemists with experience with gelatin know, aqueous macromolecular “solutions” can change easily from turgid gels to viscous liquid sols (and back again). Slight changes in local salt concentration can change both the volume and

the fluidity of the interior plasma differentially within the *A. proteus* cell. Local swelling can occur, forming an elongation called a pseudopod. Contraction in the rest of the cell, with liquefaction on the inner surface at the posterior end, then results in forward flow of the plasma. Spatially organized, alternating gelation and fluidification of the plasma can create and actuate pseudopods, propelling the cell.

The *A. proteus* cell membrane separates the cell's large molecules from its outside environment, but the cell is not isolated. The membrane is permeable to water and to small ions; the cell is an open system with respect to these small chemical species. In addition to its nucleus, an *A. proteus* cell contains a "contractile vacuole," a membrane-enclosed cavity that functions to maintain osmotic equilibrium between the cell contents and its environment. If the cell's environment is too salty, then the vacuole will release water into the cell to counteract movement of ions from the outside. If the ionic concentration of the cell contents is too low compared to its environment, then the vacuole will remove water. When the vacuole is full, it moves to the surface of the cell and expels its excess water. The overall effect of this *osmoregulation* is that *A. proteus* can tolerate moderate variation in the salinity of its environment without excessive shrinking or swelling. The cellular architecture of *A. proteus* has the ability to maintain osmotic homeostasis in a changing environment.

If *A. proteus* encounters an environment in which its survival is threatened, it may attempt to isolate itself by secreting a protective membrane, encapsulating itself and becoming a cyst. As a cyst, the cell suspends most of its metabolism until the environment becomes more suitable.

The molecular details involved in phagocytosis, osmoregulation, and cyst formation are still being elucidated. There is much yet to be learned about *how* these essential functions are initiated and carried out. Each of these functions permits *A. proteus* to optimize entropy production, or to "hunker down" until conditions permit returning to an entropy-producing state. The Fourth Law tells us *why* this microbial system obtains and metabolizes complex food sources, and *why* it protects itself from threats to its survival as an entropy producer.

*A. proteus* is a successful organism, but there are limits to its capabilities as an optimizer of entropy production. A single cell can do a great deal as a separate dissipative structure, but cellular individuality has inherent constraints. We next explore the consequences of the Fourth Law as multicellularity increases opportunities for diversifying entropic capacities among the eukaryotes.

## **Multicellular Organisms**

Life forms seize entropic opportunities relentlessly. Multicellularity among the eukaryotes is eminently predictable, since the opportunities for diversifying entropic capacities increase dramatically when cells organize in the form of multicellular communities of specialized cells. The Fourth Law predicts that macroscopic life forms will emerge. Whether a particular macroscopic organism is successful depends on how effective that organism can become as an optimizer of entropy, or how effectively that organism can participate in a larger system that optimizes entropy.

Multicellular organisms compose a phenomenal entropic repertoire, from microscopic to macroscopic, exploiting a vast range of ecological niches. We shall discuss some entropic strategies found beyond the cellular level in multicellular animals. Among multicellular organisms, insects alone represent millions of species, each species an entropic specialist. This focus on animals reflects the progression of this paper toward discussions of the entropics of intelligent animal species.

Just as in other life forms, the underpinnings of optimized entropy production in a multicellular island of life (a large organism) are *homeostasis* and the layers of systems that manage the organism and maintain its integrity. The entropic parallels among animals are stunning. Digestive systems, for example, all have the same entropic function. Nervous systems facilitate food and water recognition and acquisition (including senses of thirst and hunger, and the capacity to sense satiation of thirst and hunger), mating and reproduction, avoidance of predation, coordinated movement, and the hormonal messaging that organizes the community of an organism's cells. The evolutionary trend, as the Fourth Law predicts, is toward diversity of complex systems, and toward the evolution of tactics and capacities that maintain optimized levels of entropy production.

### Pipevine Swallowtail Butterfly

Certain insects, including butterflies, are called holometabolic organisms because their life cycles include complete metamorphosis. Each developmental stage in a holometabolic insect is entropically adapted to its surroundings, each with its own multilevel entropic dynamic. We shall examine life stages in the swallowtail butterfly *Battus philenor* (Linnaeus, 1771) in the context of the Fourth Law. *B. philenor* is commonly found in the warm climates of southeastern United States, especially in open woodlands and meadows where plants of the *Aristolochia* genus, such as *A. tomentosa* and *A. durior* (the common pipevines or Dutchman's pipes) thrive.

Adult *B. philenor* females select leaves of only a few *Aristolochia* species as depositories for their red-orange eggs. Because of this fastidious egg-laying selectivity, the insect is commonly called the Pipevine Swallowtail Butterfly. The eggs may appear dormant, but they are highly active entropic systems. They process and organize far-from-equilibrium internal resources, derived from the entropic behaviors and egg-making packaging capacities of the mother, into new dissipative forms: actively feeding larvae. These caterpillars are monophagous, feeding only on plants selected by their mother.<sup>25</sup>

Each caterpillar establishes its own entropic island, the plant leaves. Body mass increases as leaf carbohydrate and other nutrients are eaten, digested, and metabolized by the caterpillar. In addition to nutritive compounds, the leaves contain aristolochic acids, a group of alkaloids that are toxic to predators. The caterpillars sequester the alkaloids, unaffected adversely by these toxins. Larval, pupal, and adult stages all retain the sequestered alkaloids. The alkaloids are a chemical shield against predatory dissipative entities, such as birds. A bird that eats a *B. philenor* becomes violently ill; if the bird survives, it probably will not attack the same type of caterpillar or adult again. Any predatory companion witnessing the results will probably also learn to avoid this far-from-equilibrium dissipative system. Warning coloration advertises the toxicity of *B. philenor* larvae and adults. Far from being camouflaged, larvae are covered with red spines and spots that visually contrast with a black or dull-red background larval surface that shines deep red in sunlight. Adults are black with blatant orange spots on the underside of the hind wings.

Birds are not the only potential predators of *B. philenor* caterpillars. The ichneumonid wasp *Trogus pennator* attacks larvae of many swallowtail butterflies, but *B. philenor* is not without defense mechanisms. It has been found<sup>26</sup> that aristolochic acids repel the wasps. Moreover, aristolochic acids are fatal to any wasp eggs that are introduced into *B. philenor* caterpillars.

In the pipevine universe, predation is a tactic that increases entropy production by providing food for birds and a hospitable environment for developing wasps. However, optimization of entropy production by *B. philenor* requires survival of the species. Accumulation, synthesis, retention, and excretion of aristolochic

acids are effective survival tactics. The Fourth Law predicts both evolution of dissipative systems and an integrated protection of those systems.

A chrysalis of *B. philenor* may be either brown or green, protective coloration that can work well to hide the chrysalis from predators. The color appears to be determined by the environment of the caterpillar just before it begins to pupate. Among the environmental determinants are color and texture of the pupation site, as well as direction, periodicity, and intensity of illumination.<sup>27</sup> The chrysalis has a characteristic shape, with a segmented posterior end and an inward curve. The *B. philenor* chrysalis is photosensitive and temperature sensitive. It is able to sense seasonal changes. When hostile conditions are detected, it can temporarily suspend development and physiological activity (enter a diapause phase) and persist in a dormant state for a season, or indeed for years, until environmental conditions are favorable for emergence of the adult butterfly.<sup>28</sup> According to Fordyce, Nice and Shapiro,<sup>29</sup> *B. philenor* butterflies that emerge from a pupal diapause have significantly less fat but are more chemically defended with aristolochic acids, compared to those that have not undergone diapause. This is another Fourth Law trade-off, balancing greater energy reserves versus the costs of diminished chemical defense.

## Termites

Earlier, we examined a rudimentary digestive system in which an amoeba surrounds a solid food particle (by an infolding of the cell membrane), engulfs the particle and then enzymatically catabolizes the particle. An amoeba cell contains a contractile vacuole that functions to maintain osmotic homeostasis. The amoeba expels extracellularly any ingested material that is not digested.

The gut of a termite is a digestive system that is more complicated in structure than an amoeba. Yet, it is similar in function to that of amoebae in that it is an entropic enhancer. A termite's chewing mouthparts transfer food to its *foregut*. The foregut is a structure formed in the embryo by infolding of the exterior body wall; the lining of the foregut is essentially continuous with the exterior of the termite's body. The *midgut* has surfaces that secrete enzymes. It is a region for enzymatic digestion of food, and it has a semipermeable membrane lining that permits absorption of nutrients. Embryonically, the *hindgut* develops as an infolding of the body wall. The hindgut has a major role in homeostasis, removing nitrogenous compounds and regulating the absorption of water and salts from waste products in the alimentary canal. The hindgut also provides an environment in which vast numbers of symbiotic microorganisms thrive. Undigested material is expelled through the anus.

Termites are renowned cellulose feeders. Woody plants capture energy from sunlight, use that energy to synthesize cellulose, and use that cellulose as a structural material that resists decomposition. Cellulose is a stiff, rod-like macromolecular polymer of D-glucose units, contrasted with starch (a flexible, coiled macromolecular polymer of D-glucose units). The chemical difference between cellulose and starch arises because of the three-dimensional geometry of the bonding between glucose units. Cellulose has  $\beta$ -glycosidic bonds, whereas starch (and glycogen, and some other carbohydrates) has  $\alpha$ -glycosidic bonds. The geometric difference between  $\beta$  and  $\alpha$  bonds means that different enzymes are needed to cleave the bonds and convert the different polymers to glucose. Humans can quickly convert starch to glucose (with enzymes in saliva) simply by chewing, but humans can chew wood chips for hours without detecting the taste of sugar, because cellulase enzymes are not present in human saliva.

Termites feed on cellulose, and convert that cellulose to D-glucose. Most termite species produce cellulase enzymes that are active in the midgut. Beginning biology students, by laboratory dissection of termites, often obtain first-hand visual knowledge of microorganisms that fill the hindgut. Those microorganisms account for more than a third of the body weight of a termite.<sup>30</sup> Symbiotic protozoans in the

hindgut are responsible for most of the cellulose conversion. Many of these protozoa rely on symbiotic bacteria on their surfaces to synthesize enzymes necessary for this digestion.

The Fourth Law predicts that systems, such as the digestive systems of termites, will exploit energy-rich depositories of cellulose in wood and woody plant materials, creating entropy as rapidly as they can. The typical individual termite can metabolize cellulose slowly by itself, but it can metabolize cellulose a lot faster by employing protozoa and bacteria in its hindgut. This is of mutual benefit for each of these organisms. The termites graze to find food, and they provide a favorable environment for the hindgut microbes. The Fourth Law predicts that populations of termites, protozoa, and bacteria will adjust themselves to create optimized rates of entropy production. On a larger scale, the Fourth Law predicts that the cellulose synthesized by plants will not accumulate without upper limit. With the aid of termites (and other organisms), cellulose will be converted into dispersed matter and energy as rapidly as possible, within the constraint that stable populations of cellulose producers will be maintained.

## Locomotion

As we observed, an *A. proteus* cell uses shape transformations to move through its environment. Spatially organized changes in the state of the cell plasma—alternating gelation and fluidification of colloidal plasma—create and actuate pseudopods, propelling the cell. Some macroscopic multicellular organisms also use shape transformations to move, with the added feature of an organized system of muscles and a rudimentary nervous system to control locomotion. We shall examine the muscular system of *earthworms* in the context of the Fourth Law.

English naturalist Charles Robert Darwin (1809-1882), recording his detailed observations that began before 1838, was intensely interested in the natural history of earthworms and in the roles earthworms play as they convert plant materials into soil. At the conclusion of his final book, Darwin wrote:

“The plough is one of the most ancient and most valuable of man’s inventions; but long before he existed the land was in fact regularly ploughed, and still continues to be thus ploughed by earth-worms. It may be doubted whether there are many other animals which have played so important a part in the history of the world, as have these lowly organised creatures.”<sup>32</sup>

An earthworm is a cylindrical, segmented creature that burrows through soil that contains plant debris, eating its way through self-constructed underground tunnels. Cellulose and soil pass through the earthworm’s digestive system as the worm moves. Entropy is created as cellulose is degraded, and as soil materials are mixed and spread out behind the advancing worm—in Darwin’s words, as the worm ploughs the soil. Locomotion is essential if the earthworm is to forage efficiently, and if it is to plough effectively.

Each body segment has a set of circular muscles, together with tiny bristles called setae. The circular muscles (just under the skin) surround the worm’s body. Beneath the circular muscles are longitudinal muscles that run from one end of the worm’s body to its other end. When the circular muscles contract, the earthworm gets long and slender. When the longitudinal muscles contract, the worm becomes stubby and chubby. An earthworm can stretch one part of its body while contracting the other. Repetitive, coordinated stretching and contracting permit methodical movement through the soil. A different pattern of stretching and contracting is used for wriggling as a defense and escape strategy. For locomotion, the setae anchor a portion of the body when another part stretches. The setae anchor the whole worm when an early morning robin attempts to extract breakfast from a burrow.

Earthworms have a nervous system. The worms have sensory receptors in their skin to gather information about their environment, and they can utilize that information to initiate and accomplish muscular motion. Giant fibers located in the nerve cord coordinate an earthworm's rapid shortening.<sup>33</sup>

An earthworm, plant debris, and soil constitute a system that creates entropy as expeditiously as possible, consistent with preservation of the integrity of earthworms while preserving a continuing supply of plant material. Each such system is part of a larger ecological system that includes the plants that capture energy from the sun, and plants that depend on a rich, humus-laden soil to anchor and sustain their roots and their aboveground systems.

## **Reproduction**

The Fourth Law insists that every living system create entropy in the most optimized manner available to the system. This insistence means that every species must reproduce, so that its entropy-making capacity is maintained and perpetuated. We have noted that prokaryotic organisms propagate by asexual cellular replication. Each cell makes a copy of its DNA and then divides to create two identical daughter cells, each with identical DNA. Because some prokaryotes can divide every ten minutes, this mode of reproduction can produce as many identical individuals as an ecological niche can support. In multicellular life forms, there is more complexity and there are correspondingly more options for organisms.

Each butterfly, termite, and earthworm that we have discussed begins as a single cell that develops into a multicellular organism by cell divisions, by cell differentiation (specialization transformations), and by patterned localization of the specialized cells. In butterflies, a great deal of this specialization and localization is embryonic development within the egg before the egg is laid. Much more transformation occurs as the metamorphosis continues through larval, pupal and into adult stages. Even in the adult stage, cell divisions continue as other cells are repaired or replaced.

Replication, transformation, and localization of cells are reproductive ways that a multicellular organism organizes itself as an entropy optimizer. Its genetic information arises from the DNA in that original single zygote cell. The zygote in turn arises as the result of fertilization, with half the genetic information from each of two parents. The molecular details involved in reproductive systems have not yet been elucidated. We do not yet know chemically *how* these essential functions are initiated and carried out. Because fertilization, replication, transformation, and localization are essential for optimizing entropy production, the Fourth Law tells us *why* these multicellular systems self-organize to optimize entropy production.

## **Ecosystems as Island Associations**

The Fourth Law predicts associations of organisms, ecosystems, and biomes, associations that are recognizable as distinct inter-organismic entropic systems of coordinated energy dissipation. Ecosystems and biomes represent optimizations in the overall capacity of a region in space and time to dissipate energy optimally as they cycle matter from high entropy states to low entropy states. Matter is dispersed, coalesced, and re-dispersed as ecosystems behave as agents of optimized energy dispersal.

Social insects self-organize to form associations that maximize entropy formation. Each individual insect is a dissipative system. A community of social insects is also a dissipative system, and communities of insects are associated with predators and food sources that together form multi-layered dissipative systems.

We shall examine an insect community that is both an ecosystem itself, and also an integral part of a larger ecosystem.

We earlier discussed an individual termite as an example of mutualism. The termite grazes for food, and provides a favorable environment for protozoa and bacteria in its hindgut. Together, the termite and its symbiotic microbes create entropy by ingesting and metabolizing cellulose. As we often see in nature, the story of an individual is a part of an encompassing larger entropic drama. To illustrate this widespread phenomenon, we now examine a woodland with stands of pine, birch, sugar maple, pecan, and bald cypress trees, a colony of Formosan subterranean termites in that woods, and a legion of symbiotic microorganisms within the gut of each termite.

The bald cypress tree (*Taxodium distichum* (L.) L.C. Rich), found in the southeastern United States, is a tall, deciduous conifer. The bald cypress heartwood is resistant to attack by the Formosan subterranean termite (*Coptotermes formosanus* Shiraki) that thrives in the same geographical area. Bald cypress is used for heavy exterior construction, including docks, bridges, and boats. For example, cypress timbers used from 1597 to 1603 to construct the Spanish Governor's Mansion in St. Augustine, Florida, remained free of termite damage for over three centuries, although other native woods in the same framing were heavily attacked.<sup>34</sup> This specific resistance is significant, because *C. formosanus* termites are among the most destructive urban pests in the United States, eating their way through billions of dollars of pine, birch, sugar maple, and pecan each year.<sup>35</sup> *C. formosanus* attacks living plants as well as structural lumber in searching for sources of cellulose. Standing bald cypress trees defend themselves from Formosan termite attack by incorporating specific diterpenes, repugnant to *C. formosanus*, in their heartwood. Diterpenes form a class of hydrocarbons with the composition  $C_{20}H_{32}$ ; individual diterpenes differ in their geometry (their "stereochemistry").<sup>36</sup> Although defended from termite attack, *T. distichum* trees fall to human predation, precisely because lumber sawn from its heartwood contains the termite-repelling diterpenes.

The Formosan termites have their own defensive chemical agent. Chen, *et al.* report<sup>37</sup> that *C. formosanus* synthesizes the aromatic hydrocarbon naphthalene,  $C_{10}H_8$ , and may use this chemical (employed domestically by humans as a moth repellent) as a "defense against natural enemies such as ants, pathogenic microorganisms and nematodes... In termite nests, naphthalene as an antiseptic agent, as well as other nest fumigants, may inhibit the growth of such pathogenic microorganisms." They found that the fire ant *Solenopsis invicta* Buren, a major termite predator, is paralyzed at concentrations that have no visible effect on *C. formosanus*. They also observed that naphthalene elicits trail-following behavior in *C. formosanus* soldiers.

The hindgut of a Formosan termite is home for a highly complex community of prokaryotes and eukaryotes. The interactions of these organisms provide a model of mutualism, and have been intensively studied.<sup>38</sup> This community has the chemical ability to digest cellulose and other components of wood, producing glucose and other nutrients need by the host termite.

Formosan termites live in colonies that are a prime example of self-organized systems, using cooperation to exploit food sources not available to an individual insect acting alone. Husseneder, *et al.* have speculated<sup>39</sup> that flexible social and spatial organization of colonies may contribute to the success of *C. formosanus*. They found colonies (simple families) headed by a single pair of outbred reproductives, and almost as many colonies headed by multiple kings and/or queens. They also found<sup>40</sup> separate colonies that have interconnected foraging sites. It may take several years for a termite colony, which may contain millions of termites foraging for cellulosic food sources within a 400-foot radius, to attain mature size.

A typical colony contains nymphs, workers, soldiers, and reproductive individuals of both genders, sometimes containing several egg-laying queens. Worker termites are foragers, and they also have tasks

involving food storage as well as brood and nest maintenance. They are the main caste in the colony for the digestion of cellulose in food, and are the most likely individuals to be found in infested wood. The *C. formosanus* soldier caste is morphologically and physiologically specialized for defense. Mechanical weapons of the soldiers include mandibles modified for crushing. Chemical weapons include a spray ejected from an orifice at the front of the head. The spray acts both as an immobilizing glue, and also as an irritant against predators such as ants. This secretion also appears to contain an alarm pheromone that repels workers and attracts other soldiers. Chemicals in the secretion may signal workers exposed to the fluid to morph into soldiers.<sup>41</sup>

The microorganisms in the hindgut comprise a dissipative system, an island of life, which produces entropy as rapidly as possible, consistent with ensuring the integrity of the harboring gut. The foraging termite is a larger island, including the life in its gut, which produces entropy by finding, chewing, and ingesting wood products. Specialized workers, soldiers, and reproductive individuals self-organize as colonies that produce entropy faster than solitary individuals or unorganized groups of individuals. An even larger island of life includes the photosynthetic community that captures energy from sunlight and synthesizes cellulose, cellulose that is degraded by entropy producers such as termites and their symbiotes. Each of the components of the large system self-organizes, and the entire system self-organizes, so that entropy production is optimized. The system includes self-created, critical impediments, such as defense mechanisms, that ensure survival of the system.

We focused on Formosan subterranean termites to tell one compelling story about a community of interdependent organisms. This is far from a unique story. Entomologists and forestry scientists<sup>42</sup> have observed that the Southern Pine Beetle, *Dendroctonus frontalis* (Zimmermann, 1868), can exist in and house an entire community of associated species. *D. frontalis* is the most destructive pine bark beetle in the southern United States. The Georgia Forestry Commission estimates that in Georgia the beetle each year kills trees (mostly shortleaf, loblolly, and Virginia pines) with a commercial value of 7.5 million dollars. Larvae of the beetle are dependent on two symbiotic fungi—*Entomocorticium* sp. A and *Ophiostoma ranaculosum*—which grow in the vascular system of pine trees and provide food for the beetle larvae. Another fungus, *O. minus*, is a symbiont that can help the beetle overcome pine tree defenses. However, this fungus can inhibit growth of the principal *Entomocorticium* fungal food source. The beetle deals with the aggressive fungus by harboring yet another species—an actinomycete bacterium—that secretes antibiotics fatal to *O. minus*. *D. frontalis* is associated with more than fifty species of mites, including parasites, predators, fungivores, and omnivores.

This intricate, mutualistic association of host trees, beetles, fungi, mites, and antibiotic-producing bacteria is another example in which individuals self-organize, and in which a larger system self-organizes, so that entropy production is optimized. As we saw with termites, this system includes self-created, critical impediments to unbridled entropy production, impediments such as defense mechanisms that ensure survival of the system.

Research that revealed the complex mutualistic microcosm involving termites and the comparable mutualism involving bark beetles has been motivated in part by interest in fundamental science, and in part by the tremendous economic importance of these insects. These species are not unique in their symbiotic relationships. The Fourth Law predicts that communal mutualism is commonplace among the million known species in Class Insecta.

The Fourth Law also predicts that communal mutualism is commonplace among the inhabitants of every ecosystem, no matter how large the system. Ecosystems are communities of organisms that disperse matter and energy. From one trophic level to the next in an ecosystem, the main theme is dispersal. From one

trophic level to the next, 90% of the consumed energy is dispersed to the surroundings. Members of the community in an ecosystem disperse large molecules that end up being recycled as elements or biochemically reusable small molecules. For example, some large molecules in pollen end up residing in honey. Those molecules become dispersed largely as carbon dioxide and water, which are subsequently recycled in photosynthesis. Ecosystem dynamics are an impressive display of the Fourth Law.

Significantly, the Fourth Law imposes checks and balances. A healthy ecosystem expresses a dynamic balance between unbridled consumption and maintenance of the integrity of its multiple layers of self-organized community. The ebbs and flows of competition for resources produce a balanced flux. In ecosystems, as in all biological systems, the struggle of life is a struggle to balance opposing forces.

## Intelligent Species

The Fourth Law predicts a tendency toward the evolution of intelligent species on planets capable of supporting life, since intelligent species transcend purely metabolic means of increasing entropy. Human societies are very visible expressions of communal mutualism, and the Fourth Law predicts the emergence of self-organized political, social, economic, and cultural systems.

The Fourth Law affirms a transcendental confidence in consistencies of the rates and the morphologies of natural events. Many observers have expressed concern that *Homo sapiens*, with the ability to act in defiance of its own best interests, is failing miserably to act in synchrony with the Fourth Law. We have observed in laboratory petri dishes how populations of some organisms respond to an environment with fixed resources and constrained geometry. The petri dish does not self-destruct, but the organisms either adapt or perish. *H. sapiens* may have found ways to move toward uncontrolled expansion of consumption, and toward unbridled population growth.

As a *rational* intelligent species, *H. sapiens* should observe the checks and balances needed to maintain its place within the biosphere. If we do not act rationally, humans may produce the conditions for the near extinction of this latest version of the Hominid line. There seems to be no reason to assume that we are the culmination of that line. We may be just the only one that destroys itself. If we fail and our global order collapses, genetically isolated smallish populations of *H. sapiens* may be left behind. It is from isolated populations that new species arise. The Fourth Law is consistently directional; it favors the genesis of intelligence, because intelligent species are capable of creating an enormous, perhaps limitless, diversity of ideas and inventions that disperse matter and energy. The Fourth Law predicts that if we do not adjust to sustainable practices and policies, a new Hominid species may well emerge from our isolated embers, more rational, more aware of the necessity of entropic homeostasis than the former. Because the Fourth Law favors managed consumption, the new species might be more balanced and benevolent than its predecessor. In the long run, the Fourth Law favors environmental benevolence. The choice is ours—either us, or a new wiser Hominid species that reverences the environment. If we fail, that new species may look back on its ancestor with shame.

Intelligence gives *H. sapiens* tools to act in ways contrary to the long-range benefit of the species. Human societies often organize themselves with self-created barriers that restrict the benefits of being open systems. Political organizations often erect exclusionary walls that have the effect of limiting evolution. Universities, instead of functioning as dynamic intellectual ecosystems, often encourage departmentalism and separation of disciplines, and discourage interdisciplinary interaction. Intellectual barriers to dispersion of ideas often have the effect of thwarting Fourth Law imperatives. Generation after generation, it is prudent to consider the words of Emerson and “come to look at the world with new eyes.”

The messages of biological history and of the Fourth Law of Thermodynamics both seem clear. Life forms will persist and emerge on our planet, regardless of what *H. sapiens* does. We do not need to act to save the *planet*. We need to act to preserve our species and move into synchrony with a cosmically penetrant force. Neither biological history nor the Fourth Law, however, seem to provide any assurance that *H. sapiens* would be among the remaining or emerging life forms after self-inflicted attempts at its own extermination. Many biologists propose that we are engineering a sixth great extinction. If so, life will re-diversify, as it always has. The question is whether *H. sapiens* will be present in a new world.

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## References

1. Michael Faraday, *Lectures on the Various Forces of Matter, and The Chemical History of a Candle* (London: Griffin Bohn & Co., 1863).
2. R. E. Morel and George Fleck, "A Fourth Law of Thermodynamics," *Khimiya*, vol. 15, no. 4, pp. 305–308 (2006).
3. *Nature* (Boston: James Munroe and Company, 1836; 95 pages). Essay published anonymously by Ralph Waldo Emerson.
4. Vincent J. Schaefer, "Observations of an Early Morning Cup of Coffee," *American Scientist*, vol. 59, pp. 534–535 (1971).
5. Jearl Walker, "Wonders of Physics that can be found in a Cup of Coffee or Tea," *Scientific American*, vol. 237, no. 5, pp. 152–160 (November 1977).
6. Irving Langmuir, "Surface Motion of Water Induced by Wind," *Science*, vol. 87, no. 2250, pp. 119–123 (February 11, 1938).
7. Louis Nico Marie Duysens, *Transfer of Excitation Energy in Photosynthesis* (Doctoral dissertation, Utrecht, 1952).
8. Wesley Brittin and George Gamow, "Negative Entropy and Photosynthesis," *Proceedings of the National Academy of Sciences*, vol. 47, pp. 724–727 (1961); Robert G. Mortimer and Robert M. Mazo, "Irreversible Thermodynamics of Systems Containing Radiation. Application to Photochemical Reactions," *Journal of Chemical Physics*, vol. 35, no. 3, pp. 1013–1018 (1961); Wolfgang Yourgrau and Alwyn Van Der Merwe, "Entropy Balance in Photosynthesis," *Proceedings of the National Academy of Sciences*, vol. 59, pp. 734–737 (1968); Robert T. Ross and Melvin Calvin, "Thermodynamics of Light Emission and Free-Energy Storage in Photosynthesis," *Biophysical Journal*, vol. 7, pp. 595–614 (1967).
9. L. N. M. Duysens, "The Path of Energy in Photosynthesis," *Brookhaven Symposia in Biology*, vol. 11, pp. 10–25 (1958); Donald A. Bryant, ed., *The Molecular Biology of Cyanobacteria* (Dordrecht: Klumer Academic Publishers, 1994); Mamoru Mimuro, "Photon Capture, Exiton Migration and Trapping and Fluorescence Emission in Cyanobacteria and Red Algae," chap. 7 in George C. Papageorgiou and Govindjee, eds., *Chlorophyll a Fluorescence: A Signature of Photosynthesis* (Dordrecht: Springer, 2004).
10. Jouko Rikkinen and Viivi Virtanen, "Genetic diversity in cyanobacterial symbionts of thalloid bryophytes" *Journal of Experimental Botany*, vol. 59, no. 5, pp. 1013–1021 (2008).
11. R. G. Eagon, "Pseudomonas Natriegens, a Marine Bacterium with a Generation Time of less than 10 minutes," *Journal of Bacteriology*, vol. 83, pp. 736–737 (1962).
12. Barbara E. Wright, "Stress-directed adaptive mutations and evolution," *Molecular Microbiology*, vol. 52, no. 3, pp. 643–650 (2004).
13. Peter Ward, "Mass Extinctions: The Microbes Strike Back," *New Scientist*, vol. 197, no. 2642, February 9, 2008, pp. 40–43.
14. L. H. Chen, G. L. Kenyon, F. Curtin, S. Harayama, M. E. Bembenek, G. Hajipour, and C. P. Whitman, "4-Oxalocrotonate tautomerase, an enzyme composed of 62 amino acid residues per monomer," *Journal of Biological Chemistry*, vol. 267, no. 25, pp. 17716–17721 (1992).
15. M. R. Badger and G. D. Price, "The Role of Carbonic Anhydrase in Photosynthesis," *Annual Review of Plant Physiology and Plant Molecular Biology*, vol. 45, pp. 369–392 (June 1994).

16. Chetan Lad, Nicholas H. Williams and Richard Wolfenden, “The rate of hydrolysis of phosphomonoester dianions and the exceptional catalytic proficiencies of protein and inositol phosphatases,” *Proceedings of the National Academy of Sciences*, vol.100, no.10, pp. 5607–5610 (2003).
17. Jochen Brocks, *et al.*, “Archean Molecular Fossils and the Early Rise of Eukaryotes,” *Science*, vol. 285, August 13, 1999, pp. 1033–1036.
18. Andres H. Knoll, E. J. Javaux, D. Hewitt, and P. Cohen, “Eukaryotic organisms in Proterozoic oceans,” *Philosophical Transactions of the Royal Society of London, Part B* 361 (1470): pp. 1023–1038 (2006).
19. P. E. McGovern, *et al.*, “Fermented beverages of pre- and proto-historic China,” *Proceedings of the National Academy of Sciences*, vol. 101, no. 51, pp. 17593–17598 (December 21, 2004).
20. Alessandro Martini, “Origin and domestication of the wine yeast *Saccharomyces cerevisiae*,” *Journal of Wine Research*, vol. 4, no. 3, pp. 165–176 (1993).
21. Jean-Luc Legras, Didier Merdinoglu, Jean-Marie Cornuet, and Francis Karst, “Bread, Beer and Wine: *Saccharomyces cerevisiae* Diversity Reflects Human History,” *Molecular Ecology*, vol. 16, issue 10, pp. 2091–2102 (2007).
22. J. Michael Thomson, Eric A. Gaucher, Michelle F. Burgan, Danny W. De Kee, Tang Li, John P. Aris, and Steven A. Benner, “Resurrecting Ancestral Alcohol Dehydrogenases from Yeast,” *Nature Genetics*, vol. 37, pp. 630–635 (2005).
23. Patrick E. McGovern, Juzhong Zhang, Jigen Tang, Zhiqing Zhang, Gretchen R. Hall, Robert A. Moreau, Alberto Nuñez, Eric D. Butrym, Michael P. Richards, Chen-shan Wang, Guangsheng Cheng, Zhijun Zhao, Changsui Wang, and Ofer Bar-Yosef, “Fermented Beverages of Pre- and Proto-Historic China,” *Proceedings of the National Academy of Sciences*, vol. 101, no. 51, pp. 17593–17598 (December 21, 2004).
24. S. O. Mast, “Mechanics of Locomotion in Amoeba,” *Proceedings of the National Academy of Sciences*, vol. 9, pp. 258–261 (1923).
25. T. Racheli and L. Pariset, “II genere *Battus tassonomia* e storia naturale,” *Fragmenta entomologica (Supplemento)*, vol. 23, pp.1–163 (1992).
26. Karen Sime, “Chemical defence of *Battus philenor* larvae against attack by the parasitoid *Trogus pennator*,” *Ecological Entomology*, vol. 27, issue 3, pp. 337–345 (2002).
27. Sota Hiraga, “Interactions of environmental factors influencing pupal coloration in swallowtail butterfly *Papilio xuthus*,” *Journal of Insect Physiology*, vol. 52, issue 8, August 2006, pp. 826–838.
28. S. R. Sims and A. M. Shapiro, “Seasonal Phenology of *Battus Philenor* (L.) (Papilionidae) in California,” *Journal of the Lepidopterists’ Society*, vol. 37, issue 4, pp. 281–288 (1983).
29. James A. Fordyce, Chris C. Nice, and Arthur M. Shapiro, “A novel trade-off of insect diapause affecting a sequestered chemical defense,” *Oecologia*, vol. 149, pp. 101–106 (2006).
30. Carolina Biological Supply Company sells a termite study kit in which *Trichonympha* and *Pyrsonympha*, as well as other protozoa that live as symbionts in the termite’s gut, are shipped inside live termites.
31. J. B. S. Haldane, *Possible Worlds and Other Essays*, (London: Chatto & Windus, 1927).
32. Charles Darwin, *The Formation of Vegetable Mould, through the Action of Worms, with Observations on their Habits* (London: John Murray, 1881), p. 313.

33. M. B. V. Roberts, “Giant-Fibre Reflex of the Earthworm,” *Nature*, vol. 186, no. 4719, p. 167 (April 9, 1960); B. R. Coonfield, “The Peripheral Nervous System of the Earthworm,” *Transactions of the Kansas Academy of Science*, vol. 34, p. 115 (1931).
34. Benjamin R. Ellis, “Tidewater Red Cypress Resists Termites for Over 300 Years at St. Augustine,” *Southern Lumber Journal*, vol. 40, p. 22 (November 1936).
35. Juan Morales Ramos and Maria Rojas, “Growth of Young Colonies of *Coptotermes Formosanus* (Isoptera: Rhinotermitidae) Feeding on Single Versus Multiple Wood Species,” *Sociobiology*, vol. 46, pp. 155–173 (2005).
36. Rudolf H. Scheffrahn, Rwei-Ching Hsu, Nan-Yao Su, Jacob B. Huffman, Sharon L. Midland, and James J. Sims, “Allelochemical resistance of bald cypress, *Taxodium distichum*, heartwood to the subterranean termite, *Coptotermes formosanus*,” *Journal of Chemical Ecology*, vol. 14, no. 3, pp. 765–776 (1988).
37. J. Chen, G. Henderson, C. C. Grimm, S. W. Lloyd, and R. A. Laine, “Termites fumigate their nests with naphthalene,” *Nature*, vol. 392, p. 558 (April 9, 1998).
38. For examples, see Ulrich Stingl, Renate Radek, Hong Yang, and Andreas Brune, “‘Endomicroba’; Cytoplasmic Symbionts of Termite Gut Protozoa Form a Separate Phylum of Prokaryotes,” *Applied and Environmental Microbiology*, vol. 71, no. 3, pp. 1473–1479 (March 2005); Satoko Noda, Toshiya Iida, Osamu Kitade, Hideaki Nakajima, Toshiaki Kudo, and Moriya Ohkuma, “Endosymbiotic *Bacteroidales* Bacteria of the Flagellated Protist *Pseudotrichonympha grasioi* in the Gut of the Termite *Coptotermes formosanus*,” *Applied and Environmental Microbiology*, vol. 71, no. 12, pp. 8811–8817 (December 2005).
39. Claudia Husseneder, Matthew T. Messenger, Nan-Yao Su, J. Kenneth Grace, and Edward L. Vargo, “Colony Social Organization and Population Genetic Structure of an Introduced Population of Formosan Subterranean Termite from New Orleans, Louisiana,” *Journal of Economic Entomology*, vol. 98, issue 5, pp. 1421–1434 (October 2005).
40. C. Husseneder, J. K. Grace, M. T. Messenger, E. L. Vargo, and N-Y Su, “Describing the Spatial and Social Organization of Formosan Subterranean Termite Colonies in Armstrong Park, New Orleans,” *Sociobiology*, vol. 41, no. 1A [vp] (2003).
41. Masaya Ohta, Fumito Matsuura, Gregg Henderson, and Roger A. Laine, “Novel free ceramides as components of the soldier defense gland of the Formosan subterranean termite (*Coptotermes formosanus*),” *Journal of Lipid Research*, vol. 48, pp. 656–664 (March 2007).
42. Diana L. Six and Kier D. Klepzig, “*Dendroctonus* Bark Beetles as Model Systems for Studies on Symbiosis,” *Symbiosis*, vol. 37, pp. 1–26 (2004); May R. Berenbaum and Thomas Eisner, “Bugs’ Bugs,” *Science*, vol. 322, no. 5898, pp. 52–53 (October 3, 2008); Jarrod J. Scott, Dong-Chan Oh, M. Cetin Yuceer, Kier D. Klepzig, Jon Clardy, and Cameron R. Currie, “Bacterial Protection of Beetle-Fungus Mutualism,” *Science*, vol. 322, no. 5898, p. 63 (October 3, 2008).

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