LIFE AS A MANIFESTATION OF THE SECOND LAW OF THERMODYNAMICS

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ABSTRACT

We examine the thermodynamic evolution of various evolving systems, from primitive physical systems to complex living systems, and conclude that they involve similar processes which are phenomenological manifestations of the second law of thermodynamics. We take the reformulated second law of thermodynamics of Hatsopoulos and Keenan and Kestin and extend it to nonequilibrium regions, where nonequilibrium is described in terms of gradients maintaining systems at some distance away from equilibrium.

The reformulated second law suggests that as systems are moved away from equilibrium they will take advantage of all available means to resist externally applied gradients. When highly ordered complex systems emerge, they develop and grow at the expense of increasing the disorder at higher levels in the system's hierarchy. We note that this behaviour appears universally in physical and chemical systems. We present a paradigm which provides for a thermodynamically consistent explanation of why there is life, including the origin of life, biological growth, the development of ecosystems, and patterns of biological evolution observed in the fossil record.

We illustrate the use of this paradigm through a discussion of ecosystem development . We argue that as ecosystems grow and develop, they should increase their total dissipation, develop more complex structures with more energy flow, increase their cycling activity, develop greater diversity and generate more hierarchical levels, all to abet energy degradation. Species which survive in ecosystems are those that funnel energy into their own production and reproduction and contribute to autocatalytic processes which increase the total dissipation of the ecosystem. In short ecosystems develop in ways which systematically increases their ability to degrade the incoming solar energy. We believe that our thermodynamic paradigm makes it possible for the study of ecosystems to be developed from a descriptive science to a predictive science founded on the most basic principle of physics.

INTRODUCTION

In 1943 Erwin Schrödinger (1944) wrote his small book *What is Life?* , in which he attempted to draw together the fundamental processes of biology and the sciences of physics and chemistry. He noted that life was comprised of two fundamental processes; one "order from order" and the other "order from disorder". He observed that the gene with it's soon to be discovered DNA, controlled a process that generated order from order in a species, that is the progeny inherited the traits of the parent. Schrödinger recognized that this process was controlled by an aperiodic crystal, with unusual stability and coding capabilities. Over a decade later these processes were uncovered by Watson and Crick. Their work provided biology with a framework that allowed for some of the most important findings of the last thirty years.

However, Schrödinger's equally important and less understood observation was his "order from disorder" premise. This was an effort to link biology with the fundamental theorems of thermodynamics. He noted that at first glance, living systems seem to defy the second law of thermodynamics as it insists that, within closed systems, entropy should be maximized and disorder should reign. Living systems, however, are the antithesis of such disorder. They display marvelous levels of order created from disorder. For instance, plants are highly ordered structures, which are synthesized from disordered atoms and molecules found in atmospheric gases and soils.

Schrödinger solved this dilemma by turning to nonequilibrium thermodynamics, that is he recognized that living systems exist in a world of energy and material fluxes. An organism stays alive in its highly organized state by taking energy from outside itself, from a larger encompassing system, and processing it to produce, within itself, a lower entropy, more organized state. Schrödinger recognized that life is a far from equilibrium system that maintains its local level of organization at the expense of the larger global entropy budget. He proposed that to study living systems from a nonequilibrium perspective would reconcile biological self-organization and thermodynamics. Furthermore he expected that such a study would yield new principles of physics.

This paper takes on the task proposed by Schrödinger and expands on his thermodynamic view of life. We explain that the second law of thermodynamics is not an impediment to the understanding of life but rather is necessary for a complete description of living processes. We further expand thermodynamics into the causality of the living process and assert that the second law is a necessary but not sufficient cause for life itself. In short, our reexamination of thermodynamics shows that the second law underlies and determines the direction for many of the processes observed in the development of living systems. This work harmonizes physics and biology at the macro level and shows that biology is not an exception to physics, we have simply misunderstood the rules of physics.

Central to our discussion is a fresh look at thermodynamics. Since the time of Boltzmann and Gibbs there have been major advances in thermodynamics especially by Carathéodory, Hatsopoulos and Keenan, Kestin, Jaynes, and Tribus. We take the restated laws of thermodynamics of Hatsopoulos and Keenan and Kestin and extend them so that in nonequilibrium regions processes and systems can be described in terms of gradients maintaining systems away from equilibrium. In this context the second law mandates that as systems are moved away from equilibrium they will take advantage of all means available to them to resist externally applied gradients. Our expansion of the second law immediately applies to complex systems in nonequilibrium settings unlike classical statements which are restricted to equilibrium or near equilibrium conditions. Away from equilibrium, highly ordered stable complex systems can emerge, develop and grow at the expense of more disorder at higher levels in the system's hierarchy.

We will demonstrate the utility of these restatements of the second law by considering one of the classic examples of dissipative structures, Bénard Cells. We argue that this paradigm can be applied to physical and chemical systems, and that it allows for a thermodynamically consistent explanation of the development of far from equilibrium complex systems including life.

As a case study we focus on the applications of these thermodynamic principles to the science of ecology. We view ecosystems as open thermodynamic systems with a large gradient impressed on them by the sun. The thermodynamic imperative of the restated second law is that these systems will strive to reduce this gradient by all physical and chemical processes available to them. Thus ecosystems will develop structures and functions selected to most effectively dissipate the gradients imposed on them while allowing for the continued existence of the ecosystem. We examine one ecosystem closely and using analyses of carbon flows in stressed and unstressed conditions we show that the unstressed ecosystem has structural and functional attributes that lead to more effective degradation of the energy entrained within the ecosystem. Patterns of ecosystem growth, cycling, trophic structure and efficiencies are explained by this paradigm.

A rigorous test of our hypothesis is the measurement of reradiated temperatures from terrestrial ecosystems. We argue that more mature ecosystems should degrade incoming solar radiation into lower quality exergy, that is have lower reradiated temperatures. We then provide data to show that not only are more mature ecosystems better degraders of energy (cooler) but that airborne infrared thermal measurements of terrestrial ecosystems may offer a major breakthrough in providing measures of ecosystem health or integrity.

CLASSICAL THERMODYNAMICS

Because the basic tenets of this paper are built on the principles of modern thermodynamics, we start this paper with a

brief discussion of thermodynamics. We ask the reader who is particularly interested in ecology to bear with us through this discussion, because an understanding of these aspects of thermodynamics will make much of our discussion of ecology self-evident. For the reader who has mastered thermodynamics we believe that our approach to the theoretical issues of nonequilibrium thermodynamics is original and permits a more satisfactory discussion of observed far from equilibrium phenomena.

Comparatively speaking, thermodynamics is a young science but has been shown to apply to all work and energy systems including the classic temperature-volume-pressure systems, chemical kinetic systems, electromagnetic and quantum systems. The development of classical thermodynamics was initiated by Carnot in 1824 through his attempts to understand steam engines. He is responsible for the notion of mechanical work, cycles, reversible processes, and early statements of the first and second law. Clausius in the period 1840 to 1860 refined Carnot's work, formalizing the first and second law and the notion of entropy.

The first law arose from efforts to understand the relation between heat and work. Most simply stated, the first law says that energy cannot be created or destroyed and that despite the transformations that energy is constantly undergoing in nature (i.e. from heat to work, chemical potential to light), the total energy within a closed or isolated system remains unchanged. It must be remembered that although the total quantity of energy in a closed system will remain unchanged, the quality of the energy in the system (i.e the free energy or the exergy content) may change.

The second law requires that if there are any physical or chemical processes underway in a system, then the overall quality of the energy in that system will degrade. The second law of thermodynamics arose from Carnot's experiments with steam engines and his recognition that it was impossible to convert all the heat in such a system completely to work. His formal statement of the second law may be stated as: It is impossible for any system to undergo a process in which it absorbs heat from a reservoir at a single temperature and converts it completely into mechanical work, while ending at the same state in which it began. The second law notes that work may be dissipated into heat, whereas heat may not be converted entirely into work, thus proving the existence of irreversibility in nature. (This was a novel, paradigm shattering suggestion for its time.)

The second law can also be stated in terms of the quantitative measure of irreversibility, entropy. Clausius discovered that for any cyclic process[1]:

$$\int dQ/T \ \leq 0$$

where equality holds only for reversible processes (for example, a Carnot cycle).

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[1]Where Q is heat transfer in calories and T is in degrees Kelvin

Clausius, borrowing from the Greek for transformation, called the quantity $\int -dQ/T$ which measures the irreversibility of a process, the "entropy" of the process. The second law can be stated as: any real process can only proceed in a direction which results in an entropy increase. This universal increase in entropy draws the "arrow of time " (Eddington, 1958) in nature and represents the extent to which nature becomes more disordered or random.

All natural processes can be viewed in light of the second law and in **all** cases this one-sided aspect of nature is observed. Heat always flows spontaneously from a hotter reservoir to a colder reservoir until there is no longer a temperature difference or gradient; gas will always flow from high pressure to low pressure until there is no longer a pressure difference or gradient. If one mixes hot and cold water, the mixture comes to a uniform temperature. The resulting luke warm water will not spontaneously unmix itself into hot and cold portions. Boltzmann would have restated the above sentence as: it is highly improbable that water will spontaneously separate into hot and cold portions, but it is not impossible.

Boltzmann recast thermodynamics in terms of energy microstates of matter. In this context, entropy reflects the number of different ways microstates can be combined to give a particular macrostate. The larger the number of microstates for a given macrostate, the larger the entropy. Consider a ten compartment box with 10,000 marbles in one

of the ten compartments and the rest of the compartments being empty. If doors are opened between the compartments and the box is subjected to a pattern of random shaking one would expect, over time, to see a distribution of about 1,000 marbles per compartment, the distribution which has the largest number of possible microstates. This randomization of the marbles to the equiprobable distribution corresponds to the macrostate with the maximum entropy for the closed system. If one continued the shaking it would be highly improbable but not impossible for all the marbles to reseparate themselves into the low entropy configuration with 10,000 marbles in one compartment. The same logic is applied by Boltzmann to explain the macroscopic phenomena of thermodynamics in terms of microstates of matter. Systems will tend to the macrostate which has the largest number of corresponding accessible microstates.

THE EXTENDED LAWS OF THERMODYNAMICS

In 1908 thermodynamics was moved a step forward by the work of Carathéodory (Kestin, 1976) when he developed a proof that showed that the law of "entropy increase" is not the general statement of the second law. The more encompassing statement of the second law of thermodynamics is that "In the neighbourhood of any given state of any closed system, there exists states which are inaccessible from it along any adiabatic path reversible or irreversible". This statement of the second law, unlike earlier ones, does not depend on the concepts of entropy or temperature and

applies equally well in the positive and negative temperature regimes.

More recently Hatsopoulos & Keenan (1965) and Kestin (1966) have put forward a principle which subsumes the 0th, 1st and 2nd Laws: "When an isolated system performs a process after the removal of a series of internal constraints, it will reach a unique state of equilibrium: this state of equilibrium is independent of the order in which the constraints are removed". (This is called the Law of Stable Equilibrium by Hatsopoulos & Keenan and the Unified Principle of Thermodynamics by Kestin.)

The importance of this statement is that, unlike all the earlier statements which show that all real processes are irreversible, it dictates a direction and an end state for all real processes. All previous formulations of the second law tells us what systems cannot do. This statement tells us what systems will do. An example of this phenomena are two flasks, connected with a closed stopcock. One flask holds 10,000 molecules of a gas. Upon removing the constraint (opening the stopcock) the system will come to its equilibrium state of 5,000 molecules in each flask, with no gradient between the flasks. These principles hold for closed isolated systems. However a more interesting class of phenomena belong to systems that are open to energy and/or material flows and reside at stable states some distance from equilibrium.

These much more complex thermodynamic systems are the ones investigated by Prigogine and his collaborators (Nicolis and Prigogine,

1977, 1989). These systems are open and are moved away from equilibrium by the fluxes of material and energy across their boundary. These systems maintain their form or structure by continuous dissipation of energy and thus are known as dissipative structures. Prigogine showed that nonequilibrium systems, through their exchange of matter and/or energy with the outside world, can maintain themselves for a period of time away from thermodynamic equilibrium in a locally reduced entropy steady-state. This is done at the cost of increasing the entropy of the larger "global" system in which the dissipative structure is imbedded; thus following the mandate of the second law that overall entropy must increase. Nonliving organized systems (like convection cells, tornados and lasers) and living systems (from cells to ecosystems) are dependent on outside energy fluxes to maintain their organization in a locally reduced entropy state.

Prigogine's description of dissipative structures is formally limited to the neighbourhood of equilibrium. This is because his analysis depends on a linear expansion of the entropy function about equilibrium. This is a severe restriction on the application of his theory and in particular precludes its formal application to living systems.

To deal with the thermodynamics of nonequilibrium systems, we propose the following corollary that follows from the proof by Kestin of the Unified Principle of Thermodynamics. His proof shows that a system's equilibrium state is stable in the Lyapunov sense. Implicit in this conclusion is

that a system will resist being removed from the equilibrium state. The degree to which a system has been moved from equilibrium is measured by the gradients imposed on the system. *"The thermodynamic principle which governs the behaviour of systems is that, as they are moved away from equilibrium, they will utilize all avenues available to counter the applied gradients. As the applied gradients increase, so does the system's ability to oppose further movement from equilibrium."*

(In the discussion that follows we shall refer to this statement as the "restated second law". The pre-Carathéodory statements (i.e. entropy will increase) will be referred to as the classical second law)

A simple example of this phenomena is the Bénard cell. The experimental apparatus for studying the Bénard cell consists of a highly instrumented insulated container enclosing a fluid. The bottom of the container is a heat source and the top is a cold reservoir. (See Figure 1.) When the fluid is heated from below it resists the applied gradients (ΔT) by dissipating heat through conduction. As the gradient is increased, the fluid develops convection cells. These convection cells increase the rate of dissipation. (These convection cells are called Bénard cells, Chandrasehkar, 1961.)

Figure 2-c shows a plot of the gradient (Ra, the Rayleigh number, which is proportional to the gradient ΔT) against the available work which is expended in maintaining the gradient. The dynamics of the system are such that it

becomes more and more difficult to move the system away from equilibrium (that is, proportionally more available work must be expended for each incremental increase in gradient as the system gets further from equilibrium, i.e. ΔT increases).

In chemical systems, LeChatelier's principle is another example of the restated second law. Fermi, in his 1936 lectures on thermodynamics, noted that the effect of a change in external conditions on the equilibrium of a chemical reaction is prescribed by the LeChatelier's principle. "If the external conditions of a thermodynamic system are altered, the equilibrium of the system will tend to move in such a direction as to oppose the change in the external conditions" (Fermi, 1956). Fermi noted that if a chemical reaction were exothermal, i.e. (A+B=C+D+heat) an increase in temperature will shift the chemical equilibrium to the left hand side. Since the reaction from left to right is exothermal, the displacement of the equilibrium towards the left results in the absorption of heat and opposes the rise in temperature. Similarly a change in pressure (at a constant temperature) results in a shift in the chemical equilibrium of reactions which opposes the pressure change.

Thermodynamic systems exhibiting temperature, pressure, and chemical equilibrium resist movement away from these equilibrium states. When moved away from their local equilibrium state they shift their state in a way which opposes the applied gradients and moves the system back towards its local equilibrium attractor. The stronger the applied

gradient, the greater the effect of the equilibrium attractor on the system.
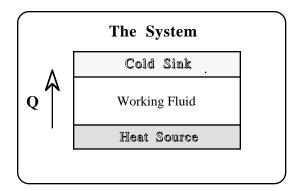
The reason that our restatement of the second law is a significant step forward for thermodynamics is that it tell us how systems will behave as they are moved away from equilibrium. Implicit in this is that this principle is applicable to nonequilibrium systems, something which is not true for classical formulations of the second law.
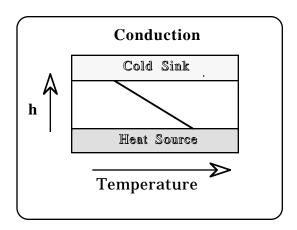
In particular our "restated second law" avoids the problems associated with state variables such as entropy which are only defined for equilibrium. Our restatement of the second law sidesteps the problems of defining entropy and entropy production in nonequilibrium systems, an issue that has plagued nonequilibrium thermodynamics for years. By focusing on gradient destruction, we avoid completely the problems encountered by Prigogine (1955), and more recently Swenson (1989), who use extremum principles based on the concept of entropy to describe self-organizing systems. Nonequilibrium systems can be described by their forces and requisite flows using the well developed methods of network thermodynamics (Katchalsky and Curren, 1965, Peusner, 1986, and Mikulecky, 1984).
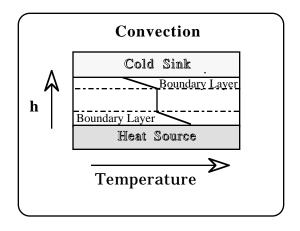
DISSIPATIVE STRUCTURES AS GRADIENT DISSIPATORS

In this section we examine the behaviour of dissipative structures in light of the restated second law. Prigogine and his colleagues have shown that dissipative structures self-organize through fluctuations, small instabilities which lead to irreversible bifurcations and new stable system states. Thus the future states of such systems are not deterministic. Dissipative structures are stable over a finite range of conditions and are sensitive to fluxes and flows from outside the system. Glansdorff and Prigogine (1971) have shown that these thermodynamic relationships are best represented by coupled nonlinear relationships i.e. autocatalytic positive feedback cycles, many of which lead to stable macroscopic structures which exist away from the equilibrium state. Convection cells, hurricanes, autocatalytic chemical reactions and living systems are all examples of far-from-equilibrium dissipative structures which exhibit coherent behavior.

The transition in a heated fluid between conduction and convection is a striking example of emergent coherent organization in response to an external energy input. A thorough analysis of these simple physical systems has allowed us to develop some general thermodynamic principles applicable to the development of complex systems as they emerge at some distance away from equilibrium. Bénard, Rayleigh, (see Chandrasekhar, 1961), Silveston (1957) and Brown (1973) conducted carefully designed experiments to study this transition.

The System

Cold Sink

Working Fluid

Heat Source

Q

Conduction

Cold Sink

Heat Source

h

Temperature

Convection

Cold Sink

Boundary Layer

Boundary Layer

Heat Source

h

Temperature

FIGURE 1: Bénard Cells

Schematics of the Bénard cell apparatus (top schematics, Q=heat transfer) and temperature profiles (lines inside apparatus in middle and bottom schematics, h = height) in the working fluid before and after the transition to convection. The fluid is heated from below and the top of the apparatus acts as a cold sink.

Initially all dissipation through the fluid occurs via conduction and molecule to molecule interaction. When the gradient reaches a critical level (Rayleigh number 1760) the transition to highly organized convection occurs.

As the gradient is increased it becomes harder and harder (more work is required) to maintain the higher rate of dissipation (see Figure 2). The further the system is moved away from its equilibrium state the more exergy is destroyed, the system produces more entropy, and more work is required to maintain it in its nonequilibrium state.
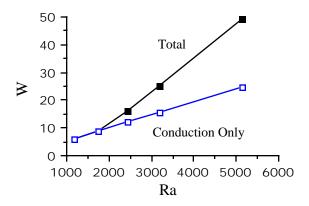
Due to the convective overturn most of the working fluid in the container becomes vertically isothermal (with little gradient) and only the boundary layers on the edge of the system carry the gradient. As the gradient is increased the boundary layers become thinner and more dissipation occurs.
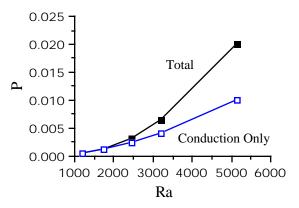
Definitions:

Nusselt Number: $Nu = Q / (k \, \Delta T / h)$

Rayleigh Number: $Ra = g \, \alpha \, \Delta T \, h^3 / \kappa \, \nu$

where Q=heat flow, k=coefficient of heat conduction, T=temperature, h=depth, g=gravity, α=coefficient of volume expansion, κ=coefficient of thermometric conductivity, ν=coefficient of kinematic viscosity.
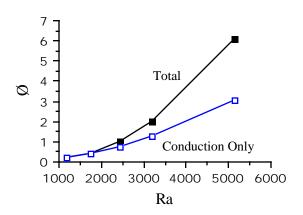
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Heat Dissipation Rate (W) vs Gradient (Ra)

Entropy Production Rate (P) vs Gradient (Ra)

Exergy Destruction Rate (Ø) vs Gradient (Ra)

FIGURE 2.

These graphs are calculations by us of entropy production and exergy destruction during heat transfer across a fluid. The data used is from the classic experiments of Silveston (1957). A fluid is heated from below. The temperature difference between the top and bottom of the fluid is increased and the heat transfer from the bottom to the top is recorded. At a Rayleigh number (a dimensionless measure of gradient) of about 1760 Bénard Cells appear, that is convection starts. As the Rayleigh number (temperature difference) increases convection becomes the dominant mode of heat transfer.

The particular analysis is for Silicon 350 at a depth of 6.98 mm. with a surface area of 0.0305 sq. m.. The first graph is the heat transfer rate (Kcal/Hour) across the fluid as a function of Rayleigh number (temperature difference). The bottom curve is the heat transfer rate without Bénard Cells and the top curve is the heat transfer rate with the formation of Bénard Cells. The point is that the emergence of the ordered structure (Bénard Cells) dissipates more energy.

The second graph is of entropy production rate (Kcal/Hour/°K) versus Rayleigh number (the gradient). Again we see the emergence of the ordered structure results in more entropy production. The third graph shows the available work[1] (exergy) (Kcal/hour) which must be provided from an external source in order to maintain the gradient. As the gradient increases a greater amount of work must be done to incrementally increase the gradient. It becomes more difficult to maintain the gradient as the system becomes more organized.

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[1]Exergy/Availability: A measure of available work content of energy.(Brzustowski and Golem, 1978, Ahern 1980, Moran, 1982) It is a measure of the potential of energy to perform useful work. It reflects the quality of the energy. Irreversible processes destroy exergy.

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The lower surface of the experimental apparatus is heated and the upper surface is kept at a cooler temperature. (See Figure 1). Hence a temperature gradient is induced across the fluid. The initial heat flow through the system is controlled by conduction. Energy transfer is by molecule to molecule interaction. When the heat flux reaches a critical value of the temperature gradient, the system becomes unstable and the molecular action of the fluid becomes coherent and convective overturning emerges. These convective structures result in highly structured coherent hexagonal surface patterns (Bénard Cells) in the fluids. This coherent kinetic structuring increases the rate of heat transfer and gradient destruction in the system.

This transition between noncoherent, molecule to molecule, heat transfer to coherent structure results in excess of 10^{23} molecules acting together in an organized manner. This seemingly improbable occurrence is the direct result of the applied temperature gradient and is the system's response to attempts to move it away from equilibrium.

Recently we studied the Bénard Cell phenomena in detail, using the original data sets collected by Silveston (1957) and Brown (1973) (which they most graciously provided us with). We believe that these analyses are significant, in that we have calculated for the first time the entropy production, exergy drop and available work destruction, resulting from these organizing events. (See Figure 2.) Our analysis clearly shows that as the gradient

increases it becomes harder to increase the gradient.

Initially the temperature gradient in the apparatus is being accommodated solely by random conductive activity. When the gradient is raised, a combination of factors including surface tension effects and gravitational fluid instability, converts the system to a mixed conductive-convective heat transfer system. The transition to coherent behaviour occurs at Ra=1760 (see definitions, Figure 1).

Figure 2 are plots of Silveston's original data using silicon as the working fluid with a separation between the hot and cold sinks of 6.98 mm. The curve labelled "Conduction" is the dissipation which would occur without the emergent coherent behaviour. The difference between the curve labelled "Total", and the one labelled "Conduction", is the increase in dissipation due to the emergence of the dissipative structure. As is shown in Figure 2, with the onset of convection there is a dramatic increase in the heat transfer rate across the system.

From the literature, especially Chandrasekhar (1961), and from our analysis of Silveston and Brown's data we note the following behavior for these systems:

1) Heat Dissipation Rate (transfer of heat between the plates) is a linearly increasing function of the gradient ΔT (see figure 2-a, recalling that Ra is proportional to ΔT).

2) Entropy production rate (P) vs ΔT increases in a nonlinear way (see figure 2-b).

3) Exergy destruction rate (Ø) vs ∆T increases in a nonlinear way, the shape of the curve being the same as P vs ∆T.

4) 2&3 imply that as the gradient increases it is harder (requires more available work, that is exergy) to incrementally increase the gradient. The further from equilibrium that the system is, the more it resists being moved further from equilibrium. In any real system there is an upper limit to the gradient which can be applied to the system.

5) Once convection occurs, the temperature profile within the fluid is vertically isothermal outside the boundary layer, i.e. the temperature in the convection cells is constant thus effectively removing the gradient through most of the fluid (see Figure 1).

6) As the gradient increases, further critical points are reached. At each critical point the boundary layer depth decreases.

7) 1 is true because the rate of heat transfer is controlled (more or less) by the rate of heat flow across the boundary layer, i.e. by conduction which is a linear process. This process is also responsible for most of the entropy production, as there will be little production due to convection. The slope change is caused by the decrease in the boundary layer depth (l) at a mode change (critical point). (Recall Q=k∆T/l thus as l decreases, slope (k/l) increases.)

8) Nu is Q/Qc = P/Pc = Ø/Øc; that is, in Bénard Cells, the increase in dissipation at any point due to the emergent process is equal to the increase in degradation at any point due to the emergent process. This is true for any process which involves only heat transfer. Otherwise degradation ≠ dissipation. (This is why Prigogine at times mistakenly uses these terms interchangeably.)

9) The principle governing these systems is not one of maximum entropy production but rather one of entropy production change being positive semi-definite as you increase the gradient. See point 7 above. The interesting question is, how much structure emerges for a given gradient, and how much resistance exists to increasing the gradient further.

As the temperature difference increases, there are a number of further transitions at which the hexagonal cells re-organize themselves so that the cost of increasing the temperature gradient escalates even more quickly. Ultimately the system becomes chaotic and dissipation is maximum in this regime.

The point of this example is that in a simple physical system, new structures emerge which better resist the application of an external gradient. The Bénard cell phenomena is an excellent example of our nonequilibrium restated second law. As we will see later, other physical, chemical, and living systems observe similar rules.

The more a system is moved from equilibrium, the more sophisticated its mechanisms for resisting being moved from equilibrium. This behaviour is not sensible from a classical second law perspective, but is

what is expected given the restated second law. No longer is the emergence of coherent self-organizing structures a surprise, but rather it is an expected response of a system as it attempts to resist and dissipate externally applied gradients which would move the system away from equilibrium. The term dissipative structure takes on a new meaning. No longer does it mean just increasing dissipation of matter and energy, but dissipation of gradients as well.

In this regard it is important to distinguish between energy dissipation and energy degradation. Dissipation of energy means to move energy through a system, as in the Bénard cell. Dissipation may or may not destroy gradients. Degradation of energy means to destroy the ability of energy to set up gradients. The ability to set up gradients is measured by the availability or exergy of the energy. Thus energy degradation means exergy destruction, that is the degradation of the ability of the energy to produce gradients that can accomplish work. In simple systems involving only heat flow, energy degradation is via energy dissipation.

The gradient reducing nature of self-organizing systems is dramatically demonstrated by a simple experimental device sold as a toy in a nationwide scientific catalog (Edmunds). Their "Tornado in a Bottle" (not to be confused with "fusion in a bottle"), consists of a simple plastic orifice that allows the connection of two 1.5 liter plastic soda bottles end to end. The bottles are connected and set on a level surface to drain with the upper bottle filled with water and the lower bottle empty. When set vertical, a thirty centimeter gradient of water exists.

Due to the orifice configuration, the bottle drains slowly requiring approximately six minutes to empty the upper bottle (i.e. to reduce the gradient in the system). The experiment is then repeated with the bottles being given a slight rotational perturbation. A vortex forms, driven by the gravitational gradient within the system, and drains the upper bottle in approximately 11 seconds. The "tornado", a highly organized structure, has the ability to dissipate the gradient much faster thus bringing the system to its local equilibrium more quickly! Here again is a manifestation of the restated second law, a macroscopic highly organized structure of 10^{23} molecules acting coherently to dissipate a gradient. The production of the highly organized system, the tornado, leads to more effective dissipation of the larger driving gradient, the gravitational differences in water levels between the bottles. As in the Bénard convection experiments, organized structures reduce gradients more quickly than random linear processes.

It should not be surprising that this simple experimental device mimics meteorological phenomena such as mesoscale weather patterns. The development of temperature gradients between a warm earth and a cooler overlying atmosphere results in highly organized convective cloud patterns which reduce the troposphere temperature gradient. The violent destructive power of tornadoes is a manifestation of the ability of these self-

organizing structures to rapidly dissipate strong temperature and barometric gradients. Hurricanes are another example of mesoscale dissipative meteorological structures.

The global weather, wind and ocean circulation patterns are the result of the difference in heating at the equator relative to the poles. The general meteorological circulation of the earth, although affected by spatial, coriolis and angular momentum effects, is driven by gradients and the global system's attempt to dissipate them and come to local equilibrium. Paltridge (1979) has suggested that the earth-atmosphere, climate system configures itself into a state of maximum dissipation and that the global distribution of clouds, temperature and horizontal energy flows are governed by thermodynamic dissipative processes similar to those described above. We see that the earth-climate system, as well as other dissipative systems, do not reach a static equilibrium state because they are open thermodynamic systems constantly receiving a supply of external energy (i.e. from the sun), which drives them and maintains them in a nonequilibrium organized state.

So far we have focused our discussion on simple physical systems and how thermodynamic gradients drive self-organization. The literature is replete with similar phenomena in dynamic chemical systems. Prigogine and the Brussel's School and others have documented the thermodynamics and behavior of these chemical reaction systems. Chemical gradients result in dissipative autocatalytic reactions,

examples of which are found in simple inorganic chemical systems, in protein synthesis reactions, or phosphorylation, polymerization and hydrolytic autocatalytic reactions.

Autocatalytic reactions systems are a form of positive feedback where the activity of the system or reaction augments itself in the form of self-reinforcing reactions. Consider a reaction where A catalyzes the formation of B and B accelerates the formation of A; the overall set of reactions is an autocatalytic or positive feedback cycle. Ulanowicz (1986) notes that in autocatalysis, the activity of any element in the cycle engenders greater activity in all the other elements, thus stimulating the aggregate activity of the whole cycle. Such self-reinforcing catalytic activity is self-organizing and is an important way of increasing the dissipative capacity of the system. Cycling and autocatalysis is a fundamental process in nonequilibrium systems.

The notion of dissipative systems as gradient dissipators holds for nonequilibrium physical and chemical systems and describes the processes of emergence and development of complex systems. Not only are the processes of these dissipative systems consistent with the restated second law, it should be expected that they will exist wherever there are gradients.

LIVING SYSTEMS AS GRADIENT DISSIPATORS

We will now focus our attention on the role of thermodynamics in the evolution of living systems. The father of statistical

thermodynamics, Boltzmann recognized the apparent contradiction between the thermodynamically predicted randomized cold death of the universe and the existence of a process (i.e. life) in nature by which systems grow, complexify, and evolve, all of which reduce their internal entropy. As early as 1886 Boltzmann observed that the gradient on earth, caused by the energy provided by the sun, drives the living process and suggested a Darwinean like competition for entropy in living systems:

"Between the earth and sun, however, there is a colossal temperature difference; between these two bodies energy is thus not at all distributed according to the laws of probability. The equalization of temperature, based on the tendency towards greater probability, takes millions of years, because the bodies are so large and are so far apart. The intermediate forms assumed by solar energy, until it falls to terrestrial temperatures, can be fairly improbable, so that we can easily use the transition of heat from sun to earth for the performance of work, like the transition of water from the boiler to the cooling instillation. The general struggle for existence of animate beings is therefore not a struggle for raw materials - these, for organisms, are air, water and soil, all abundantly available - nor for energy which exists in plenty in any body in the form of heat (albeit unfortunately not transformable), but a struggle for entropy, which becomes available through the transition of energy from the hot sun to the cold earth. In order to exploit this transition as much as possible, plants spread their immense surface of leaves and force the sun's energy, before it falls to the earth's temperature, to perform in ways yet unexplored certain chemical syntheses of which no one in our laboratories has so far the least idea. The products of this chemical kitchen constitute the object of struggle of the animal world." (Boltzmann, 1886).

As we noted in the introduction Boltzmann's ideas were further explored by Schrödinger in "What is Life?" (Schrödinger, 1944). Schrödinger, like Boltzmann, was perplexed. He also noted that some systems, like life, seem to defy the classical second law of thermodynamics. However he recognized that living systems are open and not the adiabatic closed boxes of classical thermodynamics. An organism stays alive in its highly organized state by taking energy from outside itself, that is from a larger encompassing system, and processing it to produce a lower entropy state within itself. Life can be viewed as a far-from-equilibrium dissipative structure that maintains its local level of organization, at the expense of producing entropy in the larger system it is part of.

If we view the earth as an open thermodynamic system with a large gradient impressed on it by the sun, the thermodynamic

imperative of the restated second law is that the system will strive to reduce this gradient by using all physical and chemical processes available to it. We have already shown that self-organizing processes are an effective means of reducing gradients. We have discussed that meteorological and oceanographic circulation degrades some of the energy gradients and disequilibrium from the 1580 watts /meter^2 of incoming solar energy. However there are still additional energy gradients requiring dissipation. *We suggest that life exists on earth as another means of dissipating the solar induced gradient and as such is a manifestation of the restated second law.* It is obvious that living systems are far from equilibrium dissipative systems and have great potential of reducing radiation gradients on earth (Ulanowicz and Hannon, 1987). Much of this dissipation is accomplished by the plant kingdom (less than 1% of it through photosynthesis, with most of the dissipation occurring through evaporation and transpiration).

An interesting exception to this are the deep sea vent ecosystems that derive their energy from temperature and chemical gradients emanating from the sea floor rather than from solar energy (Corliss, 1990). In these systems, life is most abundant where the chemical and temperature gradients are the greatest, thus the required gradient dissipation is the highest.

THE ORIGIN OF LIFE

The origin of prebiotic life is the development of another route for the dissipation of induced energy gradients. Life with its requisite ability to reproduce, insures that these dissipative pathways continue and it has evolved strategies to maintain these dissipative structures in the face of a fluctuating physical environment. We suggest that living systems are dynamic dissipative systems with encoded memories, the gene with its DNA, that allow the dissipative processes to continue without having to restart the dissipative process via stochastic events. Living systems are sophisticated mini-tornados, with a memory (its DNA), whose Aristotelian "final cause" may be the second law of thermodynamics. However one should be clear not to overstate the role of thermodynamics in living processes. The restated second law is a necessary but not a sufficient condition for life.

This paradigm presents no contradiction with the neo-Darwinean hypothesis and the importance of the genetic process, and its role in biological evolution. We reject the selfish gene (Dawkins, 1976), as the only process in selection and would insert the gene or species as a component in competing autocatalytic ecosystems (Weber et al., 1989), competing to degrade available energy gradients.

The origin of life should not be seen as an isolated event. Rather it represents the emergence of yet another class of processes whose goal is the dissipation of thermodynamic gradients. Life should be viewed as the most

sophisticated (until now) end in the continuum of development of natural dissipative structures from physical to chemical to autocatalytic to living systems. As we have discussed earlier autocatalytic chemical reactions are the backbone of chemical dissipative systems. The work of Eigen (1971), Eigen and Schuster (1979) connect autocatalytic and self-reproductive macromolecular species with a thermodynamic vision of the origin of life. Ishida (1981) describes Eigen's work:

"Eigen (1971) has asserted that the first steps of biological self-organization occurred in a structureless soup, certainly involving functional macromolecular structures such as nucleic acids and proteins. In accordance with this assertion he has considered a chemical system composed of a wide variety of self-reproductive macromolecules and many different energy-rich monomers required to synthesize the macromolecules. Each macromolecular and monomeric species are distributed uniformly throughout the available volume. The system is open and maintained in a nonequilibrium state by continuous flows of energy-rich and energy-deficient monomers. It is thus tremendously complex. In addition, metabolism, self-reproduction and mutability are necessary for each macromolecular species to yield the behavior of Darwinian selection at the molecular level. For each

macromolecular species, Eigen has proposed a simple phenomenological rate equation materializing these three necessary prerequisites. This rate equation, which we shall now call Eigen's equation, is interpreted in terms of the terminology of chemical kinetics."

Eigen (1971) himself says:

"Evolution appears to be an inevitable event, given the presence of certain matter with specified autocatalytic properties and under the maintenance of the finite (free) energy flow necessary to compensate for the steady production of entropy"

From the point of view of nonequilibrium thermodynamics of chemical reactions in a homogeneous system, Eigen has shown that the Darwinian selection of such macromolecular species can be linked to Glansdorff & Prigogine's stability criterion (Nicolis and Prigogine, 1977 and Peacocke, 1983). By examining the entropy changes and entropy production of such systems Ishida has formulated a nonequilibrium thermodynamics of the hypercycles. This theory is used to discuss the stability of the "quasi-species" (a solution to Eigen's equations with non-vanishing mutation terms). In principle, it is possible, using nonequilibrium thermodynamics of open systems, to put forward scenarios for the development of biochemical machinery for the duplication and translation of nucleic acids and other macromolecules essential to life.

BIOLOGICAL GROWTH AND DEVELOPMENT

Our thesis is that growth, development, and evolution are the response to the thermodynamic imperative of dissipating gradients (Kay, 1984) and (Schneider, 1988). (Which is not to say this is the only imperative governing life, survival is equally important.) Biological growth occurs when the system adds more of the same types of pathways for degrading imposed gradients. Biological development occurs when new types of pathways for degrading imposed gradients emerge in the system. The larger the system, i.e., the larger the system flow activity (Ulanowicz, 1986), the more reactions and pathways (both in number and type) are available for gradient destruction. Clearly the above principle provides a criteria for evaluating growth and development in living systems. All else being equal, the better dissipative pathway is preferred. In what follows we explore some examples of this principle.

Plant growth is an attempt, within the constraints of its genetic (and evolutionarily tested) make up and its environmental boundary conditions, to capture solar energy and dissipate usable gradients. The gradient capturing aspects of plants can be seen in phototrophism and their symmetrical shapes, designed to capture and degrade sunlight. Although each tree species has its own genetically endowed form, the energy capturing aspect of an isolated tree leads to its magnificent symmetry. Canopies of plants of many species arrange themselves into leaf index assemblies to optimize energy capture and degradation. The gross energy budgets of terrestrial plants show that the vast majority of their energy use is for evapotranspiration, with 200-500 grams of water transpired per gram of fixed photosynthetic material. This mechanism is a very effective energy degrading process with 600 calories used per gram of water transpired (Kimmins, 1987).

Data synthesized by Currie and Paquin (1987) show that the large scale biogeographical distribution of species richness of trees is strongly correlated with realized annual evapotranspiration and available energy. The more energy is partitioned among species the more pathways there are available for total energy degradation. Trophic levels and food chains are based upon photosynthetic fixed material and further dissipate these gradients by making more higher ordered structures. Thus we would expect more species diversity to occur where there is more available energy. Species diversity and trophic levels are vastly greater at the equator, where 5/6 of the earths solar radiation occurs, and there is more of a gradient to reduce.

A THERMODYNAMIC ANALYSIS OF ECOSYSTEMS

Ecosystems display the influence of thermodynamic principles in their patterns of growth and development. A thermodynamically based theory of ecology holds the promise of propelling ecology from a descriptive to a predictive science. Ecosystems

are the result of the biotic, physical, and chemical components of nature acting together as a nonequilibrium dissipative process. As such ecosystem development increases energy degradation thus following the imperative of the second law. This hypothesis can be tested by observing the energetics of ecosystem development during the successional process or by determining their behavior as they are stressed or as their boundary conditions are changed.

As ecosystems develop or mature they should increase their total dissipation, and should develop more complex structures with greater diversity and more hierarchical levels to abet energy degradation. Species which survive in ecosystems are those that funnel energy into their own production and reproduction and contribute to autocatalytic processes which increase the total dissipation of the ecosystem. In short, ecosystems develop in a way which systematically increases their ability to degrade the incoming solar energy.

In this sense the development of ecosystem maturity via succession is the result of the system organizing itself to dissipate more incoming energy with each stage of succession. Thus one would expect successional processes in ecosystems to result in systems with:

1. More energy capture:- because the more energy that flows into a system the greater the potential for degradation.

2. More energy flow activity within the system:- again, the more energy that flows within and through a system, the greater the potential for degradation.

3. More cycling of energy and material:

   A) Numbers of cycles:- more pathways for energy to be recycled in the system results in further degradation of the incoming energy.

   B) The length of cycles:- more mature systems will have cycles of greater length, i.e. more nodes in the cycle. Each chemical reaction at or within a node results in entropy production; the more such reactions the more complete the degradation.

   C) The amount of material flowing in cycles (as versus straight through flow) increases. The ecosystem becomes less leaky thus maintaining a supply of raw material for energy degrading processes.

   D) Turnover time of cycles or cycling rate decreases:- more nodes or cycles in a system will result in nutrients or energy being stored at nodes in the system resulting in longer residence time in the system. This phenomena is the same as the decrease in production/biomass (P/B) ratio decreases observed in maturing ecosystems. P/B is the residence time of material in the system. The residence time of a nitrogen atom in a simple bacterial cycle will be a matter of hours, however the residence time of a similar nitrogen atom in a rainforest will be years.

4. Higher average trophic structure:
    A) Longer trophic food chains:- energy is degraded at each step of the trophic food chain, therefore longer chains will result in more degradation.
    B) Species will occupy higher average trophic levels:- This will result in more energy degradation as energy at higher trophic levels has a higher exergy content.
    C) Greater trophic efficiencies:- energy that is passed higher up the food chain will be degraded further than energy that is shunted immediately into the detrital food chain.
5. Higher respiration and transpiration:- transpiration and respiration results in energy degradation.
6. Larger ecosystem biomass:- more biomass means more pathways for energy degradation.
7. More types of organisms (higher diversity):- more types of organisms will provide diverse and different pathways for degrading energy.

This list of ecological attributes can be explained by ecosystems behaving in such a manner as to degrade as much of the incoming energy as possible (Kay and Schneider, 1991, Kay, 1989) and provides causality for most if not all the phenomenological attributes of maturing ecosystems developed by Odum in 1969. Lotka's (1922) suggestion that living systems will maximize their energy flow, H. T. Odum's (1955) maximum power principle for ecosystems and Lieth's (1976) maximum

energy conductivity are all subsumed and explained by our theory.

If ecosystems develop into dynamic quasi-stable states, one would expect them to respond to changes in boundary conditions that perturb these states by retreating to configurations with lower energy degradation potential. Stressed ecosystems will retreat down their thermodynamic branch into more primitive systems with attributes opposite those presented above (Kay, 1991). Stressed ecosystems often appear similar to earlier successional stage ecosystems and will reside at some distance closer to thermodynamic equilibrium.

We have recently analyzed a carefully collected data set for carbon-energy flows in two aquatic tidal marsh ecosystems adjacent to a large power generating facility on the Crystal River in Florida. The ecosystems in question were a "stressed" and a "control" marsh. The stressed ecosystem is exposed to hot water effluent from the nuclear power station. The stress is an approximately 6° C water temperature increase. The "control" ecosystem is not exposed to the effluent but is otherwise exposed to the same environmental conditions. We wished to determine the effect of the change in environmental conditions on the structure of the stressed system.

Table 1 summarizes a set of ecosystem indicators. The I/O or Input/Output Measures indicate various aspects of the flows through the ecosystem. In absolute terms (the first three columns of Table 1) all the flows dropped in the stressed ecosystem. Overall the drop in

TABLE 1: Ecosystem Indicators for the Crystal River Marsh Gut Ecosystems

Crystal River	Mg/Sq m/day				Scaled by Import		
	Control	Stressed	Δ%		Control	Stressed	Δ%
Biomass	1,157,136	755,213	34.73%		157.50	125.49	20.32%
Total I/O							
Imports	7,347	6,018	18.09%		1	1	0.00%
TST	22,768	18,055	20.70%		3.10	3.00	3.19%
Production	3,292	2573.9	21.82%		0.45	0.43	4.56%
Exports	952	872	8.37%		0.13	0.14	-11.86%
Respiration	6,400	5,148	19.57%		0.87	0.86	1.80%
Living I/O							
Production	400	326	18.39%		0.05	0.05	0.37%
Exports	316	253	19.93%		0.04	0.04	2.24%
Respiration	3,566	3,078	13.69%		0.49	0.51	-5.37%
To Detritus	5,726	4,315	24.64%		0.78	0.72	7.99%
Detritus I/O					Scaled by Detritus Input		
Input from Living	5,726	4,315	24.64%		1.00	1.00	0.00%
Production	2,893	2,248	22.29%		0.51	0.52	-3.11%
Exports	636	619	2.64%		0.11	0.14	-29.19%
Respiration	2,834	2,070	26.96%		0.49	0.48	3.09%
Food Web							
Cycles	142	69	51.41%				
Trophic Levels	5	5	0.00%				

flows was about 20%, in particular the imported flows (that is the resources available for consumption) drops by 18% and the TST (the total system throughput, the total flow activity in the system) dropped by 21%. The biomass dropped by about 35%. The implication of these numbers is that the stress has resulted in the ecosystem shrinking in size, in terms of biomass, its consumption of resources, and its ability to degrade and dissipate incoming energy.

If the flows are scaled by the import to the ecosystem from the outside, (the last three columns in Table 1) the resulting numbers indicate how well the ecosystem is making use of the resources it does capture. The percentage changes in these scaled flow rates reveals that in total the stressed ecosystem is, relatively speaking, exporting more. In other words, it is losing material more quickly than the control ecosystem. It is a leaky ecosystem. Looking at the living side, the big changes are an increase in respiration and a decrease in flow to the detritus. There was a small decrease in exports. These changes indicate that the consumed resources are being more effectively

used by the living components. It also indicates the species are stressed. Looking at the detritus, a different picture emerges. There was a slight increase in production and a small decrease in respiration and a very large increase in exports. This analysis of the scaled flow rates indicates that the living components are somewhat stressed but that more importantly, there is a large break down in the ability of the ecosystem to recycle material through the detritus and thus retain and degrade its resources.

Examining the Food Web data further confirms this. (The last three rows in Table 1.) The number of cycles in the stressed ecosystem is 51% of the number in the control. Furthermore overall these cycles are shorter in length. In the effective grazing chain the number of trophic levels was not changed, but the trophic efficiencies were changed dramatically, as was the flow to the top trophic levels. These are all indicators of a stressed ecosystem (Ulanowicz, 1985).

Overall the impact of the effluent from the power station has been to decrease the size of the ecosystem and its consumption of resources while impacting its ability to retain the resources it has captured. In short the impacted ecosystem is smaller, has lower trophic levels, recycles less, and leaks nutrients and energy. All of these are signs of disorganization and a step backward in development. This analysis suggests that the function and structure of ecosystems follows the development path predicted by the behavior of nonequilibrium thermodynamic structures. A more complete

analysis of these data and the implications of this hypothesis for ecosystem health or integrity are found in Kay and Schneider (1991).

ECOSYSTEMS AS ENERGY DEGRADERS

The energetics of terrestrial ecosystems provides an excellent test of our thesis that ecosystems will develop so as to degrade energy gradients more effectively. More developed dissipative structures will degrade more energy. Thus we would expect more mature ecosystems to degrade the exergy content of the energy they capture more completely than a less developed ecosystem. The exergy drop (i.e. gradient dissipation) across an ecosystem is a function of the difference in black body temperature between the captured solar energy and the energy reradiated by the ecosystem. If a group of ecosystems are bathed by the same amount of incoming energy, we would expect that the most mature ecosystem would reradiate its energy at the lowest exergy level, that is the ecosystem would have the coldest black body temperature. (See equations next page.) The black body temperature is determined by the surface temperature of the ecosystem.

Luvall and Holbo (1989, 1991) and Luvall et al. (1990) conducted experiments in which they overflew terrestrial ecosystems and measured surface temperatures using a Thermal Infrared Multispectral Scanner (TIMS). Their technique allows assessments of energy budgets of terrestrial landscapes, integrating attributes of the overflown ecosystems,

TABLE 2. Radiative estimates from Thermal Infrared Multispectral Scanner for different ecosystem types in the H.J. Andrews Experimental Forest, Oregon. The data is presented from least (quarry) to most developed (400 year old forest). Data from Luvall and Holbo (1989).

	Quarry	Clearcut	Douglas Fir Plantation	Natural Forest	400 year old Douglas Fir Forest
K^* (watts/m^2)	718	799	854	895	1005
L^* (watts/m^2)	273	281	124	124	95
R_n (watts/m^2)	445	517	730	771	830
T (°C)	50.7	51.8	29.9	29.4	24.7
R_n/K^* (%)	62	65	85	86	90

R_n/K^*= percent of net incoming solar radiation degraded into nonradiative process.

including vegetation, leaf and canopy morphology, biomass, species composition and canopy water status. Luvall and his co-workers have documented ecosystem energy budgets, including tropical forests, mid-latitude varied ecosystems, and semiarid ecosystems. Their data shows one unmistakable trend, that when other variables are constant the more developed the ecosystem, the colder its surface temperature and the more degraded it's reradiated energy.

Table 2 portrays TIMS data from a coniferous forest in western Oregon, North America. Ecosystem surface temperature varies with ecosystem maturity and type. The warmest temperatures were found at a clearcut

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THE RADIATION EQUATIONS

$$R_n = K^* - L^*$$

where K^* = Net flux of Solar Radiation (incoming), L^* = Net Flux of long wave radiation (outgoing), R_n = Net radiation flux absorbed at surface (all measured in watts / meter^2)

and

$$R_n = H + L_e + G$$

where H = sensible heat flux, L_e = latent heat flux, G= energy flux into the ground. R_n is the energy which is degraded from radiation into molecular motion.

Furthermore:
$$L^* = \varepsilon \, [\sigma(T)^4]$$

where ε= emissivity, σ=Stefan-Boltzmann constant, T= surface temperature

IF K^* IS CONSTANT, THE SMALLER T, THE SMALLER L^* AND HENCE THE LARGER R_N AND THUS THE LARGER THE AMOUNT OF ENERGY DEGRADED.

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SURFACE TEMPERATURE (°C) VS TRANSECT DISTANCE (M)

FIGURE 3   A Thermal Infrared Multichannel Scanner (TIMS) profile over a varied landscape in the Braulio Carrillo National Park in Costa Rica (done by Luvall et al.1990). The TIMS is mounted on an aircraft measuring six thermal channels in the wave length channels of 8.2 to 12.2 μm and flown over a 400 meter transect.   Temperatures are canopy temperature values calculated from net reradiated thermal energy. Temperatures showed that forest fire burn was the warmest system (it did not degrade as much incoming energy) and the tree island the coldest (the best degrader). The pasture degraded energy in an intermediate fashion.   Airborne thermal imaging may hold great promise for rapid evaluation of terrestrial ecological integrity.

and over a rock quarry.   The coldest site, 299°K, some 26° colder than the clear cut, was a 400 year old mature Douglas Fir forest with a three tiered plant canopy.   The 23 year old naturally regrowing forest had the same temperature as the 25 year old plantation of Douglas Fir.   Even with the initial planting of the late successional species of fir, the natural system obtained a similar energy degrading capacity in a similar time.

Luvall's data allows for an interesting calculation of the percent of the net solar radiation (K^*) that is degraded into energy in the form of molecular motion (R_n).   Luvall points out that R_n is the net available energy dissipated through evaporation, sensible heat and storage. The ratio R_n/K^* is the percentage of the radiative fluxes converted to lower exergy thermal heat. The quarry degraded 62% of the net incoming radiation while the 400 year old forest degraded 90%.   The remaining sites fell between these extremes, increasing degradation with more mature or less perturbed ecosystems.

These unique data sets show that ecosystems develop structure and function that degrades imposed energy gradients more effectively.   Analysis of airborne collected

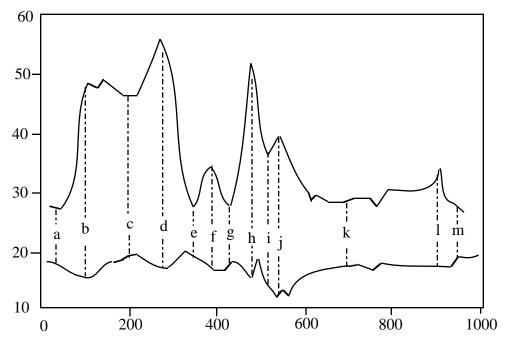## SURFACE TEMPERATURE (°C) VS TRANSECT DISTANCE (M)

FIGURE 4: Temperature profiles along a 1 km transect in the H.J. Andrews Experimental Forest, Oregon. (Luvall & Holbo, 1991) The top profile is for noon and the bottom profile is for post-sunset. The data was collected using TIMS surface temperature acquisition system. The letters on the diagram correspond to surface features:

a) edge of forest, b) narrow road, c) somewhere in a clear cut, d) a wider road, e) one side of a small shelter wood of Douglas Fir, f) a pond within the shelter wood, g) the other side of the shelter wood, h) a wide road, i) trees along the road, j) in a flat part of a clear cut, k) somewhere in a 15 year old Douglas Fir plantation, l) a trail, m) an old stand of Douglas Fir regrowth.

reradiated energy fluxes appears to be a unique and valuable tool in measuring the energy budget and energy transformations in terrestrial ecosystems. According to proposals made in this paper, a more developed ecosystem degrades more energy. Thus the ecosystem temperature or R_n/K^* may be excellent indicators of ecological integrity that can be formulated from first principles of thermodynamics and physics.

For these indices to be used to determine comparative or, hopefully, absolute measures of ecosystem integrity, much more research is needed on energy transformation in ecosystems, as well as method development to correct for system specific location dependant energy processes, i.e. rainfall and altitude. The potential for these methods to be used for remote sensed ecosystem classification and ecosystem health evaluation is apparent in Figure 3 & 4. Forest fire burn, pasture and trees have their own distinctive temperatures. More mature ecosystems are colder. Luvall has also tested algorithms to measure the thermal inertia of ecosystems, analyzed spectral variability, day night differences and evapotranspiration, all which show specific ecosystem characteristics.

AREA	Energy absorbed at surface	Energy Reradiated Long Wave	Sensible Heat Flux	Evapo-transpiratrion
Amazon	184.7	17%	15%	70%
US	220.2	18%	19%	61%
Asia	223.4	24%	26%	50%
Sahara	202	41%	56%	2%
Rain Forest	204	16%	22%	63%
Grassland	186	22%	30%	48%

TABLE 3 Energy absorbed (watts/ m^2/ day) at the surface of varied ecosystems, and the percentage of this energy which is emitted into space . Data was obtained from the satellite derived Earth Radiation Budget Experiment and from the SiB climate biosphere model of Sellers et al. (1986). This data demonstrates that a more developed ecosystem is a better dissipative structure.

These same phenomena are observed at a larger scale and exhibit the global nature of the biosphere in reducing the induced solar gradient on earth. Sato and his colleagues have recently calculated the mean surface energy budget for four large regions of the earth for 50 days in the summer. (See Table 3) The regions are a) the Amazon basin which is uniformly covered by rainforest, b) central and eastern United States which consists mainly of cultivated land, grasslands and some mixed forest, c) Asia, a heterogeneous mix of tropical rain forest, forest, cultivated land and desert, and d) the Sahara desert. Their data was obtained from the satellite derived Earth Radiation Budget Experiment and from the SiB climate biosphere model of Sellers et al. (1986). They measured insolation, albedo, net long and short wave energy absorbed at the earth's surface, net radiation or available energy and calculated important heat fluxes by modeling physiological and biological processes which influence radiation, momentum, mass, and heat transfer related to vegetation-surface atmosphere interactions. Their calculations are important because they integrate the atmosphere-biosphere as a net dissipative system and allow for the determination of the reduction of the solar induced gradient between a warm black body earth and the 2.8°K temperature of outer space.

The first four rows presented in Table 3 are arranged from the most developed ecosystem (Amazon rainforest) to the least. The re-radiated long wave radiation and the sensible heat flux represent energy which has not been degraded to the ambient and which will cause disequilibrium. Evapotranspiration represents energy which is dissipated and thus been converted to lower quality exergy. On the basis of the arguments presented in this paper, evapotranspiration should increase with ecosystem development and long wave radiation and sensible heat flux should

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FIGURE 5. The mean monthly outgoing long wave radiation (OLR) is measured by the NOAA-9 polar orbiting satellite using the infrared channel. Contours are in watts/m^2. Note the low longwave emissions over the tropical rain forests and high values over the earth's deserts.

decrease. This is borne out by the results presented in the first four rows of Table 3.

Moreover the last two rows represent running the SiB model for the rainforest and then for the same location except assuming a grassland instead of a rainforest. (Shulka et al., 1989). Again, this data shows that the more developed an ecosystem, the more the energy impinging on it is degraded to lower quality energy.

Satellite derived earth radiation data developed for global climate analysis, shows that this same phenomena may also be apparent at the global scale. The Climate Analysis Center and the Satellite Research Laboratory of the National Oceanic and Atmospheric Administration (NOAA) produce monthly maps of outgoing longwave radiation (OLR) collected from multiwave spectral scanners aboard polar orbiting satellites.

Long wave infrared emissions (L) from the earth are dependant on the surface temperature, greenhouse gasses, i.e. H_2O and CO_2, and cloud cover. Like the greenhouse gasses, cloud cover will tend to act as a blanket and trap longwave infrared.

Figure 5 is a global OLR map for February 1991. For the tropical rainforests of the Amazon, the Congo, and over Indonesia and Java, L is less than 200 watts/m^2. The deserts emit a net OLR of over 280 watt/m^2. Interestingly enough, the tropical rain forests with their coupled cloud system, with the sun directly overhead, have the same surface temperature as Canada in the winter. The low tropical rainforest OLR temperatures are due to the cold temperatures of the convective cloud tops which are generated by the underlying cooler forests.

As we have seen earlier, mature ecosystems can lower surface temperature by approximately 25°C. The low reradiation from the rainforest-cloud systems appears to be a global scale signal of solar gradient degradation. Most of the energy degradation in terrestrial ecosystems is due to the latent heat production via evapotranspiration. Tropical rain forests produce a prodigious amount of water vapor via this process, and convective induced cooling produces high clouds which tends to reinforce the cooling of the rain forests. The coupled rain forest cloud system lowers the earth to space gradient even more than the forest alone.

This phenomena may appeal to supporters of Lovelock's (1990) Gaia hypothesis, as it is an example of the coupled global biosphere-climate system. Without immersing ourselves

into the Gaiaean controversy, the coupled system does decrease the apparent earth-space gradient. Furthermore the rain forests with their attendant cloud formation act to cool the earth on a global basis and thus play an important role in global climate energy budgets. We have research underway to further quantify these propositions.

DISCUSSION

In this paper we have recast the second law of thermodynamics from the old statement of "entropy increase" into a statement that describes systems undergoing processes so that they will reach a unique state of equilibrium. This description draws on the work of Carathéodory, Hatsopoulos & Keenan, and Kestin. It allows for the discussion of system behaviour in nonequilibrium situations. It overcomes the difficulty of describing nonequilibrium systems in terms of entropy, which can only be defined in the equilibrium state. We suggest that, in nonequilibrium situations, systems will take advantage of all available means to resist the gradients responsible for the nonequilibrium condition. Furthermore, the stronger the applied gradient, the greater the effect that the equilibrium attractor will have on the system. Emergence of coherent self-organizing structures are the expected response of systems as they attempt to resist and dissipate the external gradients that are moving them away from equilibrium.

We have shown that these principles are manifested in the behaviour of physical dissipative systems (i.e. Bénard cells) and described how they apply to mesoscale meteorology. We apply these same principles to the origin of life, biological growth, the development of ecosystems, and biological evolution. Living systems are not only permissible under the restated second law of thermodynamics, but it is the restated second law which mandates living processes and is a necessary but not sufficient cause for life itself. We provide biology with a paradigm that not only describes the "why" of life but also describes the directions in which living systems will develop and evolve.

We have documented that ecological processes are driven and governed by thermodynamic imperatives; ecosystems develop and select energetic pathways that strive to degrade as much of the energy available to them as possible. We believe that these same principles extend to Darwinean selection. Margalef (1968), Odum (1969), Wicken (1987) and Schneider (1988) all observed that the strategy of succession, a short term process, is basically the same strategy as the long term evolutionary development of the biosphere. Margalef (1968) noted that:

> "evolution cannot be understood except in the framework of succession. By the natural process of succession, which is inherent in every ecosystem, the evolution of species is pushed or sucked onto the direction taken by succession. Succession is in progress everywhere and evolution follows encased in succession's frame.".

Zotin (1984) studied the bioenergetic trends of the evolution of organisms and noted that evolution has progressed in a manner such that organisms evolved with increasing energetic dissipation rates, i.e. respiratory intensity. Evolution, like ecosystems seems to select species and ecosystems that increase the global dissipation rate.

Our suggestions should not be confused with the work of Brooks and Wiley (1986). Their "increase of entropy", observed in their cladograms of evolving species, refers to an information theoretic entropy and as such explains things in terms of microstate probabilities of information states. Our work examines the thermodynamic development of natural systems and as such explains things in terms of macroscopic behaviour of energy processing.

The foundations of our work were certainly developed by Prigogine and Wiame (1946) and Wicken (1980, 1987) but we circumvent their discussions of entropy and life, and instead rely on a more appropriate approach to nonequilibrium systems, that is the development of self-organization as a means of dissipating gradients imposed on systems.

Lotka (1922) and Odum and Pinkerton (1955) have suggested that those biological systems that survive are those that develop the most power inflow and use it to best meet their needs for survival. Our work would propose that a better description of these "power laws" would be that biological systems develop in a manner as to increase their degradation rate, and that biological growth, ecosystem

development and evolution represent the development of new dissipative pathways. This work is quite different than Jørgensen's Maximum Exergy Principle (Jørgensen and Mejr,1979). He has focused on exergy concentrations, while we are investigating exergy degradation. The two concepts may be interrelated but our work has not as yet shown the linkage.

Our proposals represent a new approach to the biological synthesis. We have not been able to discuss all the ramifications these principles have for our understanding of the growth and development of biological systems. We have intentionally not discussed the application of these principles to the development and operation of genetic processes. We note that our thermodynamic description of living systems fits comfortably into the present day molecular-genetic research program. The importance of the gene and its role in morphogenesis, speciation and in carrying the message of evolution forward is vital.

Life represents a balance between the imperatives of survival and energy degradation. To quote Blum (1968):

> "I like to compare evolution to the weaving of a great tapestry. The strong unyielding warp of this tapestry is formed by the essential nature of elementary non-living matter, and the way in which this matter has been brought together in the evolution of our planet. In building this warp the second law of thermodynamics has

played a predominant role. The multi-colored woof which forms the detail of the tapestry I like to think of as having been woven onto the warp principally by mutation and natural selection. While the warp establishes the dimensions and supports the whole, it is the woof that most intrigues the aesthetic sense of the student of organic evolution, showing as it does the beauty and variety of fitness of organisms to their environment. But why should we pay so little attention to the warp, which is after all a basic part of the whole structure? Perhaps the analogy would be more complete if something were introduced that is occasionally seen in textiles-the active participation of the warp in the pattern itself. Only then, I think, does one grasp the full significance of the analogy."

What we have tried to do in this paper is to show the participation of the warp in producing the pattern of the tapestry of life. However this does not in anyway diminish the importance of the woof, which records the struggle for survival.

To return to Schrödinger, life is comprised of two processes, "order from order, and order from disorder". The work of Watson and Crick described the gene with its DNA, and solved the "order from order" mystery. Our hypothesis supports the "order from disorder" premise and connects biology with physics thus providing a unifying macroscopic theory for living systems.

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