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# Systems theory, thermodynamics and life: Integrated thinking across ecology, organization and biological evolution.

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ABSTRACT

In this paper we explore the relevance and integration of system theory and thermodynamics in terms of the Earth system. It is proposed that together, these fields explain the evolution, organization, functionality and directionality of life on Earth. We begin by summarizing historical and current thinking on the definition of life itself. We then investigate the evidence for a single unit of life. Given that any definition of life and its levels of organization are intertwined, we explore how the Earth system is structured and functions from an energetic perspective, by outlining relevant thermodynamic theory relating to molecular, metabolic, cellular, individual, population, species, ecosystem and biome organization. We next investigate the fundamental relationships between systems theory and thermodynamics in terms of the Earth system, examining the key characteristics of self-assembly, self-organization (including autonomy), emergence, non-linearity, feedback and sub-optimality. Finally, we examine the relevance of systems theory and thermodynamics with reference to two specific aspects: the tempo and directionality of evolution and the directional and predictable process of ecological succession. We discuss the importance of the entropic drive in understanding altruism, multicellularity, mutualistic and antagonistic relationships and how maximum entropy production theory may explain patterns thought to evidence the intermediate disturbance hypothesis.

## 1. Introduction

In this paper we explore the relevance and integration of system theory and thermodynamics in terms of the Earth system. It is proposed that, together, these fields account for the evolution, functionality and directionality of life on Earth.

Untangling the drivers of organization and change within the Earth system and, more fundamentally, whether there are drivers at all, have remained contested issues across the centuries. This is no more clearly demonstrated than in the thinking surrounding the origins, evolution and the very definition of life. From the blind watchmaker (Dawkins, 1996) to the Gaian hypothesis (Lovelock and Margulis, 1974), and from Vitalism (Bergson, 1911) to spontaneous generation (McNichol, 2008), many different explanations have been set out as to how and why the living world is formulated in the way that it is. These questions are not merely of importance in philosophical and scientific debate. They have urgent relevance in terms of the existential challenges humanity faces today and into our near-future.

While Raspail (1825) emphasised that life always comes from life (*omnis cellula e cellula*), this approach, much like panspermia, relies on life always having existed. To argue otherwise must assert that life must have, at some point, come from non-life (i.e., life must have originally spontaneously generated from non-life). The same difficulties arise in terms of defining the concept of a species, in that, at some point, the first member of a new species must have been conceived by a parent or parents of a different species (with the exception of the first life-form that clearly had no living parent). Such issues point to significant problems in terms of how we deal with the origins, organization and evolution of life. At its heart lies a fundamental question: how do we define life? This is a key issue that must be addressed before we can discuss these other questions relating to life.

## 2. Aims and objectives

We begin by summarizing historical and current thinking on the definition of life itself. What is the difference between the inanimate and the animate? Given that any definition of life and its levels of organization are intertwined, we explore how the Earth system is structured and functions from an energetic perspective, by outlining relevant thermodynamic theory. We explore its relevance to the organization of

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life at the levels of molecular, metabolic, cellular, individual, population, species, ecosystem and biome organization. We next investigate the fundamental relationships between systems theory and thermodynamics in terms of the Earth system, examining the key characteristics of self-assembly, self-organization (including autonomy), emergence, non-linearity, feedback and sub-optimality, all within a thermodynamic context. Finally, we examine the relevance of these areas with reference to two specific topics of study: the tempo and directionality of evolution and the process of ecological succession. The findings are summarised in the conclusion.

## 3. A brief history of the meaning of life

Attempts to define life have been debated for millennia. While most would acknowledge that biology is an outcome of physics and chemistry, life has often been viewed as something that was separate from these more basic sciences. Even today, the field of chemistry itself is often divided into organic chemistry (or biochemistry) and inorganic chemistry, paying homage to the formerly dominant idea of Vitalism. Substances were viewed as 'organic' if they irreversibly changed upon heating, and 'inorganic' if they reverted to their original forms when cooled. Furthermore, it was asserted that organic matter could not be formed from inorganic matter, and that some vital force, or *élan vital*, was thought to inhabit organic material and co-ordinate its organization (see Posteraro (2023) for a wide-ranging critique). Although mechanistic approaches to life led to the demise of vitalism, the terminology of inorganic chemistry and biochemistry still persist today.

While early (and some current) visions of the origin of life centred around a wide range of so-called 'creator myths', usually involving one or more deities who created the world and its diversity of species, Anaximander of Ancient Greece was one of the first to set out a scientific explanation, involving four elements (fire, soil, water and air), which emerged from an eternal and unchangeable cosmological essence or force that he named '*apheiron*'. Apheiron could transform into any of the four elements, producing life, and these elements could return to apheiron. He viewed this essence as both the beginning and as a ruler, directing things (Theodossiou et al., 2011).

Many of the more recent definitions of life begin with seven key characteristics that must co-exist for something to be considered truly living: reproduction, growth and development, metabolism, biological evolution, a cellular basis and response (McKay, 2004). There have been many papers written relating to the shortcomings of the 'club of seven', such as those by Luisi et al. (1998), Tirard et al. (2010) and Chodasewicz (2014).

For example, viruses are excluded from the tree of life because they are, of themselves, non-metabolic and non-cellular. Yet it is now recognized that viruses have played significant roles in many key aspects of the evolution of life at every level, such as chromatin packing (Sosa et al., 2013), the evolution of the cell (Pradeu, 2016), tissue development (Chuong, 2018) and the Biosphere as a whole (Suttle, 2007; Zhang et al., 2018). It is interesting to note that many years earlier, viruses were considered to be the first living organisms, at the base of the phylogenetic tree (see, for example, Alexander and Bridges (1928) and Haldane (1929)).

Koshland (2002) has targeted a separate set of seven pillars: program, improvisation, compartmentalization, energy, regeneration, adaptability and seclusion. However, compartmentalization would still rule out viruses, endosymbionts and obligate multi-host parasites as living things, in that all rely on other organisms to complete their life cycle and for energy and regeneration.

### 3.1. Molecular approaches

Oparin (1938) was one of the first to put forward a 'metabolism-first' view of life, defining life as a self-regulating system of catalytic reactions. Engels, writing in 1883 (1987, p.578) described life in terms of macromolecules, stating: "Life is the mode of existence of protein bodies, the essential element of which consists in continual metabolic interchange with the natural environment outside them, and which ceases with the cessation of this metabolism, bringing about the decomposition of the protein."

Interestingly, Engels emphasised the importance of the context of the molecules within the energetic (metabolic) natural environment, stressing the continuity of chemistry and physics across the living and non-living Cosmos, a point later picked up by successive thinkers, as we shall shortly see. He also recognized that the ongoing existence of the protein was dependent upon the ongoing relationship with its environment. Dawkins would move in the opposite direction, emphasising that the gene was the only meaningful entity, with the rest of the Earth system dismissed as merely an extended phenotype (Dawkins, 1982).

Another molecular approach was suggested by Joyce (1994) who viewed life as a self-sustaining chemical system that could self-replicate and undergo modification. A different molecular perspective, that of ecosystem chemistry, has been advanced by Muchowska et al. (2020), who suggest that cellularity may merely represent a way of partitioning ecosystem- or planetary-scale metabolism in order to respond to resource heterogeneity across local environments.

### 3.2. Functional approaches

Thus, ecosystem chemistry may be more important than cellular partitioning. Here, the emphasis is on function not form, and the currency of this functionality is energy, while the unit of organization is the ecosystem. This is in tune with the It's-the-song-not-the-singer (ITSNTS) theory of Doolittle and Inkpen (2018). Functionality circles around energetics and moves to a physical, rather than a chemical basis for defining life. Of course chemistry is essential, but the underlying foundations are built of physiological, process-based relationships. Dieguez (2013) focused on such an approach, defining life as a grouping of physiological processes that demonstrate homeostatic properties, very much in line with the Gaian hypothesis (Turner, 2004).

Another functional approach is taken by Farias et al. (2021), who write: "We therefore propose that life should be understood under the ontology of processes. Even if living beings are clearly material entities, they exist due to the continuity of a process. Thus, we understand that living beings consist in the materialization of a process and this process is the actual essence of the life phenomenon." Farias et al. conceptualize life as a metabolic macrocode composed of multiple inter-related layers of coding.

These functional approaches move away from individual organisms, structures and species and towards a systems approach. On this theme, Luisi (1998, p. 620) suggested the following definition for life: 'A system which is self-sustaining by utilizing external energy/nutrients owing to its internal process of component production and coupled to the medium via adaptive changes which persist during the time history of the system".

Self-organization is emphasised by Jianhui (2019) who wrote: "An entity is alive if it has an autopoietic ability to sustain, develop and/or reproduce itself under the control of information stored in it". Interestingly, sustainability of the entity is mentioned here.

## 4. The animate and the inanimate

An even more basic problem arises in determining at what point something can be considered alive. There are many moral as well as scientific issues surrounding this point. Was there a moment in history when something became alive? Is a single cell within a multicellular organism truly alive? Are reproductive cells more alive than somatic cells? Is a multicellular organism alive from the moment of conception? If not, is there an exact moment in development when it becomes alive?

These are not rhetorical nor metaphysical questions, as they can have significant legal implications. Indeed many of the papers relating to this

issue are published in legal rather than scientific journals. Many of these questions relate to the issue of viability, particularly in legal discussions surrounding termination of pregnancy in humans (Dasen, 2013; Romanis, 2020).

Haeckel (1866) stressed that there is no difference in qualities between the inanimate and the animate world (‘*Anorgane und Organismen*’) and, therefore, there is a natural and continuous flux from the one to the other. Thompson (1915, p. 858) had drawn attention to the unification of the living and non-living, with regards to the organizational forces acting upon them, noting that: “There is no essential difference between these phenomena of organic form and those which are manifested in portions of inanimate matter.” Chung et al. (2022) reflected that “there exists an organization principle common to both living and non-living systems”.

This idea of some form of continuum across the material world brings to mind a much earlier conceptualization of life by Von Humboldt. He referred to the living breath of nature (‘*lebendiger hauch der Natur*’), and he considered the natural world as emergent from the harmonious interactions between all biotic and abiotic components. Von Humboldt’s expressed goal in his book, *Cosmos*, was to “grasp nature as one great whole, moved and animated by internal forces” (Von Humboldt, 1997, p. 24). He referred to this interconnection of the physical and the cultural world as ‘*Zusammenhang*’, the idea of ‘hanging together’. Here, life is an integrated system, encompassing the animate and the inanimate, much as in Haeckel’s work. Thus, the transition from abiotic to biotic is seen as a gradient rather than a sharp step, or, as Pascal et al. (2013) put it, life emerged through states of ‘partial aliveness’.

## 5. Thermodynamics

Before considering how thermodynamics impacts upon a working definition of life, a brief recap on the basics of thermodynamics is provided. The study of thermodynamics, the science of energy, lies at the heart of many of the issues confronting us today, from eutrophication to climate destabilization, and from biological diversity to renewable energy technologies. In terms of this paper, thermodynamics forms a framework for a workable definition of life, and an understanding of evolutionary biology, organization and sustainability.

The first law of thermodynamics relates to quantity, and states that while energy can change from one form to another, the total amount of energy remains constant. The second law of thermodynamics relates to quality, stating that processes occur in the direction of decreasing quality of energy (Haddad, 2017), from high quality with low entropy, such as solar radiation, to low quality with high entropy, such as heat (Brillouin, 1960). The second law of thermodynamics has three unique features. Firstly, it is the only physical law dealing with order. Secondly, it states that time has an arrow that tracks irreversible processes. Finally, it predicts the future as statistical probabilities, not certainties.

The entropy of a system is a measure of the amount of molecular disorder within the system. Nielsen and Müller (2023) point out that entropy “can be seen either as a measure of state, i.e., as an indication of the probability in the distribution of elements or as a consequence of the change in energy quality (availability) due to the irreversibility related to a specific process, or sometimes it may be used as both.” A system can only generate, but not destroy, entropy. The entropy within a particular compartment, such as a cell or an organism, can be increased or decreased by the transport of energy across the system boundary.

As increasing entropy is exported into the environment (whatever that environment is), free energy import and material import can become more challenging. As we shall explore later, changes in the energetic context can have dramatic consequences, including regime changes and phase transitions. Free energy is more accurately an indicator of entropy that can be produced at a given temperature (Lineweaver and Egan 2008). The Earth itself is an energetically open thermodynamic system, with radiation incident upon it and heat released from it.

Each level of organization in the Earth system exports entropy, requiring the import of free energy to maintain internal order within an entropic universe. Humans transform roughly the equivalent of their own body weight in adenosine triphosphate (ATP) per day to adenosine diphosphate (ADP), maintaining a state of low internal entropy and, thus, avoiding death (Duval et al., 2020). Wolfe (2002, p.2) notes that: “The biology of (most of) the biosphere depends thus not only upon the energy from the Sun (a source at $T = 6000$ K) but also upon the ultimate sink of energy, the night sky (at $T = 3$ K).”

Berthelot (1879) demonstrated that chemical change moved in the direction of maximum heat production. Onsager (1931) suggested that thermodynamic systems reduce barriers to increasing entropy such that $dS/dt$. $I =$ maximum (where $dS/dt$ represents the rate of entropy change and I is the impediment to entropy increase). In Bénard cells (convection cells that appear spontaneously in a liquid layer when heat is applied from below), I is minimized and $dS/dt$ is maximized.

Ziegler (1963) further developed Onsager’s work, formally defining the maximum entropy production principle (MEPP). In its modern form, the MEPP states that “non-equilibrium thermodynamic systems are organized in steady state such that the rate of entropy production is maximized” (Kleidon et al., 2010). Jaynes (1983) demonstrated that the majority of the possible distributions allowed by constraints have entropies approaching the maximum value. The MEPP adds to the second law of thermodynamics by not only including the direction of change, but the rate of change. It has been widely applied to numerous levels of organization in the Biosphere, as shall be discussed below. For an overview of the historical development of the MEPP, see Chapman et al. (2016).

## 6. Thermodynamic approaches to defining life

Thermodynamics has become increasingly useful in terms of understanding life and the forces impacting on its organization, as we shall discuss. However, more basically, there have been an increasing number of attempts at using this field of study as a foundation for defining life itself. In many ways, the functional, process-driven approaches already mentioned have great resonance with such thinking, and there are many advantages in terms of inclusivity and embracing both the abiotic and biotic entirety of the Earth system.

The first attempt at exploring the centrality of thermodynamics in living systems can be found in the work of Boltzmann (1974 [1886], p. 24), who wrote that: “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.” Aristov et al. (2022) point out that Boltzmann’s theory is not limited to equilibrium states and that statistical entropy of kinetic theory can also be applied to non-equilibrium systems.

Ervin Bauer, the Hungarian theoretical biologist, distanced himself from both vitalistic and mechanistic theories of what life is, formulating the principle of permanent non-equilibrium of living systems (Bauer’s principle) in terms of thermodynamics (Elek and Müller, 2013). Bauer (1920, p.10) defined life as follows: “We call living organisms any body system that is not in equilibrium in a given environment and is so organized that it transforms the energy of its environment into such forms of energy, which act in the given environment against the establishment of an equilibrium state”.

According to Grandpierre et al. (2014), Bauer pinpointed three basic properties of living systems. Firstly, spontaneous changes occur in their states, changes not arising from external causes beyond the body of the organism. Secondly, living organisms in a changing environment display changes that are different from those displayed in inanimate systems. Interestingly, here he emphasises differences between the animate and the inanimate, without indulging in Vitalism. Finally, he emphasised

that living systems function in such a way as to oppose moving towards equilibrium that would otherwise be reached within a given environment. Elek and Müller (2024) point out that Bauer focused on the function of the organisms producing non-equilibrium and the ability of these organisms to alter their functionality in such a way that the system can arrive at a state of non-equilibrium anew. Importantly, Igamberdiev (2024) points out that Bauer's theory represents a relational theory of biological thermodynamics given that the standard to which it refers represents the actual biological function and not merely the abstract state of thermodynamic equilibrium.

Schrödinger (1944, pp. 74–76), building on the work of Boltzmann and Bauer, defined life as that which resists decaying to disorder and to equilibrium, writing: "What is the characteristic feature of life? When is a piece of matter said to be alive? … It is by avoiding the rapid decay into the inert state of 'equilibrium' that an organism appears so enigmatic; … How does the living organism avoid decay? The obvious answer is: by eating, drinking, breathing and (in the case of plants) assimilating. The technical term is metabolism … The essential thing in metabolism is that the organism succeeds in freeing itself from all the entropy it cannot help producing while alive."

Von Bertalanffy (1950, p.23) emphasised this thinking, stating that: "The cell and the organism as a whole, however, do not comprise a closed system, and are never in true equilibrium, but in a steady state". Prigogine and Stengers (1984) again resonate with Bauer, reiterating that life is an open thermodynamic system, where energy is constantly imported from the environment and entropy released into the environment, thus satiating the second law of thermodynamics.

Lovelock (1965, p. 568) underlined the unity of physics across the inanimate and the animate, writing that: "Life is one member of the class of phenomena which are open or continuous reaction systems able to decrease their entropy at the expense of substances or energy taken in from the environment and subsequently rejected in a degraded form".

In a similar vein, Vitas and Dobovišek (2019) defined life as being a self-maintaining chemical system, far from equilibrium, that is capable of processing, transforming and accumulating information acquired from the environment. Macklem and Seely (2010, p.330) defined life as a "self-contained, self-regulating, self-organizing, self-reproducing, interconnected, open thermodynamic network of component parts which performs work, existing in a complex regime which combines stability and adaptability in the phase transition between order and chaos, as a plant, animal, fungus, or microbe." Interestingly, this latter definition fails to embrace viruses, nor obligate parasites as living, as neither are self-reproducing nor, for parts of their lifecycle, self-contained.

Lucia and Grisolia (2017, p. 271) combined process, systems theory and thermodynamics, writing that life is the outcome of "system cooperation between components, with an interconnection between subsystems and super-systems, such that for survival the super-system must export equal or more entropy products than its sub-systems produces, towards maximum conversion of available exergy sources to entropy products."

These thermodynamic, systems-based definitions of life also avoid issues relating to the non-living origins (abiogenesis) of life in the first place. They place life as one of a group of subclasses of systems that remain far from thermodynamic equilibrium, thus viewing life as part of a continuum in line with the same laws of physics and chemistry as the rest of the Cosmos.

Skene (2015) writes that: "Life is merely one expression along the matter-energy continuum. Thus any discussion concerning the origin of life in a thermodynamic context need only relate to material and energy availability, since all other considerations are outcomes of the universal laws of physics."

Nielsen et al. (2020) have suggested that to be alive, the living being should contribute to a delayed energy conversion (a point also made by Vallino, 2010), giving the example of a forest whose capture of energy is distributed into a range of pools, such as standing wood, which may take many hundreds of years to break down and fully release that energy back into the environment through decay. Certainly entropy release often occurs across a broad temporal spectrum, particularly in terms of recycling, while the context of ecosystems also have significant impacts. For example, carbon turnover times range from sixty five years in tundra biomes to fourteen years in tropical forests (Carvalhais et al., 2014). It may be interesting to examine differences in this spectrum across food webs and across different environmental conditions.

## 7. Form and function

In addition to the separation of the animate from the inanimate, the debate as to whether form or function represent the fundamental basis of the organization and evolution of life has raged for centuries. The Venetian Franciscan and architectural theorist, Carlo Lodoli, stressed that form must follow function, as early as the eighteenth century (Kang, 2008). This paved the way for the utilitarian view and it was Georges Cuvier who set out the position that anatomical form followed function.

However form dominated function in key areas of biology, such as diversity, conservation, evolution, taxonomy, phylogeny and, laterally, active rewilding. The morphological basis of taxonomy, championed by Linnaeus, led to species being equivalent to forms, or morphotypes. Thus, diversity and both ecosystem and planetary well-being, became measured by the number of forms present (Skene, 2011). Form-rich habitats were given special protection, particularly if the forms were spectacular.

Lamarck and Darwin would later develop their theory of evolution based on form, featuring, in the latter case, beak morphology in Galápagos finches (though, more correctly, tanagers (Brinkhuizen, 2016)) and the artificial selection of fancy pigeons and pig breeds. Competition was very much based on form, as was sexual selection theory. Bacteria and Archaea, the two most functionally significant sets of organisms on the planet in terms of biogeochemical cycling, were until very recently, fundamentally ignored, as they had little morphological diversity and were so small as to be invisible to the naked human eye. Russell (1916, p. xi) asked: "Is function the mechanical result of form, or is form merely the manifestation of function or activity? What is the essence of life? Organization or activity?"

Form-led thinking leads to the idea of building blocks, or the 'lego complex', wherein solutions to problems can be addressed through engineering these blocks into new structures that are perceived to provide solutions to our current problems such as food shortages, floods and disease. Genetic engineering has long taken this approach. Reintroductions and new introductions of species such as the cane toad or the beaver are seen as a means of fixing the shortcomings of nature and humanity. Yet, when we examine mass extinctions, what becomes clear is that function is restored but the forms are very different before and after the event. This would clearly point to form following function. And the functioning of the planet is thermodynamic and system-based at its heart.

Systems theory and thermodynamics both point away from form as being the central basis of any understanding of life, its organization, evolution and development. Instead, process and function become foundational, with the flow of energy and information, rather than materials *per se*, becoming all-important. It is much more a functional ecology, rather than morphological diversity, that lies at the heart of the Earth system. Jørgensen and Fath (2004) explore a thermodynamic explanation for the evolution of the Galápagos finches at the level of the ecosystem.

Many of the key thinkers on form and its transformation have explored the importance of the underlying functionality and of the forces that drive morphological change. Goethe categorized three aspects of morphology: *gestalt* (form), *bildung* (formation) and *umbildung* (transformation). Goethe emphasised the use of the word 'bildung' as "pertaining to both what has been brought forth and the process of bringing forth" (Goethe [1817] in Zammito 2017, p. 483). This is very

reminiscent of the indigenous, sub-saharan philosophy of '*Ubuntu*', meaning that which is enfolded (*ubu*) and that which is unfolding (*ntu*) (Ramose, 1999, p.50). The idea reflects reality as being within the flux of becoming. This is reminiscent of the original meaning of the term 'evolution', literally, the unrolling of a scroll (Ostachuk, 2018).

In terms of transformation of forms, or *umbildung*, Goethe developed a grid upon which he drew facial profiles. By fixing the profile onto the grid, and mathematically transforming the grid, the profile would then alter. Thompson later adopted this approach, expanding its use to explore morphological transformation in nature, and demonstrated that mathematical transformation of the grid could track morphological changes across related groups of species.

He recognized that form was an outcome of changes in the forces underwriting the form, and wrote (Thompson, 1915, p. 857): "We pass from the conception of form to an understanding of the forces which gave rise to it; and in the representation of form, and in the comparison of kindred forms, we see in the one case a diagram of forces in equilibrium, and in the other case we discern the magnitude and the direction of the forces which have sufficed to convert the one form into the other.

He later expanded on this (Thompson [1917] 1942, p. 16): "Form […] of any portion of matter, whether it be living or dead, and the changes of form which are apparent in its movements and in its growth, may in all cases alike be described as due to the action of force. In short, the form of an object is a 'diagram of forces'".

Thus, we see that Thompson envisages form as merely a representation of the processes and functions that represent the unfolding and much deeper reality. This very much aligns with functional and thermodynamic approaches to defining life as noted earlier. Farnsworth and Niklas (1995, p.355) pointed to the thermodynamic property of diffusion as this force, observing, "We see evolution of design more as a process of diffusion into a space of possible solutions than as a process of scalar optimization".

Thus, not only is there a material continuity across forms, both animate and inanimate, but there is a continuity in the forces that gave rise to these forms. The question then arises as to what these forces are. The answer to this can only be found in bringing together development, evolution and ecology (Skene, 2020).

We have seen that life has been defined in terms of systems theory and thermodynamics in more recent times. This reflects a broader literature addressing ecology, biochemistry, molecular biology and evolutionary biology. Process, rather than form, has become a primary basis for modern thinking, and allows for the laws of physics and chemistry to find their place at the heart of such discussions. We now must ask how life is organized and what is the unit of life?

## 8. What is the unit of life? Levels of organization and thermodynamics

Having explored the spectrum of definitions of life, we now examine the organization of life within the Earth system, taking a thermodynamic, systems theory approach. Systems theory emphasises the interconnectedness of life and thus opens up the idea of integrity across all levels of organization. The Earth system can be seen is a complex suite of components, each interacting with the others and, as such, no single set of components (DNA, proteins, cells, organisms, populations, species, ecosystems and biomes), can be considered in isolation. Each level of organization feeds back upon itself, and is informed by and impinges upon the other levels (Salthe, 2012).

The Earth system is, energetically, an open system. This can build complexity provided that the activity creates more entropy than order in the smallest closed system within which the open system resides (Nicolis and Prigogine, 1977).

The Earth system operates under far-from-equilibrium conditions (Ivanitskii, 2017) and is reliant on the availability of free energy at all levels of organization. Any alteration to the flow of energy through the system, such as an impact winter (Tabor et al., 2020), anthropogenic eutrophication (Marques et al., 2003) or a combination of eutrophication and global warming, such as in the Eocene Azolla event (van Kempen et al., 2012), have the potential to dramatically alter the functioning and structure of the Earth system and the components within it. Energy flows through the Earth system, and the laws of thermodynamics can be seen as the architects of the system as a whole and the behaviour, evolution and development of each level of organization.

Tessera and Hoelzer (2013, p.142) noted that: "The emergence of each of these macroscopic levels of material and dynamical organization involved the initiation of systematic networking among agents at a lower level of organization. The examples listed above required the functional integration among genes in genomes, among cells in multicellular organisms, and among coadapted species in ecosystems." In this section we will examine the importance of thermodynamics in each of the component levels of organization.

### 8.1. Nucleic acids

The genetic code has been seen as the key foundation for the central dogma and neo-Darwinian evolutionary theory. Energy lies at the heart of this genetic material. DNA base pairing is entropy-driven and is coupled to the enthalpy-driven van der Waals base pair stacking (Privalov and Crane-Robinson, 2020). Mutations are frequently the result of random changes through ultraviolet radiation. The code becomes increasingly entropic in terms of its sequence as a result. Correction mechanisms such as base excision repair, mismatch repair, direct damage reversal, recombination repair and nucleotide excision repair while-suboptimal at the code level, help reduce informational entropy, but convert free energy to entropy (Salamon and Konopka, 1992), being energetically expensive processes. Sub-optimality in repair, where some mutations fail to be corrected, provides the basis of increasing genetic variation, though these can also lead to terminal consequences for the organism concerned.

Skene (2020, p.7) suggests that the central dogma acts as an entropy transition mechanism, "with increasing internal information entropy (as the genetic code is continuously randomized), and with increasing external entropy production (as increasingly more complicated structures and functions are produced in the form of new protein morphologies, again determined by the bioenergetic context). The loss of information at the genetic level results in potential gains in information at the protein level."

These changes can be envisioned as leading to the diffusion of life into ecological, population and developmental space, akin to Brownian motion, where changes in protein structure and function are a product of increasing informational entropy within the code, acting across informational, functional and structural levels with consequences for the entire system. See Adami (2002) and Abel (2008) for some interesting thoughts on the importance of information in systems theory and evolutionary biology.

Skene (2020) referred to this as the genetic entropy paradox, wherein DNA increases in internal information entropy, as the genetic code is randomized through mutation, and yet has the potential to increase external entropy production, as increasingly more complex structures and functions are produced, along a path of increasing entropy in the form of new protein morphologies and metabolic pathways and increasing organismal complexity, allowing greater access to ecological space and therefore greater potential for entropic output. We will return to the significance of this when we consider the thermodynamics of evolutionary biology.

Fariselli et al. (2021) state that the physical features of double stranded DNA in conjunction with the maximum entropy production principle can explain patterns and symmetries without any recourse to biological or environmental evolutionary pressure. They state that "the leading force shaping the DNA sequence in the genomes is entropy and that the major cause of all these symmetries is the randomness …

whereas the selective biological processes act as soft drivers, which only under extraordinary circumstances overtake the overall entropy content of the genome."

Michaelian (2011) suggested a cell-free early DNA replication mechanism may have initially formed, akin to PCR, where fluctuating temperatures near the surface of early ocean can lead to strand separation, stating that "the entire replication process is driven by entropy production resulting from the absorption and dissipation of UV photons."

Michaelian and Simeonov (2015) envision that many of the key molecules of life, such as RNA and DNA, the aromatic amino acids and enzymatic cofactors, originally evolved as UV-C dissipators, arguing for a thermodynamic dissipation theory for the origin of life.

One caveat to this idea is that until an ozone layer had formed as a result of oxygenic photosynthesis, damage to the DNA would be considerable at the surface of the ocean. However, the mechanics of replication and genomic organization could have continued as an early molecular experiment, quite independently from any coding function. The coding could become stabilized much later by ozone protection, with the original driving force being the dissipation of high energy radiation. Here, these early molecules can be seen as an exaptation, adopting different roles over time, with changing conditions.

Marenduzzo et al. (2006) concluded that "the second law of thermodynamics acts through nonspecific entropic forces between engaged polymerases to drive the self-organization of genomes into loops containing several thousands (and sometimes millions) of base pairs." Kak (2023), examining entropy relations in codon redundancy, found that "the use of maximum entropy transformation creates new constraints that are likely the reasons for the non-uniform codon groups and codons with no redundancy".

### 8.2. Amino acids

Early abiogenic amino acids form along a thermodynamic gradient (Higgs and Pudritz, 2009; Szőri et al., 2011). Thermodynamic constraints, relating to the availability of amino acids, limited early coding. Over time, increased entropy of formation became possible, potentially leading to the evolution of biogenic amino acids (Akashi and Gojobori, 2002; Seligmann, 2003). Thus, early coding would have involved a much smaller pool of amino acids whose entropy of formation was lower, with additional amino acids becoming available as more sophisticated anabolic pathways evolved, utilizing more free energy and with increased entropy of formation (Saier, 2019).

Hatzimanikatis et al. (2005) demonstrated that the native metabolic pathways for phenylalanine, tyrosine and tryptophan were thermodynamically more favourable than the alternative possible pathways, suggesting that these metabolic pathways have evolved under the pressure of thermodynamic constraints. It is likely that amino acids existed before the genetic code and so thermodynamics provides the best explanation in terms of their prevalence and evolution through time (Vranova et al., 2011). In this scenario the genetic code maps onto the thermodynamic outcome of amino acid synthesis (Trifonov, 2004), where a peptide world predates an nucleic acid world (Fried et al., 2022).

### 8.3. Proteins

While there is broad acceptance that the folding and function of proteins is thermodynamically determined (Anfinsen, 1973; Lazaridis and Karplus, 2002), Sorokina et al. (2022) point out that the native state of proteins is impacted by the local fluctuating free energy landscape and thus will not occupy a global free energy minimum. This point is important at every level of organization, wherein local interactions and environments are themselves outcomes of the complex interactions across the Earth system, and are unlikely to resemble reductionist experimental systems. Thus, protein structure and function are seen to emerge from the particular thermodynamic context in which the structure exists. In most cases this is the immediate cellular environment, but contextualized within the wider interactions of the Earth system. Arango-Restrepo et al. (2018b) demonstrate that while enzymatic evolution can be seen to enhance kinetics, more fundamentally, it maximizes total entropy production.

### 8.4. Metabolism

Unrean and Srienc (2011) demonstrated that metabolic pathway fluxes are redistributed in such a way as to achieve the maximum rate of entropy formation (see also Srienc and Unrean, 2010). Du et al. (2018) point to key roles played by pathway thermodynamics and cofactor use in the evolution of metabolic network structures and pathway choices. Working on some of the earliest metabolic pathways, tracing back to the last universal common ancestor, Wimmer et al. (2021) discovered a unique thermodynamic link between the geochemical environmental conditions of early Earth and the core biochemical pathway network, noting that: "The biosynthetic reactions of the last universal common ancestor represent a natural thermodynamic tendency of metabolism to unfold from energy released by reactions of $H_2$, $CO_2$, $NH_3$ and $H_2S$ in the presence of phosphate".

Nath (2019) reported that in oxidative phosphorylation, ATP synthesis, a key biochemical reaction, was compatible with the maximum entropy production principle. Similar results were found for the forward rate constants in β-Lactamase enzymes (Dobovišek et al., 2011), metabolic networks in *Saccharomyces cerevisiae* (Bordel and Nielsen, 2010) and the activation of signalling proteins (Weber et al., 2015).

### 8.5. Viruses

Given that viruses are excluded from the categorization of living organisms by many definitions because of their lack of cellularity, their reliance on other species cellular machinery and their overall lack of autonomy, we include a brief summary of some recent research on thermodynamics in the field of virology. We have seen that each and any component of the Earth system is dependent upon other components, both in terms of evolution, functioning and organization. Koonin and Starokadomskyy (2016) comment that: "The entire history of life is a story of parasite-host coevolution".

it is worth noting that all eukaryotic life is reliant upon mitochondria, while the chloroplast represents the major free-energy acquisition mechanism, and thus the ability to remain far from equilibrium, across the Biosphere. Both of these organs began as independent organisms before either being swallowed (Sagan, 1967) or infecting (Skene, 2023) their proto-eukaryotic host.

An increasing number of studies have shown the centrality of thermodynamics in understanding viral capsid assembly (Katen and Zlotnick, 2009; Alexander et al., 2013; Perlmutter and Hagan, 2015), infectivity (Gale, 2018; Popovic, 2022; Popovic et al., 2023), pathology (Dutta and Chattopadhyay, 2021; Tempera and Lieberman, 2021) and evolution (Jones et al., 2015; Tenthorey et al., 2022; Popovic, 2023).

Popovic and Minceva (2020) not that: "By comparing the Gibbs energy of growth of viruses and their hosts, it has been found that a virus always has a more negative Gibbs free energy of growth than its host, implying that synthesis of viral components is more thermodynamically favourable."

### 8.6. Cells

Living cells are best understood as open, dissipative and far-from-equilibrium systems that lower the internal entropy through an influx of energy and material. Compartmentalization is an important property. Entropy production and export of entropy requires a supply of free energy and the presence of electrochemical potential gradients to maintain a metastable far-from-equilibrium state.

Being open thermodynamic systems, the maintenance of gradients is essential, otherwise they would dissipate to equilibrium. Phospholipid membranes, together with proteins, provide the wherewithal to achieve this, using free energy in terms of active transport (Marína et al., 2009; Davies et al., 2013). Marína et al. (2009) note that: "To reach and maintain different concentration of solutes in cell compartments consumes energy and the global process is dissipative, obviously resulting in net production of entropy". Compartmentalization may well be the main contributor to low internal entropy.

Bich et al. (2016) note that while kinetic control represents a transition from systems driven towards equilibrium by thermodynamics laws towards equilibrium to systems with much more improbable molecular species, through the conversion of free energy to work, releasing entropy, this control is only possible with spatial control through compartmentalization. This in turn allows the control of the thermodynamic flow of energy and matter, maintaining the system far from equilibrium. Cellular metabolic networks and cell organization have also been found to evolve towards maximum entropy production (Unrean and Srienc, 2011; Day et al., 2022).

### 8.7. Individuals

The delineation as to what an individual consists of and where its boundaries really end is a contested subject. Is it a meaningful level of organization? Some ninety percent of plants are mycorrhizal, living with fungal partners and, often, connected to other plants, sometimes of different species. Bacteria share DNA through plasmid transfer, and often live in complex communities called biofilms. Lichens consist of a fungal and algal partnership locked together, while Cnidaria share their identities with dinoflagellates. Then there are clonal organisms, such as many plants, produced from vegetative reproduction.

Even if we consider an organism to be a unique individual, their reliance upon a source of free energy, nutrients and water along with access to sufficient habitat to acquire these things means that they are essentially dependant on their environment for existence. This is more than a philosophical point. The supply chains upon which a particular individual organism requires, potentially including a mate for sexual reproduction, mean that there is an obligate interaction with many components within the Earth system. This is what results from existing far-from-equilibrium in an entropic universe.

We propose that the glue holding the various components together, be they lichen, mycorrhiza, or food webs, is the increased dissipation of free energy achievable through such interactions. Thus, 'altruism' is driven by the second law of thermodynamics as are the many other relationships found throughout the Earth system. The entire system is driven by this. Bienertová-Vašků et al. (2016) demonstrated that entropic production follows the logistic path of maximum entropic production in individuals, where entropic production rises then levels off towards an asymptote. This is likely to be best explained by the maximum entropy production principle (MEPP).

### 8.8. Populations

We encounter similar logistic growth in populations, which again follows the MEPP, wherein K (the carrying capacity) can be seen to represent $S_{max}$ (maximum entropic output) (Skene, 2013). Increased free energy availability allows population increase within ecosystem constraints (Aoki, 1995). Here we can see that constraints limiting the maximum entropic production can be changed, altering this maximum. In terms of population dynamics, Andrae et al. (2010) demonstrate that entropy production can successfully characterize ecological systems with cyclic population dynamics.

Cooperative behaviour, the costly provision of benefits to others, is a common trait in many populations. Again, the costs are converted to entropy production, and therefore would be expected in a complex dissipative system, representing another form of entropy-generating interconnectedness.

### 8.9. Species

The species concept is a contested issue, as much so as is the definition of life or of the individual (Clarke and Okasha, 2013). Exploration of ecospace through random mutations delivers increased diversity, expressed as speciation if reproductive barriers are in place (though many 'species' can breed with other species). Speciation is a eukaryotic trait, since bacteria share DNA plasmids between taxa making the traditional species concept redundant for prokaryotes (Cohan, 2002; Skene, 2009).

Pierce (2002), building on the work of Wicken (1980), argues that speciation is a result of bifurcation points due to increasingly complex and disorganized information leading to a type of tipping point, represented by a new species. The entropic drive to randomness pushes the system to a new state.

### 8.10. Ecosystems

Ecosystems are self-organizing, self-regulating, self-contained, open thermodynamic networks built from components that evolve as complex systems, combining adaptability and stability in the phase transition between order and chaos (Jordan, 2022). Ecological succession (the predictable, directional development of an ecosystem) follows the MEPP (Aoki, 1987; Ludovisi, 2004; Meysman and Bruers, 2007) with ecosystems moving towards maximum entropy production (Skene, 2013 and references within). The MEPP has been demonstrated to play an important role in ecosystem processes such as hierarchical organization, trophodynamics, zonation, hydrology, spatial organization and spatial interactions (see Vallino, 2010; Ma and Qian, 2015; Skene, 2017).

It is argued that the directionality in ecosystem development is an outcome of the entropic drive. Many questions have been asked relating to if complexity increases with time (see McShea, 1991). In thermodynamic terms, all that is required is dissipation, an outcome of export of entropy from dissipating structures. This entropic drive leads, invariably, to increasing complexity, but increasing dissipation, not complexity, is the direction of travel.

Increasing complexity brings increasing entropic dissipation at the individual level. The advent of multicellularity, cellular specialization, increasing size and homeothermy all increase entropy production (Davies et al., 2013). Kondepudi et al. (2020) state that "dissipative structures come into existence in the service of degrading energy potentials." Gross and net primary productivity of forests is positively correlated with structural complexity (Gough et al., 2019; Toda et al., 2023) leading to increased exergy uptake, exergy storage, entropy production and increased adaptability of the ecosystem (Seidel and Ammer, 2023).

The maximum entropy possible is determined by constraints, much as in evolutionary biology (Skene, 2015). These constraints represent physical limits from the environment of the system, such as limitation of availability of chemical resources, space and energy. In a multi-level hierarchical system, constraints represent feedback from every other level of organization. The lower level is subject to the constraints by the upper level, and one may assume that it is the upper-level sub-system itself that creates these constraints (Auger, 1989).

### 8.11. Biomes

Ecosystems are located within biomes, and these impact hugely in terms of what lies within them. Energy and surface topography, including the angle of any given position on the globe to the incident radiation, are key determinates of biome function. Biome conditions are determined by solar radiation density, driving the hydrological cycle and forming the context within which any given ecosystem is shaped (Kleidon, 2009; Skene, 2013). Seasonality, temperature and rainfall

characteristics then impact on other important properties such as soil development, nutrient availability and wind direction and strength. Global circulation patterns, climate systems, marine biogeochemical cycles and hydrological processes follow the MEPP (Paltridge, 1979; Polyakov, 2001; Herbert et al., 2011; Westhoff et al., 2014; Vallino and Algar, 2016). Thus, physical properties of biomes are, fundamentally, outcomes of energetic variation across the planet and operate within the MEPP.

## 9. System properties and thermodynamics

Having seen how each level of organization in the Earth system is shaped by thermodynamics, we next need to understand how these different levels combine, producing the Earth system as we know it. To do this we will consider the role of thermodynamics in six important characteristics of any complex system: self-assembly, self-organization (inc. autonomy), emergence, non-linearity, feedback and sub-optimality.

### 9.1. Self-assembly

Complex systems self-assemble. Each component within the system also assembles within the context of the greater system. Thus, we cannot understand component assembly without reference to the assembly environment, both in terms of energy and resources. The environment is itself an outcome of the system. In terms of origins of the components of the early Earth system, there are many unknowns, both in terms of the conditions at the time and in terms of the historical pathways taken as the system assembled and grew in complexity.

Resources, information and energy must be contemporaneously available at appropriate temperatures. Furthermore, once assembled, components may become resources for the assembly of other components. From molecule to ecosystem, there is a continuous process of self-assembly. This has been elegantly demonstrated by Arango- Restrepo et al. (2018a, 2019a, b). Non-equilibrium self-assembly is accompanied by energy dissipation (van Rossum et al. (2017). Indeed, it has been demonstrated that knowledge of energy and matter dissipation related to the formation of self-assembled structures allows their architecture to be determined (Arango-Restrepo et al., 2019b).

The building blocks of non-equilibrium self-assembling units (NESAs) also serve as non-equilibrium self-assembling units, each operating within the maximum entropy production principle, given barriers and feedback (Bezryadin and Kountz, 2016), while contributing physically to the next level of organization. Thus, self-assembly is an ongoing process throughout the system.

### 9.2. Self-organization

Self-organization can be defined as the difference between the information the system receives (input) and the information the system produces (output). Schrödinger (1944) proposed that biological self-organization and thermodynamics would be reconciled by the study of living systems from a non-equilibrium perspective. This was important in that it emphasised systems theory as well as thermodynamics as important elements in any understanding of life.

Living systems should increase in organization, complexity and order as an outcome of the entropic drive from the second law of thermodynamics (Brooks and Wiley, 1988). Vitas and Dobovišek (2019) highlight thermodynamics as the underlying self-organizing principle of any system that lies outside thermal equilibrium. Self-organization is a system level phenomenon, and each component level should only be understood within the greater system (Bechtel, 2007). Odum (1995) states that “during self-organization, system designs develop and prevail that maximize power intake [and] energy transformation”.

Dincer and Cengel (2001, p. 123) point out that “systems that exchange entropy with their exterior do not simply increase the entropy of the exterior, but may undergo dramatic spontaneous transformations to self-organization." Thus, thermodynamic laws dictate that any system that delivers an irreversible flow of entropy will undergo self-organization (Prigogine et al., 1972; Henry and Schwartz, 2021).

Fränzle (2000) noted that the formation of gradients, such as temperature leading to heat flux, or chemiosmotic and electrochemical gradients in terms of chemical reaction rates, are some of the most conspicuous representations of self-organization.

Autonomy is a system property, rather than that of any individual component. All components are defined by their system context. Ruiz-Mirazo and Moreno (2004) define autonomy as the capacity of a system to modify, control and regulate self-constructive processes assembly and the exchange of material and energy with its environment. Thus, the system must be able to generate and regenerate all of the constraints that in turn limit the entropic output throughout.

Deacon and García-Valdecasas (2023) comment as follows: “This leaves us with a conundrum. In order to generate and maintain organization, living processes must take advantage of self-organizing processes, and yet they must also prevent these processes from depleting the very gradients that drive them. So, how can life both use self-organization at the same time that it prevents or holds off its terminal tendencies? This conundrum can only be resolved by recognizing that different self-organizing dynamics interact in ways that complement one another.”

### 9.3. Emergence

Perhaps no property is discussed more than is emergence. Emergent systems display characteristics and responses that belong to the whole, rather than the parts (Bedau and Humphreys, 2008). They are so important because they lie at the heart of what is referred to as wicked problems. In the human sphere, emergent properties make it extremely challenging in terms of predicting outcomes and directly interceding. They lie at the heart of the precautionary principle (Van der Sluijs et al., 2005; Rechnitzer, 2022). Thus emergence presents ethical as well as scientific challenges.

Emergent properties are both consequential upon the underlying components and autonomous from them (Bedau, 1997). Emergence can be considered as a measure of the information that a system produces, relative to the information that the system receives. Ontology is the study of the emergence of being, becoming, and of existence itself. Van den Berg et al. (2022) observe that: “Emergent properties—patterns or functions that cannot be deduced linearly from the properties of the constituent parts—underlie important ecological characteristics such as resilience, niche expansion and spatial self-organization.”

Patten (1998) has demonstrated that cycling of energy leads to intricate, emergent properties, while Roach et al. (2019) assert that the generation of complexity and natural organization is an emergent property of entropy in systems maintained far from equilibrium. Overly complex systems lead to excessive energy leakage while over-simplified systems lead to fragility in the face of a dynamic environment, due to the lack of redundancy.

This is akin to the intermediate disturbance hypothesis, and suggests a thermodynamic basis for this idea. Certainly, this balance between excessive and insufficient complexity will play a key role in the sub-optimality observed in systems, and, more fundamentally, as a constraint setting limits to the maximum entropy production possible within a given system. We see this in many other aspects, such as trophodynamics (Banville et al., 2023), mutation rates (whether directed or otherwise) (Skene, 2017), fire ecology (He et al., 2019) and population dynamics (Frazier et al., 2006; van den Berg et al., 2022).

### 9.4. Non-linearity

Systems can exist at the ‘edge of chaos’, meaning that slight changes to initial conditions can bring about unpredictably different outcomes.

This has been labelled the 'butterfly effect', and can be seen to underpin non-linearity (Lorenz, 1972). In complex adaptive systems, there is the potential for multiple basins of attraction, wherein the system can shift suddenly to a completely different arrangement (re-organization), sometimes irrevocably. Such dramatic shifts or bifurcations can occur rapidly and without warning and are some of the most concerning aspects of Earth system dynamics for components such as humanity, representing unintended consequences of human activity (Arnold 1994; Schefer et al., 2009; Rocha et al., 2015).

Heylighen (2001) highlights the fact that feedback across the components of a complex system mean that any self-organizing system will typically experience non-linearity. Non-linear systems may have a number of possible stable states, and this number tends to increase as the system is pushed farther from its thermodynamic equilibrium by increasing inputs of energy. The dynamic environments within which all components of a system exist mean that to function adequately, enough stable states must be available to respond to all of the perturbations but not so many as to lead to chaos. This is another situation that resembles the intermediate disturbance hypothesis.

Such transformations are thermodynamically driven. Under far-from-equilibrium conditions, a particular state can become unstable (Kondepudi et al., 2020). When this occurs the system can make a transition to an alternative dissipative state, governed by feedback from across the Earth system. This can be seen in phase transition in ecological succession (see below). Given the complexity and dynamic nature of such feedback, we are dealing with a black box situation with significant unpredictability in terms of the emergent temporal and spatial outcomes. Oster et al. (1971) suggest the use of network theory to form a bridge between systems theory and thermodynamics.

### 9.5. Feedback

Feedback is the lifeblood of any complex system, forming the connection across space and time. Feedback is legion, with many different types of feedback acting simultaneously, impacting specifically and more generally, positively and negatively (often simultaneously), directly and indirectly. Feedback operates throughout the system, not just at any particular locus of component organization.

Regulation, according to Bich et al. (2016), requires that the self-maintaining organisation generates additional dedicated subsystems whose function is to handle dynamic feedback. However, while feedback plays an essential role in self-organization, non-linearity means that feedback does not ensure resilience nor regulation. This is because it is the system as a whole that is the emergent entity. Thus, regulation is by no means optimized for any given component. Sub-optimality, as we shall see, is an essential property of any fully functioning system. This is key to understand regulation at different levels of organization.

Thus, regulation, homeostasis, sustainability, evolution, resilience, resistance and robustness are properties of the system, not the components, and cannot be designed or imposed at the component level (Skene, 2021). Hence, we must focus on Earth system sustainability and evolution if we are to understand component sustainability and evolution. Integrated functionality, not individual form, is the basis of all of this in a thermodynamic, system-based universe.

Feedback lies at the heart of change and continually challenges systems, sometimes driving them to dramatic transition (non-linearity). Feedback loops are central to cybernetics. However, the idea of a loop can be misleading, given the sheer complexity and interactivity of feedback at so many spatial and temporal levels. We suggest that 'feedback networks' would be a better term. Emergence results from the complexity of such feedback networks, while trade-offs are fundamental requirements in order to meet such a disparate array of challenges. Feedback can operate across a vast time scale, from the immediacy of molecular interactions through to the post-glaciation isostatic shifts or ecological relaxation following the disappearance of land bridges, which can act over millennia (Whitehouse, 2018; Chen et al., 2023).

Components that build relationships with other components create the opportunity to either metabolise formerly unavailable free energy, increase that metabolism through accessing key nutrients that were previously limiting metabolism, access previously unavailable ecospace, or all of the above. This is an important observation, emphasising the significance of the entropic drive in understanding collective functioning, such as mycorrhizal symbiosis, endosymbiosis, nitrogen fixation, altruism, multicellularity, ecosystem functioning and autonomy of the whole. Thermodynamic feedback leads to the directionality so evident in so many components of the Earth system.

### 9.6. Sub-optimality

The concept of efficiency or optimality in biology generally relies on a linear, reductionist notion of the planet. This idea has become widespread, with terms such as eco-efficiency appearing regularly in ecological and sustainability literature. However, in any complex system, sub-optimality is an inherent property of any given component because of the myriad of challenges facing that component and the dynamic landscape in which it exists. We have already noted that Farnsworth and Niklas (1995, p.355) observed that: "We see evolution of design more as a process of diffusion into a space of possible solutions than as a process of scalar optimization". Bejan (2023) noted that even a one percent imperfection in performance results in a sizable capacity to arrive at an achievable design approaching perfect performance. Bajan concludes that: "The evolutionary designs reveal the physics behind the phenomenon of diminishing returns in the vicinity of the mathematical optimum".

No single process can be individually optimized because of trade-offs with other processes. Sub-optimality operates at a number of levels: thermodynamic sub-optimality, evolutionary sub-optimality and process sub-optimality.

#### 9.6.1. Thermodynamic sub-optimality

Sub-optimality lies at the heart of the second law of thermodynamics, wherein the conversion of free energy to work is inefficient because of the loss of some of that energy as heat (Kondepudi et al., 2020). It can be argued therefore that inefficiency is a measure of entropy production. Thus, the second law demands sub-optimality. However, trade-offs throughout a system are also consequences of the inability to respond to any single challenge optimally, because other challenges require a response too.

Eco-inefficiency represents the reality that since life is a dissipative process, waste is its signature (Skene, 2017). These processes are thermodynamic outcomes. As a result, asymptotes do exist and limitations are evidenced by the maximum entropy production principle, wherein, a ceiling in entropy production is evidenced. Chodera and Mobley (2013) note that entropy and enthalpy often trade-off in what is known as 'entropy-enthalpy compensation'. We see this also in trophodynamics with food pyramids representing loss of some ninety percent of the free energy between each trophodynamic level.

#### 9.6.2. Evolutionary sub-optimality

Trade offs shape biological evolution in many ways. In evolutionary terms, a trade-off represents a concomitant increase in fitness delivered by a change in one trait being impacted by a decrease in fitness due to a change in a second trait. Life history traits are sub-optimal, as a result of trade-offs, and a balance must be reached. In *Drosophila melanogaster*, early fecundity leads to decreased longevity, while lactating red deer have reduced overwintering survival (Zera and Harshman, 2001). Mooney et al. (2010) conclude that trophic control is driven by evolutionary trade-offs in plants, rather than herbivore density or carnivore predation of herbivores.

Evans (2010) found that smaller, less ornamented (less colour spots) guppies produce faster swimming sperm than larger, more ornamented

fish, defying sexual selection arguments. This is the result of limitations in energy availability, wherein the brightly coloured guppies must invest energy into production of this ornamentation, leaving less energy for investment in sperm, and thus impacting on reproductive fitness.

Mautz et al. (2013) conclude that: "There is thus little support for secondary sexual characteristics being honest indicators of ejaculate quality contra predictions of the phenotype-linked fertility or fertility-benefits hypotheses."

#### 9.6.3. Process sub-optimality

There are trade-offs between catalytic activity and protein solubility as evidenced by the fact that mutations that increase protein solubility decrease catalytic activity (Klesmith et al., 2017). Furthermore, Bigman and Levy (2020) found that allosteric pathways may be abolished as a result of a trade-off between increased stability and decreased flexibility.

In their native states, natural proteins are not optimized for thermal stability. This is thought to be because this would impact on the ability to degrade proteins when necessary. Interestingly, a similar principle relates to designing long-life products in manufacturing. While they may reduce the need for material turnover in replacing short life products, the energetic and chemical demands in ultimately recycling them would be extremely high. Thus, generally in the Earth system, rapid turnover is favourable, freeing up resources and allowing access to otherwise locked-up materials.

Haynie (2001, p.307) writes that "Assuming proteins must be optimized for something, maybe that something is compatibility with all aspects of its existence as a biological entity, from the availability of amino acids to folding on the ribosome, to transport, biological function, and degradation." We would extend this further, to Earth system functioning. Bigman and Levy (2020) suggest that trade-offs are not solely related to biophysical properties of the proteins but also to evolutionary and functional aspects. Such system-based limitations are thought to explain the limitations upon protein function, often called 'protein frustration' (Ferreiro et al., 2014). Ulanowicz et al. (2014) state that by operating in a sub-optimal way, ecosystems can avoid becoming unstable.

Trade-offs are found at every level of organization and are essential for the stability of the Earth system as a whole, limiting excessive responses to environmental perturbation. Mutation correction mechanisms, if perfect, would lead to a lack of genetic variation. Indeed, inefficiency and sub-optimality are central to the functioning of any ecosystem (McCaughey and Tomback, 2001). Ecosystem redundancy plays a key role in resilience (Cowling et al., 1994).

Sub-optimality is a clear fingerprint of a functioning system. Multiple processes cannot be individually optimized. As the number of challenges increase upon a process, only solutions that are increasingly sub-optimal for each challenge will work. We would further suggest that sub-optimality will also explain what has been identified as intermediate disturbance, in that a balance between optimality and chaos will be found at a system level, allowing the maximum entropy production to be achieved within the dynamic constraints present, with adequate, emergent trade-offs to allow the continued function of the dissipative system as a whole.

## 10. Evolution

Focus on thermodynamics as an explanation as to how life evolved has existed for well over a century. As early as 1886, we have noted that Boltzmann asserted that the struggle for life was not for materials or free energy, but for entropy, through energy dissipation, in line with the second law of thermodynamics and the entropic drive. Lotka (1922, p. 149–150) wrote that: "Evolution, in these circumstances, proceeds in such direction as to make the total energy flux through the system a maximum compatible with the constraint", adding that "life must have tended to increase rather than decrease dissipation."

Pike (1929) argued that thermodynamics provided the driving force for organic evolution, while Blum (1935) pointed to the laws of thermodynamics as explaining the directionality of evolution. More recently, Layzer (1988) pointed to the second law for directionality, writing: "All physical laws, with one exception, fail to differentiate between the two directions of time. The one exception is the second law of thermodynamics, which asserts that all physical processes generate entropy. Therefore, it seems logical that evolution, which more than any other natural phenomenon distinguishes between the direction of the past and the direction of the future, could ultimately derive its 'arrow' from the second law." Wicken (1986) noted that the entropic drive underlies the phenomena of both speciation and variation, chiding Darwin for separating biology from nature's overall dynamics.

Many recent authors have written detailed reviews of current thinking in the field of evolutionary thermodynamics, building on these earlier foundations (see, for example, Prigogine et al., 1972; Skene, 2009, 2015; Kondepudi et al., 2020; Nielsen et al., 2020; Martyushev 2021).

Evolution occurs over vast time scales and it is impossible to examine this experimentally, due to the complexity of the Earth system and the dynamic conditions across billions of years. However, natural events through the history of the Earth have allowed us to examine the tempo of evolution, namely, mass extinction events (Skene, 2015). Following such huge perturbations to the Earth system, often driven by a dramatic drop in incoming solar radiation due to impact winters, the diversity of life collapses, as the Earth system, an open, far-from-equilibrium system, is dependent upon free energy to persist in an entropic universe. There is then a rapid diversification, where life diffuses into available ecological space, creating further ecological space through niche expansion (Sexton et al., 2017; Sjödin et al., 2018). Entropy production increases in a parallel fashion (Skene, 2015). When all available ecological space is filled, the diversification rate levels off at an asymptote (Walker and Valentine, 1984), aligned to the maximum entropy production. The trajectory resembles a logistic curve (Sepkoski, 1982; Aberhan and Kiessling, 2012; Song et al., 2018).

A diffusional model of evolution, rather than a competitive selection model, has come to the fore recently, which is predicted from thermodynamic considerations (Skene, 2015). Benton (1996) found that expansion into empty space, in the form of new niches, was the key factor in tetrapod evolution rather than competition-driven displacement, while Venditti et al. (2010) noted that most biodiversity emerges not from evolutionary conflict, but from rare and infrequent events, particularly extinction events, where empty ecological space is created and where diffusion into that empty ecospace is seen as the most likely scenario.

Brusatte et al. (2008) again place no importance on competitive superiority, instead viewing historical contingency as key, while Alizon et al. (2008) observe that competition for resources actually slows down the rate of evolution, as happens during recovery from a mass extinction event, when approaching maximum entropy production. Mahler et al. (2010), working on the evolution of Greater Antillean anoles, again recognize opportunity, not competition, as being of central importance. Finally, Phillimore and Price (2008, p.1) similarly write, relating to bird evolution, that "speciation slows as the ecological opportunities and geographic space place limits on clade growth".

Hence, we see a picture continually emerging from the fossil record of life diffusing into available space, increasing in complexity as ecosystems develop, followed by a slowing down of diversification as opportunities decrease and as selective pressures increase. This is exactly what is predicted through thermodynamics and system theory, as entropy production builds to a maximum allowable within the constraints and then enters a dynamic equilibrium, as does diversity, until the next significant perturbation or tipping point. As the components self-assemble and as the Earth system self-organises, in the direction dictated by the entropic drive, we can see that thermodynamics explains both the structure and functioning of the levels of organization, and the interactive properties across the Earth system.

Sub-optimality, feedback, emergence and non-linearity can be seen as the architects of the plan, but the client, whose demands and direction completely guide the architect, is the second law of thermodynamics. Natural selection is a symptom of one phase of the process, the asymptote, signifying the approach of the system toward maximum entropy production. However, diversification is dependent on available ecospace and the opportunity this represents, not competition, and is a diffusive process within the multidimensionality of the Earth system, where network feedback leads to emergent properties throughout the system, including life itself, and whose directionality is the outcome of the entropic drive.

## 11. Succession and thermodynamics

Ecological succession represents the predictable, directional development of ecosystems either from newly available substrates such as sand accumulation at the sides of a river estuary (primary succession) or following natural or anthropogenic perturbation. Both predictability and direction point towards a meaningful *bauplan* acting at a level far removed from individual, species or populations. Rather we see a system-wide development whose directionality belongs to the system, not the components.

Succession is so important because it traces the assembly and evolution at a level beyond the species or population, and is a key determinant of which species exist together. Across this developmental process, there is no place for many of the Darwinian concepts in terms of fitness and competition. Instead, whole suites of species disappear and new species appear at regular intervals during the developmental process, in what is referred to as phase transitions. This continues, phase after phase, until a more stable long-lasting community eventually emerges, such as an oak forest, which will remain in place until perturbed by, for example, fire, resetting the whole process.

Another form of ecosystem development is cyclical succession. In Scottish uplands, lichens initially invade bare soil before declining. The soil is then invaded by bearberry, which is then replaced by heather. After around thirty years, the heather dies back and is replaced by lichens and the whole process repeats (Barclay-Estrup and Gimingham, 1969). This process can be disturbed by nitrogen pollution.

In both these situations, how fit a particular individual or population is will have no impact in terms of their continued existence. The outcomes are determined at the ecosystem level, not the level of the gene, individual nor population. Species must fit into a succession at an appropriate phase if they are to find their place within an ecosystem. The evolution of species must therefore be seen within the context of ecosystem succession. A further point is that the suites of species existent in a mature forest are mostly connected by mycorrhizae which form an underground network. Plant species that are not connected to this network will find it difficult to establish themselves successfully (McGuire, 2007; Liang et al., 2020; Guy et al., 2022).

Margalef (1968, p.81) 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."

The phase transitions can be understood as non-equilibrium changes where a change in some thermodynamically critical point is reached, punctuating the stasis and leading to regime change (Michaelian, 2005), a classic example of non-linearity. Directionality can be clearly seen in terms of increasing complexity and heterogeneity (Averiss and Skene, 2001) and increasing entropic output. Ecosystem also move along particular functional gradients through time (see, for example, Odum (1969), Neutel et al. (2007) and van de Koppel et al. (1997)). Thermodynamic constraints also operate across food webs throughout succession. Lindeman (1942) demonstrated that there was a reduction in energy availability at each trophodynamic level, due to thermodynamic constraints on energy flow, where only a small fraction of the energy in one trophic level was available to the next one, due to waste.

Thermodynamics best explains what underpins this directional, predictable process of succession, acting at every level of organization, and underpinning evolution as well as ecology (Skene, 2017). The MEPP has been shown to hold for the process of ecological succession in Mediterranean, lake, marine sediment and tropical rain forest ecosystems. Here, entropy production increases slowly during early stages, increasing rapidly before reaching a maximum at the climax, following a logistic curve in each case (see Skene, 2013 and references therein). Such logistic curves occur at many levels of organization and it has been argued that this recurrent pattern, whether across ecological succession, determinate development in individuals or population growth curves, result from the maximum entropy production principle (Martyushev and Axelrod, 2003).

## 12. Conclusions

This paper sets out an argument for the direction, evolution, function, organization and definition of life on Earth lying within and emerging from the dynamic relationship between system theory and thermodynamics. We have shown that a thermodynamic, system-based definition of life offers huge advantages in contrast to other approaches, particularly in terms of embracing the grey areas between animate and inanimate, species, the integration of the different levels of the Earth system to each other, directionality, issues relating to what an individual actually represents and of function and form.

Each level of organization within the Earth system can be seen to function within the laws of thermodynamics, while being part of an integrated system. Paredes et al. (2023) emphasize the necessity of studying entropy and complexity as integral organic descriptors. Forms represent physical representations of diffusion into ecospace, driven by random mutations in nucleic acids. The entropic drive provides direction at each of these levels. Function, rather than form, is restored following mass extinction events.

Systems theory bring an important set of processes to the table, and we have seen that thermodynamics underpins such characteristics as self-assembly, self-organization, emergence, non-linearity, feedback and sub-optimality. The integration of systems theory and thermodynamics provides the full explanatory power with which to understand the evolution, functioning, structure and organization of the Earth system.

Finally, we explored how evolutionary biology and ecological succession lie at the heart of any understanding of thermodynamics and systems theory, and provide clear evidence of the superior explanatory power of the entropic drive as the driver and direction of change. The integrated relationship across both evolutionary biology and ecological succession provides a significant unifying explanation for both fields, a truly unique outcome in comparison to other approaches such as the selfish gene hypothesis. We also note the importance of the entropic drive in understanding collective functioning, such as mycorrhizal symbiosis, endosymbiosis, nitrogen fixation, altruism, multicellularity, ecosystem functioning and autonomy of the whole. Sub-optimality and the MEPP can be seen to explain observed patterns formerly identified as the intermediate disturbance hypothesis.

Bauer's contribution, in terms of non-equilibrium, runs throughout this paper and he is recognized as a foundational thinker in terms of the now rapidly developing field of biological thermodynamics.

## CRediT authorship contribution statement

**Keith R. Skene:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

## Declaration of competing interest

I hereby notify the journal, Biosystems, that there is **no** financial/personal interest or belief that could affect the author's objectivity. As the author, I state explicitly that **no** potential competing interests exist.

## Data availability

No data was used for the research described in the article.

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