



In pursuit of the framework behind the biosphere: S-curves, self-assembly and the genetic entropy paradox



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ABSTRACT

The origins, evolution and functioning of the Biosphere have occupied humankind for as long as recorded history has existed. In this paper we examine the claims of thermodynamics to be the framework within which we can understand the evolution, functioning and development of the Biosphere, exploring the evidence from ecology, molecular science and evolutionary biology, and particularly focussing upon the maximum entropy production principle (MEPP), and its explanatory potential in terms of many of the logistic relationships found within the Biosphere. We introduce the genetic entropy paradox, where the DNA increases in terms of internal information entropy, as the genetic code is continuously randomized through mutation, and yet this leads to increasing external entropy production, as increasingly more complicated structures and functions are produced in the form of new protein morphologies and metabolic pathways (again determined by the bioenergetic context). We suggest that the central dogma acts as a form of entropy exchange mechanism, but at the core of this is change in information entropy, which increases within the genetic code, and decreases within the organism. This would appear to be a truly unique event, and highlights a key interaction between two levels of organization within the Biosphere, the genome and the proteome, in terms of entropy production. The Biosphere is seen as being composed of a series of self-organizing sub-groups, each maximizing entropy production within the constraints of time, feedback and system constraints. The entropic production of the Biosphere is thus an emergent property.

“We rise from the conception of form to an understanding of the forces which gave rise to it”

(Thompson, 2011: 33)

1. Introduction

The concept that there is a force that separates the animate from the inanimate world stretches back through time. As early as 440 BC, Empedocles asserted that life derived from ether (McGirr, 1992). Aristotle discussed the *pneuma*, or vital heat, as a heat that is not fire. He also suggested that this force was linked to the material that was thought to fill the space beyond our planet (*aether*) and to body temperature (*therma*) (Solmsen, 1957). This idea of a life force, or Vitalism, was not only found in philosophy. It also pervaded early chemistry, leading to a division between organic (substances that changed irreversibly when heated) and inorganic (substances that reverted to their original form upon cooling) chemistry. Not only did organic matter possess this weightless, invisible substance, or vital force, but also organic matter could not be made from inorganic matter. It was special and different.

Surely the synthesis of an organic compound from an inorganic compound would put an end to vitalistic chemistry? In 1828, Frederick Wohler did just this, synthesising urea from cyanic acid and ammonium, with Justus von Liebig, in his 1837 address to the British Association for the Advancement of Science, pronouncing the feat as extraordinary and inexplicable (von Liebig, 1837).

During the first half of the nineteenth century, the debate around the origins of life continued. The theory of spontaneous generation set out that life can arise spontaneously without reproduction, either through abiogenesis, which emphasised its origin as inorganic, or through heterogenesis, which posited that life arose from organic but dissimilar parental material.

While Pasteur is perhaps best known for demonstrating that if a broth containing bacteria was boiled, no new bacteria would emerge, thus showing that life could not spontaneously regenerate, others, such as John Needham, found that there was life after boiling. It was John Tyndall, the Irish physicist, who finally settled the argument, showing that by repeated boiling, ensuring that heat-resistant spores were killed, no life could spontaneously generate. Briefly, Vitalism was again re-suscitated. Life could only come from life.

Vitalism continued to dominate concepts of life and its origins.

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Henri Bergson (1907), in his influential book, *L'evolution Créatrice*, argued that an *élan vital*, or life force, was found in all living things, guiding the organic processes. Hans Driesch (1908), the eminent embryologist, proposed the presence of a substance in living organisms that directed development, applying the word '*entelechy*' to this substance, a word coined by Aristotle, meaning something working to be itself.

Today, Vitalism is completely discredited as a theory, and the search for the origins of life lie in the transition between inorganic and organic chemistry. It was Alexander Oparin (1938), the Russian biochemist, who suggested that early Earth would have had a strongly reducing environment, and so organic molecules could form from readily available inorganic molecules such as methane, water, ammonium and hydrogen. Miller and Urey (1959) carried out this experiment, using electrical discharge to mimic a perpetual lightning storm, and, after several weeks, found that amino acids such as glycine and alanine had formed. Oró (1961) synthesised adenine, one of the four bases in DNA, from hydrogen cyanide and ammonia. The remaining three bases in DNA were later synthesised in a similar manner.

Yet problems persisted. The conditions optimal for the production of bases are not optimal for the production of sugars. Ribose sugars are not easily made and usually occur as by-products. The other sugar products formed with ribose inhibit RNA replication and synthesis. Furthermore, in DNA and RNA, the sugars must all be of the same enantiomer (right-handed). If a left-handed ribose attaches, chain elongation is terminated. Yet equal numbers of left- and right-handed enantiomers are formed on Earth. Furthermore, pyrimidines do not react well with ribose sugars, while phosphate, central to DNA, RNA and ATP, is scarce. See Shapiro (1984) for a summary of these issues.

And so, the formation of organic molecules and their subsequent integration into a living organism are challenging subjects. However, we know that life must have begun from something that was not living, and that even if Panspermia is brought into the argument, we are only delaying the second inevitability, that it must have come from somewhere.

The chemistry of life abides by the same laws as the rest of the Cosmos and the atoms that make up life are the same as those that make up the rest of the universe (Tielens, 1990). The entirety of the Biosphere falls under these same laws (Trevors, 2010). Therefore, the processes of emergence, evolution and functionality across the Biosphere must surely also obey these rules.

While physicists and chemists willingly embrace this reality, the ghosts of Vitalism seem to haunt the thinking of biologists in particular. Evolutionary biologists are hesitant to move away from a purely biological set of laws, those of natural selection, and of the selfish gene, both very much anthropomorphic concepts. Some scientists have deliberately excluded thermodynamics from the evolutionary debate. It was Demetrius (2000) who wrote that the science of thermodynamics only could be applied to inanimate matter. Others, such as Molchanov (1967), felt that, in fact, natural selection could explain physics as well as biology, elevating it to a universal and unifying theory.

Yet there is a growing consensus that the story of the origins and evolution of life need only be routed in physics, and particularly, in thermodynamics. D'arcy Thompson, the polymath and developmental theorist, emphasised the need to rise from our obsessions with the forms of biology, and focus instead on the processes or forces, as quoted at the start of this paper (Thompson, 2011).

So, is there an organizational driver behind things, something that tempers extremes, manages continuity and enables the scroll of life to unfold (*evolve*, the original meaning of the word evolution)? If this is the case, what is the nature of this driver and what is required for it to initiate and guide the construction of a biosphere? Does the Goldilocks principle hold in terms of the rare earth hypothesis (Ward and Brownlee, 2000), where the chances of conditions being such that a biosphere could arise are extremely rare, or could there be suitable conditions for life in many solar systems in the universe?

In this paper, we set out to examine if thermodynamics, and, in particular, the maximum entropy production principle, might be that driver behind the Biosphere.

2. Evolution and thermodynamics

Entropy is a state function, meaning that the path taken to the present state is irrelevant. If we take two states, X and Y , then state X has a value for the state function of entropy of $S(X)$, and state Y has a value of $S(Y)$. The difference in entropy between these states is simply calculated as:

$$\Delta S = S(X) - S(Y) \quad (1)$$

and is independent of the path taken.

A given system (a macrostate) is made up of many components that can be arranged in a range of ways. Take a container filled with gas. Depending on the concentration of gas, there will be more or less gas particles. Temperature also impacts here, with higher temperatures meaning the gas particles will have a higher mean velocity. If we consider the total number of microstates to mean the number of different possible arrangements of molecular position and momentum, in the case of an ideal gas with no internal coordinates, at a particular thermodynamic state, then any process that leads to an increase in the number of microstates, such as an increase in temperature, increases the entropy. Boltzmann summed this up as follows:

$$S = k \log W \quad (2)$$

Where k = Boltzmann's constant ($1.38 \times 10^{-23} \text{ m}^2 \text{ kg s}^{-2} \text{ K}^{-1}$), and W = number of microstates. Thus, if $W = 1$ (such as at absolute zero, where no kinetic movement occurs and the particles are 'frozen' in space and time), there will be no entropy, and so $S = 0$. The benefit of using microstates as a basis for understanding entropy is that we can also apply this to information, as we shall see in section 7.

Boltzmann was the first to describe the struggle for existence in thermodynamic terms, when he wrote that the general struggle of animate beings was for entropy, not for raw materials nor energy (Boltzmann, 1974). Boltzmann used the term 'struggle' in deference to the dominant Darwinian dogma of the time. Lotka (1922a, 1922b) also sought to embed thermodynamics within Darwin's thesis, theorizing that natural selection led to an increase in both energetic efficiency and total energy throughput. Vallino and Algar (2016) note that Lotka's work is consistent with recent developments in non-equilibrium thermodynamics, wherein complex systems will organize toward maximum entropy production (MEP).

Prigogine (1976) was one of the first to set out a completely independent concept of thermodynamic evolution, without recourse to Darwinian theory. He referred to life forms as dissipative structures, and argued that early organisms evolved from non-living, far-from-equilibrium structures.

The second law on its own can appear like a runaway train, increasingly chaotic and ultimately heading for a heat death. And indeed, the universe may well end up in such a plight, as suggested by Thomson (1857). Yet on this planet, as on many billions of others, our proximity to a radiation-emitting star, itself working its way towards its own heat death, means that we receive free energy that can be used to do work, thus supporting complexity within an entropic universe. Indeed, this complexity, as a dissipating structure, increases the entropic state of the universe.

Thus, if sufficient free energy is available, then the emergence of life is in line with the laws of thermodynamics, as is its increasing complexity. Ulanowicz (1997) wrote that energy dissipation always leads to the creation of structure and complexity, while Annala and Salthe (2010: 301) went further, claiming that "the theory of evolution by natural selection is herein subsumed by the 2nd law of thermodynamics."

Certainly, evidence has been growing in terms of the role of

thermodynamics in the origins, functions and evolution of the Universe itself (Wall, 2013), and of the Biosphere, from the molecular level to the ecosystem level of organization (see Skene (2015) for a review). And the most recent development in thermodynamic theory, the maximum entropy production principle (MEPP), has begun to play an increasingly central role in this work (Matsuno and Swenson, 1999). We now turn briefly to the background and meaning of this principle.

3. The maximum entropy production principle

The history of the MEPP is fascinating in that many workers in quite different fields of physics began to converge on the idea, each building on a different set of foundations. Not all of these foundations were robust, but the same set of fingerprints kept being found, leading these researchers to similar conclusions. Berthelot's principle of maximum work, a thermochemical rather than a thermodynamic theory, stated that all chemical changes occurring without the intervention of outside energy tend towards the production of bodies, or of a system of bodies, which liberate more heat (Berthelot, 1879).

As early as 1903, Luginin (see Kolesov, 1992) demonstrated that if a reaction has several paths, all of which are accompanied by the release of heat, the reaction will inevitably choose the path leading to the maximum release of heat. He based this on the Berthelot principle rather than the second law of thermodynamics.

It was Ziegler (1963, 1976) who formally set out the maximum entropy production principle, stating that where an irreversible force, X_i , is prescribed, the actual flux, J_i , which satisfies the condition $\sigma(J_i) = \sum_i X_i J_i$, maximizes the entropy production. Ziegler derived this formulation from von Mises' theory of plasticity, which states that the dissipation rate of mechanical energy in a unit volume during plastic deformation is at a maximum in a truly stressed state among all stressed states allowed by the given condition of plasticity (von Mises, 1928).

Application of the MEPP to the Earth system first occurred in the field of climatology, in a series of papers by Paltridge (1975, 1979), who was examining heat flow in the atmosphere of the Earth. Paltridge had tried a number of approaches before finding that by maximizing the entropy production rate, his models came close to describing actual observations (2005). While critics have pointed out that Paltridge failed to account for radiation absorbed at the Earth's surface (e.g. Essex, 1984), later work by Shimokawa and Ozawa (2001) and Ozawa et al. (2003) demonstrated that entropy production due to absorption of solar radiation in the climate system was irrelevant to the maximized properties associated with turbulence. Indeed, the more complex the system being considered, the greater number of potential pathways, which allows the pathway generating the greatest production of entropy to be the most likely one. And nothing on Earth is as complicated as the Biosphere.

A fundamental issue that emerged from the MEPP was, as Virgo (2011) pointed out, that results differ depending on what processes you include in the system under consideration. This is because any calculation of the entropy of a system depends on how much we know about the system. However, fundamental here is the reality that any open system is really a sub-system, and part of a greater system. Thus, only when the over-arching isolated system is considered in its entirety, will the laws of thermodynamics be fully understood.

Of course, the Universe, if it is a closed thermodynamic system, is so complex that it would be impossible to fully include all of its properties. However, many aspects of physics have similar issues, for example the Uncertainty Principle of Heisenberg, where one cannot know all things about a particle at one time. But this doesn't undermine the entirety of physics. This reflects Kurt Gödel's (1964) theorem of incompleteness, which observes that any sufficiently complex consistent theory has a statement in it that can be neither proved nor disproved within this theory. Dyke and Kleidon (2010) further examined the epistemological basis of the MEPP.

Bezryadin and Kountz (2016) have emphasised that although the

MEPP can be shown to hold in general terms, there can be significant deviation from maximization in three situations: (1) if the evolutionary process is not allowed to continue for a sufficient length of time; (2) if the metastable state of high entropy production rate is separated from the disordered state with a low entropy production rate by a barrier to reconfiguration; (3) if the driving thermodynamic potential is outside of some system-specific range in which the self-assembly tendency overcomes all the destructive tendencies, such as, e.g., thermal fluctuations or gravity.

While S represents a state variable, the journey to a given macrostate passes through a series of microstates. It is this journey that is described by the Maximum Entropy Production Principle, not the final macrostate. The second law of thermodynamics states that any equilibrium thermodynamic system has a unique state function of entropy S : $T\delta S = dQ$ (although this equation is correct only if no work is done on the system and there is no change in mole numbers, e.g. through chemical reactions). The MEPP requires a system to have many degrees of freedom that produce the same entropy-producing microstate. The MEPP states that systems will tend to follow the pathways that maximize entropy production at the steady state, where the steady state is defined as the circumstance in which there is no accumulation of energy or mass within the control volume, and the properties at any point within the system are independent of time. It is the rate, not the total entropy produced, that is involved here. While still lacking a theoretical foundation, and, as we have seen, with ongoing questions surrounding its universality, the MEPP appears to hold for non-linear autocatalytic systems, of which the Biosphere is an example. Ongoing careful analysis of the continuously emerging literature is essential in any field, but particularly in terms of a rapidly developing area such as this.

4. Fingerprints across the Biosphere

E. H. Moore (1908: 98) discussed the idea of abstraction when unifying fields of study, writing: "The existence of analogies between central features of various theories implies the existence of a general abstract theory which underlies the particular theories and unifies them with respect to those central features". Any good detective examines the evidence and looks for correlations and intersections as means of placing the suspect at a particular locus at a particular time. This very much relates to what Moore was writing.

Aberhan and Kiessling (2012: 16) noted that "A hierarchical approach, in which processes are nested according to multiple spatial and temporal scales, with different variables emerging at different levels, shows great promise for understanding the multifarious patterns of biodiversity". Thus, if we examine these levels of organization and identify common patterns that emerge from each level, this could lead to a beginning in terms of identifying a general abstract theory for the evolution and functionality of our biosphere and other exo-biospheres.

To untangle how the various levels of organization, such as genomes, proteomes, organisms, populations and ecosystems, can exhibit sub-optimal entropy production relative to an over-arching maximum entropic production at the level of the Biosphere, we must first begin with the fact that the Biosphere is a system and not a reductionist construction. Two important properties of systems are that they are emergent and that they self-organize (Cilliers, 2001).

Systems are interactive wholes, wherein emergent properties are not merely the additions of component parts, but rather can be more or less than the sub-system contributions (Morin, 2007). Thus, systems theory would predict that the total (added across all subsystems) entropy production can be maximized by a set of non-maximized entropy production subsystems. However, the important word here is 'maximized'. Each sub-system is maximized within the local conditions, which includes feedback from its environment and the component sub-systems that make up any given subsystem. Bezryadin and Kountz (2016), as already encountered, note that limitations to entropy maximization apply to every level of organization, and to the system as a whole.

However, more fundamentally, it is important to remember that properly functioning systems are non-linear, sub-optimal, emergent and reliant on feedback (Skene, 2018).

The other essential quality of systems that is relevant here is the fact that they exhibit autopoiesis, or self-organization (Varela et al., 1974). The most elementary steps in the evolution of living beings are based on self-organization (Prigogine and Nicolis, 1977), resulting from the natural thermodynamic imperative of increasing the entropy production of the Earth within the context of its solar environment (Michaelian, 2011b).

At the foundation of the evolution of life, and at all levels of organization of the Biosphere, lies the concept of self-assembly, wherein a given level of organization requires building blocks, which then self-assemble in order to produce a self-organizing unit or sub-system. Each sub-system, in turn, becomes a building block. Importantly, these building blocks themselves have already undergone self-assembly and have formed a self-organized unit or subsystem. However, this is not a reductionist system, because each sub-system is an emergent property, whose architecture and function are outcomes not only of its constitutive building blocks, but of self-organization. This paper suggests that the MEPP is the framework around which such organization occurs, the invisible hand behind autopoiesis. The MEPP has been observed in many of the sub-systems of the Biosphere, from ecosystems to biochemical pathways, and in crystalline solids, electrical currents, the climate system and thermal convection (see Meysman and Bruers, 2007; Skene, 2013, 2015, 2017; Arango-Restrepo et al., 2019a and refs therein).

In fact, from molecule to ecosystem, there is a continuous process of self-assembly and self-organization. This has been elegantly demonstrated by Arango-Rostrepo et al. (2018, 2019a). The hierarchical order of structures results from different interactions and feedback at each stage of the assembling process. van Rossum et al. (2017) clearly demonstrate that energy dissipation and entropy production accompany non-equilibrium self-assembly. The building blocks of non-equilibrium self-assembling units (NESAs) are themselves 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. Arango-Rostrepo et al. (2019b) demonstrate that the architecture of self-assembled structures can be determined from knowledge of the energy and matter dissipation inherent in their formation.

This also explains why time is needed to build such a system, as highlighted by Bezryadin and Kountz (2016), and why during this building process, maximum entropy production of the system as a whole will not be reached, given the constraints of a complex, developing system. This by no means contradicts the MEPP, but rather sets it within the context of systems theory. Arango-Rostrepo et al. (2019a) point to the development of feedback loops as the key factor in transitioning from self-assembly to self-organization. These processes of self-organization are also frequently observed in flocking birds, swimming bacteria and microtubules assemblies (Desai and Mitchison, 1997; Papaseit et al., 2000). Galaxies and structures composing them are viewed as self-organizing structures dissipating matter (Nozakura and Ikeuchi, 1984; Pakter and Levin, 2019) and we would suggest that they too should be viewed within this entropic framework.

We can envisage the Biosphere as a multi-armed seesaw (Fig. 1), wherein a balance is reached between the hierarchical levels, each impacting on each other through constraints, but ultimately leading to a balanced biosphere. Lucia (2015) points to the fact that the flows within the Biosphere, in terms of energy, mass, ions and chemicals, represent the communication channels between the system and environment. Bejan and Lorente (2010), emphasise that the Biosphere is configured in such a way as to move and flow as a conglomerate of 'engine and brake' designs. This forms the basis of their constructal law, which states that "for a finite-size flow system to persist in time (to live) it must evolve such that it provides greater and greater access to the

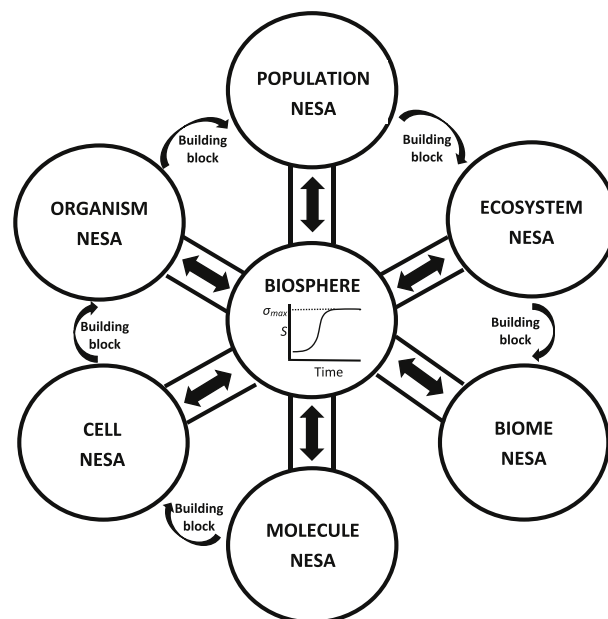


Fig. 1. The multi-armed seesaw analogy of the Biosphere. Here, each level of organization finds an appropriate level of function, informed by real-time feedback between all levels, adjusting its activities to achieve maximum entropic production (σ_{max}) within the constraints of the system. Each level forms the building blocks for the next level, and each level self-assembles and self-organizes within the MEPP. Emergence, sub-optimality and non-linearity are core outcomes of these constrained opportunities, and can be seen throughout the Biosphere. NESAs: Non-equilibrium self-assembling unit.

currents that flow through it" (Bejan and Lorente, 2010: 1335).

The entropy production of the Biosphere is maximized, within the constraints of the system, as is entropy production within each level of organization, but maximum entropy production (σ_{max}) in each case is constrained by the interactions between all of these levels. The asymptote at each level of organization is an emergent property of the self-organizing system as a result of a multitude of interactions. The Earth system itself can be perturbed by macro-scale events such as large-scale volcanism, asteroids and comets, continental configurations, disruptions in nutrient cycling and cosmic rays from supernovas (Large et al., 2015; Korschinck, 2016; Bond and Grasby, 2017). These will all impact on every level of organization.

5. Logistic curves in the Biosphere

By far the most well-researched example of a logistic curve in biology is the Verhulst-Pearl-Reed model of self-limiting growth of a biological population. Originally developed by Pierre François Verhulst in three papers (1838, 1845, 1847), the relationship was re-discovered by Raymond Pearl and Lowell Reed (1920). K , the carrying capacity, is an expression of the maximum population that can be maintained in a given habitat, assuming conditions remain constant, which, of course, they do not.

Populations of living organisms are dependent on the flow of energy fundamentally and are defined and constrained by their energetic contexts. Populations are therefore members 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 (Schrödinger, 1944; Bernal, 1951).

Given that this population represents an open system, then under the conditions of the MEPP, we would expect K to be equivalent to a state of maximum entropy production (σ_{max}) (Fig. 2). If constraints are constant, then perturbation of this population, say by the killing of a

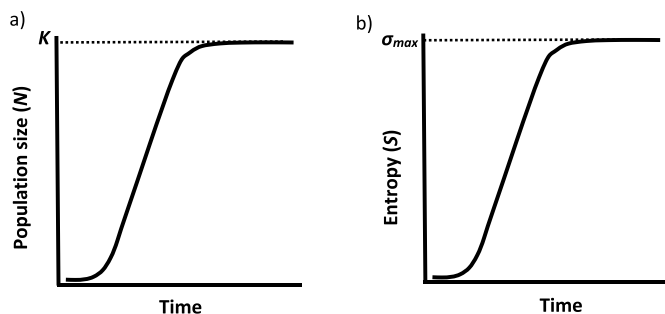


Fig. 2. a) Verhulst logistic curve and b) its MEPP equivalent. K : carrying capacity; σ_{max} : maximum entropy production.

number of the individuals, will result in a recovery back to K , or σ_{max} . An increasingly large population will require concomitantly more energy to support it, increased maintenance respiration and reproductive respiration varying in line with the density-dependent proclivity to procreate. Luo et al. (2001) combined a bioenergetics and water quality model to explore the spatio-temporal dynamics of the clupeid, *Brevoortia tyrannus*. Yen et al. (2015) found that thermodynamics explained density-dependent energy use in both populations and communities.

It should be noted that K refers to the carrying capacity of a given population out of a set of populations which define the ecosystem. However, there may exist numerous states (sets of populations or sets of K values) which give different or the same entropy production for the ecosystem. Here, we examine the impact of thermodynamics at each level of organization within an open system, which also is made of a series of open sub-systems, each set within the context of each other. Thus, the laws of physics are acting at all levels simultaneously, while the connectivity of these levels has implications for each level. It is thus suggested that the value of K will mostly be informed by the energetics of the context within which any population exists, and is clearly a dynamic concept. It can be reduced to a thermodynamic consideration, given the universality of the laws of thermodynamics, the relevance of the MEPP to non-equilibrium autocatalytic systems such as the Biosphere, the benefits of a reduction in the number of variables when studying a complex system and the fundamental concept of thermodynamic directives representing the framework within which the Biosphere can be understood. These points were used in Michaelian (2005) to justify the grounding of any understanding of ecosystem stability within non-equilibrium thermodynamic theory.

Thus, we suggest that σ_{max} should replace K , and will better reflect the energetic changes occurring, while focussing on the key underpinning energetic framework within which populations fundamentally function. If we change the boundary conditions and constraints, by providing more or less food, allowing the habitat to become degraded or setting fire to the forest, changes in free energy availability will occur, leading to a decrease in entropy production. The system will then re-constitute to return to σ_{max} .

The asymptote is determined by the system's context. Here, constraints and opportunities feed back from all levels of organization, informing and constraining the availability of microsites and determining the overall maximum rate at which complexity, and therefore microsite availability can operate at. If, for example, too much free energy is supplied, such as is the case in nutrient pollution in a lake, then a particular population of cyanobacteria may overshoot the maximum rate of reproduction and entropy generation, leading to a destabilization of the system and, ultimately, in its collapse. The pond, both as an ecosystem and as a collection of populations, would then need to re-develop through secondary succession.

Interestingly, mass-extinctions usually lead to a collapse of entire ecosystems due to a sharp cut in incident free energy from the Sun, meaning that there is a significant drop in rates of entropy production,

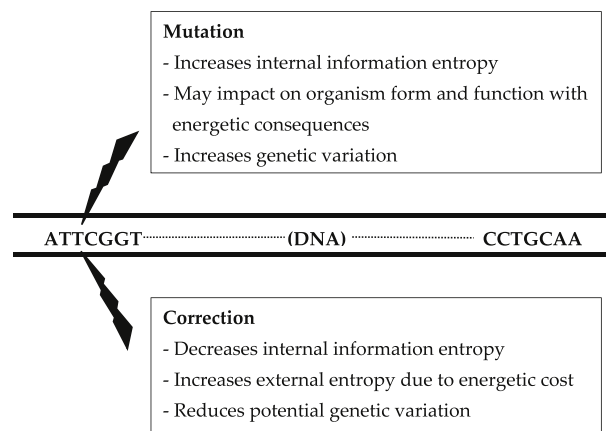


Fig. 3. Entropic relations in DNA mutation and correction.

essential for complexity, and thus complexity is lost. However, the current collapse of the Biosphere is actually driven by anthropogenic activity, increasing entropy production through agricultural fertilization and increased agricultural productivity even if this means undermining the stability of the stationary state of the present Biosphere. Agriculture is, fundamentally, a manipulation of energy flow, maximized towards particular target populations such as crops or cattle.

Reproduction ensures the continuation of life forms which are, individually, ultimately defeated by increasing internal entropy, be that through mutations (see Fig. 3) or the gradual increase in chaos that follows from a life lived within the constraints and impacts of a thermodynamic universe. Furthermore, at times, a reduction in reproductive output is key to survival, particularly at σ_{max} . Populations make these adjustments within an ecological context. These are energy-controlled. For example, predator-prey interactions are fundamentally energetic (where the prey represents free energy), and their population densities are dynamically linked. Such feedback is a typical system characteristic, and has significant indirect impacts in terms of ecosystem stability.

Thus, it is argued that σ_{max} is a better measure of population dynamics than K , encompassing not only the changes in population, but giving a mechanistic understanding of what is occurring as part of an energetic system.

We can now visualize the landscape as providing opportunity for entropic production, and the population as converting free energy into released entropy. Importantly, the relationship between landscape and population is one that moves towards a maximum state of entropic production (σ_{max}), constrained by the many factors that increasingly limit population growth, where population density is an outcome of this feedback. At the ecosystem level of organization, the organisms and abiotic environment are one, rather than separate actors. This aligns with actor-network theory, where the animate world cannot be seen in isolation from what makes them purposeful (Law, 1987; Callon, 1999; Latour, 2005). In many ways, this is the final death of Vitalism, as inorganic and organic are united within a thermodynamic framework.

Thus, in Fig. 1, interactions between all levels of the Biosphere are key, leading to the overall entropic production of the Biosphere and of each level of organization within it being maximized within the constraints arising from real-time feedback. Entropy production is not as large as it could possibly be at any level of organization, but moves towards becoming as large as it can be within the bounds of system stability. It is important to realize that there are multiple stationary states available to the non-linear system and each may have a different entropy production. The system may leave one stationary state and evolve to another depending on the size of the perturbation and local stability.

Complex systems need sub-optimality at each level to function (Skene, 2018). Farnsworth and Niklas (1995) and numerous other

authors (for example, Parish and Edelstein-Keshet, 1999; Evans, 2010; Shoval et al., 2012; Tendler et al., 2015; Du et al., 2018) clearly demonstrate that as a system becomes more complex, each challenge is solved more sub-optimally, because the system cannot optimise for any given challenge due to the necessity of trade-offs. Compromise is part of working within a system. Thus, σ_{max} is an emergent property. These classic system characteristics, non-linearity, emergence, sub-optimality and real-time feedback are all clearly seen in action.

The implications of the MEPP underpinning the logistic curve of population growth go further. Del Monte-Luna et al. (2004) point out that important properties emerge from the logistic model of population growth, including stability (the drive towards the state of dynamic equilibrium (McCann, 2000)) and resilience (the time needed for a return to stability (Holling, 1973)). We suggest that both of these properties are the outcomes of the MEPP, rather than carrying capacity. Michaelian (2005) suggests that the markedly different stability characteristics of polar and tropical ecosystems may be explained by classical irreversible thermodynamics. The enhanced stability of low latitude ecosystems has been linked to the constancy of external constraints (such as incident radiation) at the equator, as compared to the extreme seasonality, and concomitant instability, of polar ecosystems.

6. The fossil record – diversity as a diffusive process with σ_{max}

Two major models have been put forward to account for the processes underpinning the evolution of global biodiversity. Firstly, the equilibrium model, set out by Sepkoski (1978), suggests that in the aftermath of mass extinction events, diversity collapses dramatically, then recovers, following a trajectory resembling a logistic curve, where there is an initial lag, then an accelerated diversification, followed by a slowing of the rate of diversity to an equilibrium (Walker and Valentine, 1984). This was demonstrated for the Cambrian, Palaeozoic and modern faunas, with exponential diversification and subsequent slowing of diversification as the niches became filled (Sepkoski, 1984, 1998). This resembles the equilibrium model of island biodiversity (MacArthur and Wilson, 1963). In the other corner is the expansion model, where global biodiversity increases with no predictable limit (Benton, 2009).

Song et al. (2018) demonstrated that following the Permian mass extinction, biodiversity underwent a logistic recovery. This recovery was also noted by Aberhan and Kiessling (2012), working on marine genera, who determined that there have been two upper limits, one in the Devonian and one in the late Cretaceous. They concluded that sampling and preservation biases had led to support for the expansion model, but when these biases were taken into account, it was the equilibrium model that best accounted for changes in biodiversity over time.

The trajectory of marine ordinal diversity during the Phanerozoic can also be modelled by a logistic equation, where maximum diversity was reached in the late Ordovician (Sepkoski, 1978). A similar pattern is observed for the Mesozoic-Cenozoic (Aberhan and Kiessling, 2012).

So, is there the equivalent of a carrying capacity at the ecosystem level, controlling the diversification of species following perturbation? Do ecosystems show stability and resilience akin to populations, and is there an underlying and similar fingerprint at this hierarchical level? Any given ecosystem has a limited amount of available free energy and niche space. Larger areas have more niche space, leading to the species-area effect (Schoener, 1976). Furthermore, there is clear evidence that the species-area relationship is logistic in nature (Preston, 1962; Wissel and Maier, 1992; Lomolino, 1999).

Aberhan and Kiessling (2012) concluded that the concept of a global carrying capacity, itself an outcome of resource-limited, concerted local carrying capacities, has the potential to explain constraints on global diversity. Skene (2015) instead suggested that it is the MEPP that best explains logistic patterns of diversification over evolutionary time, just as it does population dynamics. Here, the diversity diffuses into

available niche space (Paine, 1966; Tilman and Downing, 1994), until a maximum entropic production level, σ_{max} , is attained by the community as a whole.

Vallino (2010: 1417) states that ecosystems are “self-organizing molecular machines that function to maximize entropy production at the ecosystem level of organization”. Skene (2013) demonstrated that logistic patterns observed in entropic production during ecosystem succession are also explained by the ecosystem moving towards σ_{max} , representing a quasi-stable climax. At this point, a dynamic equilibrium is reached. Perturbation, such as a forest fire or a hurricane, leads to secondary succession, where the system self-organizes to regain σ_{max} . Per capita community productivity is very high during the initial phases of succession, and decreases progressively as an upper limit to biomass is reached (Margalef, 1974).

In dealing with punctuated equilibrium theory, first developed by Eldredge and Gould (1997), and relating this to phase changes during ecological succession, Michaelian (2005) discusses this within the context of non-equilibrium phase transitions, wherein the punctuation of stasis may be brought about by a sudden change of external constraints through a thermodynamically critical point. Michaelian suggests that by combining Swenson’s (1989, 2000) principle of maximum entropy production and punctuated stasis, framed within a non-equilibrium thermodynamic context, the shifts observed in ecological succession towards more complex, larger phases, culminating in a more highly complex ecological steady state, may be explained. This ecological steady state may represent a particular manifestation of the thermodynamic stationary state.

del Jesus et al. (2012) point out that the application of MEPP at the ecosystem scale results in maximum productivity (for example, maximum canopy photosynthesis). They found that the spatial organization of functional vegetation types in river basins naturally evolves toward configurations corresponding to local maxima of the maximum productivity of the ecosystem, in accordance with the MEPP. Annala and Kuismanen (2009) conclude that hierarchically organized energy transduction systems develop as a way of increasing energy dispersal.

By combining evolutionary and ecological findings, the MEPP can be seen as a unifying concept across both domains, acting as the driver of change in space and time (Skene, 2017). This resonates with E.O Wilson’s concept of consilience, literally a jumping together of knowledge from different disciplines that resonates and forms the foundations for a broader, unifying framework (Wilson, 1998). This is not to say that density-dependent population growth and species diversification are the same thing. They are not. Rather, the point is that the MEPP acts on both levels, leaving the same fingerprint across both populations and ecosystems, spatially and temporally. The Biosphere evolves towards highly ordered systems from low ordered systems despite the increase in entropy of the universe (Fujiwara, 2003). Annala and Annala (2008) note that over the course of evolution, the system moves towards an ever-larger and more diversified energy transduction system.

And the fingerprints of the MEPP are found in levels well below populations and ecosystems. Unrean and Sreinc (2011), working on metabolic networks, concluded that cells evolve to redistribute metabolic pathway fluxes in order to achieve a maximum rate of entropy formation, which they describe as asymptotic (see also Sreinc and Unrean, 2010). The process of ATP synthesis in oxidative phosphorylation, probably the most important biochemical reaction, is compatible with the MEPP (Nath, 2019), as is activation of signalling proteins (Weber et al., 2015). Bordel and Nielsen (2010) demonstrated that the metabolic network in *Saccharomyces cerevisiae* (yeast) tends to maximize the entropy production rate while satisfying mass balances and maximal rate constraints. Dobovišek et al. (2011) reported that the forward rate constants in β -Lactamase enzymes approximate to those obtained by using the MEPP.

Even more fundamentally, absorption and dissipation of UV light around 260 nm was probably the primordial thermodynamic function of the first RNA or DNA single strand molecules floating on the ocean

surface (Michaelian, 2011a).

7. Information and entropy

While thermodynamics is clearly at play at molecular, population and ecosystem levels, if the MEPP is to be a truly unifying theory for Biosphere form, function and evolution, we must understand how it plays the role of the engine of diversity. This is where information entropy comes into play.

This paper posits that information, channelled through real time feedback, is what knits the various organizational levels of the Biosphere together, and thus sets the context for determining what value σ_{max} takes in each of these levels. In our seesaw analogy (Fig. 1), information pathways play the role of the structure of the seesaw, through which the forces act. Positive and negative feedback are core properties of any self-organizing system. Thus, σ_{max} can be seen as an emergent property, arising from the multiple feedback loops existing across the entire Biosphere and beyond, such as the changes in the Earth-Sun relationship, as seen in the Milankovitch cycles (Bennett, 1990).

As σ_{max} adjusts in each and every logistic relationship as a result of changing contexts and concomitant constraints, be it evolutionary diversification, population growth or ecological succession, so too will associated emergent properties such as stability and resilience. A self-organizing system is dynamic, emergent and non-linear fundamentally because of real-time feedback that courses through the system, contextualizing everything. And information lies at the heart of this.

Information (I) in a thermodynamic sense can be defined as the difference between the entropy (S_0) of a system whose components are at equilibrium and the entropy of the system (S) when assembled, thus (Lovelock, 1975):

$$I = S_0 - S \quad (3)$$

In 1867, Maxwell developed a thought experiment that sought to challenge the second law of thermodynamics. In it, he imagined a container divided into two sections by a wall with a tiny door. Each section is full of gas at the same temperature. The population of gas molecules in each section are made up of individual particles all travelling with different speeds. Now imagine a highly intelligent but tiny demon (Maxwell's demon), who can follow individual particles in space and time. He picks out the swifter ones and opens the door, allowing each one to pass from section A to section B. He does the same for slower particles, this time only allowing them to move from B to A. As a result, without doing any work, he will raise the temperature in B and lower the temperature in A. Maxwell claimed that this would contradict the second law of thermodynamics. For those unfamiliar with this experiment, and the importance of how it was resolved, please see Bennett (1987).

The central lesson from the Maxwell's demon thought experiment is that the selection, filtering and discernment of information are all thermodynamically expensive operations. Information costs energy to obtain, maintain and manage. It was Szilard (1964) who first highlighted that in the case of Maxwell's demon, the only way for the second law of thermodynamics to hold is if knowledge acquisition produced entropy. For a detailed account of the relationship between information and entropy, see Tribus and McIrvine (1971), Michel (2013) and Karnani et al. (2009).

Take the genetic code as an example. The code itself, a chain of bases which codes for proteins through transcription and translation, undergoes random mutations. The continuous battle between DNA damage and DNA correction is ongoing throughout an organism's life. Such damage can result from hydrolysis, methylation, oxidation or irradiation. In a typical mammalian cell, there can be anything between 10 000 and 20 000 changes each day in the double stranded DNA. Of course, only some 5% of the DNA in mammals can be expressed (exons), the rest remaining permanently inactive (introns). But this still amounts

to a substantial number of errors that need correcting if a mutation is not to occur.

Of course, mutations are the basis of genetic variation, essential in generating new information at the protein, population and species level. Much like blind-folded monkeys typing, what is written may be nonsense or make some sense within the multiple layers of context that represent the Biosphere. But the typing continues, night and day, and as the genetic code continues to degrade, in spite of correction, the text is changed, subtly or otherwise.

DNA synthesis itself generates entropy. Gaspard (2016a) estimates that the free energy required to add one nucleotide during DNA syntheses is equivalent to two ATP molecules. He later calculated (Gaspard, 2016b) that the total entropy generated per nucleotide addition could be calculated as:

$$\Sigma = \frac{1}{R} \frac{\delta_i S}{\delta t} - \nu A \geq 0 \text{ with } A = \epsilon + D(\omega|\alpha) \quad (4)$$

(Σ , entropy production; R , molar gas constant; S , entropy; A , affinity or entropy production per nucleotide; t , time, ν , mean growth velocity; $D(\omega|\alpha)$, conditional Shannon disorder per nucleotide of the copy ω with respect to the template α ; ϵ , mean free-energy driving force per nucleotide).

There are three classes of mutations: substitutions, insertions, and deletions. These can result in a number of outcomes: missense mutations, nonsense mutations, duplications, frameshift mutations, repeat expansions and silent mutations. While mutations act on the genetic coding material (be that DNA or RNA (in RNA viruses for example)), they generally only come into physical expression during the translation process, when protein sequence is produced from this code. An exception here is structural RNA. Recent work has highlighted the importance of thermodynamics in any consideration of mutations. Lakshmanan et al. (2018) demonstrated that thermodynamics lies at the mechanistic centre of understanding deletion mutations in mitochondrial DNA, presenting evidence from five different species (nematodes, mice, rats, rhesus monkeys and humans). They showed that the deletion breakpoint positions are most consistent with a mutagenesis mechanism that is driven by thermodynamics. Recent work has also focused on the thermodynamics of DNA repair (Miroshnikova et al., 2016; Kládova et al., 2019).

What is really interesting is that at the heart of the central dogma lies a process of increasing internal information entropy, which forms the foundation for a biosphere where complexity is maintained by exporting entropy to the environment, thus maintaining complexity within an entropic universe. Correction of mutations is an energetically expensive process and leads to entropy being released and exported externally.

This battle between mutation and correction is thus a balance between generation of internal and external entropy (Fig. 3). And it is the increasing internal information entropy that results in genetic and, subsequently, phenotypic variation, which underpins variation at the population level. Thus, the coding of proteins from DNA is also a transition between increasing internal entropy (genetic variation), representing a loss in information, and the fundamental structural and functional proteins that represent increasing information and a means of externalizing entropy while processing free energy.

We suggest that the central dogma is, fundamentally, 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, though nonsense mutations (such as the generation of a stop codon at the wrong point) can lead to failure in the process.

While Fenchel (1974) demonstrated that the increasing complexity of life on Earth followed an increasingly dissipative path, with

increasing complexity reflecting increasing external entropy production, underpinning the phenotypic informational complexity is an increasingly chaotic genetic code with increasing internal entropy. In many ways it resembles a fridge: the cooler the temperature inside the fridge, the greater the heat dissipated outside the fridge.

Thus, the central dogma acts as an entropy exchange mechanism, but at the core of this is change in information entropy, which increases within the genetic code. Changes here either result in silent mutations (i.e. no change in protein sequence and function as a result of codon redundancy), failure of protein structure and protein function or alteration in protein structure and function. In the latter case, we would expect changes that delivered increased entropy production at the metabolic pathway level and beyond to be favoured, contributing to increased complexity, ultimately at the ecosystem level. Furthermore, over time, changes in protein structure that increase stability at the organismal level, as a result of entropy export into the environment (Lovelock, 1965), would be likely to be favoured, though within the context of higher organizational levels of the hierarchy that represents the Biosphere. This would appear to be a truly unique event, what we will call the genetic entropy paradox.

Our new protein is a structural entity. As mutations continue to randomise the genetic sequence, diffusing into coding space, so too, proteins explore folding space. Thermodynamically determined, proteins fold depending on their energetic context. An unfolded protein has higher entropy and enthalpy than a folded protein. Indeed, if we change that context, by, for example, heating the solution in which the protein resides, the protein may unfold and denature, or change its folded state. Many active transport proteins, such as the sodium-potassium pump, alter their folded state upon phosphorylation, involving ATP (Skou, 1957).

Functional proteins (enzymes) take their places within metabolic pathways, whose main role is the management of energetic relations within a cell and organism (one and the same thing in the case of unicellular organisms). Once again, thermodynamic considerations lie at the heart of things here. Recent work has focused on conformational entropy and its impact upon protein-protein interactions and thermal stability (Steinbrecher et al., 2017; Bej et al., 2018; Rietman and Tuszyński, 2018).

The organism, be it unicellular or multicellular, then finds itself within two contexts: populations and ecosystems. This is the macro-level of organization. Once again, thermodynamic considerations take centre stage. We suggest that population dynamics can best be understood as a thermodynamic process, where, as we have already seen, the carrying capacity can be better understood in terms of maximum entropic production, σ_{max} .

Vallino (2010) notes that distributing genomic information across many species and individuals at a low copy number, much of which is not immediately relevant to the current ecosystem state, allows for storage of resilience and for resistance to change, ready to use, in what is known as the rare Biosphere. It was Sogin et al. (2006) who suggested that the huge number of rare organisms within a given ecosystem acted as stores of information for that ecosystem, providing a bank of solutions to problems encountered over evolutionary time, and providing resilience and resistance to dynamic changes that may have been encountered.

It is often said that there is nothing new under the Sun, and, during the 3.8 billion years of life on Earth, just about every eventuality has been faced and learned from. The importance of this distributed intelligence would not register in a typical neo-Darwinian approach, where such rare organisms should be selected against if their toolbox was deemed irrelevant at a given time. However, the rare Biosphere finds its place secure within a distributed intelligence model from a thermodynamic perspective.

Vallino (2010) goes on to make the point that by maximizing entropy production instantaneously, complexity cannot occur. Thus, information stored within the metagenome (the collective genome of a

community) manages the maximization process over time, rather than at a specific point in space-time. Vallino further notes that such spatio-temporal averaging actually means that biological systems outperform abiotic processes in terms of maximizing entropy production.

Karlin et al. (2013) examined information loss during disturbance in the Arid Chaco region of Argentina, using Lyapunov coefficients (L). Lyapunov coefficients are a measure of the Lyapunov exponent, which is the rate at which information about the initial conditions is lost. Here, increasing values of L represent increasing disturbance of an ecosystem, requiring greater exergy (available energy) to restore it. In the nineteenth century, Guoy (1889) demonstrated that the exergy lost in a process is proportional to the entropy generated. The further away from σ_{max} a given community is, the greater amount of exergy is needed to restore it to σ_{max} . Karlin et al. have suggested that Lyapunov coefficients may be more precise succession indicators than biodiversity indexes, representing the amount of exergy needed for a vegetation state to reach the reference condition (i.e. quasi-stable climax, or σ_{max}). Sciubba and Zullo (2019) stress that a process takes place spontaneously only if the system/systems find a way to destroy exergy and that disequilibrium represents the driver of such processes.

While information entropy is important, it is almost always a negligible component of the total entropy of a chemical system. Karnani et al. (2009) envisage communication as one of many ways in which to disperse energy and as a mechanism for energy transduction. Here, communication plays a role in connecting different levels of organization, assisting in flattening energy landscapes, as the second law of thermodynamics dictates. In this present paper, an increase in information entropy through random mutations in the genetic material is expressed, through transcription and translation, into changes in the physical reality of protein chemistry, and onwards throughout the Biosphere. Thus, we suggest that increases in information entropy at the genetic level leads to diffusion of protein structure, and then, through metabolic pathways, to changes in organismal physiology. This then drives diffusion of life into ecological space, leading to increasing complexity, with increasing output of entropy into the environment, as dictated by the second law. Lovelock (1965: 568) defines life as follows: "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." Thus, while information entropy increases in the genetic material, this then leads to a decrease in entropy within the organism and an increase in entropy within the environment, the genetic entropy paradox.

8. Conclusions

Much work has been done to explore the potential role of MEPP within s-curves and logistic relationships (see Skene, 2013, 2015, 2017 and refs therein). From a thermodynamic perspective, ecological succession is driven at the ecosystem level and, ultimately, by the MEPP, moving towards σ_{max} . If we examine the fossil record, as we have seen, during recovery from mass extinction events, species diversification also follows a logistic curve. The most rapid speciation occurs far below niche saturation (σ_{max}) and thus competition and natural selection do not really kick in until speciation slows. Therefore, these foundation stones of the modern evolutionary synthesis may be seen as outcomes of reaching the asymptote, as niche space fills, rather than drivers of speciation.

Rather, speciation occurs in the empty marketplaces, not in the crowded back-alleys (Skene, 2009). Opportunity, not competition, characterizes this phase. Thus, natural selection can be seen as a symptom of niche saturation, a σ_{max} property, not the driver of diversity. Benton (1996) concluded that displacement via competition probably played a minor role in the history of the tetrapods and that family originations were most often associated with expansion into new or recently empty niches, in what we would call diffusion into free

space.

Mahler et al. (2010) found that the rate of phenotypic diversity declines with decreasing opportunity, as did Phillimore and Price (2008), finding that in bird evolution, speciation slows as ecological opportunities and geographic space limit the clade growth. Alizon et al. (2008) demonstrated that under resource competition, there is an exponential slowdown of the apparent rate of evolution. Brusatte et al. (2008) claimed that contingency, rather than prolonged competition or general superiority was the prime factor in the rise of the dinosaurs. Jablonski (1986) wrote that the reason for species being removed during mass extinctions was essentially random, rather than being ecologically related.

All of these observations point towards a thermodynamic framework for evolutionary tempo, where life diffuses into available niche space. Evolution is most rapid in conditions of low selection and slows in conditions of high selection. Thus, competition inhibits diversification, which should be expected, as it reduces variation. Cornish-Bowden and Cárdenas (2019) emphasise that thermodynamics is so important that it must play a central role in any consideration of the origin and evolution of life.

Hence, the MEPP as a framework provides a physical explanation of so many of the facets of biosphere evolution, development and function. It satisfies Moore's and Wilson's outlines of what makes a general abstract theory, operating from molecular to ecosystem levels, and at the level of the Cosmos, tied together by information and energy. This is an area of ongoing and much-needed research rather than a solved problem and it is important to reflect that this paper represents a beginning rather than a conclusion, in terms of opening up an understanding of the Biosphere through physics and systems thinking, rather than natural selection and reductionist thinking.

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