



Thermodynamics, ecology and evolutionary biology: A bridge over troubled water or common ground?



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ABSTRACT

This paper addresses a key issue confronting ecological and evolutionary biology, namely the challenge of a cohesive approach to these fields given significant differences in the concepts and foundations of their study. Yet these two areas of scientific research are paramount in terms addressing the spatial and temporal dynamics and distribution of diversity, an understanding of which is needed if we are to resolve the current crisis facing the biosphere. The importance of understanding how nature responds to change is now of essential rather than of metaphysical interest as our planet struggles with increasing anthropogenic damage. Ecology and evolutionary biology can no longer remain disjointed. While some progress has been made in terms of synthetic thinking across these areas, this has often been in terms of bridge building, where thinking in one aspect is extended over to the other side. We review these bridges and the success or otherwise of such efforts. This paper then suggests that in order to move from a descriptive to a mechanistic understanding of the biosphere, we may need to re-evaluate our approach to the studies of ecology and evolutionary biology, finding a common denominator that will enable us to address the critical issues facing us, particularly in terms of understanding what drives change, what determines tempo and how communities function. Common ground, we argue, is essential if we are to comprehend how resilience operates in the natural world and how diversification can counter increasing extinction rates. This paper suggests that thermodynamics may provide a bridge between ecology and evolutionary biology, and that this will enable us to move forward with otherwise intractable problems.

1. Introduction

Ecology and evolutionary biology are enduring areas of scientific research, focusing on the spatial and temporal dynamics and distribution of diversity. Both of these fields have developed rapidly over the last century and continue to do so. Originally relevant in terms of basic survival (in our earlier guise as hunter gatherers dependent on understanding seasonality of foodstuffs and migration tempo) and as explanations for why the natural world looks and functions the way that it does, these subjects now occupy a more exigent role, predicting the impact of environmental perturbation on the biosphere as a whole, in terms of ecosystem service provision, resilience and diversity. It is as important to understand the processes of species diversification in functional and morphological space and time as it is to understand the processes of species extinction. The relationship between ecology and evolutionary biology has itself evolved over the last one hundred and fifty years.

It has long been recognized that spatial variation in diversity results from the combination of both ecological and evolutionary mechanisms acting over time (MacArthur, 1972). Hutchinson (1965) described this

relationship as the ecological theatre and the evolutionary play. Since then, efforts have been made to elucidate the relative importance of these mechanisms (see, for example, Terborgh and Faaborg, 1980; Graham et al., 2014; Kozak and Wiens, 2016; Suárez-Atilano et al., 2017).

Yet for all of the common ground that they occupy, ecological and evolutionary studies differ, specifically in the approaches and underpinning philosophy that scientists employ in each of these fields. Their academic foundations differ significantly, with the modern evolutionary synthesis (MES) and its conspecific concepts such as the selfish gene relying, ultimately, on a reductionist, empiricist approach, whereas ecology has more recently utilized a system theory approach, embracing emergence. This has resulted in a conceptual and experimental gulf developing between these two fields, in spite of their seeking to address questions with mutual implications.

The Modern Evolutionary Synthesis (MES) focuses on the gene as the unit of selection, and advocates a selfish gene approach, wherein fitness is measured by the success of genetic variants being expressed in successive generations. Dawkins (1982) comments that “the organism is a tool for DNA, rather than the other way around”. This molecular

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approach has been successfully applied at individual and population levels in particular environments, but fails to find a role at ecosystem and biome levels. The extended evolutionary synthesis (EES), though by its very title acting as an extension of the MES rather than a revision, attempts to embrace some systems aspects while maintaining the core elements of the MES.

The gene-centric approach is perceived by some to have shortcomings in terms of accounting for the drive and direction in ecological succession, post-mass extinction recovery, the broader tempo of diversification over geological time and the more fundamental importance of replacement rather than displacement as the basis for the emergence of new lineages (Benton, 1996; Brusatte et al., 2008; Mahler et al., 2010; Venditti et al., 2010; Percival et al., 2017).

Many researchers recognize that ecology does impact upon evolution. It is now recognized that adaptive radiation is dependent on ecological context (Pires et al., 2015). Any understanding of post-extinction recovery must begin with ecological succession (Solé et al., 2002). Bell (2013) argues that traditional approaches of relative fitness fail to form a sufficient basis for population genetics, instead advocating the need to combine ecology, population genetics and population dynamics, embracing absolute fitness.

Evolution is also viewed by many to impact upon ecology. Recent research has shown that evolution can affect species diversity (Schreiber et al., 2011; Pantel et al., 2015), population demography (Reznick et al., 2012), ecosystem function (Bassar et al., 2012; ter Horst et al., 2014) and the outcome of species interactions (Yoshida et al., 2003; ter Horst et al., 2010). ter Horst and Zee (2016) conclude that it is impossible to understand the ecology of a community without understanding concurrent evolutionary change.

Spatial and temporal considerations dominate both fields. Function tends to feature more in ecological thinking, with the fields of eco-physiology and functional ecology becoming significant areas of recent research over the latter part of the 20th century (e.g. Calow, 1987; Keddy, 1992; Buchmann, 2002; Norling et al., 2007).

Given the differences in these two fields and the fact that an understanding of how nature responds to change is now of essential rather than of metaphysical interest as our planet struggles with increasing anthropogenic damage, there is an emerging need to unify our approach, in order to fully understand the processes of diversification, change and function within our biosphere. Ceballos et al. (2015) warn that: “Averting a dramatic decay of biodiversity and the subsequent loss of ecosystem services is still possible through intensified conservation efforts, but that window of opportunity is rapidly closing”. However, without a unified theory of evolution and ecology, it is hard to unravel the patterns and processes that generate and maintain the biotic diversity of our planet, a necessary basis for any ambition toward maintaining ecosystem services.

1.1. Bridge building?

Calls for an integrative understanding of biological processes have been made for many years in the literature, from Dobzhansky's (1973) famous quote, “Nothing in biology makes sense except in the light of evolution”, to current, more focused statements that evolution itself only makes sense when viewed in its ecological context (e.g. Coulson et al., 2006; Saccheri and Hanski, 2006; Johnson and Stinchcombe, 2007; Metcalf and Pavard, 2007; Pelletier et al., 2007; Grant and Grant, 2008). Pelletier et al. (2009) went further by claiming that nothing in evolution or ecology makes sense except in the light of the other. However, Levin (1998) concluded that the disciplinary links between ecological studies and evolutionary biology are among the weakest in the biological sciences.

There have been recent attempts at building bridges between the two fields (see Matthews et al. (2011) for a summary). Weber et al. (2017) call for more work to develop diversification models that include a mechanistic understanding of how ecological and evolutionary

processes interactively influence speciation and extinction. As early as 1976, Antonovics (1976) announced the brave new world of ecological genetics. Thuiller et al. (2013) emphasise the importance of eco-evolutionary processes in biodiversity models. Elser (2006) employed stoichiometric theory as a chemical bridge between ecosystem ecology and evolutionary biology, while Kokko and López-Sepulcre (2007) turned to ecogenetic feedback loops. Laland et al. (2008) and Matthews et al. (2014) suggested a more complicated triple bridge between evolution, development and ecology, suggesting that niche construction could provide a “useful conduit” between evolution and development. Valladares et al. (2006) focused on phenotypic plasticity as a bridge while Gonzalez et al. (2013) suggest that evolutionary rescue lies at the intersection between ecology and evolution.

Yet bridges do not unify nor do they reach all parts of the discursive landscape. Given the significant philosophical and material differences that exist (such as reduction contrasting with emergence, a single unit of selection compared with interactive levels of organization, the emphasis of form contrasting with function, the importance and significance, or otherwise, of energy and material flow), the two discourses would appear so different that bridges are unlikely to help unify the fields.

Schoener (2011, p. 426) questions whether such bridge building is valid at all, writing: “We still don't know if the evolution-ecology pathway is frequent and strong enough in nature to be broadly important”. Johnson and Stinchcombe (2007) concluded that no study has convincingly demonstrated that rapid evolution in one species affects community dynamics in the field, and stated that “The importance of bridging community ecology and evolutionary ecology has not yet been convincingly demonstrated”.

Another issue relates to the timescales of micro- and macro-evolution. Jablonski (2008) points out that attempting to study any interplay of ecological and evolutionary dynamics is problematic due to mismatches in scale and level. Research into the interactions between ecological and evolutionary dynamics has largely focused on relatively simple ecological communities and on local spatial scales (Urban et al., 2008). Difficulties relating to how the short term ecological impacts of rapid evolutionary change really inform macro-evolution as well as how the origins of species diversity relate to macro-evolutionary events are discussed by Weber et al. (2017). Fussmann et al. (2007) concluded that no study had come close to providing empirical support for eco-evolutionary community dynamics. Weber et al. (2017) counter this viewpoint, concluding that “Ignoring the role of evolution in community studies may be inappropriate in many cases”.

This paper explores the idea that pursuing common ground may be more productive than isolated bridge building. Given that ecology and evolutionary biology are focused on the one biosphere, and that this biosphere is made of the same components as the rest of the universe, subject to the same physical laws and is an open system dependent on energy mostly from our neighbouring star, then this common ground may not be so mysterious. Starting with the premise that the biosphere is merely an extension of the rest of the universe in terms of its drives, functioning and development, we examine the significance or otherwise of the laws of thermodynamics as a common ground that could unify evolutionary biology and ecological science.

We begin by summarizing the key developments in the field of thermodynamics, before examining the existent literature on thermodynamic theory relating to ecology and evolution. Next, we explore the importance of thermodynamics in each level of biosphere organization, before considering the potential of such common ground in addressing key issues in both fields.

2. Thermodynamics and the MEPP

Thermodynamics is the study of the energy flow, heat and movement in structures within the universe. In 1824, Carnot published his book, *Réflexions sur la Puissance Motrice du Feu* (Carnot, 1824), in

which he concluded that heat could neither be created nor destroyed, that the total heat of the universe was constant, that when a temperature gradient exists, work can be done and that there can be no such thing as perpetual motion. It would be another thirty years before Rudolf Clausius (1850) and William Thomson (1851) would formally develop the first and second laws of thermodynamics. Clausius gave these laws their simplest and clearest definitions. The first law states that the energy of the Universe is constant, while the second law states that the entropy of the universe tends towards a maximum (Clausius, 1867). The term entropy, meaning transformation, is a measure of the thermal energy of a system per unit temperature that is unavailable for doing work. Entropy production is proportional to the degree of the conversion of energy from high-quality forms (energy able to do work) to low-quality forms (dissipated energy) (Kuricheva et al., 2017). Importantly, diffusion, a key element in both physical and biological processes, produces an increase in the entropy of a system, as predicted by the Second Law. Indeed, it is the second law of thermodynamics that drives the diffusive process (Supplee, 1980). This will become important when we look at potential drivers in evolutionary biology.

2.1. The maximum entropy production principle (MEPP)

Early in the history of thermodynamics, the concept of the maximum entropy production principle (MEPP) appeared. Berthelot (1875) argued that chemical change shifted towards maximum heat production. Onsager (1931), building on earlier work by Rayleigh (1876), made the observation that thermodynamic systems reduce barriers to increasing entropy: $dS/dt = \text{maximum}$ (where dS/dt represents the rate of entropy change and I is the impediment to entropy increase). Using Bénard cells, Onsager demonstrated that I is minimized and dS/dt is maximized with time. Ziegler (1963) developed these ideas further and is often credited with formally defining the MEPP. Jaynes (1983) showed that the majority of the distributions (e.g. of positions and velocities of individual atoms) permissible by constraints have entropies near the maximum value.

In its modern expression, 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). Importantly, the MEPP adds to the second law of thermodynamics by not only indicating the direction of change, but the rate of change. Kleidon and Lorenz (2004) and Martyushev and Seleznev (2006) concluded that open systems interacting with the external environment in non-linear ways are stabilized in such a way as to maximize entropy production. Serizawa et al. (2014) note that open systems existing in a state far from equilibrium become stabilized when entropy production is maximized and this is facilitated by the emergence of dissipative structures. Importantly, dissipative structures with access to free energy will reduce internal entropy and thus become more ordered by externalizing entropic output to the environment. Thus, complexity and dissipation are, in effect, two sides of the one coin, with increasing complexity generating increased entropic output, due to concomitant increases in growth and maintenance respiration (Skene, 2017). Lucia and Maino (2013) demonstrated that entropy generation not only increases but increases as quickly as possible towards an asymptote, its maximum rate, based upon the probability of individual elementary modes distributed in accordance with the Boltzmann distribution.

Dyke and Kleidon (2010) argue that because all Earth system processes operate within the constraints of conservation of energy, mass and momentum, then the MEPP should be applied to all Earth system processes, assuming local thermodynamic equilibrium at the relevant scales. For a detailed historic analysis of the development of the MEPP, we recommend Vallino and Algar (2016).

The MEPP was first applied to the Earth system by Paltridge (1975, 1979), following on from the work of Lorenz (1960). Since then, the MEPP has been applied in a wide range of non-equilibrium systems, ranging across present and past climate (Mobbs, 1982; O'Brien and

Stephens, 1995; Paltridge, 2001; Herbert et al., 2011), oceanic circulation (Polyakov, 2001; Shimokawa and Ozawa, 2007), the organization of watershed development (Zhao et al., 2016), monsoon behaviour (Wang et al., 2016), linguistics (Berger et al., 1996), macroeconomics (Aoki, 1996), earthquake predictions (Dong et al., 1984), photosynthesis (Juretić and Županović, 2004), plant evapotranspiration (Wang and Bras, 2011), critical zone processes (Quijano and Lin, 2014), metabolic networks (Srienc and Unrean, 2010; Unrean and Srienc, 2011), nucleotide sequences (Salamon and Konopka, 1992; Schmitt and Herzog, 1997), developmental biology (Grabec, 1998), bacterial chemotaxis (Županović et al., 2010), enzyme kinetics (Dobovišek et al., 2011), ATP synthase enzyme design (Dewar et al., 2006), and chemical replicators (Martin and Horvath, 2013). Extra-terrestrial applications have included atmospheric models for Titan and Mars (Lorenz et al., 2001; Ozawa et al., 2003).

3. Thermodynamics and ecology

The significance of thermodynamics in ecology dates back over one hundred years, to Ludwig Boltzmann, (1886), Sergei Podolinsky (Cleveland, 1999; Podolinsky, 2004), Alfred Lotka, (1922a) and Vladimir Stanchinskii (Weiner, 1984). Since the laws of thermodynamics lie at the heart of any understanding of energetics in both biotic and abiotic systems, it is unsurprising that the concept of thermodynamics has become increasingly important in recent ecological literature.

Morowitz (1968) examined energy flow from organic molecules to ecosystems, demonstrating that systems subject to external energy gradients, be they thermal, chemical, or electromagnetic, have a tendency to develop internal material cycles, driving the system further from equilibrium and to lower entropic states. Ecosystems are now known to maintain their structure through converting low-entropy solar radiation into high-entropy forms of energy, such as long-wave radiation and latent and sensible heat (Kleidon and Lorenz, 2004). Schrödinger (1944) observed that internal order can only be maintained at the expense of increasing disorder in the environment. So not only do ecosystems move to reduce entropy within themselves (hence moving further from energetic equilibrium), but in doing so they move towards maximizing external entropy increase. Central to this process is the maximum entropy production principle (MEPP). Odum and Pinkerton (1955) set out the maximum power principle as a foundation for systems ecology, claiming that the principle was universally applicable. This states that “during self-organization, system designs develop and prevail that maximize power intake [and] energy transformation” (Odum, 1995).

The MEPP has now been applied to a wide range of ecosystem level characteristics (Harte, 2011; Harte and Newman, 2014; Chapman et al., 2016), including spatial organization (Phillips et al., 2006; Harte et al., 2008; del Jesus et al., 2012), spatial interactions (Volkov et al., 2009), semi-arid system heterogeneity (Schymanski et al., 2010), soil hydrology (Porada et al., 2011), food web structure (Schneider and Kay, 1994a,b; Meysman and Bruers, 2010; Yen et al., 2016), hierarchical organization (Annala and Kuismanen, 2009), ecosystem biogeochemistry (Vallino, 2010; Vallino and Algar, 2016), zonation in paludification gradients (Kuricheva et al., 2017) and ecological succession in Mediterranean (Celeste and Pignatti, 1988), lake (Aoki, 1987, 1989, 1990; 2006; Ludovisi, 2004), marine sediment (Meysman and Bruers, 2007) and tropical rainforest (Holdaway et al., 2010; Lin et al., 2011) ecosystems, where entropy production increases during earlier stages before reaching a maximum at maturity. As ecosystems transition into a mature state (or pseudo-steady state where $P:R = 1$), entropic output follows a logistic trajectory, levelling off at S_{max} (maximum entropic output), in accordance with the MEPP (Holdaway et al., 2010; Skene, 2013). Here, the ecosystem has organized either to consume all available energy (energy limited), or to consume as much energy as available resources allow (resource limited). The latter case is expressed as Liebig's law of the minimum (though more correctly, Sprengel's Law of

the Minimum (Sprengel, 1828)). In effect, the Law of the Minimum represents an expression of the MEPP, indicating one of the limiting factors defining S_{\max} , the asymptote (Skene, 2013).

Recent investigations have found that energy dissipation in ecosystems depends on the type of plant community (Lin et al., 2009; Maes et al., 2011; Norris et al., 2012; Stoy et al., 2014), canopy architecture (Miedzijko and Kędziora, 2014), weather conditions (Song et al., 2013), seasonality (Lin et al., 2009; Norris et al., 2012), level of disturbance (Svirezhev, 2000; Lin et al. 2017) and stage of succession (Skene, 2013; Stoy et al., 2014).

4. Thermodynamics and evolutionary biology

Boltzmann was the first to describe the struggle for existence in thermodynamic terms, when he wrote: “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” (Boltzmann, 1886).

The idea that thermodynamics might somehow influence biological evolution gained further support from Lotka (1922a; b; 1925). He focused on the energy flow in evolutionary processes, claiming that natural selection led to an increase in both energetic efficiency and total energy throughput. Schrödinger (1944) further developed the concept that evolution was driven by maximization of useful energy flow, stating that life forms imported negative entropy (or negentropy) and released positive entropy into their environments. He further suggested that thermodynamics and biological self-organization would be reconciled by the study of living systems from a non-equilibrium perspective. Fenchel (1974) demonstrated that the evolution of life on Earth followed an increasingly dissipative path, the specific energy needs per unit biomass being higher for multicellular organisms than for unicellular organisms, and for homeothermic (warm-blooded) animals in comparison to poikilothermic (cold-blooded) animals.

Prigogine (1976) referred to life forms as dissipative structures, and argued that early organisms evolved from non-living, far-from-equilibrium structures, increasing in complexity through increased entropy production. Ulanowicz (1997) further linked the evolution of diversity and complexity with thermodynamics when he wrote: “In any real process, it is impossible to dissipate a set amount of energy in finite time without creating any structures in the process”. Wiley and Brooks (1982) argued that evolution is, itself, an entropic phenomenon. Annala and Salthe (2010) went further, claiming that “the theory of evolution by natural selection is herein subsumed by the 2nd law of thermodynamics.” Swenson (1989) demonstrated that much of the behaviour that is generally attributed to either cultural or biological systems is, instead, generic to the physics of the expanding universe.

Pujol (2002) found that the application of the MEPP to the Daisy-world simulation of Watson and Lovelock (1983) led to increased temperature stability across a range of solar insolation values, thus creating improved conditions for life. Pujol (2002) further points out that although the MEPP may be a favourable principle for the existence and continuation of life, its nature is independent of the existence of living organisms. Rather it is a physical driver based on the laws of thermodynamics. Wicken (1987) concluded that entropic dissipation propels evolutionary structuring, while Schneider and Kay (2005) contended that evolving life represents order emerging from disorder in the service of causing even more disorder.

Phylogenetics also acknowledges the importance of thermodynamics in evolution. Butler and King (2004) point out that, although it is not always clearly stated, Brownian motion, which is an outcome of the second law of thermodynamics (Neumann, 1980; Roos, 2014), is the underlying model of evolution in nearly all phylogenetic comparative methods such as maximum likelihood (ML) methods for ancestral

character state reconstruction, phylogenetic regression, phylogenetic autocorrelation, simulation methods and weighted least squares parsimony.

5. Entropic production and dissipative structures at each level of organization: in search of common ground

The biosphere is arranged in a series of levels of organization (DNA, proteins, cells, organisms, populations, species, ecosystems and biomes), each level feeding back upon itself and impinging on the other levels (Salthe, 2012). Each level is an open system in energetic terms, and the entire biosphere is also an open system. The flow of energy through the system is essential for its continuance. Lovelock (1965) stated: “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 free energy taken from the environment and subsequently rejected in a degraded form.” The MEPP acts locally at each of these levels of organization in any complex open system, while the asymptote at which maximum entropic production (S_{\max}) is set will be defined by its surroundings, namely, the other levels of organization. These interactions limit the entropic production at any given level (i.e., there is sub-optimality), allowing the maximum entropic production possible, given these restrictions, at the level of the biosphere. For example, a population will be impacted by nutrient availability, energy availability, predator-prey interactions, disease organism populations, genetic diversity, successional stage, biome characteristics and many other constraints. Each level of organization contributes towards evolutionary, ecological and physiological outcomes.

This paper explores the proposition that the structure and functioning of each level of biosphere organization is shaped and driven by thermodynamics, and to examine the evidence for this, I now review the relevant scientific literature.

5.1. DNA

Genetic material is unique in biological terms in that, over time, information entropy increases within the molecule (as randomization increases with each mutational event) and out with it (due to energetic requirements in production, maintenance and error correction). It is the internal information entropy increase that contributes significantly to variation and drives phenotypic change and diversification. Normally life as a process reduces internal entropy by converting low entropy energy to high entropy waste (Lovelock, 1965). Yet with genetic material, random mutations produce increased information entropy within the genetic sequence (Tessera and Hoelzer, 2013). In eukaryotes, mutations must occur in germline cells in order to be passed on to the next generation, although mutations in somatic cells can lead to death, thus impacting reproduction through, for example, cancer.

Germline mutation depends on a complex combination of related biological timescales. These include the efficiency of DNA repair, the cycle times of cellular processes in gametogenesis, the ages of puberty and reproduction, the duration of fertility and the duration of key stages in embryonic development, each potentially differing by sex or species (Sally, 2016). Of course, DNA repair processes, such as direct damage reversal, base excision repair, nucleotide excision repair, mismatch repair and recombination repair (Hoeijmakers, 2001), help reduce informational entropy within the sequence, but this in turn comes at an energetic cost, leading to increased physical entropic production (Salamon and Konopka, 1992). Thus, the generation of variation (an outcome of the balance between mutation, producing informational entropy and repair, producing physical entropy, both thermodynamic events) within the genetic material, a foundation stone of evolutionary theory, is, fundamentally, a thermodynamic process and the second law of thermodynamics acts as a signpost in terms of increasing genotypic complexity and cost, both in terms of production, maintenance and repair. Ultimately it is the sub-optimal repair of DNA damage that

controls the passage of these mutations into the proteotype, underpinning and driving phenotypic diffusion into structural and functional ecological space, or ecospace (Bambach et al., 2007).

5.2. Amino acids

Amino acids form the building blocks of life. Early abiogenic amino acids were shown to form along a thermodynamic gradient (Higgs and Pudritz, 2009; Szőri et al., 2011). Early coding was constrained thermodynamically in terms of concentration and availability of amino acids, while later biogenic amino acids would produce increased entropy of formation (Akashi and Gojobori, 2002; Seligmann, 2003). Since amino acids are likely to have existed prior to the formation of the genetic code (Vranova et al., 2011), it is important to note that their prevalence and temporal appearance is most easily explicable on thermodynamic grounds. Thus, the genetic code appears to map onto this thermodynamic outcome (Trifonov 2004).

Indeed, the resulting abundance pattern produced from thermodynamic considerations may well have provided important constraints on the nature of the genetic code that ultimately appeared (Higgs and Pudritz, 2009). A final interesting observation at this level is that due to unexpected trade-offs in the codon table, energetically cheaper nucleotides encode on average energetically more expensive amino acids (Chen et al., 2016).

5.3. Proteins

The folding and function of proteins is thermodynamically determined (Anfinsen, 1973; Lazaridis and Karplus, 2002). It is important to remember that the genetic code does not produce the final global protein structure. Rather, the thermodynamic context determines this. Furthermore, changes in protein configuration, essential for proteins involved in active transport, occurs because of a change in the thermodynamic context, not in the amino acid sequence. Thus, increasing entropy within the genetic code can produce changes in the protein sequence, but the functional and structural outcomes are shaped by another thermodynamic context, as outcomes of interactions between the other levels of organization. Hence, proteins structurally explore physical and temporal space and this exploration is driven by thermodynamics. Functionally, again their roles are defined thermodynamically.

5.4. Cells

Cellularity allows the reduction of entropy within cells, providing the stability needed for cellular physiology (Davies et al., 2013). Cells also export high levels of entropy (Marín et al., 2009). To live, cells need a temperature difference between them and their environment and this temperature difference is the driving force for the flow of energy (the energy that is available to be used) (Lucia, 2014). Cellular metabolic networks evolve towards maximum entropy production (Unrean and Srien, 2011).

There are several novel structural features of the eukaryotic cell compared to prokaryotic cells, including significant increases in cell volume and DNA size, the appearance of mitochondria or chloroplasts, the nucleus and the complex cytoskeletal network (Maynard Smith and Szathmáry, 1999). With the increase in size, the internal network structures were able to grow and become increasingly more complex (Suki, 2012), as expected from the second law of thermodynamics - increasing complexity requires greater growth and maintenance respiration, converting larger amounts of free energy to waste. The endosymbiosis of proteobacteria as mitochondria and as chloroplasts has greatly aided the development of these vastly more entropy-exporting cell types (Lane, 2005).

5.5. Individual organisms

The organism is a unit of organization that brings together the cells as an operational whole. Dawkins (1982) has claimed that “The organism is a physically discrete machine ... it takes decisions as a unit”. This could not be completely correct. Organisms are open systems as are all levels of organization in the biosphere, and their path is determined by the greater interactive network within which they exist. If organisms were discrete, independent decision makers, then population dynamics, ecological succession and other supra-organismal emergent properties would be inexplicable. Organisms do not sit at the top end of the organizational hierarchy, but rather find themselves within the network, contributing and being shaped by all around them. No man is an island, and the same applies to all organisms. Thermodynamics reaches through all. Schrödinger (1944) demonstrated a correlation between the entropy of living organisms and the environment. Living organisms decrease their own entropy at the expense of the increase of the entropy of the environment. Access to available energy from the environment through food webs determines the survival of the organism within a thermodynamic universe. Such access requires the organism to be firmly bedded within its ecology.

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). Form represents structural diffusion into ecospace, explaining the vast number of morphotypes on our planet through evolutionary time, estimated at some 30 million species (Skene, 2015), while function conforms to laws of thermodynamics. Function is much more conservative than form.

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. Lenart and Bienertová-Vašků (2016) suggest that the relationship between aging and entropic production may be explained by double strand breaks, caused by heat dissipation over time, which are in turn known to play an important role in the process of aging, thus forming a bridge between aging and increased entropic production (i.e. heat dissipation).

5.6. Populations

Evolutionary biologists tend to focus on genetic diversity within populations whereas ecologists tend to focus on community dynamics, ignoring evolution (Urban et al., 2008). However, population ecology and genetics have been demonstrated to overlap. Both insertion-deletion (Sung et al., 2016) and substitution (Sung et al., 2012) mutation rates have been shown to be inversely proportional to population size. Populations are shaped, primarily, by energy and resource availability, where increased energy availability raises the carrying capacity. Individual organisms are part of populations or meta-populations. Increased free energy availability allows population increase within ecosystem constraints (Aoki, 1995). Logistic growth of populations follows the MEPP, wherein K (the carrying capacity) can be seen to represent S_{max} (maximum entropic output) (Skene, 2013). In terms of population dynamics, Andrae et al. (2010) demonstrate that entropy production can successfully characterize ecological systems with cyclic population dynamics.

5.7. Speciation

The concept of species as a unit of organization is not as clear cut as has been thought. Speciation is, at best, a eukaryotic trait, since bacteria share DNA plasmids between taxa making the species concept redundant for prokaryotes (Skene, 2009). Horizontal gene transfer actually operates between phylogenetic kingdoms. Mitochondria and chloroplasts represent the remnant of entire prokaryotic organisms that

have been transferred into eukaryotes (Cavalier-Smith, 1987; Moreira et al., 2000; Gray et al., 2001). Even within eukaryotes, the reproductive species concept breaks down. Hybridization occurs in 25% of plant species and 10% of animal species, with much higher figures (42.9% in birds of paradise and 24% in American warblers) in given families (Mallet, 2005). However, given the importance of the species in evolutionary theory, we include it here.

Exploration of ecospace through random mutations delivers increased diversity, expressed as speciation if reproductive barriers are in place. Skene (2015) used four physical laws and processes (the first and second laws of thermodynamics, diffusion and the maximum entropy production principle) to approximate species diversity across evolutionary time. Given that open systems such as ecosystems will move towards maximizing dispersal of energy, we should expect biological diversity to increase towards a level, D_{max} , representing maximum entropic production (S_{max}). This thermodynamic approximation, combining diversification, post-extinction recovery and likelihood of discovery in the fossil record, has a highly significant correlation with the observed fossil record over the last 500 million years ($r = 0.866$, $p < 0.001$) (Skene, 2015). It is suggested that increasing competition and natural selection are indicators of proximity of diversity to maximum entropic production, wherein as the system approaches maximum entropic production, speciation reduces, as diversification slows. Alizon et al. (2008) observe that “under resource competition there is an exponential slowdown of apparent evolution”, while Phillimore and Price (2008) conclude that “speciation slows as ecological opportunities and geographic space place limits on clade growth”.

Thus, we see that thermodynamics offers a unique insight into the history of speciation on our planet, something that a gene-centric approach cannot possibly deliver. Furthermore, the tempo of evolution can be accounted for on a thermodynamic basis (Skene, 2015), something that neither ecological nor evolutionary theory can explain.

5.8. Ecosystems

As we have examined in detail earlier, the maximum entropy production principle has been demonstrated to play an important role in ecosystem processes such as spatial organization, spatial interactions, soil hydrology, food web structure, hierarchical organization, succession and zonation in a wide range of studies. Trophic relationships, eutrophication and other ecosystem processes are all thermodynamic in their essence (Ma and Qian, 2015; Skene, 2017). Directionality in succession has long been of interest to ecologists, where there is a predictable, directional, spatial and temporal change in ecosystem development. Species are replaced by other species over time. However, the maximum entropy production principle, wherein community structure changes to maximize entropy production, can be seen to offer an explanation as to the drive underpinning ecosystem succession, not towards a climax community but towards one offering maximum entropic output within a given environmental context (Skene, 2013).

5.9. Biomes

Biome conditions are determined by solar radiation density, interacting with the hydrological cycle, and forming the backdrop within which ecosystems types develop (Kleidon, 2009; Skene, 2013). It is at the biome level of organization that we see physics at its purest, determining temperature, seasonality, and rainfall characteristics that then impact on other important properties such as wind direction and strength, soil development and nutrient availability. Climate, global circulation patterns, hydrology and tectonic activity have all been shown to follow the MEPP (Paltridge, 1975, 1979; Dong et al., 1984; Polyakov, 2001; Herbert et al., 2011; Westhoff et al., 2014). Thus, biomes are, fundamentally, outcomes of energetic variation across the planet and operate within the MEPP.

6. Can thermodynamics form the common ground?

Alfred Lotka published two important papers on the role of thermodynamics in ecosystem organization and evolution. In the first paper (Lotka, 1922a), he suggested that ecosystems will organize to maximize energy flux while in the second (Lotka, 1922b), he further suggested that increasing energy flow also provides directionality to evolution. Hence, he saw energetics as a common ground, shared by both biological evolution and ecology.

We now examine a number of ecological and evolutionary areas which may benefit from a thermodynamic approach.

6.1. Direction and drive at spatial and temporal levels explained including succession, post-extinction recovery and evolutionary tempo

Direction and drive are clearly apparent in ecological succession (Facelli and D'Angela, 1990; Demetrius, 2000; Platt and Connell, 2003). However, evolutionary tempo is also clearly evident, particularly in terms of post-extinction recovery, where, following a brief lag, diversification passes through an exponential phase, before levelling off at an asymptote (approximating a logistic curve). This can be seen throughout evolutionary history (Sepkoski, 1996; Solé et al., 2002). Eldredge and Gould (1972) highlight punctuated equilibrium, wherein there is an alteration of ‘stasis’ phases and accelerated phases. Of interest here is what happens within the accelerated phases. A detailed discussion relating to asymptotes in evolutionary time can be found in Benton and Emerson (2007).

Furthermore, although species composition can change significantly across mass extinction events (for example, the rise of the dinosaurs following the end-Triassic event (Percival et al., 2017) and the rise of the primates following the K/T event (Heads, 2010)), there is a restoration of functional groupings every time. New species of primary producers, herbivores, carnivores and detritivores appear, restoring functional integrity. The functional resilience of nature is most likely due to the significance of energy flow in the continuance of life on Earth. It is free energy that must be acquired for growth and maintenance, and the production of entropy is a cosmic requisite. The increase in complexity (requiring increasing amounts of maintenance respiration) along with increasingly energetically expensive life histories is expected within a thermodynamic cosmos, provided that free energy is available. If the availability of free energy is reduced (for example due to dust from bolide impacts or significant volcanic activity) then complexity will be reduced (the process of ecological simplification), but upon restoration of incident energy levels, complexity can once again increase, up to a point of maximum entropy production. Thus, the evolutionary tempo over millions of years can be seen to be an outcome of thermodynamic considerations (Skene, 2015).

6.2. Alignment across ecology and evolution

Given that ecology and evolutionary biology relate to the same biosphere, it is a strategy of doubtful value to consider them as separate lands. Thermodynamics offers common ground, within which both subjects can be explored together. As we have seen, thermodynamics works across all levels of biosphere organization, and as such produces a system-based emergent outcome, rather than a reductionist one where the selfish gene dominates over the extended phenotype. This may be the most challenging issue for evolutionary biology to accommodate. An important issue relates to the emergent nature of ecology and evolution, in terms of fine detail at the micro level contrasting with general diffusive patterns at the macro level. However, just as in the greater cosmos, thermodynamics applies at all levels of organization, and so the foundations for both ecology and evolution remain the same. Not knowing the specific velocity and position of every particle in a diffusing cloud does not mean that we cannot measure diffusion.

6.3. Alignment with universal drivers

Some have held that the inanimate and animate worlds are completely different, and governed by different principles. For example, Demetrius (2000) wrote that “The science of thermodynamics is concerned with understanding the properties of inanimate matter”. Pross (2011) stated that neither the behaviour of a stalking lion nor the single cell phenomenon of chemotaxis is explicable in terms of the second law.

Others have sought to extend the principle of natural selection to the inanimate world. Molchanov (1967) wrote: “By now enough facts have been gathered to show that the main principles of Darwinism are applicable to all evolving systems, from elementary particles to galaxies”. Prigogine et al. (1972) emphasised that while natural selection can be expressed in thermodynamic terms, thermodynamics cannot replace natural selection as an under-riding evolutionary principle.

Yet surely it would seem more likely that already acknowledged cosmic laws will reach as far as our planet and the chemistry and biology existent on it. Since life itself is a thermodynamic concept (Schrödinger, 1944), then it makes sense that the evolution of life should also be best understood through a thermodynamic lens. Thermodynamics penetrates into the very particles from which life and the rest of the universe are constructed, and controls core processes such as diffusion, gravity and Newton's laws (Neumann, 1980; Verlinde, 2011; Roos, 2014). Thus, as a common ground, it holds a strong, penetrative and authoritative position. As we have seen, experimental and theoretical evidence points to the fact that at every level of organization of the biosphere, thermodynamics plays a central role, acting as the architect of structure, function and change. Furthermore, natural selection, unlike thermodynamics, fails to account for direction in ecological succession, a fundamental process in both ecology and evolutionary biology, where species (and therefore genes) are turned over, rather than maintaining themselves in any selfish way.

6.4. Sub-optimality and eco-inefficiency in nature

A key feature of the biosphere is sub-optimality, be it in terms of DNA correction (if optimized there would be no primary variation) to sub-optimal predation. Sub-optimality is a clear fingerprint of system theory, wherein multiple processes cannot all be optimized. As the number of challenges increase upon a process, only solutions that are increasingly sub-optimal for each challenge will work (Farnsworth and Niklas, 1995). Indeed, inefficiency and sub-optimality are both central to the functioning of any ecosystem (Abbott and Quink, 1970; Forget, 1992; Tomback, 2001). Eco-inefficiency represents the reality that life is a dissipative process fundamentally, and therefore waste is its signature (Skene, 2017). These processes are thermodynamic outcomes. Nature is not optimal and asymptotes do exist.

6.5. The significance and meaning of form and function in evolutionary biology and ecology

Finally, thermodynamics offers a meaningful basis for understanding the difference between form and function in evolutionary biology and ecology. Form has dominated evolutionary considerations since Linnaeus set out the modern system of binomial taxonomy (Skene, 2011). Diversity has been equated to morphotype, and species were identified based on form. Phylogenetics utilizes this taxonomic system. Only more recently has DNA sequencing become important. Yet in terms of evolution, there are a myriad of forms. In terms of the processes underlying the generation of form in eukaryotes, the increasing informational entropy within the genetic material, brought about by random mutations, plays a central role. This results in the diffusion of the proteotype and the phenotype into energetic space, much as Brownian motion drives the distribution of gas particles in a jar. In turn, diffusion and Brownian motion are thermodynamic outcomes, as we have seen.

However, the ultimate determination as to whether a given phenotype can survive is if it can meet the demands of thermodynamics in terms of maintaining order in an increasingly disordered universe. It is its ability to acquire free energy and expel waste energy that is essential, and this is the domain of physiology. Physiology is much more conservative than form, because the laws of thermodynamics are focused on energy handling, the very tenet of physiology. Thus, form is a diffusive process, whereas function is an energy-transforming process. While generation of form is a consequence of entropic increase within the genetic material and the subsequent diffusion of the phenotype into ecospace, physiology is the process of reducing entropy within the organism, and exporting it into the environment. As in all diffusive processes, there is direction and drive in diversification and a dynamic equilibrium is reached in a given context, such as in a jar. Thus, we see the diversification of life through time as a diffusive process, whereas the functioning of life is a waste expulsion process.

Returning to Hutchinson's (1965) ecological theatre and evolutionary play, we can instead view the story of life as a functional play with the forms as the players (Skene, 2009). Each actor brings their own flair and interpretation to the part, but the script ultimately determines their role. After each mass extinction event, new organisms take on the characters of carnivores, herbivores, detritivores and producers. However, the overall script is the same. This is because the levels of organization are, ultimately, functional in essence and forms diffuse into functional space, acting out their parts. If you don't stick to the script, you won't be in the production. Thus, the tight functional play resumes after each interruption, and is conservative in nature in spite of the diverse cast assembled. Thermodynamics scripts and directs the production.

7. Conclusions

We suggest that each level of organization in the biosphere operates in accordance with the maximum entropy production principle, both in spatial and temporal terms. Thus, thermodynamics can claim to be the common ground underpinning the structure and function of life on Earth, and in addition, provides the drive and temporal context for change, be that in ecology or evolutionary biology.

The concept of genetic determinism arises from a belief that genes, unlike other causal factors, are instructions, not just materials, and are directed towards outcomes they help to produce (Oyama 2000 a; b). However, genes are incapable of directing many of the outcomes in life, such as ecological succession, post-extinction recovery patterns, evolutionary tempo, functional redundancy, community resilience, biome characteristics and patterns of diversification. These cannot be explained as merely an expression of an extended phenotype (Dawkins, 1982), and they cannot be dismissed as contexts, but rather as properties of a system from which life emerges. For system theory has no place for a reductionist unit of selection and for good reason, because such an approach fails completely to account for the emergent properties of life. We suggest that a more appropriate common ground is thermodynamics, allowing ecology and evolutionary biology to be understood as a unified whole, and paving the way for research and applications to address the significant challenges currently facing the biosphere.

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