Title: On the thermodynamics of multilevel evolution

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Abstract

Biodiversity is hierarchically structured both phylogenetically and functionally. Phylogenetic hierarchy is understood as a product of branching organic evolution as described by Darwin. Ecosystem biologists understand some aspects of functional hierarchy, such as food web architecture, as a product of evolutionary ecology; but functional hierarchy extends to much lower scales of organization than those studied by ecologists. We argue that the more general use of the term “evolution” employed by physicists and applied to non-living systems connects directly to the narrow biological meaning. Physical evolution is best understood as a thermodynamic phenomenon, and this perspective comfortably includes all of biological evolution. We suggest four dynamical factors that build on each other in a hierarchical fashion and set the stage for the Darwinian evolution of biological systems: 1) the entropic erosion of structure; 2) the construction of dissipative systems; 3) the reproduction of growing systems; and 4) the historical memory accrued to populations of reproductive agents by the acquisition of hereditary mechanisms. A particular level of evolution can underpin the emergence of higher levels, but evolutionary processes persist at each level in the hierarchy. We also argue that particular evolutionary processes can occur at any level of the hierarchy where they are not obstructed by material constraints. This theoretical framework provides an extensive basis for understanding natural selection as a multilevel process. The extensive literature on thermodynamics in turn provides an important advantage to this perspective on the evolution of higher levels of organization, such as the evolution of altruism that can accompany the emergence of social organization.

Key Words

Multilevel evolution; Multilevel selection; Thermodynamics; Physical evolution; Self-organization; Dissipative systems; Entropy
1. Introduction

In Biology the term “evolution” refers to the changes in heritable information within populations over time and the dynamics of population origins and extinctions. This view of evolution naturally focuses on the evolution of living systems, which fundamentally involves reproduction of bio-molecules, cells and whole organisms. Therefore, our understanding of processes affecting biological evolution (e.g., natural selection, drift…) usually center on patterns of reproductive success. In physics, however, the evolution of a specific system can be more generally defined as its unfolding change in form and/or function over time.

Thermodynamically speaking, any ensemble composed of a certain quantity of matter and energy (i.e. a physical system) in an initial state at time $t_0$ will change over time towards a new state at time $t_1$. Physical systems, including living systems like organisms and ecosystems (Schneider and Kay, 1994), are typically ‘open’ with exchanges of matter/energy/information between the system and its local environment flowing in both directions. They have been called complex systems because interactions among the components of the system sustain the form of ‘the complex’ in a ‘far from equilibrium’ state (Coveney, 2003). Prigogine provided a rationale for the self-organization (origin and sustenance) of such systems based on non-equilibrium thermodynamics. He argued that localized spatial gradients in matter/energy provide opportunities for the emergence of coherent systems that dissipate the gradient, consistent with the second law (Nicolis and Prigogine, 1977). Familiar examples include the emergence of vortexes and convection cells in the atmosphere when the hot air at the earth’s surface is sufficiently hotter than the cold air at higher altitudes. These atmospheric dissipative systems effectively reduce the strength of the heat gradient by vertically pumping and mixing the air masses. The emergence of a dissipative system represents increasing local order (Schrödinger, 1944), but this remains consistent with the second law as long as the system generates more entropy through
dissipation than is lost through self-organization. This thermodynamic requirement effectively makes dissipative systems irreversible (Zenil and Marshall, 2012).

So while biologists often consider populations of reproducing agents to be necessary for evolution to occur, physicists extend the term to include the evolution of singular self-organizing systems. The development of individual organisms would fit the more general definition of evolution, although it is usually considered an utterly different phenomenon by biologists. This semantic difference is not just an arbitrary one that demands a choice when one uses the term “evolution”, because reproduction itself involves thermodynamic processes that require energy and increase entropy. In other words, reproduction is another kind of activity molecules and organisms can perform involving the dissipation of physical gradients. One conventional way to think about this is that the free energy used in reproduction is obtained by breaking down ordered macromolecules and degraded energy is ultimately dissipated to the environment in the form of heat. Furthermore, constraints on system growth (e.g., cells, organisms...) would thermodynamically favor reproduction in particular when the gradients fueling system dynamics persist. Biological cells and organisms typically have mechanisms for energy storage that can carry them through short periods without resource input. In contrast, the fuel for atmospheric convection cells is fleeting. Their dissipating action can substantially diminish the local heat gradient, and local solar heating of the earth’s surface stops as the storm rotates to the dark side of the earth. Given the connections between reproduction and thermodynamics, Hoelzer et al. (2006) argued that natural selection itself is a thermodynamic process in the same sense that we would describe convection in a thermodynamic context. Abiotic selection improves the efficiency and effectiveness with which agents (e.g., organisms) capture and utilize matter/energy. Coevolution among populations gives form to ecosystems, such as food web structure (e.g., McKane and Drossel, 2006), resulting in more efficient and effective
dissipation (e.g., of solar energy; Hoelzer et al., 2006) at the global scale. Complex adaptive systems also require stochastic factors (Gros, 2008), which are provided by mutation and drift. With this set of evolutionary processes in place, it is generally expected that higher levels of organization will emerge (e.g., Okasha, 2012), and the process of evolution would be manifested throughout the hierarchy.

In this paper we suggest some key levels of biological evolution from a thermodynamic perspective. We adopt a broad view of multilevel evolution (MLE) in which multilevel selection (MLS) would be one of several (thermodynamic) evolutionary processes. We suggest a hierarchical set of evolutionary levels that are quite different from the ones previously considered by most biologists, although we do not see any conflict between our categories and alternative paradigms. An important benefit from our new framework is that it helps to expose biological evolution as a phenomenon that emerged from ongoing earthly thermodynamics, as opposed to starting de novo with the chance origin of molecular replication, and it provides a physical basis for MLE.

2. Theory

2.1 Level-1 evolution

The second law of thermodynamics sets the most generic tendency of change as the simple instability of structure, hence we use this as our most basal level of physical evolution. Local gradients in temperature, pressure, chemical potential and composition tend to irreversibly decrease according to the second law of thermodynamics (Feynman et al., 1964, 1966). Accordingly, the second law states that entropy can only increase or remain stable within an isolated system. It is a trivial consequence of the equal prior probability postulate. The entropy of an isolated system in thermal equilibrium containing an amount of energy (E) is:
\[ S = k_B \log [\Omega (E)] \]  

(1)

Where \( k_B \) is the Boltzmann constant and \( \Omega (E) \) is the number of quantum states in a small interval between \( E \) and \( E + \delta E \) (Nagle, 2010). This means that the structure of isolated systems will progressively vanish over time. Thus level-1 evolution involves monotonic and deteriorative change.

### 2.2 Level-2 evolution

Of course, not all change is deterioration. Dynamical systems exist and new ones are frequently constructed throughout the universe. Constructive processes create local order (Schrödinger, 1944), which would not be possible at the scale of a whole closed system. In contrast, open systems exchange matter/energy/information with their external environment can be constructive, as long as their activity creates more entropy than order in the smallest closed system within which the open system resides (Nicolis and Prigogine, 1977). Open systems can continuously fill their fuel tanks by extracting free energy as they facilitate the increase in entropy and they can use it for construction (self-organization, including maintenance) and system behavior. In other words, self-organizing systems can use the free energy they obtain from accelerating the production of entropy to move still further from thermal equilibrium. Nevertheless, as a dissipative system needs the continual input of energy, it is a meta-stable pattern and breaks down without this input (Johnson and Lam, 2010).

Systems that actively maintain or increase their level of organization by using matter and free energy obtained from the external environment are called self-organizing (SO) systems because the order of the system is constructed by the internal dynamics of the system itself (Smith, 2008). The potential for the emergence of SO dissipative structures exists wherever there are sufficiently concentrated spatial gradients in free energy (Hoelzer
et al., 2006). Convection cells and vortices (e.g., thunder storms and tornadoes) forming in the atmosphere when heat builds up at the earth’s surface are familiar examples of such simple SO systems (Hoelzer et al., 2006). In particular tropical cyclones form when the energy released by the condensation of moisture in rising air causes a positive feedback loop over warm ocean waters (Gray, 1988). On earth these systems do not “survive” more than days, but there are examples of such convection systems that last much longer such as the red spot on Jupiter (observed for the first time in 1870). We suggest that dissipative self-organization should be classified as level-2 evolution.

2.3 Level-3 evolution

The emergence of SO dissipative structures requires the inflow and outflow of matter/energy (Pulselli et al., 2009). About 4 billion years ago, specific local conditions, such as hydrothermal vents akin to the Lost City Hydrothermal Field (LCHF), might have favored the emergence of dissipative systems organized on a macroscopic level and generated by a flow of matter and energy that is continuously consumed (Tessera, 2011 and Russell et al., 2010). Indeed, observations and experiments show that lipid vesicles could have formed in environments like those at hydrothermal vents (Rushdi and Simoneit, 2001, Baaske et al., 2007, Proskurowski et al., 2008, Martin et al., 2008, Amend and McCollom, 2009, Budin et al., 2009 and Konn et al., 2009) where the fuel for self-organization is provided by persistent thermal and molecular (e.g., hydrogen and methane) gradients. Moreover, experimental data from bi-layer vesicle models show that the vesicles can grow and bud (a kind of reproduction) even before a directed synthetic chemical system is established (Luisi et al, 2004, Rasi et al., 2004, Walde, 2006 and Weber, 2010). Thus the population size of such vesicles can increase over time due to the positive feedback between individual reproduction and population growth (individual reproduction adds to population growth, which results in more reproducing individuals, and so on).
macroscopic system into two, including diverse biological processes like cellular division and viviparous birth, directly increases entropy by increasing the number of microstates manifested by the living system. Of course, directing metabolic energy into building and using reproductive mechanisms further accelerates entropy production; but reproduction is unusual among the behaviors systems can perform in its direct contribution to entropy. For this reason, we expect the tendency for growth to typically be accompanied by reproduction, unless material constraints lead the system to simply fall apart or stop growing instead. From a thermodynamic perspective, the origin of reproduction by vesicles wrapped in lipid bilayers with the tendency to grow is not surprising and does not require special circumstances. However, the characteristics of vesicles in the population (e.g., the composition of the vesicle membrane) are fully dependent on the environment experienced by each individual vesicle. Evolution in populations of the simplest reproductive systems would be level-3 evolution.

2.4 Level-4 evolution

The evolution of the experimental lipid vesicles is limited as they do not contain a mechanism of storing hereditary information. They have little in the way of inherent qualities that could be filtered by natural selection (Tessera, 2011). The vesicles could reproduce, but they might have later acquired heritable structure/function properties (Tessera, 2011). As dissipative systems, the vesicles are free to access and dissipate any local gradients, including chemical ones. Spontaneous chemical reactions generate entropy (Ott and Boerio-Goates, 2000), so vesicles facilitating chemical reactions inside of their membranes (e.g., autocatalytic sets; Ulanowicz, 1997 and Kauffman, 2000) would be thermodynamically favored over other vesicles. Indeed cellular metabolism is recognized as an example of entropy-generating dissipation (Davies et al., 2013). The spontaneous growth and replication of polymers (e.g., DNA, RNA, proteins…), particularly if this was part of autocatalysis, is precisely the kind of chemical reaction that could be facilitated within
vesicles, induce functional qualities in vesicles, and provide a mechanism of phenotypic inheritance that is relatively independent from variation in the local environment. Any mechanism of heritability in processes of reproduction or replication will be error-prone, so it seems likely that mutation rates were probably very high in early emerging mechanisms of inheritance and subsequently reduced through evolutionary adaptation (Lieberman and Feldman, 1986). In addition, the phylogeny of early microbial evolution was more web-like (less tree-like) than the familiar metazoan phylogenies due to extensive horizontal gene transfer (Martin, 2011). The horizontal transfer of genes would have also facilitated the spread of heritable structure/function properties among the lineages of the vesicles (e.g., by fusion of the vesicle membranes).

Despite occasional horizontal transfers, such properties led to the emergence of distinctive lineages of systems and thus the potential for selection among lineages. In other words, natural selection acting at multiple levels of organization was an emergent process founded on the thermodynamically driven origin of a birth/reproduction/death cycle (Hoelzer et al., 2006 and Holland, 1976). Natural selection helped to orchestrate the metabolisms of these dissipative systems. In physic-chemical systems there are also examples, such as crystallization, in which the formation of structural irregularities, such as dislocations, can enable some crystals to grow faster and reproduce copies of themselves and their faults (Cottrell, 1979). However the evolution of crystal populations is strongly limited by the structural homogeneity of crystals within populations, which cannot offer the heterogeneous structural diversity provided by carbon-based structures, such as lipid vesicles. Level-4 evolution, then, builds on level-3 by adding a mechanism(s) for the storage of hereditary information across many generations.

2.5 Higher levels of evolution

Higher levels of evolution appeared with the emergence of the genetic code. The
thermodynamic perspective suggests this was driven by the increase in the diversity of microstates created by the diversification of genetic lineages. As biodiversity grew the genetic and ecological combinatoric possibilities exploded. This potentiated the emergence of new evolutionary mechanisms, such as genetic transfers and endosymbiosis, and even larger scales of macroscopic organization, such as multicellularity. Ecological structures (i.e., ecosystems) also emerged; a process that has been effectively described in a thermodynamic framework (Schneider and Kay, 1994). The emergence of each of these macroscopic levels of material and dynamical organization involved the initiation of systematic networking among agents at a lower level of organization. The examples listed above required the functional integration among genes in genomes, among cells in multicellular organisms, and among coadapted species in ecosystems.

Most of the literature on MLE focuses on MLS (the proposition that the process of natural selection operates on >1 level of biological organization) and whether this is a valid or useful way to understand the evolution of altruism in social systems (Sober and Wilson, 1998 and Wilson and Wilson, 2007). We think natural selection is best understood as a thermodynamic process (Hoelzer et al., 2006 and Wicken, 1998) that can manifest in any population of reproductive agents exhibiting heritable variation for fitness (a positive function of survival and reproductive rate), just as the process of convection can manifest in any fluid system exhibiting a sufficiently strong thermal gradient. Social systems guide and constrain the kinds and rates of interactions among their constituent agents (e.g., individual organisms), so they induce metabolic energy processing at the level of social groups (Wicken, 1998). In this way sociality fits neatly into our thermodynamic perspective of evolution as the emergence of a physically structured system of entropy production. Social systems can grow and reproduce (e.g., social group fission in Old World monkeys and apes; Chepko-Sade and Sade, 1979, Henzi et al., 1997 Okamoto and Matsumura, 2001, Lehmann...
and Boesch, 2004 and Sueur et al., 2012), so they can exhibit fitness at the group level
(Sober and Wilson, 1998). They can also influence the fitnesses of the constituent agents,
because an individual’s fitness may depend in part on the identity of the social group(s) to
which they belong, which is largely generated by the structure of interactions among group
members. It is this kind of functional integration among agents that leads to the emergence
of higher-level agents. Altruism can be an effective aspect of social integration, so it can
contribute to the self-organization of social groups and their role in entropy production.
Altruism, and sociality in general, are fully consistent with the hierarchical thermodynamic
perspective on evolutionary dynamics, which provides a physical basis for understanding
nature that connects a great diversity of macroscopic phenomena. This logical consistency
with thermodynamics supports multilevel selection and, more generally, multilevel
evolution with a well established theoretical framework in physics.

3. Conclusion

The term "evolution" is a generic term that can be understood as the change over time of
dynamical systems. We argue that thermodynamics drive change (i.e., evolution) in physical
systems, including the diversity of life on earth. Specifically we aimed to show that there
are different levels of evolution, from simple to more complex, taking into account the level
of interaction between systems and populations of systems (i.e., agents) and their local
environments.

We described four fundamental levels of evolution with the most basic level
corresponding to the monotonic degradation of isolated systems, which excludes all
interaction with the external environment. When systems can interact with the local
environment through inputs and outputs they can oppose degradation through self-
organizing dynamics. We identify self-organization as the second level of evolutionary
dynamics, because the complexity of self-organization results confers much greater
persistence on the system. Self-organizing systems tend to grow as they receive environmental inputs, as long as the inputs outweigh the outputs, but growth ultimately destabilizes systems as internal dynamics become uncoordinated. This can result in large systems splitting into two smaller systems. We identify reproduction of self-organizing systems as the third level of evolution because it transforms individual systems into populations of systems, which further extends persistence of the system's dynamical cascade. The fourth fundamental level we describe corresponds to Darwinian evolution through the addition of imperfect (i.e., mutable) hereditary mechanisms that increase the correlation between phenotypic similarity and filial relatedness while also promoting the emergence of genetically and ecologically diverse lineages. We do not claim that these four fundamental levels of evolution are a complete list or that alternative schemes would be erroneous. Nevertheless, we think our scheme effectively illustrates how biological evolution is logically connected to the general thermodynamic complexification of evolutionary dynamics.

Evolution explains the emergence of many levels of organization in the biosphere, from genes to genomes to cells to multicellular organisms to social groups of organisms, and all of these phenomena are fueled by the production of entropy. From this perspective, evolutionary processes, like natural selection, are also thermodynamic processes (Hoelzer et al., 2006 and Wicken, 1998) that can be manifested at any level of biological organization subject to the material constraints of that context. Given that the biosphere has many hierarchical levels of reproducing agents, the process of natural selection can manifest at each of these levels. This is the essence of multilevel selection theory (Sober and Wilson, 1998), which goes hand-in-hand with the thermodynamic view of multilevel evolution. Therefore, research based on multilevel selection theory is more deeply connected to our understanding of physics than alternatives, such as single-level selection (e.g., gene-level:
Williams, 1966 and Dawkins, 1976) or kin selection (Hamilton, 1964). We think that the multilevel selection approach offers a greater potential for connecting models of social evolution to more general models of biological evolution and to even more general models of thermodynamics.

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