

The Logic of Life

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Abstract In this paper we propose a logical connection between the physical and biological worlds, one resting on a broader understanding of the stability concept. We propose that stability manifests two facets - time and energy, and that stability's time facet, expressed as persistence, is more general than its energy facet. That insight leads to the logical formulation of the Persistence Principle, which describes the general direction of material change in the universe, and which can be stated most simply as: *nature seeks persistent forms*. Significantly, the principle is found to express itself in two mathematically distinct ways: in the replicative world through Malthusian exponential growth, and in the 'regular' physical/chemical world through Boltzmann's probabilistic considerations. By encompassing both 'regular' and replicative worlds, the principle appears to be able to help reconcile two of the major scientific theories of the 19th century – the Second Law of Thermodynamics and Darwin's theory of evolution – within a single conceptual framework.

Keywords Thermodynamic stability · Dynamic Kinetic stability · Second law of thermodynamics · Darwinian evolution · Natural selection · Persistence principle

Introduction

The Second Law of Thermodynamics, particularly in its statistical mechanical formulation, and Darwin's theory of evolution, could together be considered the two profound scientific

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advances of the 19th century. These two theories offered fundamental insights into the basis for material change in the world, the former primarily in the physicochemical world, the latter in the biological world. Yet, despite their revolutionary impact on scientific thinking, these two grand theories have not cohabited comfortably. The Second Law, though necessarily encompassing all material change, both within the living and non-living worlds, seems strangely detached from Darwinian thinking. Typical biological images, whether a nesting bird or a predator stalking its prey, images so readily explained in Darwinian terms, are incongruent when viewed through the lens of thermodynamics. Thermodynamics, as Lotka (1922a) already pointed out almost a century ago, is unable to tell us what *will* happen, just what *cannot* happen. Seemingly, there exist two orthogonal dimensions to the nature of material change, with the animate and inanimate worlds somehow bound by different principles. Despite persistent attempts over the years, thermodynamics has been unable to explain the existence of the highly complex, far-from-equilibrium, energy-consuming material forms that we categorize as life (Lineweaver and Egan 2008). As Lotka (1922b) himself noted very early in the debate, the clear evolutionary drive in living systems to *minimize* energy dissipation does not sit well with the thermodynamic view of life as yet one further energy dissipation system. And recent advances in non-equilibrium thermodynamics (Nicolis and Prigogine 1977), though insightful in themselves, have not been able to resolve the life conundrum. No wonder then that, despite the profound impact that thermodynamics has had on our understanding of the energetics of material change, several of the great physicists of the 20th century found biology to be physically inexplicable, and were led to speculate as to the likelihood of as yet undiscovered physical laws (Wigner 1970; Schrödinger 1944; Bohr 1933).

In recent work we have attempted to help bridge the animate-inanimate conceptual gap through the characterization of an alternative stability kind, dynamic kinetic stability (DKS) (Pross and Khodorkovsky 2004; Pross 2005, 2009, 2011, 2012; Pascal 2012; Pascal et al. 2013; Pross and Pascal 2013; Pascal 2015), a stability kind applicable solely to replicating systems, whether chemical or biological, and quite distinct from the more conventional thermodynamic stability. By building on the DKS concept we obtain the valuable insight that the two seemingly separate processes – life's emergence (abiogenesis), and biological evolution – may well constitute one single physicochemical process with a common driving force, the drive toward greater DKS. That unification enables the chemical roots of evolution to be uncovered, at least in principle, thereby narrowing the conceptual gap that continues to separate those two seemingly incongruent worlds. It is evident that the ability to relate abiogenesis and biological evolution through an understanding of the physicochemical process by which inanimate was transformed into animate, would be a major step toward the integration of the two worlds within a single coherent framework.

But the very idea of an alternative stability kind in nature, DKS, raises an immediate question: why two stability kinds? Are other stability kinds possible? And how do these two empirical stability kinds relate to one another? Is one stability kind preferred over the other? Is there some overriding principle that can unify these two seemingly distinct stability kinds? In this paper we argue that such a principle does indeed exist, that its basis is logical/mathematical rather than empirical, and that its formulation is able to provide a logical underpinning for the existence of two material forms in nature – living and non-living (Pascal and Pross 2015; Pross and Pascal 2014).

Discussion

The concept of stability is central to thermodynamic thinking: systems of lower Gibbs (free) energy (or higher entropy) are considered more stable than those of higher Gibbs (free) energy (or lower entropy). Though thermodynamics started off as an empirical science in the earlier part of the 19th century, Boltzmann's insight that the thermodynamic stability of a system is grounded in probability theory transformed thermodynamics from an empirical science to one resting on a mathematical/logical base. Through its statistical mechanical formulation, the concept of stability was given a logical and quantifiable interpretation (Sewell 1980).

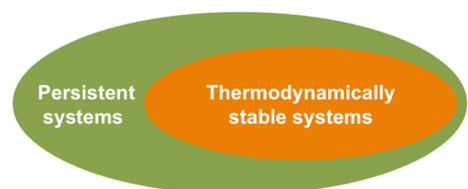
But despite the importance of energetic considerations in governing stability, the stability concept has another facet - a time facet, one not necessarily related to energy/entropy. A system that is persistent, unchanging over time, is also considered stable even though that system may be unstable in a thermodynamic sense (Pascal and Pross 2015). Indeed, DK stability, as described above, manifests such a stability kind. A replicating population can be stable in the sense of being persistent, maintaining a continuing presence over extended periods of time, even millions of years, despite the fact that the individual entities which make up that population are energetically unstable and continually turn over.

So given that stability can express itself through two distinct facets, how do these two facets relate to one another? Can one be considered more fundamental? Surprisingly, it turns out that the stability's time facet is more general than its energy facet and this is illustrated by the Venn diagram in Fig. 1. From the diagram it can be seen that thermodynamic stability is just a subset of the more general group of persistent/time stable systems. Whereas thermodynamically stable systems are necessarily persistent (having reached the equilibrium state), persistent systems are not necessarily thermodynamically stable, and the existence of DK stable systems as discussed above, exemplifies that situation. But the realization that stability's more general expression is through its time facet means that both thermodynamic stability and DK stability can be linked, as *both* stability kinds manifest the drive toward increasingly persistent forms. Stability as persistence then allows the two seemingly distinct stability kinds to be viewed in the same terms and allows the formulation of a general principle, the Persistence Principle, governing change in both the 'regular' physicochemical world and the world of certain replicating systems.

The principle may be formulated as follows: *systems will tend from less stable (persistent) to more stable (persistent) forms*, or, more concisely: *nature seeks persistent forms*. The statement has a logical base in that *less* stable/persistent systems will, by definition, be *more* likely to change, while *more* stable/persistent systems will be *less* likely to do so. Or, put more simply, changing things will change until they change into things that do not.

We see therefore that through the persistence principle a unified framework for the nature and direction of change in both inanimate *and* biological worlds can be set out. Evolutionary change takes place in both worlds – toward greater persistence – even though the physical/

Fig. 1 Schematic diagram illustrating the set of thermodynamically stable systems as a sub-set of the more general set of persistent systems



mathematical basis for change can be different. Within the physiochemical world the driving force toward increased persistence is dictated solely by the Second Law with its probabilistic directive toward maximum entropy, while in the replicative world the change is (under conditions facilitating the DKS state) governed by replicative variation and the math of exponential growth. Imperfect replication leads to variation and, as was pointed out some years ago (Eigen and Schuster 1979; Szathmáry and Gladkih 1989; Lifson 1997), competing exponential replicators cannot coexist. The math is unambiguous – the more DK stable replicators drive the less DK stable ones into extinction leading to increasingly stable/persistent replicating populations, i.e., to an evolutionary process.

In other words nature is able to achieve greater persistence by either of *two* mathematically governed processes, one that governs change in the ‘regular’ world, the other that is effectively operational in the replicative world. However, since the math of evolutionary change in the two worlds is different, the mechanism of evolutionary change is also different. Within the physicochemical world, change takes place toward the equilibrium state, the state of maximum entropy, while in the replicative world, change (toward increasing DK stability) involves a process of complexification, though the term is notoriously difficult to define or quantify (Corning and Szathmáry 2015; Adami 2002; Gell-Mann 1995). Simple replicators are fragile so that replication only takes place in laboratories, and is highly dependent on those laboratory reaction conditions (Pross 2013). In contrast complex replicators (living forms) are highly robust and able to replicate almost anywhere – no labs, no postdocs or students required! Indeed, in that respect, the degree of complexification in the replicative world can be thought of as mirroring the entropy function in the non-replicative world. Increasing entropy and increasing complexity – two parallel means by which greater persistence is achieved, each in its respective world (Pascal and Pross 2015).

As noted above, a central feature of the replicative world is that it involves far from equilibrium systems dependent on a continual energy source to maintain that non-equilibrium steady-state. However, the origin of life is usually studied in terms of prebiotic chemistry, in which intractable mixtures containing diverse classes of monomers and polymers are usually produced through abiotic organic reactions (Benner et al. 2012). The stochastic emergence of thermodynamically unstable living entities from these mixtures is considered highly improbable (Morowitz 1992; Pascal et al. 2013). In any case simply considering these systems as mixtures does not give any information regarding the thermodynamic state in which they are formed. Presumably whatever species are formed from within such mixtures, whether at equilibrium, or in some metastable state, they will primarily have come about through favorable covalent and/or non-covalent interactions within molecular adducts or supramolecular assemblies. Furthermore, under these conditions the system will continue to evolve towards minimal Gibbs energy according to the Second Law. Of course, such thermodynamically-directed assemblies clearly play a role in living organisms, as for example in the formation of lipid bilayers and many other structures found in the cell. But this process does not explain the formation of biopolymers (nucleic acids, proteins) from their components, which in most case do not correspond to thermodynamic minima, since they are formed in aqueous environments by dehydration processes. On the contrary, we must explain how a connection can be made between abiotic processes of thermodynamic self-organization, and the main feature of living organisms expressed under far from equilibrium situations in which these dissipative systems

maintain their non-equilibrium state at the expense of free energy received as nutrients from the environment.

It is more likely that a principle of continuity, already invoked by Darwin (De Beer 1959; Peretó et al. 2009) was at work, allowing kinetic selection of species expressing kinetic rather than thermodynamic stability, before life could emerge (Pascal et al. 2013). As mentioned earlier, the selection of efficient reproducing species is operating provided that those entities undergo Malthusian growth giving rise to that other form of stability, DKS (Pross 2012). Unsustainable exponential growth requires that the reverse process does not dampen the reproduction cycle, otherwise it would be governed by thermodynamics, rather than by exponential kinetics. On the contrary, provided that no other limitation is present (von Kiedrowski et al. 1991), kinetically irreversible (i.e. far from equilibrium) chemical reproducing systems, corresponding to exergonic processes that behave in an autocatalytic fashion, can express exponential growth, at least until compensating decay processes lead to the establishment of a dynamic steady-state. Under such conditions competing systems able to replicate would only be selected according to their reproductive efficiency (Lifson 1997) and independently of the initial conditions (Szathmáry and Gladkih 1989). The more efficient reproducing entities will persist, as reflected in an increasing number of members, giving rise to time stability and, thereby, to an expression of the persistence principle. Provided that some variability is possible among the population of replicating entities, open-ended evolution can emerge through a process analogous to natural selection, and, following (Lotka 1922a), we can consider that the Persistence Principle corresponds to a physical principle based on a mathematical and logical law, rather than to an independent biological principle.

Conclusion

Through a more detailed consideration of the stability concept we reach the surprising conclusion that the life phenomenon is far from being an inexplicable material form seemingly at odds with thermodynamic logic. In fact, life as a material phenomenon can be seen to rest on an extra-thermodynamic (kinetic) base, one that derives directly from mathematical/logical considerations. Life, first and foremost, is a self-sustained replicative network of chemical reactions whose evolutionary roots lie in some simple primordial replicative system whose identity has long faded in the mists of time. But once such a simple (but persistent) replicating system was able to emerge from the materially diverse environment that was manifest on our planet some four billion years ago, the logic of the persistence principle, supported by the math of exponential growth, led inevitably to an evolutionary process of increasing complexity, both within the individual replicating forms (protocells and cells), and through network formation between those individual forms. Increasing complexity for increasing stability/persistence, as described recently (Pross 2013). Thus life's mystery lies not in the actual existence or evolution of that complex replicative network we term life, but rather in the contingent conditions that would have facilitated the initial step - the emergence of some primal dynamic steady-state replicative system on which the evolutionary process of complexification was able to commence.

Systems chemistry (von Kiedrowski et al. 2010), that emergent area of chemistry that deals, *inter alia*, with relatively simple replicating chemical systems, is in its infancy, and our understanding of such systems remains rudimentary. To date no persistent replicating system

(energy consuming, maintaining a non-equilibrium steady-state) of any kind has been artificially created from its components. Recent work of van Esch and colleagues (Boekhoven et al. 2015; Boekhoven et al. 2010) on non-equilibrium chemical steady-state systems, though non-replicative, constitutes an important step forward in this direction. But it is only once we are able to outline the range of chemical systems able to establish dynamic replicative networks, the ease with such networks can spontaneously form, and the means by which such systems were able to couple up with an energy source, that the answer to the perennial question regarding life's likely existence beyond our planet may be finally addressed.

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