The Thermodynamic Considerations of Evolution; the Role of Entropy in Biological Complexity

Eva Deli[1]

1 University of Debrecen

Abstract

Darwin's theory of biological evolution became a cornerstone of modern biology. Predictable fluctuations in entropy, genetic diversity, population number, and resource availability in ecosystems turn evolution into a cyclic process, making the ecosystem's thermodynamic analysis possible. The sun's energy input drives a closed theoretical process, the reversed Carnot cycle. The Carnot cycle is divided into four distinct phases with standard features. The first phase is a low entropy, fast-changing environment, spurring phenotypic plasticity (phase 1). In phase 2, the population growth increases entropy, forming nutrient cycles via symbiotic, parasitic, predator-prey, and other interdependent relationships. In phase 3, the overpopulated, stressed ecosystem outgrows its boundaries; competitive and chaotic interactions spread genetic innovations through horizontal gene transfer. Finally, in phase 4, extinction purges the non-evolvable genomes, but the surviving species carry the cycle's genetic innovations and make renewal possible. Therefore, compression and expansion of the ecospace by energy fluxes (i.e., ecosystem dynamics) are potent drivers of change. Thus, the Darwinian concept is a cyclic sequestering of the sun's energy into genetic complexity. The second law of intellect shows that genetic complexity either increases or remains constant; it never decreases.

Eva Deli

University of Debrecen, Department of Anatomy, Histology and Embryology

Eva.kdeli@gmail.com

https://orcid.org/0000-0003-1126-1970

Keywords: Darwinian evolution, extinction, evolution modeling, entropy in evolution, thermodynamics of evolution, reversed Carnot cycle.

Definitions used in the text

Social or psychological temperature: Temperature indexes internal energy, and social or psychological temperature measures arousal (Escobar et al., 2021; O'Neill & Schoth, 2022: Deli and Kisvarday, 2020; Deli et al., 2021). Therefore,

individual organisms are analogous to particles, and their individual histories (even in complex organisms) are analogous to thermal fluctuations. For example, the focus is stable at low arousal, but information overload or stress causes an erratic oscillation across multiple subjects, resulting in aggravation, aggression, and risky behavior. In addition, the environment has an essential role because effective population size and supply abundance determines the nature of the interaction, therefore, arousal (Deli et al., 2021; Roos, 2014; Sella and Hirsh, 2005). For example, abundance allows low social temperature, such as cooperation and generosity (Tkadlec et al., 2020), but supply shortage causes competition, enhancing social temperature (Crokidakis, 2017).

Temporal field: Fields associate each point in space with a specific physical quantity. For example, gravity is a vector field, ensuring spatial organization stability. Likewise, the stability of biological organisms and social, cultural, and intellectual organizations rely on temporal fields (Deli 2015). We propose that the genetic material represents an information field with a temporal extension. As the genetic material represents an organizational memory, the neural system enables the accumulation of individual experience. Further regulatory layers might be writing and the internet, representing increasing potential for organization and support.

Genetic complexity: Genetic complexity is the structure and properties of genotype-to-phenotype maps enabling the quantitative comparison of the relative complexities of genetic systems (Charlesworth, 2001; Thompson and Galitski, 2012).

Introduction

Thermodynamics can predict the behavior across all physical systems with an axiomatic approach and a minimum of assumptions. The second law of thermodynamics states that the total entropy of a system either increases or remains constant in any spontaneous process; it never decreases (reviewed by Boojari, 2020). The law has inspired the analysis of entropy (Lotka, 1922. a, b; Annila & Baverstock, 2014; Pross & Pascal, 2017; Sherwin, 2018; Skene, 2020; Gladyshev, 2017) and thermodynamics in evolution (Ao, 2005 and 2008; Barton & Coe, 2009; Vopson, 2022). The increasing complexity and organization during biological evolution, particularly the human brain's complex organization, is a blatant offense to the second law of thermodynamics. The most famous analogy is Maxwell's demon, a theoretical tool that can separate warmer particles from colder ones and illegally decrease system entropy. Maxwell's demon highlights the problem of decreasing entropy in biological systems. As a result, genomes' information entropy and the entropy of the organism appear to decrease, challenging the Darwinian concept (Vopson, 2022).

Darwin recognized that all species share a common ancestor. In the generational change in heritable traits of biological populations, the fittest individuals are more likely to survive and create offspring (Darwin, 1859). However, irrational behavior can hasten the individual's demise or even the extinction of the species. According to the Darwinian theory of evolution, only natural selection determines which mutations are beneficial, and there is no deterministic correlation between any parameter and the probability that these mutations will occur. Nevertheless, genetic changes, such as the

emergence of toeless lizards or humanity's switch to agriculture, have no selective advantage. Organisms often lose the functions of organs, yet evolution never proceeds toward the lesser organization. For example, whales have lost many functions during a macroevolutionary transition to the water (Werth, 2020), but they did not lose their mammalian complexity by turning into cold-blooded fish. For example, excessive reliance on the host causes anagenetic endoparasites' structure and physiological function simplification.

Biological systems utilize energy and materials from the environment for building tissues in an inherently systemic and dynamic process. Ubiquitous adaptive cycles reflect endogenously generated self-organization dynamics (Sundstrom & Allen, 2019). Higher levels influence and constrain the dynamics of lower levels in organizational hierarchies (Walker and Davies, 2012), allowing simple laws to give rise to a complex organization. How is life assembled? The problem of calculating the thermodynamic cost of the ecosystem by summing the chemical energy accumulated in the biological matter and the information conserved in the genetic material fails to account for the complexity. Life's molecular assembly encodes information and uses that information to determine the system's future state. According to Bennett, complex objects contain internal evidence of a nontrivial causal history (Bennett, 1986).

Furthermore, logical depth is intimately related to algorithmic complexity, the length of instructions needed to decompress a file in a context-dependent, causal manner. Therefore, a causal chain can represent a complex object. Likewise, assembly theory or causal set theory explains the emergence of life via complexity science; causal graphs explain relationships between the origins of objects.

Another difficulty is that evolution proceeds by long nearly-static periods punctuated by sudden "inventions" of novel phenotypic solutions on the macroevolutionary timescale. It is a multi-phase process with varying phase lengths (McMahon & Ivarsson, 2019) and periodicities (Roberts & Mannion, 2019). For example, cichlid diversification occurred by consecutive trait-specific pulses of morphospace expansion (Ronco et al., 2020). Although evolutionary processes are nonlinear, they show certain regularity of entropy and population number, which allows modeling by thermodynamics and statistical mechanics of equilibrium systems. In particular, the increase of disorder accompanying the increase of entropy can occur in microscopic degrees of freedom (e.g., thermal motion of molecules). At the same time, highly complex and organized structures emerge out of macroscopic degrees of freedom (Jeffery et al., 2019). Metastable states correspond to local minima of the free energy functional and can persist on different time scales. An information-theoretic description, for instance, is the mutual information between various macroscopic observables (Jeffery et al., 2019).

In sufficiently large populations, individual organisms are analogous to particles, and their histories are analogous to thermal fluctuations, resulting in predictable collective effects. Therefore, the maximum entropy principle, according to which the distribution of any quantity in a large ensemble of entities tends to the highest entropy distribution subject to the relevant constraints, can conceptualize relationships in biology, chemistry, economy, and consciousness science (Deli & Kisvarday, 2020; Deli et al., 2021; Fry, 2017; Jiang et al., 2016; Klimek et al., 2019) and even evolution (Frank, 2009; Frank and Smith, 2011; Vanchurin et al., 2021). The system's statistical tendency to increase entropy creates an entropic force. We speculate that the environment's entropic force pushes life toward the more efficient use of entropy, inadvertently increasing life's complexity and intellect ((Jeffery et al., 2019: Roos, 2014; Schrödinger, 1945).

Evolution transforms the sun's continuous energy input into a stepwise increase in genetic complexity. Each evolutionary cycle can be divided into well-separable phases characterized by predictable entropy, population number, resource availability, and genetic diversity. First, extinction bottlenecks compress the ecosystem's genetic potential while conserving entropy. Low entropy populations (phase first) accelerate the order and complexity of the genetic material. However, horizontal gene transfer spreads genetic elements in high-entropy ecosystems, allowing selection to play a crucial role.

Considerations of Entropy

Photosynthesis, the dominant energy source in most ecosystems, converts light to C-H bonds in organic material, serving cell complexity, movement, and intellect. Therefore, endothermic processes, such as biological organization, depend on exothermic operations (Ménendez, 2021; Ramstead et al., 2018). Moreover, biological systems accumulate energy in the genetic material, which forms a stable field unaffected by the chaotic environment. Compartmentation also applies to metabolites and the reductions in entropy from metabolic equilibrium (Sabater, 2022). Landauer's principle shows that information storage is analogous to a temperature decrease or "phase transition." Thus, the genetic material, which acts as a field, separate from the system (Figure 1), represents Maxwell's demon.

The role of entropy in evolution is a particularly sought-after problem (Bartlet, 2017; Cohen & Marron, 2020; Kondepudi et al., 2020; Pross & Pascal, 2017; Sherwin, 2018; Skene, 2015; Roach et al., 2020; Roach, 2020; Torday, 2021; Wong, 2020). Entropy measures the variety of existing possible configurations within a system.

$$S = -k_B \sum_i p_i \log p_i$$

where S is the entropy, k_B is the Boltzmann constant and p_i is the current state of the system.

Because entropy production directs all changes toward equilibrium, it is connected to time's arrow (Andrieux et al., 2007; Gaspard, 2005; Roldán and Parrondo, 2010). Therefore, time can be defined as the entropy generation rate (Kostic, 2014). Free energy (von Helmholtz, 1882) defines the maximum amount of work a thermodynamic process on a constant volume can perform. For example, organisms require materials from the environment for generating energy and building tissues; energy fluxes (i.e., ecosystem dynamics) can drive complexity (Bush & Pruss, 2013).

An entropic force, derived by Neumann, is an emergent phenomenon resulting from the tendency of a thermodynamic system to maximize its entropy via Brownian motion. In an ecosystem, the species distribution in an ecological niche follows a Brownian distribution.

$$F\left(X_0\right) = T\nabla_x S(X)\big|_{X_0} \qquad (1)$$

where T is the temperature, S(X) is the entropy associated with the macrostate X and X_0 is the present macrostate.

Genetic diversity corresponds to the number of microstates (Boltzmann entropy) (Sailer & Harms, 2017; Roos, 2014). The

entropic force enhances the number of microstates in the ecosystem. Then, at a critical state, it precipitates extinction, with the sharp reduction of entropy and genetic diversity. Because only the genes are transmissible across generations, genetic information represents an independent medium (i.e., field). Therefore, the thermodynamic changes and the devastation of extinction preserve the cycle's genetic innovations. Therefore, the cycle can repeat with the same state variables of entropy, genetic diversity, social temperature, and resource density, turning evolution into a forced, complexity-increasing harmonic motion (Table I). Therefore, evolution is driven by the entropy generation of the physical world (Schrödinger, 1945; Jeffery et al., 2019).

At equilibrium, mutations often remain silent (the genetic acceleration is zero); the dynamical ecosystem does not generate evolutionary changes. However, a non-equilibrium bias towards maximum instantaneous entropy production moves the ecosystem toward higher-entropy macroscopic states. Therefore, mutation frequency shows an initial decrease during eras with low genetic concentration and subsequently changes parallel with the population number (Vahdati et al., 2017). The genetic (i.e., field) modifications are significant in the low entropy phase, but the population number is low. In contrast, in the high entropy phase, the genetic changes are minor, but the population density is high. Therefore, notable evolutionary changes are increasingly likely at the cycle's low and high entropy sections.
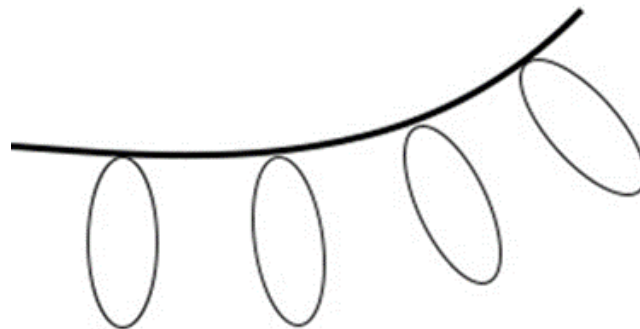

Figure 1. The thermodynamic origin of genetic complexity as a field. The thermodynamic cycle (indicated by an oval) represents a fluid, chaotic and reversible process. The energy field (solid line) represents the increasing complexity of the genetic material.

Table I. Comparison of the evolutionary cycle and genome representing an orthogonal field

The evolutionary cycle	The genome as an orthogonal field
The cycle can be divided into well-defined entropy, social temperature, and resource density phases.	The genome represents stable and unique energy (complexity).
The cycle's phases are chaotic, noisy, and often reversible.	The complexity field satisfies the second law of intellect.
The cycle forms a discrete loop; therefore, it must end.	The cycle's innovations become an indelible part of a heritable material.

The Carnot Cycle as an Evolutionary Model

The Carnot cycle is a closed thermodynamic cycle; therefore, it can only exchange energy with its environment. Further, it is an idealized theoretical process between two heat reservoirs with vanishing net entropy production, where the phases repeat precisely. The macroscopic variables, such as temperature, pressure, and volume, are quantifiable characteristics without details on individual molecule dynamics. For example, the temperature manifests particles' kinetic energy, but the social temperature is the fierceness of competition, driven mainly by hunger and lack of living space (Deli et al., 2021; Roos, 2014). Anxiety and aggravation represent significant energy requirements (Gao et al., 2022; Saarimäki et al., 2017). The above characteristics apply to emotional animals, but stress causes aberrant, erratic behavior in all animals, plants, and living things.

The Earth receives solar radiation from the sun, causing an energy influx, the difference between absorbed and emitted radiation. The ecosystem consists of all solid ground, water, and air, which theoretically can satisfy the ecosystem's nutrient needs. This way, the ecosystem is a closed system where the sun's energy input sets the limit of achievable computational efficiency (biological complexity gain) during the cycle. Moreover, genetic complexity resists extinction; therefore, it is a conserved quantity (Thompson and Galitski, 2012). Although the gene pool's intergenerational stability ensures the species' constancy, it manifests the organism's evolutionary history and represents a potential for its future.

We must note another crucial element here. A constant stimulus can produce fluctuating parameter outcomes, such as self-organized criticality. For example, in the famous "sandpile experiment" (Lang and Shkolnikov, 2019), a slowly building conical sandpile triggers an avalanche of sand in a completely unpredictable fashion. Likewise, mass extinctions act as avalanches, which turn the sun's biomass generation periodic. According to recent studies, evolution consists of extended periods of stasis that accumulate mutations without producing significant phenotypic change, followed by rapid morphological jumps (Bakhtin et al., 2020; Katsnelson et al., 2019; Lowery & Fraass, 2019; Rosenberg, 2022). As a result, radiations and extinctions are decoupled in time (Cuthill et al., 2020; Fan et al., 2020; Lynch et al., 2016), and genetic innovations precede Darwinian selection.

The fossil record testifies that the cycle of death and birth, extinction and origination, is a constant source of change and renewal in the living world (Babcock et al., 2015; Marshall, 2017). Major extinctions cause the vanishing of specific taxa but spare species with adaptive evolution capacity (Bush et al., 1977; Wagner, 2020). Therefore, extinction events are crucial in the increasing complexity transformation of the ecosystem (Boggs & Gross, 2021; Parry, 2021). Furthermore, extinction events section the geologic time into eons, eras, and periods, with specific genetic and morphological features (Figure 2; notice the similarities to figure 1). Therefore, both shorter and longer cycles terminate in extinctions.

Capricious evolution trajectories enhance the probability of either extinction or innovation because the demise of less evolvable genomes allows flexible genomes to survive. These "survivor" genomes carry the genetic and morphological innovations of the cycle. Therefore, extinction events accelerate evolution because genetic streamlining formulates a radically new and more complex biosphere (Lehman & Miikkulainen, 2015). In the rapid expansion through vacated niches, the genotype-phenotype maps determine the long-term evolutionary trends (Ahnert, 2017).

The entropic force pushes entropy into biological systems and ultimately accumulates complexity in the genetic material, an "invisible" factor in the ecosystem's structural relationships (Figure 1). Gravity, the most fundamental field, underlines all of space, but information fields are temporal. For example, genetic information directs the cell's organization and life's progression. Therefore, in contrast to gravity, temporal fields represent a gradation of complexity. Moreover, the complexity must either remain the same or increase in the limit of a reversible process (Vopson, 2022; Vopson & Lepadatu, 2022). The temporal field's resistance to complexity loss leads to a tendency for energy accumulation, the second law of intellect (Figure 3). The second law of intellect explains organisms' increasingly efficient use of entropy via an upward complexity spiral. Therefore, the second law of thermodynamics, the environment's entropic drive, can explain the complex facets of evolution and the evolutionary, technological, and social progress.

A healthy ecosystem depends on the equilibrium of nutrients, wastes, air, energy, and other resources (Table II). An ideal evolutionary cycle can be divided into four well-defined phases based on recurring state variables: entropy, species number, genetic diversity, and resource-richness (Crokidakis, 2017; Sundstrom & Allen, 2019; Wong, 2020). We model the ideal evolutionary cycle via the reversed Carnot cycle, which absorbs heat from the low-temperature reservoir and deposits it in the hot-temperature reservoir via an energy-requiring process (Figures 4, 5). The cycle starts with adiabatic compression (A-B). Then, heat is rejected during the reversible isothermal compression (B-C). Next, reversible Adiabatic expansion expands the ecosystem slowly until the social temperature drops to T1 (C-D). Finally, isothermal expansion absorbs heat (D-A). The following discussion will focus on animals, but plants form a similar evolutionary progression.
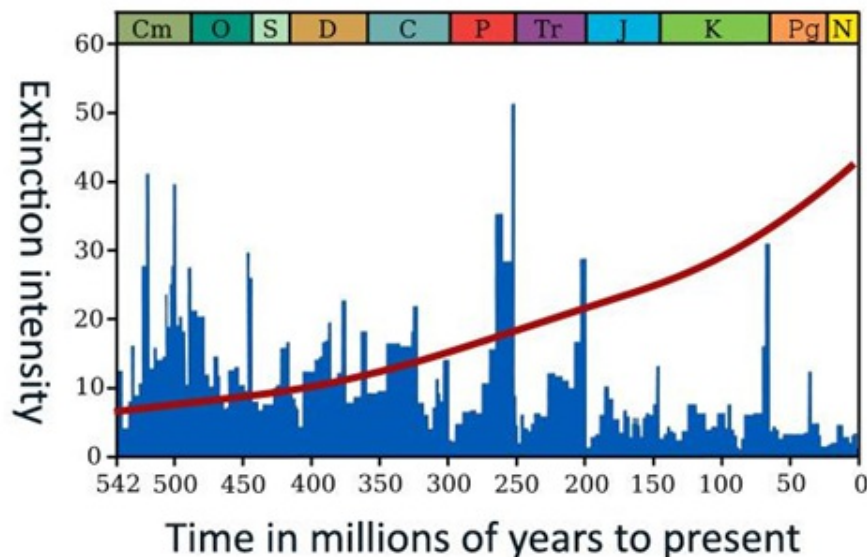

Figure 2. The field representation of complexity throughout evolution (Marine extinction intensity during the past five hundred million years). Over time, the increasing genetic complexity demonstrates an upward trend (red line).
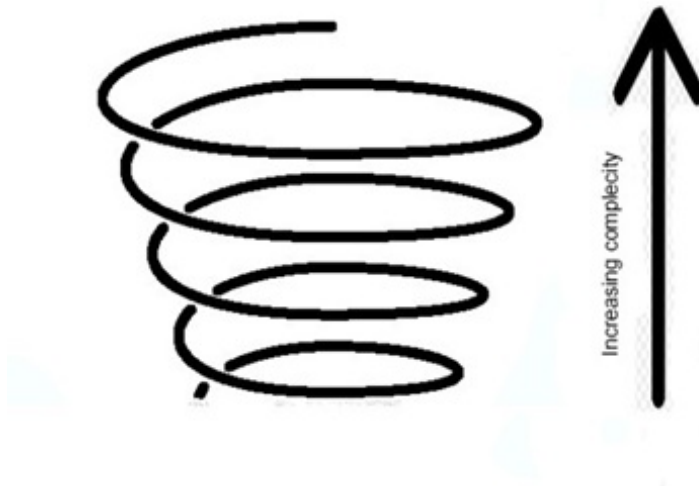
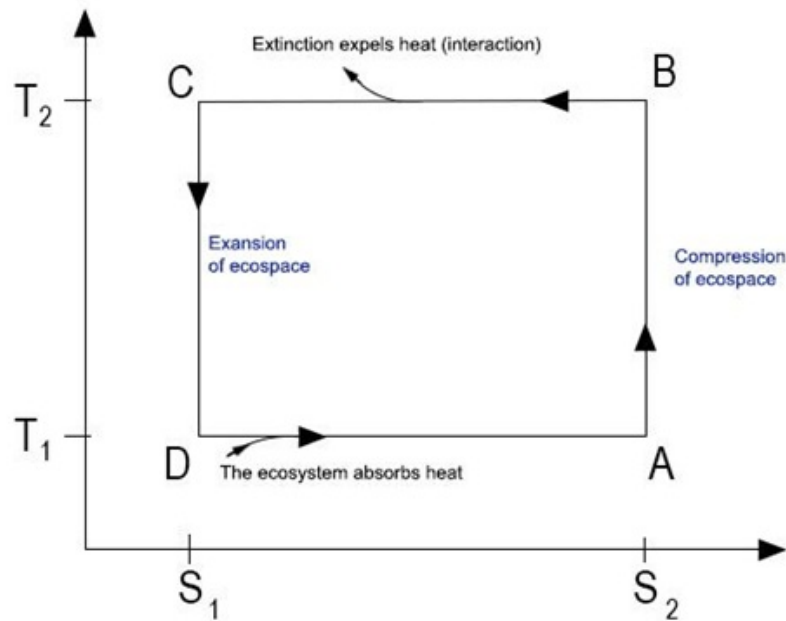**Figure 3.** The hierarchic field structure

Figure 4. The reversed Carnot cycle representation of the evolutionary cycle The genetic and morphological complexity of the biosphere increases in discrete steps. (A-B) Overpopulation generates competition, increasing social temperature. (B-C) Extinction reduces genetic diversity and population (rejecting genetic material as heat). (C-D) The survivors occupy isolated pockets of the segregated environment. (D-A) The sun's energy input increases the population and genetic variety (D-A).
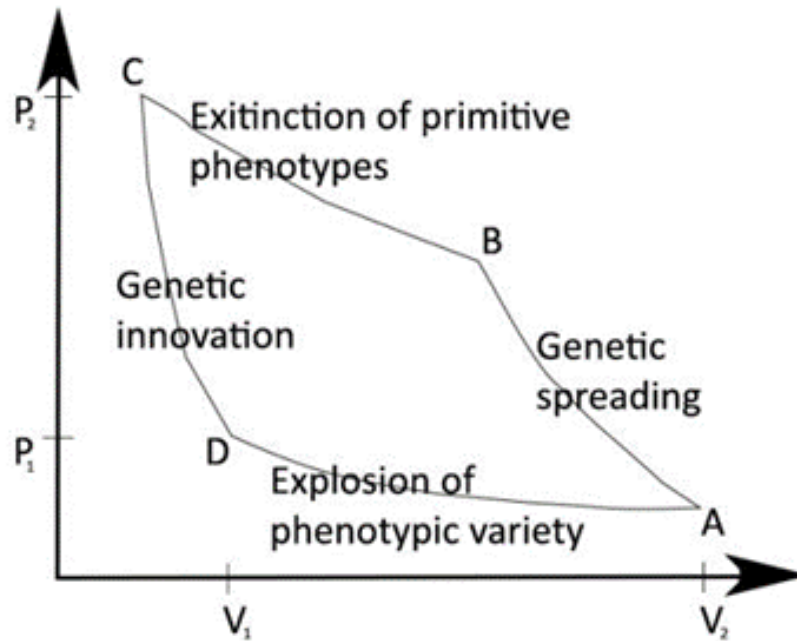
Figure 5. Phenotypic and genotypic changes shape the evolutionary phases In the first phase (C-D), low entropy spurs genetic ordering and complexity-increasing transformations. In the second phase (D-A), population expansion into diverse environments leads to phenotypic and genotypic variety explosion. The place within the food chain drives the diversification of the phenotype. In the third phase (A-B), stress and social anxiety cause competition, spreading genetic elements in the ecosystem. Environmental degradation increases social pressure and temperature. In the fourth phase (B-C), extinction eliminates the non-evolvable genetic elements.

Table II. The characterization of a typical evolutionary cycle

	Phase One (A-B)	Phase Two (B-C)	Phase Three (A-B)	Phase Four (B-C)
Social temperature	↓ (Ecospace expansion decreases social temperature)	Low	↑ (Increasing with population expansion)	High
Population number	Low	↑ Population growth	High	↓ Extinction
Entropy	Low	↑ (Increasing)	High	↓ (Falls)
Evolutionary changes	Complexity, order	Perfection of the species	Specialization, small genetic changes	Survival of the fittest
Heat flow	Adiabatic	A growing population absorbs the sun's energy.	Adiabatic	Extinction, heat loss

Evolutionary Phases

Phase 1 (C-D). Start of a New Cycle

The clear separation in the fossil record indicates that mass extinctions coincide with the destruction of the biosphere. Extinction comes for "free," acting as heat rejected by the system. Thus, by sealing the fate of evolutionary approaches that no longer work, extinction creates a "clean slate" (LaBar & Adami, 2016; Kirchner & Weil, 2000), where fast evolution can take place. In the first phase of evolution, resource abundance represents energy dominance (Figure 6), leading to three essential qualities that make renewal possible.

1, First, nature abhors a vacuum. Extinctions, acting as rejected heat, open a population vacuum in empty niches. Geographic isolation facilitates the evolution of co-adapted alleles at multiple physically unlinked loci (Waters and McCulloch, 2021). Newly mixed gene pools may enrich the adaptive genetic variation and allow for fast adaptation. When alleles involved in adaptation to alternative environments are present in high frequencies in the population, reassembling these ancient alleles can trigger a rapid and parallel ecological differentiation.

Although evolution depends on many factors, the availability of resources is one of the most critical environmental factors shaping developmental processes. In the late eighteen hundreds, Peter Kropotkin (1902) observed that biological richness inspires generosity and cooperation in ants, bees, falcons, and people (Connelly et al., 2017; Tkadlec et al., 2020). High resource density encourages maximizing individual power via experimentation, play, and organization. Cooperation positively affects reproduction and survival (Arlettaz et al., 2017; Katsnelson et al., 2018; Liao et al., 2019; Tkadlec et al., 2020; Wolf et al., 2018). In game theory, prisoner's dilemma studies support the above ideas (Lee et al., 2018).

2, Second, fast-changing environments spur evolution. The changing environment can trigger phenotypic plasticity (Boggs & Gross, 2021; Zhang et al., 2021). Over the past decades, evidence has shown surprisingly fast adaptation, such as re-using the same genes, in changing environments (Burtsev et al., 2022). Inversely, extreme phenotypic changes, speciation, or other evolutionary innovation require significant environmental changes, such as adaptations to a novel niche (Burtsev et al., 2022; Brun-Usan et al., 2021; Boggs & Gross, 2021; Pentz et al., 2020; Ng & Kinjo, 2022; Zhang et al., 2021). Furthermore, evolutionary innovations generate rapid expansion (Lehman & Miikkulainen, 2015; Nevo & Beiles, 2011); adaptive plasticity improves survival in changing environments by improving organizational function, such as the Ediacaran increase of diversity (635 to ca 580–550 yr) (Knoll et al., 2006). Computer studies also support a plasticity-led evolution (Ng & Kinjo, 2022; Levis & Pfennig, 2019a, b; Burtsev et al., 2022; Brun-Usan et al., 2021; Rago et al., 2018).

Underlying trait architectures and demographic characteristics of natural populations can constrain adaptation through different mechanisms. For example, exaptation in complex organisms, the recruitment of junk DNA, and widespread mobile element presence can generate complexity (Lynch and Conery, 2003). In addition, mobile elements can shift the function of a trait, dramatically increasing evolutionary potential (Koonin, 2016). For example, SARS-CoV-2 structural proteins changed substantially in the initial months and stabilized later as the virus adapted to the global human population (Ghanchi et al., 2021; Santoni et al., 2021).

3, Third, genetic diversity corresponds to the number of microstates (Boltzmann entropy) (Sailer & Harms, 2017; Roos, 2014). In phase 1, the low genetic diversity population represents low entropy when order-increasing genetic changes

coalesce into new functions and utilities (Andersson et al., 2015; Kondepudi et al., 2020; Xia et al., 2020) (Table I). Selfish genetic elements and gene duplication due to errors in DNA replication and repair machinery significantly increase evolvability (Jouffrey et al., 2021). Preexisting genetic variation can spur rapid and often parallel ecological adaptation. For example, gene duplication serves as degeneracy in the evolution of new functions (reviewed by Magadum et al., 2013) and other complexities (Katsnelson et al., 2019). Conversely, preexisting molecular architecture can converge toward functional utility or new organisms and species by reorganizing genetic material, such as parts of the nervous or muscle system (Morris, 2010).

When multiple populations colonize seemingly similar habitats, they may evolve similar genes, traits, or functions. Evidence shows a rapid evolution of complex behavior, such as the parallel evolution of emotions and thermoregulation (Soslau, 2019), in birds and mammals (Burtsev et al., 2022). The two species evolve the same traits in the same (Marques et al., 20222) or different environments.

The two-step process of initial divergence in an ancient and potentially isolated population and subsequent admixture putatively also applies to other examples of fast and repeated ecological divergence. Repeated ecological divergence at the same loci has been reported in some iconic examples of parallel evolution, such as stickleback, cichlid fishes, and Heliconius butterflies (Van Belleghem et al., 2018). Convergence might generate repetitive evolution among species, depending on gene flow among populations and the phylogenetic relatedness of the lineages involved (Waters and McCulloch, 2021). Parallel and convergent evolution suggests that evolution is not an accidental series of events but a constant search for opportunities to increase complexity.
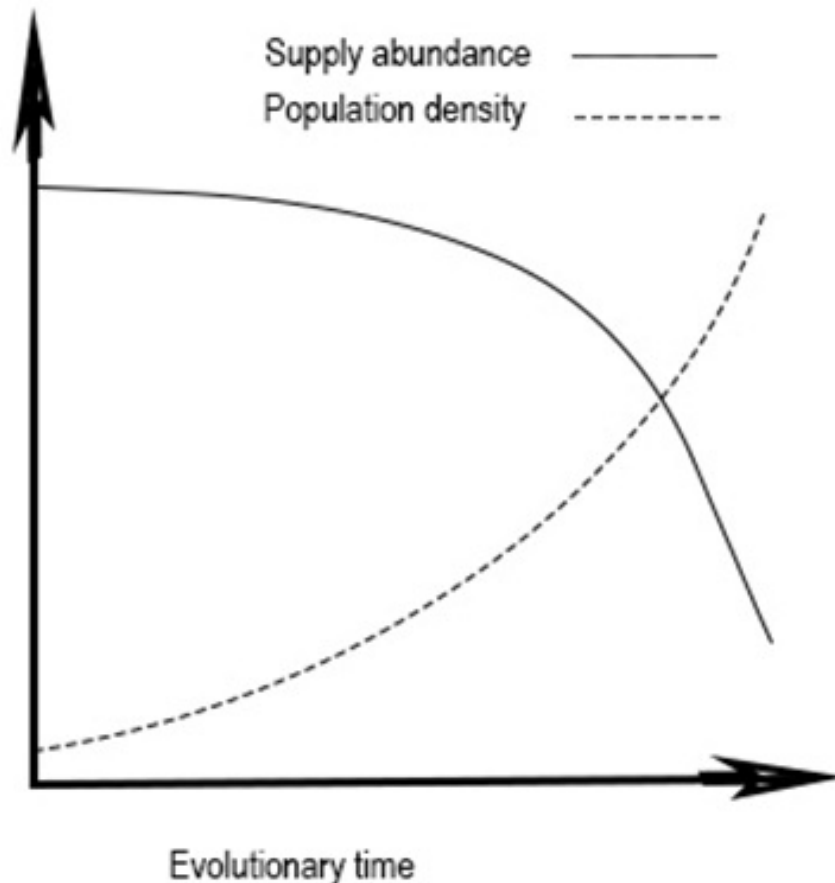
Figure 6. Supply availability in the ecosystem as the function of population density during an ideal evolutionary cycle

Phase 2 (D-A). Expansion

The Second phase of the evolutionary cycle forms an equilibrium position. Low social temperatures allow a close interdependence between the nutrient supply and the demands of the ecosystem. Environmental resources and the sun's heat input engender rapid population growth and diversity, which correlates to microstates in physics. For example, laboratory studies produced aggregate multicellularity (Márquez-Zacarías et al., 2021; Pentz et al., 2020), but organizational changes required genetic intervention (Daane et al., 2021).

The growing ecosystem's regular and organized interactions gradually fill the ecological niches. The highly structured processing and recycling of nutrients, wastes, air, energy, and other resources between producers and users give rise to food chains (Kingsbury & Hong, 2020), forming the backbone of the ecosystem. Symbioses and predator-prey cycles form equilibrium points with perfect interdependence, dynamic stability, and fitness (Good et al., 2017; Koonin, 2016; Vahdati et al., 2017). Populations of predators and their prey usually follow predictable cycles, which designate the species' place within the ecosystem.

The species must adapt to a new environment or perish. The meaningful mutation steps from the origin (p) form the

system's state and increase the number of microstates. With the increasing entropy, we lose information about the system's initial state, making it challenging to retrace the exact evolutionary path. The Kullback-Leibler divergence can express the genetic distance between the current algorithm (p) and the expected (final) output (q). A species (p) can adapt to a new environment by evolving into (q).

X = discrete random variable in genetic signal space X.

$p(x) \geq 0$, q (x) > 0 = probability distribution of species x, where

$p(x)$ = probability distribution of species x at time 0,

$q(x)$ = probability distribution of species x at equilibrium.

$$D_{KL}((p(x)\|q(x)) = \sum_{x \in X} p(x)\ln\frac{p(x)}{q(x)} \geq 0 \qquad (1)$$

where $\ln\frac{p(x)}{q(x)}$ is the significance of the change. Genetic updating depends on $D_{KL}((p(x)\|q(x)) \geq 0$ and disappears when q = p.

The ecosystem's endothermic energy production depends on the solar energy input; S is the entropy, and T is the social temperature for an isolated system, $dS = \frac{\delta Q}{T}$. The system moves toward high entropy equilibrium using free energy

The population number changes as a function of fitness.

$$\frac{dP_i}{dt} = F_i\, p_i \qquad (2)$$

where $F_i\, p_i$ is the fitness and the prospect of the ith species

$$\frac{dP_i}{dt} = \left(F_i - <F>\right)p_i \qquad (3)$$

where <F> is the mean fitness at equilibrium.

The system's state has been formed by the meaningful mutation steps from the origin (p) and the factor for the increase in the number of microstates (divergence).

Phase 3 (A-B). Overpopulation

Biological systems are messy, but excessive details leave higher-level organizations stable. Both small and large—but not intermediate-sized—populations tend to evolve larger genomes, allowing subsequent increases in phenotypic complexity (LaBar & Adami, 2016). Noise generates diversity; chaotic environmental and chemical changes, such as error-prone polymerases, provoke transient mechanisms for generating adaptive phenotypes (Ronco et al., 2020). Finally, entropic effects push cryptic (hidden) variations into otherwise-inaccessible regions of the adaptive landscape (Vahdati et al., 2017; Zheng et al., 2019).

Microscopic fluctuations drive the system towards more probable states; horizontal gene transfer spreads the genetic elements (Rosenberg, 2022; Sakaue et al., 2017), dispersing potential for new functions and morphologies (Sailer & Harms, 2017) and species formation (Woods et al., 2020; Suh, 2021). Entropy increases with time (Cohen & Marron, 2020; Jennings et al., 2020), generating disorder, which has diffusional effects on gene spreading (LaBar & Adami, 2016; Kimura, 1968; Sailer & Harms, 2017) without producing substantial evolutionary change. Therefore, entropic force represents microstate fluctuations of the gene pool, a trend that reverses the low entropy first phase.

The ecosystem has well-defined boundaries beyond which the population cannot expand. For example, fish cannot live on land; land animals might be confined by mountains or bodies of water, while the range of their food source binds birds. Population explosion causes a sharp decline in the availability of food and other resources (Figure 6). In Phase Three, the perfect equilibrium of Phase Two is upended by energy shortage. When the dwindling supplies reach a tipping point, defections sweep through the population, and generosity disappears (Gorban et al., 2021; Hoek et al., 2016; Kropotkin, 1902). Competition for resources increases the social temperature. High social temperature is less stable and more volatile, causing a sharp transition from cooperation to competition (Figure 3). Hierarchical interactions create winners and losers. Resource scarcity prompts stress, food fights, within-group scramble, and behavioral and other physiological effects (Gorban et al., 2021; Harris et al., 2010; Hoek et al., 2016). The degradation and environmental destruction of resources exhaust the ecosystem. In a complicated relationship between mutation frequency and population number (Cui & Yuan, 2020; Vahdati et al., 2017; McAvoy & Allen, 2020), competition creates stochastic patterns, giving rise to evolution's statistical and unpredictable nature (Sailer & Harms, 2017; Roos, 2014).

At the start of the period (T=0), all the survivors have an equal opportunity at evolution. The system evolves through a Markov process. As the distribution (x) changes over time, the transition leaves the state unchanged at the equilibrium position.

$$x_t \sim x_{t=1} \sim x_{t=2} \sim x_{t=3} \cdots \qquad (5)$$

where x_t is the distribution at time T.

In a chaotic, stressed environment, evolutionary change is limited to arbitrary gene flow, with the ability to stabilize the species' genome. At high entropy and social temperature, the cycle's free energy is minimized and must end.

Phase 4 (B-C). Extinction

In the overstretched ecosystem, environmental stressors can disrupt predator-prey cycles, symbiotic relationships, and homeostatic mechanisms, exposing cryptic genetic variation and allowing natural selection to act (Nijhout et al., 2017). The species ideally suited for their environment, "ideal phenotype," and species with lower genetic diversity are most vulnerable to extinction (Boggs & Gross, 2021; Ørsted et al., 2019), and the two conditions often coexist. Therefore, mass extinctions affect only the most specialized (inflexible) genomes, reducing genetic diversity (the number of microstates). Inversely, survivors are non-ideal phenotypes living in the margins. For example, proto-mammals lived in the shadow of better-adopted dinosaurs.

Repeated environmental shocks can squeeze vulnerable organisms' ecological niches (Dakos et al., 2019), causing marked reductions in population size, preceding the purported geological "extinction" event (Chiarenza et al., 2019; Dakos et al., 2019). For example, the onset of the Siberian Traps and South China intensive volcanism may have diminished communities' ecological resilience and functions well before the end-Permian mass extinction (Shen et al., 2018). Because the species' fitness was declining for tens of thousands of years, a single environmental disturbance could collapse the ecosystem (Boggs & Gross, 2021; Parry, 2021). Indeed, extinctions are generally connected to ecospace destruction (Lehman & Miikkulainen, 2015) and decoupled from mass radiations (Cuthill et al., 2020; Fan et al., 2020; Lynch et al., 2016). Supercomputer fossil record analysis can validate the different dynamics of extinctions and diversifications (Fan et al., 2020; Wagner, 2020).

While neutral mutations have no fitness effects, selection pressure enhances the likelihood of deleterious mutations (LaBar & Adami, 2017) and decreases the probability of fixation (Cui & Yuan, 2018). Therefore, mutations can weed out failed evolutionary experiments and find optimal genotypes. Furthermore, evolutionary selection of the fittest requires equilibrium entropy, which exists in phases three and four of the evolutionary cycle, and thus satisfies the classic Darwinian concept (Roos, 2014; Skene, 2020). Thus, detailed studies of the evolutionary phases might be a promising area of study (Tkadlec et al., 2019).

During the expansion of the ecosystem, it moves from state q to p, the peak of population growth. During Phases 1-3, the species best adapted to the ecosystem has better prospects, but the advantage disappears during dramatic environmental changes (Phase 4); the best-adapted species go extinct first.

Discussion and Conclusions

Throughout biology, at every level, cells, tissues, neurons, viruses, plants, and animals solve problems and achieve goals by flexibly navigating metabolic, physiological, genetic, cognitive, and behavioral needs. However, extinctions testify to the failure of the living world to adapt to environmental changes. We have shown that ecosystems are subjected to physical laws. A non-equilibrium physical system's bias towards maximum instantaneous entropy production applies to ecosystem evolution toward higher-entropy macroscopic states. Evolution's endothermic cycle shows the existence of a physical relationship between intelligence and entropy maximization.

The cell's biochemical flows and reactions can run both ways, yet life is about growth and development. Similarly, often confusing and arbitrary ecosystems generate complexity-increasing macroevolution with periodicities on many scales in space and time (Roberts & Mannion, 2019). Although a single mutation can produce surprising changes in the organism's characteristics, environmental changes and the state of other genes are significant (Ng & Kinjo, 2022; Burtsev et al., 2022; Brun-Usan et al., 2021). Therefore, although entropy has diffusional effects on gene spreading (LaBar & Adami, 2016; Kimura, 1968; Sailer & Harms, 2017), substantial evolutionary change might require extinction caused by repeated, catastrophic environmental shocks (Dakos et al., 2019).

Extinction reduces the number of microstates. In the first phase of evolution, the species is not well-adopted to its niche, limiting the degrees of freedom. The "liquid phase" of the cycle dictates low degrees of freedom for the organisms; they must closely "follow" the possibilities provided by the environment. Considering organisms as "particles" with small kinetic energy, the least energy path represents generosity and altruism. As the species' genetic makeup and morphology stabilize, it adapts to its unique habitat. Increasing population numbers engage in more combative and heated interactions indicating greater degrees of freedom. The evolutionary stability of the current ecosystem supports the conclusion that low entropy conditions are necessary for significant evolutionary jumps.

The imperfect copying and selection of neural informational patterns according to the Darwinian process cannot solve intelligent computations, such as the traveling salesman problem (Czégel et al., 2021). Therefore, in its current form, the Darwinian Theory is an incomplete description of the evolutionary process. Utilizing thermodynamic methods permit us to generalize the Darwinian Theory, which, on a fundamental level, is a crucial piece in the so-far unexplained emergence and nature of intellect.

Mutations in larger populations (Phase Three) find optimal genotypes by weeding out the failed evolutionary experiments, while the genetic and morphological innovations remain part of the "survivor" genomes. Therefore, the Darwinian concept, such as random mutations and selection of the fittest, requires equilibrium, the cycle's high entropy three and four phases. Distinguishing order-increasing (low entropy) and disordered (high entropy) transformations can usher in a more nuanced study and understanding of evolution.

Genetic information represents a temporal field that remains stable in changing environmental conditions. Nevertheless, its evolvable organization endows the organism with adaptability. Occasional simplifications of the genome do not erase the species' evolutionary classification. Therefore, the second law of intellect is the temporal field's tendency to accumulate energy as complexity. Evolution is the saga of individual organisms' increasingly efficient use of entropy.

The sun's continuous energy boosts self-replicative entities with a concomitant decrease in internal entropy (increased complexity) via periodic changes in the ecosystem's operating parameters, such as temperature and entropy. Despite or because of chaotic environmental noise, the sun's energy influx operates a forced complexity-increasing harmonic motion that accumulates energy in the genetic organization. The dramatic swings in entropy, population number, and resource density are necessary for the increasing biological complexity.

Energy fluxes (i.e., ecosystem dynamics), due to the ecosystem's compression and expansion, are very effective in driving either extinction or evolution. Therefore, extinction coupled with entropic effects is a powerful generator of substantial evolutionary change. Although the details and implications of the model remain to be worked out and validated with empirical data, the temporal field structure represents a general evolutionary trend of an unending upward complexity spiral. Moreover, computer simulations, such as supercomputer analysis of fossil records and long-term evolution studies, can verify its points.

_____

The authors declare no competing interests.

References

- Ahnert, S. E. (2017) Structural properties of genotype–phenotype maps. J. R. Soc. Interface. 142017027520170275 http://doi.org/10.1098/rsif.2017.0275

- Andersson, D., Jerlström-Hultqvist, J., & Näsvall, J. (2015). Evolution of new functions de novo and from preexisting genes. Cold Spring Harbor perspectives in biology, 7 6.

- Andrieux, D., Gaspard, P., Ciliberto, S., Garnier, N., Joubaud, S. and Petrosyan, A. (2007) "Entropy production and time asymmetry in non-equilibrium fluctuations," *Phys. Rev. Lett,* no. 98:150601.

- Annila, A., & Baverstock, K. (2014). Genes without prominence: a reappraisal of the foundations of biology. Journal of The Royal Society Interface, 11.

- Ao, P., (2005). Laws in Darwinian evolutionary theory. Physics of Life Reviews 2: 117-156.

- Ao, P., (2008). Emerging of stochastic dynamical equalities and steady state thermodynamics from Darwinian dynamics. Communications in Theoretical Physics 49: 1073-1090.

- Arlettaz, R., Christe, P., & Schaub, M. (2017). Food availability as a major driver in the evolution of life-history strategies of sibling species. Ecology and Evolution, 7(12), 4163–4172. https://doi.org/10.1002/ece3.2909.

- Babcock, L., Peng, S., Brett, C., Zhu, M., Ahlberg, P., Bevis, M., & Robison, R.A. (2015). Global climate, sea level cycles, and biotic events in the Cambrian Period. Palaeoworld, 24, 5-15.

- Bartlett, J. (2017). Evolutionary Teleonomy as a Unifying Principle for the Extended Evolutionary Synthesis. Bio-complexity, 2017.

- Barton, N.H., & Coe, J.B. (2009). On the application of statistical physics to evolutionary biology*Journal of theoretical biology, 259 2*, 317-24.

- Bennett, C. H. (1986). On the nature and origin of complexity in discrete, homogeneous, locally-interacting systems. Foundations of physics, 16(6), 585-592.

- Boggs, T.E., & Gross, J.B. (2021). Reduced Oxygen as an Environmental Pressure in the Evolution of the Blind Mexican Cavefish. Diversity, 13, 26.

- Boojari, M.A. (2020) Investigating the Evolution and Development of Biological Systems from the Perspective of Thermo-Kinetics and Systems Theory. Orig Life Evol Biosph 50, 121–143.

- Brun-Usan, M., Rago, A., Thies, C. *et al.* (2021) Development and selective grain make plasticity 'take the lead' in adaptive evolution. *BMC Ecol Evo* **21,** 205.

- Burtsev, M.S., Anokhin, K., & Bateson, P. (2022). Plasticity facilitates rapid evolution.*bioRxiv*.

- Bush, A., & Pruss, S. (2013). Theoretical Ecospace for Ecosystem Paleobiology: Energy, Nutrients, Biominerals, and Macroevolution. The Paleontological Society Papers, 19, 1-20.

- Bush, G.L., Case, S.M., Wilson, A., & Patton, J. (1977). Rapid speciation and chromosomal evolution in mammals. PNAS, 74 9, 3942-6.

- Charlesworth, B. (2001). The genetic complexity of life. *Nature* **412**, 682.

- Chiarenza, A.A., Mannion, P., Lunt, D., Farnsworth, A., Jones, L.A., Kelland, S., & Allison, P. (2019). Ecological niche modelling does not support climatically-driven dinosaur diversity decline before the Cretaceous/Paleogene mass extinction. Nature Communications, 10.

- Cohen, I. R., & Marron, A. (2020) The evolution of universal adaptations of life is driven by universal properties of matter: energy, entropy, and interaction. F1000Research, 9, 626.

- Connelly BD, Bruger EL, McKinley PK, Waters CM. (2017) Resource abundance and the critical transition to cooperation. J Evol Biol. 30: 750–761. pmid:28036143.

- Crokidakis, N., (2017) Non-Equilibrium Phase Transitions Induced by Social Temperature in Kinetic Exchange Opinion Models on Regular Lattices. Reports in Advances of Physical Sciences Vol. 1, No. 1 (2017) 1740001

- Cui, F., Yuan, B. (2018). Fixation probability of a beneficial mutation conferring decreased generation time in changing environments. BMC Syst Biol 12, 48.

- Cuthill, J.F., Guttenberg, N., & Budd, G. (2020). Impacts of speciation and extinction measured by an evolutionary decay clock. Nature.

- Czégel, D., Giaffar, H., Csillag, M., Futó, B., & Szathmáry, E. (2021). Novelty and imitation within the brain: a Darwinian neurodynamic approach to combinatorial problems. Scientific Reports, 11.

- Daane, J.M., Blum, N., Lanni, J., Boldt, H., Iovine, M.K., Higdon, C.W., Johnson, S.L., Lovejoy, N.R., & Harris, M.P. (2021). Modulation of bioelectric cues in the evolution of flying fishes. Current Biology, 31, 5052-5061.e8.

- Darwin, C., (1859). On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life. John Murray, London.

- Deli, E. and Kisvarday, Z. (2020) The Thermodynamic Brain and the Evolution of Intellect: The Role of Mental Energy. Cognitive Neurodynamics, 14(6), 743-756. DOI: 10.1007/s11571-020-09637-y

- Deli, E., Peters, J., and Kisvarday, Z. (2021) The thermodynamics of cognition: A Mathematical Treatment. Computational and Structural Biotechnology Journal. https://doi.org/10.1016/j.csbj.2021.01.008

- Erwin Schrödinger (1944), What Is Life?: The Physical Aspect of the Living Cell. Cambridge University Press

- Escobar, F.B., Velasco, C., Motoki, K., & Wang, Q. (2021). The temperature of emotions. PLoS ONE, 16.

- Fan, J., Shen, S., Erwin, D. et al. (2020). A high-resolution summary of Cambrian to Early Triassic marine invertebrate biodiversity. Science, 367, 272 - 277.

- Frank, S. A. and Smith, E. (2011). A simple derivation and classification of common probability distributions based on information symmetry and measurement scale. J. Evol. Biol. 24, 469–484.

- Frank, S. A. (2009). The common patterns of nature. J. Evol. Biol. 22, 1563–1585

- Fry, R., (2017) Physical Intelligence and Thermodynamic Computing. Entropy, 19, 107.

- Gao, Z., Cui, X., Wan, W., Zheng, W. and Gu, Z. (2022). "Long-range correlation analysis of high frequency prefrontal electroencephalogram oscillations for dynamic emotion recognition," Biomedical Signal Processing and Control,

- Gaspard, P. (2005) "Brownian motion, dynamical randomness and irreversibility," *N. J. Phys.* vol. 7, no. 77.

- Ghanchi, N.K., Nasir, A., Masood, K.I. (2021). Higher entropy observed in SARS-CoV-2 genomes from the first COVID-19 wave in Pakistan. *PLoS ONE, 16.*

- Gladyshev, G. (2017). On General Physical Principles of Biological Evolution.

- Good, B. H., McDonald, M. J., Barrick, J. E., Lenski, R. E., & Desai, M. M. (2017). The dynamics of molecular evolution over 60,000 generations. Nature, 551(7678), 45–50.

- Gorban, A.N., Tyukina, T.A., Pokidysheva, L.I., & Smirnova, E.V. (2021). Dynamic and thermodynamic models of adaptation. Physics of life reviews, 37, 17-64.

- Hoek, T.A., Axelrod, K., Biancalani, T., Yurtsev, E.A., Liu, J. & Gore, J. (2016). Resource availability modulates the cooperative and competitive nature of a microbial cross-feeding mutualism. PLoS Biol. 14: e1002540.

- Jeffery, K., Pollack, R. and Rovelli, C. (2019) "On the statistical mechanics of life: Schrödinger revisited," entropy, 21, 1211,

- Jennings, R.C., Belgio, E. & Zucchelli, G. (2020) Does maximal entropy production play a role in the evolution of biological complexity? A biological point of view. Rend. Fis. Acc. Lincei 31, 259–268.

- Jiang, W., Wu, J., Wang, G. and Zheng, H. (2016) "Forming Opinions via Trusted Friends: Time-Evolving Rating Prediction Using Fluid Dynamics," in IEEE Transactions on Computers, vol. 65, no. 4, pp. 1211-1224, doi: 10.1109/TC.2015.2444842.

- Jouffrey V., Leonard A. S. and Ahnert S. E. (2021) Gene duplication and subsequent diversification strongly affect phenotypic evolvability and robustness R. Soc. open sci. 8201636201636 http://doi.org/10.1098/rsos.201636

- Katsnelson MI, Wolf YI, Koonin EV (2018) Towards physical principles of biological evolution. Phys Scr 93:043001. https://doi.org/10.1088/1402-4896/aaaba4

- Katsnelson, MI. Wolf, YI. And Koonin, EV. (2019) On the feasibility of saltational evolution, PNAS 116 (42) 21068-21075

- KIMURA, M. (1968). Evolutionary Rate at the Molecular Level. Nature 217, 624–626

- Kingsbury, L. and Hong, W. (2020) A Multi-Brain Framework for Social Interaction Trends in Neurosciences, 43 (9) 651-666.

- Kirchner, J., & Weil, A. (2000). Delayed biological recovery from extinctions throughout the fossil record. Nature, 404, 177-180.

- Klimek, P., S. Poledna, S., and Thurner, S. (2019) Quantifying economic resilience from input–output susceptibility to improve predictions of economic growth and recovery, Nature Communications 10, 1677.

- Knoll, A. H., Javaux, E. J., Hewitt, D., & Cohen, P. (2006). Eukaryotic organisms in Proterozoic oceans. Philosophical transactions of the Royal Society of London. Series B, Biological sciences, 361(1470), 1023–1038. https://doi.org/10.1098/rstb.2006.1843

- Kondepudi, D.K., Bari, B.D., & Dixon, J.A. (2020). Dissipative Structures, Organisms and Evolution. Entropy, 22.

- Koonin EV. Are there laws of genome evolution? PLOS Computational Biology. 2011;7:e1002173

- Koonin, EV. (2016) The meaning of biological information Phil. Trans. R. Soc.A.37420150065 http://doi.org/10.1098/rsta.2015.0065.

- Kostic, M. "The Elusive Nature of Entropy and Its Physical Meaning" *Entropy,* vol. 16, pp. 953-967, 2014.

- Kropotkin, P., Mutual Aid: A Factor of Evolution, 1902.

- LaBar, T., Adami, C. Evolution of drift robustness in small populations. Nat Commun 8, 1012 (2017).

https://doi.org/10.1038/s41467-017-01003-7

- Lang, M. and Shkolnikov, M. Harmonic dynamics of the abelian sandpile. *Proceedings of the National Academy of Sciences*, 2019.

- Lee HW, Malik N, Mucha PJ. Evolutionary prisoner's dilemma games coevolving on adaptive networks. J Complex Netw. 2018 Feb;6(1):1-23.

- Lehman, J., & Miikkulainen, R. (2015). Extinction Events Can Accelerate Evolution. PLoS ONE, 10.

- Levis, N.A., & Pfennig, D.W. (2019). Plasticity-led evolution: A survey of developmental mechanisms and empirical tests. *Evolution & Development, 22*, 71 - 87.

- Levis, N.A., & Pfennig, D.W. (2019). Plasticity-led evolution: evaluating the key prediction of frequency-dependent adaptation. *Proceedings of the Royal Society B, 286*

- Liao, M.J., Din, M.O., Tsimring, L.S., & Hasty, J. (2019). Rock-paper-scissors: Engineered population dynamics increase genetic stability. *Science, 365*, 1045 - 1049.

- Lotka, A.J. Contribution to the energetics of evolution. Proc. Natl. Acad. Sci. USA 1922.b, 8, 147–151.

- Lotka, A.J. Natural selection as a physical principle. Proc. Natl. Acad. Sci. USA 1922.a, 8, 151–154.

- Lowery, C.M., Fraass, A.J. Morphospace expansion paces taxonomic diversification after end Cretaceous mass extinction. Nat Ecol Evol 3, 900–904 (2019).

- Lynch M, and Conery J (2003) The Origins of Genome Complexity, Science 302:1401–1404. DOI:10.1126/science.1089370.

- Magadum S, Banerjee U, Murugan P, Gangapur D, Ravikesavan R. Gene duplication as a major force in evolution. J Genet. 2013 Apr;92(1):155-61.

- Marques, D.A., Jones, F.C., Palma, F.D., Kingsley, D.M., & Reimchen, T.E. (2022). Genomic changes underlying repeated niche shifts in an adaptive radiation. *Evolution; International Journal of Organic Evolution, 76*, 1301 - 1319.

- Márquez-Zacarías, P., Conlin, P.L., Tong, K. et al. Why have aggregative multicellular organisms stayed simple?. Curr Genet 67, 871–876 (2021).

- Marshall, C. (2017). Five palaeobiological laws needed to understand the evolution of the living biota. Nature Ecology &Evolution, 1.

- McAvoy, A. and Allen, B. Fixation probabilities in evolutionary dynamics under weak selection. arXiv preprint arXiv:1908.03827, 2019.

- McMahon S, Ivarsson M. A New Frontier for Palaeobiology: Earth's Vast Deep Biosphere. Bioessays. 2019 Aug;41(8):e1900052. doi: 10.1002/bies.201900052. Epub 2019 Jun 26. PMID: 31241200.

- Ménendez, S. (2021). A hierarchical thermodynamic imperative drives the evolution of self-replicative life systems towards increased complexity. bioRxiv.

- Morris, S. C. (2010). Evolution, like any other science is predictable. Phil. Trans. R. Soc. B., 365, (1537): 133–145.

- Ng, E.T., & Kinjo, A. (2022). Computational Modelling of Plasticity-Led Evolution. arXiv:2208.00649v1 [q-bio.PE] 1 Aug 2022

- Nijhout, H.F., Sadre-Marandi, F., Best, J., & Reed, M.C. (2017). Systems Biology of Phenotypic Robustness and Plasticity. Integrative and comparative biology, 57 2, 171-184.

- O'Neill, J., & Schoth, A. (2022). The Mental Maxwell Relations: A Thermodynamic Allegory for Higher Brain Functions. Frontiers in Neuroscience.

- Ørsted M, Hoffmann AA, Sverrisdóttir E, Nielsen KL, Kristensen TN. Genomic variation predicts adaptive evolutionary responses better than population bottleneck history. PLoS Genet. 2019;15:e1008205.

- Parry, L.A. (2021). Evolution: No extinction? No way! Current Biology, 31, R907-R909.

- Pentz, J.T., Márquez-Zacarías, P., Bozdag, G.O., Burnetti, A.J., Yunker, P.J., Libby, E., & Ratcliff, W.C. (2020). Ecological Advantages and Evolutionary Limitations of Aggregative Multicellular Development. Current Biology, 30, 4155-4164.e6.

- Pross, A.; Pascal, R. Beilstein J. Org. Chem. 2017, 13, 665–674.doi:10.3762/bjoc.13.66

- Rago, A., Kouvaris, K., Uller, T., & Watson, R.A. (2018). How adaptive plasticity evolves when selected against.*PLoS Computational Biology, 15*.

- Ramstead, M.J., Badcock, P., & Friston, K.J. (2018). Answering Schrödinger's question: A free-energy formulation. Physics of Life Reviews, 24, 1 - 16.

- Roach, T., Nulton, J., Sibani, P., Rohwer, F., & Salamon, P. (2019). Emergent structure in a stochastic model of ecological evolution. Ecological Modelling, 401, 129-133.

- Roach, T.N. (2020). Use and Abuse of Entropy in Biology: A Case for Caliber. Entropy, 22 12.

- Roberts, G.G., & Mannion, P. (2019). Timing and periodicity of Phanerozoic marine biodiversity and environmental change. Scientific Reports, 9.

- Roldán, É. and Parrondo, J. M. "Estimating dissipation from single stationary trajectories,"*Phys. Rev. Lett.,* no. 105:150607. DOI: 10.1103/PhysRevLett.105.150607, 2010.

- Ronco, F., Matschiner, M., Böhne, A. et al. Drivers and dynamics of a massive adaptive radiation in cichlid fishes. Nature (2020). https://doi.org/10.1038/s41586-020-2930-4

- Roos, N. (2014). "Entropic forces in Brownian motion." American Journal of Physics. 82 (12): 1161–1166.

- Rosenberg, E. (2022). Rapid acquisition of microorganisms and microbial genes can help explain punctuated evolution. *Frontiers in Ecology and Evolution*.

- Saarimäki, H. and et al., "Distributed affective space represents multiple emotion categories across the brain," bioRxiv, 2017.

- Sabater, B. (2022) Entropy Perspectives of Molecular and Evolutionary Biology. Int J Mol Sci. 23(8):4098.

- Sailer, Z.R., & Harms, M.J. (2017). Molecular ensembles make evolution unpredictable. PNAS, 114, 11938 - 11943.

- Sakaue, H., Kinouchi, T., Fujii, N., Takata, T., and Fujii, N. (2017) Isomeric replacement of a single aspartic acid induces a marked change in protein function: The example of Ribonuclease A ACS Omega 2, 260– 267 DOI: 10.1021/acsomega.6b00346

- Santoni, D., Ghosh, N., & Saha, I. (2021). An entropy-based study on mutational trajectory of SARS-CoV-2 in India. *Infection, Genetics and Evolution, 97*, 105154 - 105154.

- Schrödinger, E (1945). What Is Life? The Physical Aspect of the Living Cell. The University Press.

- Sella, G. and Hirsh, A. E. The application of statistical physics to evolutionary biology. Proc. Natl. Acad. Sci. U.S.A. 102, 9541–9546 (2005).

- Shen, S., Ramezani, J., Chen, J., Cao, C., Erwin, D.H., Zhang, H., Xiang, L., Schoepfer, S.D., Henderson, C.M., Zheng, Q., Bowring, S.A., Wang, Y., Li, X., Wang, X., Yuan, D., Zhang, Y., Mu, L., Wang, J., & Wu, Y. (2018). A sudden end-Permian mass extinction in South China. *GSA Bulletin*.
- Sherwin, W. (2018). Entropy, or Information, Unifies Ecology and Evolution and Beyond. Entropy, 20.
- Skene, K.R. (2015). Life's a Gas: A Thermodynamic Theory of Biological Evolution. Entropy, 17, 5522-5548.
- Skene, K.R. (2020). In pursuit of the framework behind the biosphere: S-curves, self-assembly and the genetic entropy paradox. Bio Systems, 104101.
- Soslau, G. (2019). The role of the red blood cell and platelet in the evolution of mammalian and avian endothermy. Journal of experimental zoology. Part B, Molecular and developmental evolution.
- Suh, A. (2021). Horizontal Transfer of Transposons as Genomic Fossils of Host-Parasite Interactions. Topics in Geobiology.
- Sundstrom, S., & Allen, C. (2019). The adaptive cycle: More than a metaphor. Ecological Complexity, 39, 100767.
- Tara R. Harris, Colin A. Chapman, Steven L. Monfort, Small folivorous primate groups exhibit behavioral and physiological effects of food scarcity, Behavioral Ecology, Volume 21, Issue 1, January-February 2010, Pages 46–56.
- Thompson EG, Galitski T. Quantifying and analyzing the network basis of genetic complexity. PLoS Comput Biol. 2012;8(7):e1002583.
- Tkadlec J, Pavlogiannis A, Chatterjee K, Nowak MA. Limits on amplifiers of natural selection under death-Birth updating. PLOS Computational Biology. 2020;16(1):e1007494.
- Tkadlec, A. Pavlogiannis, K. Chatterjee, and M. A. Nowak. Population structure determines the tradeoff between fixation probability and fixation time. Communications Biology, 2, 2019.
- Torday, J.S. (2021). Cellular evolution as the flow of energy. Progress in biophysics and molecular biology. https://doi.org/10.1016/j.pbiomolbio.2021.06.011
- Vahdati, A. R., Sprouffske, K., & Wagner, A. (2017). Effect of Population Size and Mutation Rate on the Evolution of RNA Sequences on an Adaptive Landscape Determined by RNA Folding. International journal of biological sciences, 13(9), 1138–1151.
- Van Belleghem, S.M., Vangestel, C., De Wolf, K., De Corte, Z., Möst, M., Rastas, P., De Meester, L., & Hendrickx, F. (2018). Evolution at two time frames: Polymorphisms from an ancient singular divergence event fuel contemporary parallel evolution. *PLoS Genetics, 14*.
- Vanchurin, V., Wolf, Y.I., Koonin, E.V., & Katsnelson, M.I. (2022). Thermodynamics of evolution and the origin of life. Proceedings of the National Academy of Sciences of the United States of America, 119.
- Dakos, V., Matthews, B., Hendry, A. P. et al. (2019) Ecosystem tipping points in an evolving world. Nature ecology & evolution, page 1.
- von Helmholtz, H. (1882). Physical memoirs, selected and translated from foreign sources. Taylor & Francis.
- Vopson, M.M., & Lepadatu, S. (2022). Second law of information dynamics. *AIP Advances*.
- Vopson, M.M. (2022). A Possible Information Entropic Law of Genetic Mutations. *Applied Sciences*.
- Wagner, P. (2020). High-resolution dating of Paleozoic fossils. Science, 367, 249 - 249.
- Walker, S.I., & Davies, P.C. (2013). The algorithmic origins of life. Journal of The Royal Society Interface, 10.

- Waters, J.M., & McCulloch, G.A. (2021). Reinventing the wheel? Reassessing the roles of gene flow, sorting and convergence in repeated evolution. *Molecular Ecology, 30*, 4162 - 4172.

- Werth, A.J. (2020). Cetaceans as Exemplars of Evolution and Evolutionary Ecology: A Glossary.

- Wolf, YI, Katsnelson, MI, Koonin, EV (2018) Physical foundations of biological complexity PNAS 115(37) DOI: 10.1073/pnas.1807890115.

- Wong, T.W. (2020). Sources of evolutionary contingency: chance variation and genetic drift. Biology & Philosophy.

- Woods, LC., Gorrell, RJ. Taylor, F., Connallon, T., Kwok, T. and McDonald, MJ. Horizontal gene transfer potentiates adaptation by reducing selective constraints on the spread of genetic variation, Proc Natl Acad Sci U S A. 2020 Oct 27; 117(43): 26868–26875.

- Xia, S., VanKuren, N.W., Chen, C., Zhang, L., Kemkemer, C., Shao, Y., Jia, H., Lee, U., Advani, A.S., Gschwend, A.R., Vibranovski, M., Chen, S., Zhang, Y., & Long, M. (2020). Genomic Analyses of New Genes and Their Phenotypic Effects Reveal Rapid Evolution of Essential Functions in Drosophila Development. bioRxiv.

- Yuri Bakhtin, Mikhail I. Katsnelson, Yuri I. Wolf, Eugene V. Koonin, (2020) Punctuated equilibrium as the default mode of evolution of large populations on fitness landscapes dominated by saddle points in the weak-mutation limit. DOI: 10.1101/2020.07.20.212241

- Zhang, L., Reifová, R., Halenková, Z., & Gompert, Z. (2021). How Important Are Structural Variants for Speciation? Genes, 12.

- ZHENG, J., PAYNE, JL. WAGNER, A. (2019) Cryptic genetic variation accelerates evolution by opening access to diverse adaptive peaks. SCIENCE 365(6451):347-353 DOI: 10.1126/science.aax1837.