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Natural patterns of energy dispersal

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Abstract

Universal patterns such as power-law dependences, skewed distributions, tree-like structures, networks and spirals are associated with energy dispersal processes using the principle of least action. Also ubiquitous temporal courses such as sigmoid growth, bifurcations and chaos are ascribed to the decrease of free energy in the least time. Moreover, emergence of natural standards such as the common genetic code and chirality consensus of amino acids are understood to follow from the quest to maximize the dispersal of energy. Many mathematical functions that model natural patterns and processes are found as approximations of the evolutionary equation of motion that has been derived from statistical physics of open systems. The evolutionary processes can be described as flows of energy that run from high energy sources to low energy sinks in the least time. However, the equation of evolution cannot be solved in general because the flows of energy and their driving forces are inseparable. Since the energy of the system keeps changing, the paths of evolution cannot be integrated from a given initial state to a final state. Although evolutionary courses of these non-Hamiltonian systems with two or more alternative ways of dissipation cannot be predicted, the flows of energy will search and naturally select paths of least action, known as geodesics, to consume free energy in the least time. The scale-invariant natural patterns follow from this natural law that impinges on processes at all scales of space and time.

Keywords: Entropy; Evolution; Free energy; Least action; Natural selection; Power law; Scale-free; Self-similarity; Thermodynamics

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1. Introduction

Diversity in nature is staggering but not arbitrary. We recognize regularities as scale-independent patterns, notably power laws, skewed distributions and tree-like structures that branch out in logistic manner as well as spirals that wind out in logarithmic manner. These universal patterns are familiar, for example, from ecology where a power law relates the number of species to the size of the area on which they live [1]; from physiology where Kleiber's law associates the metabolic rate of a species with its body mass [2]; from linguistics where Zipf's law relates the number of words with their frequency of use in human languages [3]; and from social sciences where the Pareto principle links the number of owners to the amount of land which they possess [4,5]. The scale-free power laws are recognized also in the forms of electrostatic and gravitational potentials as well as in the form of ubiquitous 1/f noise. The skewed, nearly log-normal distributions account for variation among individuals in a population and the body size-species richness patterns [6] and for the income of households in an economy just as for the size dispersion of galaxies in space and velocity distribution of gas molecules in a container [7–9]. Examples of ubiquitous tree-like, self-similar structures are the pulmonary structure of our lungs that branches out just like a river estuary [10,11] and an electric discharge of a lighting that fans out in a fractal manner. In turn, a marine shell exemplifies the spiral shape that winds around itself just as a tornado or galaxy wraps around itself [12]. Also closed trajectories, sometimes interpreted as modified circles, are common in nature [13]. These forms are familiar from the steady-state metabolic cycle in cells, or from the nutrient cycle in ecosystems, just as from vortices in Bernard cells, or orbiting planets in solar systems.

Not only are the self-similar spatial patterns ubiquitous but also copious temporal processes are recurrent. Sigmoid growth patterns of organisms and developmental stages of individuals resemble evolutionary epochs of ecosystems that burst by punctuations and settle to stases [14]. These time lines are familiar, for example, from microbiology where bacterial growth on a Petri dish follows an S-curve, and from economics when a nascent industry initiates and matures [15]. The typical temporal courses are also familiar from environmental events. For example, an outburst from a reservoir launches flooding that will eventually level off by filling the basin just like an outbreak of immigrant species unleashes expansion that will ultimately even out by populating the habitat. Moreover, animate developmental sequences diversify by bifurcations and at times take off even on chaotic trajectories. Populations of species may oscillate in an ecosystem [16] just like populations of chemical compounds may oscillate in a reaction vessel [17,18] and occupancies of electronic states of noble gas atoms may vary in oscillatory manner in an optical cavity [19]. Also economic systems tend to go through up- and downswings.

Moreover, diversity in nature displays standards and conventions rather than spreading out at random. The natural standards are familiar, for example, from biochemistry where chirality convention of amino acids and the genetic code are ubiquitous just like from contemporary economies where a common currency is adopted to facilitate transactions, and from telecommunications where competing manufacturers have agreed upon protocols to facilitate data transfer. Also many standards of social systems such as languages, and cultural codes such as symbols, and habits such as greetings, can be regarded as standardized ways for individuals to facilitate interaction with each other.

The universal spatial and temporal patterns as well as ubiquitous standards have attracted many to contemplate a profound principle that would rationalize these rules and regularities of nature amid diversity and complexity. It is not a new thought to suspect that the scale-free patterns and allometric laws [20,21] emerge from processes that follow the maximum entropy production principle [22–32] or the principle of least action [33,34]. According to Hamilton's principle [35] the differential equation of the second law of thermodynamics and the integral equation of least action

are equivalent [36–38]. The thermodynamic tenet sees no demarcation line between animate and inanimate but pictures all processes as flows of energy that level off energy differences in the least time. In other words, the natural processes will spontaneously direct along paths of least action by consuming free energy as fast as possible. Many mathematical models account well for these motions and yield reasonably representative distributions of populations as well as outline approximately their cumulative curves [39–41]. After all, natural patterns are rarely ideal to follow precisely a particular mathematical function and allometric laws are seldom exact, but the patterns are preferably described as propensities or tendencies.

In this study the objective is not to repeat reviewing various mathematical models but to provide a holistic physical portrayal of nature that clarifies, by the supreme law of nature, why natural processes result in patterns that are recognized in diverse disciplines. Since no theory may go against the second law by the words of Eddington [42] we do not question the natural law itself but merely analyze its equation of motion to draw conclusions about the fundamental origin of the natural patterns. In this way it is easy to understand why most commonly used mathematical functions are so successful models of natural processes. Thus we do not aim on calculating some particular natural patterns rather we will disclose the underlying thermodynamic processes that produce these patterns. In fact we will clarify why it is impossible to predict precisely natural processes and their ensuing patterns.

2. Dispersal of energy

The general law of nature is preferably communicated using most general concepts. To this end physics relates energy to everything that exists and associates an energy difference to a force between any two things. The energy difference is known as free energy. It forces energy to flow [43]. This is the essence of the second law of thermodynamics which simply states that energy flows from high energy densities to low energy densities. Usually it is emphasized by the maximum entropy production principle that the energy differences will level off at a maximal rate. The same basic law of thermodynamics is also stated by the principle of least action which says that the flows of energy will naturally select the paths that will take to the state of minimum free-energy, equivalent to the state of maximum entropy in the least time.

Here this universal imperative to transform energy in the least time is inspected, together with the conservation of energy, i.e. the first law of thermodynamics, to understand the basis of natural patterns and standards. To this end the second law of thermodynamics is derived from statistical physics of open systems and formulated as an equation of motion. The evolutionary equation is analyzed and compared to mathematical formulas that are commonly used to model natural processes and patterns. The comparison reveals that the mathematical models are approximate expressions of the fundamental evolutionary equation.

2.1. Energy transduction systems

A difference in energy manifests itself when there is some mechanism, direct or indirect, which conducts energy from one repository to another. For example, a flow of electric current reveals that a battery is charged up relative to a reference potential, e.g. the common ground level. Conversely without an energy flow, the potential will remain concealed. An energy transduction system comprises densities-in-energy $\phi = \exp(G/k_BT)$ [44] that are coupled to each other by flows of energy in one way or another. An entity of the system is referred to as the *j*-entity. It is associated with energy G_j . The value of G_j is relative to the common reference level k_BT , the average energy per entity of the affine system. The energy density in a pool of N_j identical *j*-entities is $\phi_j = N_j \exp(G_j/k_BT)$. To obtain a scale-independent formulation for a system of interacting entities, each entity is regarded as a result of earlier evolutionary processes [45]. For example, a molecule in a cellular system results from its substrates via chemical syntheses just as an individual in an ecosystem emerges from various ingredients via myriad processes. Therefore the probability P_j for the *j*-entity to exist depends on ingredients that are available in its surroundings. Thus the existence of *j*-entity depends on other entities, referred to as the *k*-entities, each of which is associated with energy G_k as well as on energy that couples from the surroundings to *jk*-transformations. The formula of P_j that describes the status due to the mutual dependence of entities and energy from the surroundings is defined by statistical physics of open systems as [46,47]

$$P_j = \left(\prod_k \left(N_k e^{-(\Delta G_{jk} - i\Delta Q_{jk})/k_B T}\right)^{g_{jk}} / g_{jk}!\right)^{N_j} / N_j!.$$
(2.1)



Fig. 1. An energy transduction system is depicted as a level diagram. Each level, indexed by j, is occupied by entities numbered N_j and assigned with energy G_j . The occupancies N_j and N_k change in jk-transformations where horizontal arrows indicate changes in scalar potential and vertical wavy arrows denote changes driven by vector potential differences. The bow arrows denote isoenergic exchange of indistinguishable entities. The probability P distribution outlines the partition of the diverse j- and k-entities. For a quasi-stationary system, P_j depends up to a good approximation on the population N_j since the amount of free energy is small compared to the energy bound in N_j . The system evolves, step-by-step, via absorptive or emissive jk-transformations facilitated by the functional entities themselves, toward a stationary-state energy balance in which the levels are populated so that the average energy k_BT equals that in the system's surroundings. A sufficiently statistical system will evolve gradually because it is not greatly perturbed in its energy content by a single step of evolution where energy is absorbed to or emitted from the system. Hence at each step of evolution the quasi-stationary partition of entities is close to the maximum-entropy distribution.

The recursive form is self-similar so that the *j*-entity is a product $\prod N_k$ of embedded *k*-entities, each distinct type available in numbers N_k . In other words, if any one of the vital k-ingredients is missing, the j-entity cannot be assembled $P_i = 0$. The energy difference between the *j*-product and *k*-substrates is as usual $\Delta G_{ik} = G_i - G_k$ [48]. The k-entity copies that remain indistinguishable (symmetric, exchangeable) in the assembled *j*-entity are numbered by degeneracy g_{ik} so that $g_{ik}\Delta G_{ik} = G_i - g_{ik}G_k$. The energy influx that couples to the *jk*-transformation as a stream of photons from the surroundings to the system is denoted by ΔQ_{ik} . Energy in this form is customarily known as the vector potential whose force carriers are photons [49]. In the *jk*-transformation from one state to another electromagnetic field couples orthogonally, hence indicated by i, to the scalar part ΔG_{ik} of the bound forms of energy (Fig. 1). The orthogonal relation between the scalar and vector potential is familiar from the Poynting's theorem which describes, for example, a situation in which an electron radiates perpendicular to its path while plunging down along the electric potential gradient. Likewise in photosynthesis light couples orthogonal to electron orbits when lifting an electron from the ground state to an excited state. Moreover, the notation by complex number will guarantee the conservation of energy by defining the coordinates of space and time as mutually orthogonal [50]. For example, in a chemical reaction the scalar (chemical) potential is transformed to the vector potential (heat) (or vice versa). Finally, it is worth noting that the photon flux to a macroscopic system is small compared to the energy content of the system, hence the system will evolve from one state to another gradually. Therefore many distributions of evolving natural systems, such as populations of species are quasi-stationary, i.e. close to the maximum entropy partition. These optimal partitions are the skewed distributions of animate just as inanimate entities. Only when the population is small, i.e. not sufficiently statistical, evolution does not advance smoothly but the step size in energy is comparable to the energy that is bound to the system. For example, when a new species appears or an old one goes extinct, the probability P_i for the particular species will change abruptly.

The total probability P, as the energetic status measure for the entire system, is a product of P_j over all *j*-levels and *jk*-paths of transformations [46,47]

$$P = \prod_{j} P_{j} = \prod_{j} \left(\prod_{k} \left(N_{k} e^{-(\Delta G_{jk} - i\Delta Q_{jk})/k_{B}T} \right)^{g_{jk}} / g_{jk}! \right)^{N_{j}} / N_{j}!.$$
(2.2)

The self-similar form of P describes a hierarchy of interacting systems within systems [51] (Fig. 2). The status measure is conditional because it depends on the energetic conditions within the system and in its surrounding systems. Since populations are non-negative so is P. Since the energy content of an evolving system is changing, so is P. Therefore the probability of an evolving system cannot be normalized to unity. Consequently no unitary transformation can be found that would remove the time dependence. In other words evolution toward free energy minimum is



Fig. 2. Hierarchical organization of nature is pictured as energy transduction systems within systems. Each system is circled to depict its motions. The open systems evolve along spiral trajectories via net flows of energy to or from the surroundings. Evolution proceeds by systemic transformations that either emit energy to or absorb energy from its surroundings. A stationary system is in balance with or eventually isolated from its surroundings and executes steady-state reversible dynamics on closed orbits.

directional with time. First, at a stationary state, P is constant and can be normalized to unity, as usual, dividing by an invariant partition function. Then it is possible to find a unitary transformation to remove the time-dependence. In other words dynamics at the free-energy minimum state is completely reversible.

The above definition of probability in terms of energy may seem strange to some because traditionally P is regarded merely as an invariant number that represents ideal realizations. For example, the probability of any given face of a dice to show on top is ideally equal for all faces. In other words, because pips are indented, the faces are energetically equivalent, i.e. indistinguishable in interactions between the dice and a table. However for players the faces are distinguishable, e.g. due to differences in observed reflections of light that differ for the number of pips on each face. When combinatorial possibilities are energetically equivalent, there is no practical reason to recall that P is in fact physical. However, the physical portrayal of P as the system's status measure clarifies that the natural processes, both animate and inanimate, direct toward the free energy minimum by dissipative transformations from one state to another, more probable one. Irreversibility follows from the net dissipation. The evolutionary process terminates at the free energy minimum where the net dissipation vanishes and motions become reversible. According to the thermodynamic maxim the free energy minimum state is the maximum-entropy state [52,53]. At the maximum-entropy state entities populate the energy levels so that all free energy is consumed. At the free-energy minimum state the dispersal of energy by the available mechanisms of transduction is maximal (Fig. 1). A chemical reaction mixture at the chemical equilibrium is an example of a free-energy minimum state and an ecosystem at the climax state is another example of a free-energy minimum system.

2.2. Entropy as a statistical measure of energy dispersal

A state of a large repository of energy will not change much when few quanta are absorbed from or emitted to the surroundings. Such a sufficiently statistical system [54] can be assigned with additive logarithmic probability measure known as entropy [46,47]

$$S = k_B \ln P = k_B \sum_{j} N_j \left(1 - \sum_{k} A_{jk} / k_B T \right)$$
(2.3)

where Stirling's approximation $\ln N_j! \approx N_j \ln N_j - N_j$ valid for $N_j \gg 1$ has been used. However, when N_j is small, e.g. when a new species emerges or an old one goes extinct, the use of statistical approximation is not warranted. This volatility is typical of small populations. For example, an endangered species may go extinct merely due to unusual weather conditions whereas an abundant species tends to populate numerous and diverse habitants that are not all affected by local bad weather. The free energy $A_{jk} = \Delta \mu_{jk} - i \Delta Q_{jk}$, is also referred as affinity or exergy [55] where the scalar potential difference $\Delta \mu_{jk} = \mu_j - \sum \mu_k$ is the difference between the *j*-product's μ_j and the *k*-substrate's μ_k as well as *k*-byproduct's $-\mu_k$, and ΔQ_{jk} denotes difference in the vector potential relative to the surroundings (Figs. 1 and 2). It becomes apparent, when multiplying Eq. (2.3) with temperature *T*, that entropy is a state measure in terms of energy which is bound in the systemic entities $\sum N_j k_B T$ minus $\sum N_j A_{jk}$ which is still free to be consumed by evolutionary processes. When all affinities $A_{jk} = 0$ have vanished, Eq. (2.3) reduces to the familiar expression of maximum entropy $S_{max} = k_B \sum N_j^{ss}$ that sums up from the stationary-state populations N_j^{ss} [46]. Energy that is bound in the steady-state populations equals $T S_{max}$.

Importantly, entropy is not a measure of disorder, i.e., decoherence [56]. The common misconception gives rise to erroneous thoughts of animate processes leading to a decrease of entropy within the living system at the expense of increasing entropy in its surroundings. This conjecture would in fact violate the conservation of energy because the system and its surroundings share the same flows of energy via mutual interface. Thus the entropy of the system, just as entropy of its surroundings, will increase when the flow of energy levels off mutual differences in energy densities. The confusion between entropy and order originates from the failure to distinguish states from phases. The distinct states differ from each other by energy whereas a state may be composed of $N_i \ge 1$, i.e. one or more isoenergetic configurations, known also as microstates, that differ from each other only by relative phases (Fig. 1). When all configurations are in the same phase ($\Delta \varphi = 0$), the degree of order is at its maximum and the system moves coherently. Then actions are fully synchronized. Conversely, the phase dispersal is maximal for randomly spread configurations. Then the system is fully disordered and it moves incoherently. A change in configuration, i.e. a change in phase φ is energetically conserved $\Delta Q_{ik} = 0$ whereas a transition from one state to another is dissipative $\Delta Q_{ik} \neq 0$ [47]. Obviously, the phase of motion is not immaterial for the outcome of an energy transduction process between the system and its surroundings. For example, an observer may couple to the system in a particular phase of its motion so that the received, coherent flows of energy interfere constructively or in another phase where the interference is destructive. Motions of a microscopic system such as a set of magnetic moments, due its small number of entities, may readily be brought to a coherent phase. The principle is no different for a macroscopic system, such as a colony of cells, which can also be triggered or driven to move in a synchronized manner [57]. Also predators tend to move in-phase with their prey. The phase-dependence in energy transduction between the macroscopic system and the observer is obtained by computing the expectation value of the operator that drives the detected transition [58]. Moreover, when a microscopic system couples to its surroundings, it may abruptly lose its coherence due to the transition while a macroscopic system has usually many ways to exchange quanta with its surroundings and consequently its motions will gradually become incoherent due to random to-and-fro flows of energy between the system and its surroundings.

2.3. Equations of evolution

When Boltzmann formulated thermodynamics from first principles, he came up with an astounding idea of nature being in motion toward more probable states. He placed probability as a corner stone of statistical mechanics. However, rather than developing the notion of conditional probabilities pioneered by Bayes, Boltzmann adopted the isoenergetic concept of invariant probabilities [59]. Consequently, statistical mechanics was formulated so that it is limited to closed, conserved systems. Nonetheless, the theory delivers a stationary-state partition using the method of Lagrange multipliers that associate with the fixed energy and invariant number of entities in the system [46]. Due to this incomplete understanding of probability, Boltzmann's formulation included no free-energy and conversely excluded all changes of state. Hence, dynamics remained limited to isoenergetic phase precession which is reversible and inapplicable to describe irreversible evolution. Moreover, due to the misunderstanding about the change of state and the change of phase, the entropy concept was mixed up with the notion of disorder because the formalism devised for conserved systems allowed only for dispersal of phases due to sporadic exchange of quanta between a coherent system and incoherent surroundings but not changes of state.

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Statistical physics of open systems is based on the physical probability concept as defined in Eq. (2.2). The equation of motion is obtained by straight-forward differentiation $(dP_j/dN_j)(dN_j/dt)$ [46,47]

$$\frac{dP}{dt} = LP \quad \Rightarrow \quad \frac{dS}{dt} = k_B L \ge 0; \qquad L = \frac{1}{k_B T} \sum_{j,k} \frac{dN_j}{dt} (-\Delta \mu_{jk} + i\Delta Q_{jk}) = -\sum_{j,k} \frac{dN_j}{dt} \frac{A_{jk}}{k_B T}.$$
 (2.4)

In accordance with the principle of increasing entropy, the differential of *P* is always non-negative. When the force $A_{jk} > 0$ (<0), the flow $dN_j/dt < 0$ (>0) will aim to level off the force. Evolution expires first at the stationary state dS/dt = 0 where free energy has been consumed $A_{jk} = 0$ and thus populations do not vary $dN_j/dt = 0$. In the absence of net dissipation, detailed balance [50] holds for isoenergetic phase precession and phase dispersal.

Curiously, the simple equation for a sequence of changes of state, i.e. evolution cannot be solved when there are two or more alternative paths for the *jk*-transformations. For example, when a stock food, such as a prey population, can be consumed by two or more predator populations, the two predator populations are interdependent. When one succeeds in game, odds for the other will fall. Technically speaking, such an evolutionary system has three of more degrees of freedom for dissipative transitions. When the forces depend on flows, the system is non-Hamiltonian. Its equation of motion cannot be solved because the forces cannot be separated from the flows. By consequence, when variables such as the size of population N_i and the free energy A_{ik} which is a function of N_i cannot be separated, the evolutionary equation of motion cannot be integrated to a closed from. This is familiar from the three-body problem [60] as well as from problems that display computational intractability such as the traveling salesman problem [61] and the protein folding problem [62]. Since the energy content of an evolving system is either increasing or decreasing, there is no norm that would be required in order to find a unitary transformation to extract eigenvalues [63]. Simply said, the motional (eigen) modes cannot be determined because they keep changing during evolution. This is familiar from an elementary physical system where frequency of a vibrating string increases with increasing tension. Likewise changing environmental conditions drive changes in animate populations and animate behavior. A well-known example is Blue Tits that learned from the 1960s to open traditional British milk bottles with foil tops to get at the cream underneath. Recently though, this behavior has become less motivated among the tits because the available energy is less. Skimmed milk is consumed nowadays. In general, evolutionary courses are inherently non-deterministic when motions affect driving forces and vice versa. This type of unpredictability is familiar, e.g. from fractal growth which is often modeled by nonlinear iterative equations [39] and from phenomena that display self-organized criticality [64]. However, the equation of evolution is non-deterministic unlike its approximate deterministic models such as the logistic equation [65] and iterative maps that model bifurcations and a set of differential equations that mimic chaos [66,40].

A change dN_j/dt in the population N_j of a sufficiently statistical system is proportional to the free energy A_{jk} by a particular mechanism that facilitates the transformation from the k-substrates to the j-products [46,47]

$$\frac{dN_j}{dt} = -\sum_k \sigma_{jk} \frac{A_{jk}}{k_B T}.$$
(2.5)

The coefficient of conductance σ_{jk} is characteristic of the transformation mechanism. For example, an enzyme is a mechanism at molecular level just as an individual is a mechanism at another level of hierarchy since both facilitate energy transduction processes. The quest to diminish energy differences as fast as possible entails that evolution at every moment and at every level of hierarchy points toward maximizing dS/dt. This imperative is the maximum entropy production principle. Along the path of least action the transformation rate is maximal. Thus, the optimal change in population along the geodesic is obtained from Eq. (2.4) as

$$\frac{d^2S}{dt^2} = 0 \quad \Leftrightarrow \quad \frac{1}{k_B T} \frac{d}{dt} \sum_{j,k} \frac{dN_j}{dt} (-\Delta \mu_{jk} + i\Delta Q_{jk}) = 0 \quad \Rightarrow \quad \left(\frac{dN_j}{dt}\right)^2 \frac{\partial^2 U}{\partial N_j^2} = \frac{\partial^2 Q}{\partial t^2} \tag{2.6}$$

where the differences in the scalar $\mu_j = \partial U/\partial N_j$ and vector $Q_j = \partial U/\partial N_j$ potential components are understood as orthogonal, continuous derivates so that the directional gradient $(dN_j/dt)\partial/\partial N_j$ equals the temporal derivative $\partial/\partial t$. However, the maxim given by Eq. (2.6) applies only at the spacetime point. If the formula was applied over a period of time, it would erroneously entail that the energy flow would not drain the sources and fill the sinks. This invariance also be stated so that the spacetime point retains symmetry. Therefore, a formal integration of Eq. (2.6) to a closed form would not properly describe evolution which is a symmetry breaking process along the open path that keeps redirecting itself on its way from one state to more probable one.

The law of mass-action [67] is often used to model population changes instead Eq. (2.5). This common model of kinetics assumes that the rate dN_j/dt would be proportional to concentrations or populations N_k and N_j in powers of stoichiometry. In this form, which is also familiar from differential equations due to Lotka and Volterra [40], forward and backward rate constants are distinct from each other just like Einstein's rate coefficients [49] are distinct for emission and absorption in transitions between electronic states. Consequently, when the rate is not given correctly as proportional to the free energy, kinetics and thermodynamics are incompatible with each other. Then transitions between states cannot be described as flows of energy funneling through passages, each characterized by the conductance σ_{jk} . Instead, transitions are pictured to cross over some high-energy barriers. Then, for instance, the conventional view of a catalyst as an agent that lowers the high-energy transition state is somewhat misleading because the notion implies that something were moving on the energy landscape rather than the energy landscape itself being in motion during the natural process. When the natural process is properly formulated, a mechanism, for example a catalyst, provides increased conductance in both directions and remains invariant during the course of a reaction.

According to the self-similar thermodynamic description, the conduction mechanism itself is a system that has emerged from an earlier evolutionary process. For example, an enzyme is a result of protein folding [68] just as a polypeptide is a result of chemical synthesis. During evolution, the mechanism does not necessarily remain intact, e.g. when a protein accumulates mutations, its function may change. A pioneering mechanism is superseded by more effective means of transformation characterized by a higher coefficient σ_{jk} . The flow of energy will naturally select [69] superior conduction mechanisms because then a faster decrease of free energy is facilitated [70,71]. For example, an electric discharge that spreads by ionizing a medium can be regarded as a superior conduction mechanism over miniscule currents that funnel through the medium. Likewise, a tornado can be regarded as a superior mechanism over a laminar flow to diminish atmospheric temperature differences. These examples reveal that for a highly effective mechanism to form and propagate, a high gradient in energy is required. Conversely, when the gradient has been exhausted, the highly effective species will go extinct.

When a new mechanism branches out from a linage of mechanisms, its ancestral mechanism is forced to evolve further apart from the course taken by the offspring. In a bifurcation process mutual interactions will directly or indirectly force both mechanisms to co-evolve so that they will soon draw from distinct sources to maximize the total consumption of free energy. The bifurcation process in ecosystems is referred to as speciation but similar processes are common in economies where they are known as product diversification or specialization in business, e.g. via outsourcing. The path to self-organized complexity follows the characteristic scale-invariance of a power law [72]. At the phase transition from a stationary state to another, the system evolves from one symmetry to another [63,73]. At a branching point the tangent, i.e. the derivative of the path is inexact which is in thermodynamics denoted as T dS = dO. This is a characteristic of path-dependent processes. The ingredients of a novel function that emerge in the transition are not only the prior systemic constituents but also include the influx of energy from surroundings that couples to the transformation. Conversely, when a system decays, its functions are lost along with efflux to the surroundings. For example, during starvation eukaryote cells lose functions by internalizing their molecular mechanisms [74] just as during a draught an ecosystem cannot support all but it will lose species. Since the energy content of an evolving system varies, there are no invariants of motion. Consequently the evolutionary equations of motion, e.g. the Navier-Stokes equation, cannot be solved to predict transition from laminar to turbulent flow [63]. Likewise, it is in principle impossible to predict precisely when a new species appears to an open ecosystem.

2.4. The steady-state system

An evolving system will ultimately attain the energy density of its surroundings through absorptive or emissive transformations. In the minimum state of free energy, entropy *S* is at its maximum. In the state of perfect balance (dS/dt = 0), net dissipation is zero. The stationary state is stable according to Lyapunov [40,55] since any perturbation δN_j away from the steady-state population N_j^{ss} will lead to decrease in $S(\delta N_j) < 0$ and increase in $dS(\delta N_j)/dt > 0$. When $N_j > N_j^{ss}$, the restoring force $A_{jk} > 0$ will develop and the flow $dN_j/dt < 0$ will further reduce N_j , and vice versa. When the influx is exactly balanced by the efflux, the steady-state partition of entities is given by Le Chatelier's

condition $A_{jk} = 0$ which yields from Eq. (2.4) [46]

$$\mu_j = \sum_k \mu_k + i \Delta Q_{jk} \quad \Leftrightarrow \quad N_j = \prod_k \left(N_k e^{-(\Delta G_{jk} - i \Delta Q_{jk})/k_B T} \right)^{g_{jk}}$$
(2.7)

where \prod_k is over all k-substrates in stoichiometric powers g_{jk} and k-coproducts with the opposite (-) sign. In ecology the μ_k and ΔQ_{jk} supplied by the surroundings are mostly referred to as food and light and in economics as raw materials and fuel. Likewise, the surrounding sinks, e.g. byproducts are referred to as excrement and waste. The population is steady (N_i^{ss}) when the influx matches the efflux exactly over the period of integration. The flux through the maximum-entropy system manifests itself as motion on closed, steady-state orbits [73]. In other words when energy of the system is conserved, the system obeys a conservation law and it is invariant under a group of symmetry operations. For example, a cell will display steady metabolic cycles when steadily provided with food. Likewise, a mature ecosystem will circulate nutrients. These motions on closed circular trajectories are invariant under a group of symmetry operations such as periodic sampling of the status. When the system is stationary, an eventual sporadic decline in the population will yield a surplus of food which subsequently serves to increase the population, and vice versa. A sporadic influx of energy to the system from its surroundings results in a step of evolution along an opening trajectory but the ensuing opposing force causes a subsequent efflux which returns the system along a reversed path to the original state. Thus incoherent or coherent exchange of energy, i.e. to-and-fro flows of energy between the system and its surroundings, cause fluctuations or periodic changes in population but the system remains in the thermodynamically stationary state over its characteristic period of motion. For example, biota can be regarded as stationary over a year although the system follows the annual, latitude-dependent variation in isolation. The same principle of free energy minimum has been suggested to underlie global homeostasis that has lasted over eons [75,76].

The product form in Eq. (2.7) shows that the population N_j as a class of *j*-entities is a result of *k*-multiplicative operations. The *j*-class differs from its neighboring classes j + n in a distribution of energy-densities by the number *n* of multiplicative operations where the *j*-products are assembled from the basic *k*-constituents. The multiplicative form is the characteristic of log-normal distribution and its cumulative curve follows a power law [9,77]. An evolving system, that is sufficiently statistical, does not depart at any moment much from the balance given by Eq. (2.7) because $A_{jk} \ll k_B T$. When a high-energy system evolves by emissions toward the balance in its low-energy surroundings, the skewed distribution will shift to lower classes. Conversely, when a low-energy system evolves by absorptions toward the balance in its high-energy surroundings, the distribution will shift to higher classes. This distribution's dependence on the average energy is most familiar from the temperature dependence of velocities in the Maxwell–Boltzmann distribution and from the black-body radiation spectrum [49] but it is also recognized in temporal changes during ecological succession [78,79], economic development [80,81] and cultural changes [82,83].

2.5. Continuous energy density in evolution

The above formulation of evolution as a series of step-by-step transformations toward a stationary state in respective surroundings applies for diverse natural processes. Nonetheless it is worth to rewrite the equations for a continuum form because many inanimate natural processes are described that way. In the convenient limit of potential differences as continuous gradients the equations are the familiar formulas of mechanics, but these equations can also be derived directly from Newton's second law of motion $\mathbf{F} = d\mathbf{p}/dt$ where momentum $\mathbf{p} = m\mathbf{v}$. The straight-forward differentiation in a Cartesian basis and multiplication by the components of velocity \mathbf{v} yields the equation for the flows of energy [38,84]

$$\sum_{j,k} v_j \frac{dp_{jk}}{dt} = \sum_{j,k} v_j m_{jk} a_k + \sum_{j,k} v_j \frac{\partial m_{jk}}{\partial t} v_k \quad \Leftrightarrow \quad \frac{d}{dt} 2K = -v\nabla U + i\frac{\partial Q}{\partial t}$$
(2.8)

where the acceleration is $a_k = dv_k/dt$ and the non-rotational part of the force is the scalar potential U gradient $m_{jk}a_k = -\partial U/\partial x_k$ whereas the divergence-free part is the vector potential Q gradient $(\partial m_{jk}/\partial t)v_k = \partial Q/\partial x_k$. The flow equation satisfies conservation of energy by stating that the change in the potential U concurrent with dissipation $\partial Q/\partial t = v^2 \partial m/\partial t$ is balanced by the change in kinetic energy $2K = mv^2$ as has been conjectured already a long time ago [85,86]. A comparison of Eqs. (2.4) and (2.8) associates T dS/dt with d2K/dt. Since 2K is the integrand of the principle of least action [33], indeed the stationary condition d2K/dt = 0 is equivalent to the maximum entropy production principle.



Fig. 3. Nature in evolution is pictured as an evolving free energy landscape that is leveling off in a series of transformation (from left to right) by transforming the scalar potential U to dissipation Q in order to match the energy density at its surroundings. The flow of energy directs (from top to bottom) along the geodesic where change in the kinetic energy 2K is maximal toward the free energy minimum. Due to the net dissipation to the surroundings, the process is irreversible. In other words, when the system dissipates, there is not enough free energy to reach back to the past points. In general the evolutionary process is intractable because the path-dependent process itself changes the surroundings that either accept or provided the dissipated quanta.

It is convenient to regard the flow equation (Eq. (2.8)) as a differentiable energy landscape spanned by the orthogonal directional spatial gradients $\mathbf{v} \cdot \nabla$ and vector gradients along time $\partial/\partial t$ that together add up to the change d/dt in the kinetic energy. The quest for the free energy minimum is understood as a process where the free energy landscape is leveling toward the flat stage d2K/dt = 0 where only stationary-state, conserved currents prevail [73] (Fig. 3). In general the landscape is curved and evolves to become even. The landscape notion is also used in biology to describe evolution [87]. Here the fundamental basis of this thinking is provided. When the landscape does not curve much, the 2K-resultant is, to a good approximation, the square root of its squared U- and Q-components. The Lorentzian relationship for the conservation of total energy and momentum is familiar from four-vectors in spacetime. Thus within this approximation the equation for can be solved. However, in general the non-Euclidean curvature signifies the presence of the rotational force component, i.e. electromagnetic radiation that results from dissipative transitions until the landscape evens out at a dynamic stationary state. The special point of balance is an isoenergic orbit. At the stationary state the net dissipation vanishes in accordance with viral theorem 2K + U = 0. The even and invariant landscape has the Euclidean norm and thus there is a unitary transformation to solve the characteristic equation for eigenvalues and motional modes.

When the system is at the stationary state, the condition of no net dissipation in Eq. (2.8) yields

$$2K = -U + iQ \tag{2.9}$$

where the energy in interactions Q carried by photons between bound forms of energy is explicitly denoted. For example, the steady-state condition 2K + U = 0 and $\partial Q/\partial t = 0$ yield $\mathbf{v} \cdot \nabla U = -U$ which is satisfied by a central 1/r potential. Then Eq. (2.9) yields the familiar expression due to Kepler $\tau^2 \propto r^3$ for the orbital period $\tau = \omega^{-1}$. Likewise, when light traverses a homogenous medium, it does not experience forces and propagates in a straight line. The conservation of energy requires that the directional spatial and temporal derivatives are equal in magnitude, i.e. $c\nabla \cdot = \partial/\partial t$, so that for light Eq. (2.8) reduces to $-\partial U/\partial t + c\nabla \cdot \mathbf{Q} = 0$. This form of symmetry, in turn, is recognized as the Lorenz gauge by the equivalent magnitudes $\phi = c |\mathbf{A}|$ of the scalar field $\phi = U/\rho$, i.e. the potential divided by charge density ρ , and the vector potential $\mathbf{A} = \mathbf{Q}/c\rho$ [88,47].

During evolution the energy density differences are diminishing in the least time so that the landscape is changing at the maximum rate. The condition as above (Eq. (2.6)) at a given spacetime point on the geodesic

$$\frac{d^2}{dt^2} 2K = 0 \quad \Leftrightarrow \quad v^2 \nabla^2 U = \frac{\partial^2 Q}{\partial t^2} \tag{2.10}$$

yields the well-known wave equation [48]. The motion plunges along the geodesic. However, Eq. (2.10) describes only a spacetime point, thus its formal integration to a closed form would not describe properly evolution along the open path that keeps redirecting itself. The field equation for light in the absence of charges is invariant under the spatial and temporal transformations. This is familiar from Maxwell's equations. The medium's energy density is characterized by the permittivity ε due to the electric and the permeability μ due to the magnetic components relative to the vacuum where $\varepsilon \mu = c^{-2}$. When a homogenous medium is dilutes, $\nabla^2 U$ decreases and $\partial^2 Q/\partial t^2$ increases but the ratio $(\varepsilon c)^{-1} = \sqrt{\mu/\varepsilon}$, known as the impedance of a diaelectric, remains a constant α , normalized by the quantum of action \hbar and proportional to the square of the elementary charge *e*. The above analysis reveals that the main characteristics of evolution are exposed also by continuum mechanics. This result emphasizes that there is no fundamental difference between animate and inanimate processes.

3. Patterns of energy dispersal

When the second law of thermodynamics in the form of the evolutionary equation as given above (Eqs. (2.4) and (2.8)) is analyzed, the universal spatial and temporal patterns of nature as well as natural standards can be understood as consequences of the maximal energy dispersal. Many familiar mathematical functions that are used to model natural processes and patterns are then recognized as approximate forms of the evolutionary equation. Moreover, the scale-invariant character of the universal patterns is found in the recursive, self-similar form of the probability (Eq. (2.2)) that describes nature as a nested hierarchy of systems within systems. The same scale-free form of spatial structures and temporal courses as well as the similarity between distributions in space and time follow from the conservation of energy. The dissipative flows of energy that level off the potential energy differences between distinct spatial loci form the arrow of time [47]. This correspondence between the directional spatial gradient and the time derivate, i.e. $\mathbf{v} \cdot \partial/\partial \mathbf{x} = \partial/\partial t$, is, of course, self-evident from its elementary integral form $\mathbf{x} = \mathbf{v}t$. The flows of energy plough least-time paths from diverse sources to sinks and yield tree-like structures and networks.

3.1. Power-law dependences

The origin of ubiquitous power laws can be identified to the maximal energy dispersal when the equation for the evolving probability dP/dt = LP (Eq. (2.4)) is analyzed. Its mathematical form shows that the initial rate of probability change dP/dt is increasing to a good approximation exponentially since at an early stage of the process the free energy A_{jk} , denoted in the process generator L, has hardly been consumed yet. Therefore, within this approximation, the variables P and t can be separated for integration that gives an exponential growth. Evolution punctuates off when a transformation mechanism appears in the system for the first time and taps into a nascent reservoir of free energy. For example, the initial growth of a colony of bacteria is exponential. Conversely, when the natural process is about to arrive at a stationary state, evolution is decreasing to a good approximation exponentially since evolution has by then nearly exhausted all free energy. Evolution settles toward a stasis when the transformation mechanism draws the remains from the free energy reservoir. For example, the colony of bacteria will gradually attain a maximum population density which depends on the amount of steadily available food.

In practice, it is not a particular probability P_j of the master equation (Eq. (2.4)) but the corresponding population N_j that is monitored. For the kinetic equation (Eq. (2.5)) to be consistent with the conservation of energy, the rate of population change dN_j/dt must be proportional to the free energy A_{jk} . The exponential rate approximation is valid when the nascent population N_j is still small in comparison with the mature population N_j^{ss} . When the system is sufficiently statistical, the change in the free energy $\sum_k \partial A_{jk}/\partial t = \sum_k \sigma_{jk}$ can be taken as constant, independent of the energy flow that is feeding the population growth by draining the source of energy. This deterministic, zero-order approximation

$$\sum_{k} \frac{\partial A_{jk}/k_B T}{\partial t} = \frac{dN_j}{dt} \sum_{k} \frac{\partial A_{jk}/k_B T}{\partial N_j} \approx \sum_{k} \sigma_{jk} \quad \Rightarrow \quad \frac{dN_j}{dt} = \sigma_j N_j, \quad \text{when } A_{jk}(t) \approx A_{jk}(0) \tag{3.1a}$$

yields, after separation of variables and integration from 0 to t, the exponentially increasing initial growth $N_j(t) = N_j(0) \exp(\sigma_j t)$. Conversely, the decreasing exponential approximation holds when energy in the maturing population $N_j(t)$ has almost attained $N_j^{ss}(\infty)$ at the stasis where $A_{jk}^{ss} = 0$ so that the change $\sum_k \partial A_{jk}/\partial t = -\sum_k \sigma_{jk}$ can be taken as a constant

$$\sum_{k} \frac{\partial A_{jk}/k_{B}T}{\partial t} = \frac{dN_{j}}{dt} \sum_{k} \frac{\partial A_{jk}/k_{B}T}{\partial N_{j}} \approx -\sum_{k} \sigma_{jk} \quad \Rightarrow \quad \frac{dN_{j}}{dt} = -\sigma_{j}N_{j},$$

when $A_{jk}(t) \approx A_{jk}^{ss} = 0.$ (3.1b)



Fig. 4. During a natural process a *j*-species populates along a sigmoid course (solid line). Initially, when consuming nascent resources of free energy A_j (dotted line), the specific species N_j will populate its surroundings nearly exponentially. Soon, when the source of free energy begins to narrow, the growth will turn to follow a power law (central section). Eventually when remains of the free energy are being extracted, the growth declines exponentially. The overall course follows closely a logistic curve. The rate of change dN_j/dt of the cumulative curve is approximately log-normal (dashed line).

When variables are separated and N_j is integrated from $N_j(0)$ to N_j^{ss} , the exponentially decreasing form $N_j(t) = N_j^{ss} - N_j(0) \exp(-\sigma_j t)$ of the late stage is obtained.

In the intermediate region between the initial increase and the final decrease the population N_j is given by Eq. (2.7). It is valid for a sufficient statistical system which means that any *j*-entity of the quasi-stationary system can be described in a recursive manner as being assembled by multiplicative operations from some basic constituents (e.g. atoms) in numbers N_1

$$N_{j} = \prod_{k} \left(N_{k} e^{-A_{jk}/k_{B}T} \right)^{g_{jk}} = N_{1}^{j} \prod_{1 \le m, n \le j} e^{-A_{mn}/k_{B}T} = \alpha_{j} N_{1}^{j}, \quad \text{when } A_{mn} \ll k_{B}T$$
(3.1c)

where $\alpha_j = \prod_{m,n} \exp(-A_{jk}/k_BT)$ is taken as a constant over available *m*, *n*-indexed transformation paths. The multiplicative form (3.1c) is recognized as a power law. The corresponding time course about a quasi-stationary point A_{jk}^{qs} is obtained, as before, using the approximation $\sum_k \partial A_{jk}/\partial t = \partial A_j/\partial t = -\sigma_j$

$$\frac{dN_j}{dt} = \frac{dN_j}{dN_1}\frac{dN_1}{dt} = \alpha_j j N_1^{j-1}\frac{dN_1}{dt} = \frac{jN_j}{N_1}\frac{dN_1}{dt} \quad \Rightarrow \quad \frac{dN_j}{N_j} = \frac{jdN_1}{N_1}, \quad \text{when } A_{mn} \approx A_{jk}^{qs}. \tag{3.1d}$$

When the variables are separated, the integration yields $\ln N_j = j \ln N_1 + a$ constant. On the log–log scale the curve follows a straight line which is the characteristic of scale invariance. The basic constituent's exponent is its stoichiometry. This functional form is familiar from the law of mass-action. However, here it is emphasized the transformation of energy is not driven by concentration differences of substances or population differences of animate species but by the free energy A_{jk}/k_BT . Consequently, when the law of mass-action is used for the kinetic equation, the forward and backward reaction coefficients are erroneously deemed as changing during the course of reaction whereas in reality it is the free energy that is decreasing and the conduction coefficient σ_{jk} in Eq. (2.5) is a constant. It is worth emphasizing that the evolutionary equation (Eq. (2.4)) is non-deterministic, unlike its deterministic mathematical models that can be integrated to closed forms. Often the overall sigmoid course is, to a good approximation, also given by the logistic equation (Fig. 4). The above analysis of the evolutionary equation (Eq. (2.4)) and the associated kinetic (Eq. (2.5)) and balance equations (Eq. (2.7)) for the initial, intermediate and final stages of growth (or decline), shows that the ubiquitous power laws are consequences of the natural principle of the least-time energy dispersal.

3.2. Bifurcations and chaos

Many living systems display not only a single sigmoid growth curve but a series of time-dependent processes. For example developmental processes [89] and ecological succession due to a series of immigrant species [1,79] as well as long-lasting economic growth due to a series of technological innovations [15,81] display a series of sigmoids, each punctuating when a new mechanism appears in the system. Remarkably also the overall course follows to a good approximation a power law which emphasis the scale-free character of natural processes. According to thermodynamics the advent of a new mechanistic species is motivated when it will yield a larger entropy increase

than could be obtained by increasing any of the existing population N_j of *j*-species (Eqs. (2.3) and (2.4)). The new species will either tap into a new supply of free energy or consume the existing supplies more rapidly than its ancestors, or both. It is worth emphasizing that the advent of a new species will change the living conditions of all other species in the system. After the critical event of bifurcation, the stem species in particular will face substantial evolutionary forces due to the offspring that is operating in the same environment and consuming largely the same resources but more effectively. Therefore, to escape extinction, the stem species are forced to specialize in energy transduction further apart from the offspring rivalry. For the same reason, when two species equipped with (largely) similar phenotypes appear on a common ground, one of them will gain the ground. In ecology this manifestation of the natural law is known as the competitive exclusion principle [1]. During the natural process it is these mutual interactions that cultivate distinct identities to maximize overall energy transduction. This will result in phylogenic trees branching to diversity.

The familiar mathematical models of speciation or bifurcation in general can be rationalized by the thermodynamic imperative when the entropy change dS/dt (Eq. (2.5)) is replaced with difference $S_{n+1} - S_n$ taken at consecutive time steps t_{n+1} and t_n of dissipative *jk*-transformations indexed by *n*. However, usually not entropy, but a change in population is monitored. To account for the interdependence among population change, i.e. flow and evolutionary force, free energy is modeled to the first-order by the approximation $\sum_k \partial A_{jk}/\partial t = \sigma_j - \beta_j N_j$ which delivers the recurrence relation

$$\frac{dN_j}{dt} \sum_k \frac{\partial A_{jk}/k_B T}{\partial N_j} = \frac{1}{N_j} \frac{dN_j}{dt} \approx \sigma_j - \beta_j N_j \quad \Rightarrow \quad N_j(n+1) = N_j(n) \big[\sigma_j - \beta_j N_j(n) \big],$$
when $A_{jk} \ll k_B T$
(3.2a)

for population change for the consequent time steps.

The mathematical model of Eq. (3.2a) is the familiar, quadratic recurrence relation that gives an iterative map [90]. When the parameters σ_i and β_i are assigned with values that satisfy the approximation of a sufficiently statistical system, evolution will converge to a stationary point where the j-entities have either survived and settled to N_i^{ss} or gone extinct $N_j = 0$. By contrast, the mathematical model will display peculiar phenomena when the tangent of the map exceeds unity, i.e. $\sigma_{ik}A_{ik}/k_BT > 1$. Thus the physical reason for the intriguing behavior is that the system is not sufficiently statistical. The changes in energy are comparable to energy that is bound in the population. The ensuing oscillatory or even chaotic motion can be understood from Eqs. (2.5) and (3.2a) so that the mechanism of energy transduction, i.e. the particular *j*-species is more effective in consuming the free energy than its vital k-reservoirs of energy are refilling up. In other words, the effects of inseparable flows and forces are pronounced when predators consume prey much faster than the prey reproduces. This is seen as recurrent passages about a point that is pictured as optimal by the mathematical model. The physical portrayal of motion is however somewhat different than that by a deterministic mathematical model. Namely, the energy landscape is not stationary but due to the effective consumption of free energy, the concave landscape deforms past the minimum, or equivalently the convex entropy surface morphs past the maximum. The ensuing oscillations exemplify that the driving forces and energy flows are inseparable (Fig. 5). The oscillations are rarely symmetric about the past and future [91] because the energy landscape of a complex system is seldom highly symmetrical. When there are three or more degrees of freedom, the path-dependent process is nondeterministic. For example, when a single prey succeeds to escape, the future of the predator population is affected. The failure to make a kill may cause pups to be lost and consequently the number of predators may fall even below that what is required for effective hunting. Thus even a small initial change may affect later trajectories substantially. This is a characteristic of chaos.

3.3. Skewed distributions

The skewed distributions are characteristic of numerous animate populations just as inanimate partitions [7–9]. The natural distribution can be found from the thermodynamic stationary-state condition $(d \ln P = 0)$ using Eq. (3.1c). When logarithm is taken, the distribution is found linear on a semi-log scale [9,77]

$$\ln N_{j} = \ln \prod_{k} (N_{k} e^{-(\Delta G_{jk} - i\Delta Q_{jk})/k_{B}T})^{g_{jk}} = j \ln N_{1} \sum_{1 \le m, n \le j} -A_{mn}/k_{B}T \propto j \ln N_{1},$$

when $A_{mn} \ll k_{B}T.$ (3.3a)



Fig. 5. When a highly-effective energy transduction mechanism, a species named j, survives only by consuming a high-energy gradient (A_j , dotted) representing a stock of supplies (N_k , dashed), the species may populate (N_j , solid), even due to sporadic fluctuations, over its resources. Then the *j*-species may lose its vital transduction mechanisms that draw from specialization and collaboration, and fails to reproduce itself in previous numbers. Thus the decline in the impoverished surroundings is inevitable until the surroundings have been replenished to allow for a new rise.

Each *j*-entity in the hierarchy (Fig. 1) is as a result of its developmental or other evolutionary processes ultimately composed of some basic constituents N_1 . It follows from this recursive form that the population N_j embodies an energy density

$$\phi_j = N_j e^{G_j/k_B T} = N_1^j e^{j(G_1 + i\Delta Q_1)/k_B T} = e^{j(\ln\phi_1 + i\Delta Q_1/k_B T)} \quad \Leftrightarrow \quad \ln\phi_j = j\ln\phi_1', \tag{3.3b}$$

where the number of quanta $j \Delta Q_1$ incorporated in the assembly of ϕ_j are conveniently included in the notation of ϕ'_1 . Likewise, the population of an adjacent (j + n)-class has the density

$$\phi_{j+n} = \exp\left[(j+n)\phi_1'\right] = \phi_j \exp\left(n\ln\phi_1'\right) \quad \Leftrightarrow \quad \ln\phi_{j+n} = (j+n)\ln\phi_1'. \tag{3.3c}$$

This form yields a distribution of energy densities $\phi_{j-n...j+n}$ over adjacent classes j - n ... j + n about ϕ_j according to

$$\ln \phi_{j-n...j+n} = \ln \phi_j + \sum_n n \ln \phi'_1.$$
(3.3d)

When $n \ll j$, the form of the function is normal according to the central limit theorem. The condition of small variation is effectively the criterion of classification that is used when the distribution is compiled. For example, a genus is a class where a relatively small variation in *n* during the assembly process yields related species. Conversely, when the number of multiplicative steps for any two species differs significantly, the two species will differentiate significantly from each other during the growth process and thus they will fall into two distinct distributions. Any given natural distribution deviates from the log-normality in the way it tails off both at low and high ends where the characteristic functional mechanism becomes increasingly ineffective as a means of energy transformation (Fig. 6). For this reason the sigmoid cumulative curve deviates from the power law at both the low and high ends as explained in Section 3.1. For example, the species–area relationship [92–95] is a cumulative curve that totals from distributions of species in a genus that populates increasing larger areas [96]. The relationship follows mostly a power law but toward the low end the resources on a small area are marginal to support any species in the particular genus, as well as toward the high end the resources are large but scattered on a large area that no species of that genus is equipped with effective enough mechanisms to harvest them (Fig. 6) [97–103].

Since a sufficiently statistical system evolves gradually, i.e. $A_{jk} \ll k_B T$, the stationary-state condition holds to a good approximation also during evolution and the natural distribution at a quasi-stationary state retains its characteristic, nearly log-normal form. When the system evolves by absorbing energy from its surroundings, the skewed distribution will shift gradually to peak at higher classes. Conversely when the system degrades by dissipation, its distribution will shift to peak at lower classes. This dependence on average energy $k_B T$ is most familiar from Maxwell–Boltzmann as well as from Planck's distribution but accounts also for distributions compiled from data collected from ecosystems and economic systems.

Natural distributions have been modeled by many mathematical functions. For example, the beta-function, which follows a power law for large values of either of its gamma-function arguments [104], mimics the recursive form of the cumulative probability distribution (Eq. (2.2)). Moreover, when the scale-free cumulative distribution $\sum k^{-\alpha}$ is stationary, it is proportional to the Riemann zeta function $\zeta(\alpha)$ [5] which, in turn, has been associated to the stationary states by the thermodynamic principle [63]. However, these and other mathematical models [105] rarely account for



Fig. 6. A natural probability distribution tails off at the low (red) end beyond which no one entity is capable of contributing to the energy transduction. Conversely the distribution tails off at the high (blue) end above which no one mechanism is able to access the free energy from the other entities in the partition and from the surroundings to support its existence. The cumulative curve $\sum P_j$ (dashed) follows mostly a power law on a log–log plot. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

the entire span of a natural distribution that tails due to the mechanistic limits of energy transduction. For example, the Gutenberg–Richter law as a cumulative power-law distribution for the distribution of earthquake magnitudes does not scale to infinity because a finite amount of energy in the Earth's crust limits the maximum size of an earthquake [106]. The low end cut-off is usually referred to as the finite-size effect [107]. When no mechanistic classification criterion for the energy transduction is imposed, the cumulative distribution, such as 1/f noise, extends over many orders of magnitude, ultimately being limited by the finite Universe and the finite constant of action \hbar .

3.4. Tree-like structures

Many tree-like structures and networks are scale-free [108]. These natural patterns can also be understood by the imperative to consume free energy in the least time. Evolution as the path-dependent energy dispersal process directs from heights to lows along the paths of least action. The natural process for the maximal energy dispersal results in a non-deterministic tree-like structure, when the total flow from a source is distributed on multiple paths toward multiple sinks. Conversely, the tree-like structure also emerges when multiple flows from several sources drain to a common sink. In turn, a network forms when nodes as complex entities are both sources for some flows and sinks for other. In general, when there are degrees of freedom, the natural process of energy dispersal is non-deterministic. Only when there is a single path from a source to a sink, the process is deterministic. Consistent with thermodynamic reasoning about intractability, it is known that the fractal scaling requires the number of edges connected to a given vertex to be at least three, i.e. the degree $k \ge 3$ [109]. While for a given *j*-source and a set of k-sinks (or vice versa) the overall tree-like structure can be anticipated, the details, e.g. specific branching points cannot be predicted. The treelike and network structures can be regarded as an evolving energy landscape. Evolution is not predetermined but the functional structure will morph by whatever means and mechanisms there are to level off energy density differences in the least time. For example the food web of an ecosystem is an energy transduction network that will adapt to changes in surrounding conditions, e.g. to a climate change. Likewise we witness rapid changes in communication networks when wireless connections are replacing wired structures. Low-cost connections enable more intense and more frequent interactions.

The self-similarity in the flow of energy through the tree-like structures follows from the conservation of energy, i.e. a mainstream must supply all estuaries. At any given radius of curvature away from the source toward the sinks, the free energy consumption distributes on the energy landscape along paths that maximize dS/dt (Eq. (2.4)). For example, when the curvature is large, the mainstream will flow with velocity v_j along its steepest spatial gradient $\partial/\partial x_j$. Conversely when the landscape is almost flat, the main flow will branch out repeatedly to finer and finer estuaries which will together channel the total $\sum v_k \partial/\partial x_k$ along their spatial gradients $\partial/\partial x_k$. Likewise, numerous trickles at the upriver, each following the steepest available directional spatial gradient $v_k \partial/\partial x_k$, combine to form larger and larger flows downstream. The total transmission takes least time when each class (bin) in the natural distribution of transduction mechanism channels as much as any other (Eqs. (2.7) and (3.3)). The nearly log-normal distribution of conduction mechanisms implies that the natural tree-like patterns branch out in a self-similar manner



Fig. 7. Flows of energy branch from a source (top) to multiple sinks (bottom). The resulting tree-like geodesic structure levels off the free energy landscape in the least time. The natural distribution P of diverse paths, each associated with energy G_j , is limited at the high end (blue) by the single stem capacity whereas the flow is limited at low end (red) by the finest twigs that barely serve as conductors. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

(Fig. 7). The distribution tails off at the low end since the very fine twigs are not functional enough to disperse energy further. Conversely, the distribution tails off at the high end since the total flow at the stem cannot exceed the flow at the branches. This natural tree-like structure also characterizes a food chain where the population at a particular level is smaller than the one at the level below it. The pyramid structure is a mere consequence of conservation of energy.

Networks such as cellular metabolism, food webs or telecommunication networks organize to maximize energy dispersal from diverse sources to various sinks in the least time by adapting the degree of nodes, i.e. the number of connections from a node to other nodes and their conduction capacity. Indeed, many real networks display degree distributions that follow a power law [110]. The natural selection for the maximal conduction that accounts for the scale-free characteristics is often referred to as the mechanism of preferential attachment. For example, stationary-state currents of an electric circuit can be obtained from the condition dS/dt which is equivalent to the Kirchhoff's law [111]. Likewise, a through-flow system of a mature cell is at a stationary metabolic state just as a mature ecosystem displays steady circulations of nutrients.

Fractals, as mathematical constructs, mimic the scale-invariance of the natural tree-like patterns. These continuous but non-differential curves account both for the continuity and emergent phenomena of natural processes. The physical portrayal of natural processes makes it apparent that the continuity means conservation of energy and that the inexact derivatives associate with the branching points. Moreover, it is of interest to note that the fractals, such as Césaro and Koch–Peano curves as space-filling curves, are generated by affine transformations defined by a complex number [112]. This notation combines the two orthogonal components just like the natural processes are described by mutually orthogonal scalar and vector potential differences that are combined to the complex free energy. Also selfsimilar graphs model the scale-invariant trees and networks, but it is worth emphasizing that energy transduction is functionally, not structurally self-similar. The specific structures at adjacent levels of hierarchy are not scaleindependent copies of each other vet all structures function to maximize energy dispersal. The three-like pattern, when referred to as a directed acyclic graph, emphasizes the flow-through nature of the system. Its topological ordering relates to the principle of least action so that the geodesic distances are the optimal paths from a source to sinks. Also a Bayesian network [113] contains the essential idea of a natural process with extensive degrees of freedom. The Bayesian formalism regards nodes of a path-dependent process as probabilistic events. However, the probabilities are usually regarded merely as odds in choosing one or the other among alternatives but the decision making could also be regarded as a physical process and formulated accordingly in energetic terms.

Despite the established mathematical correspondence between the characteristic outcomes of natural processes, it may still appear perplexing that an energy transduction system would develop an approximately power-law branching pattern when placed on an arbitrary terrain. In fact it would not but the quest for free energy minimum will result in the power-law characteristics. Initially flows will adapt to the particular terrain but they will also begin to shape the terrain via dissipative transformations, e.g. by wearing the supporting ground. Therefore the natural terrains themselves



Fig. 8. The spiral distribution of densities-in-energy (color coded) embodies the least-time trajectory of an evolving system. The spiral form of energy dispersal relates to a skewed distribution (left) by the phase angle φ so that the spiral opens out up to the maximal radius ρ corresponding to the low (red) energy density end beyond which there is no density to be dissipated or no mechanism to dissipate it. Conversely, the spiral closes in at the maximal path length λ corresponding to the high (blue) end beyond which no dissipative mechanism is able to form that would be able to access even more free energy, e.g. by transforming the other entities in the distribution. The cumulative curve (dashed) of the logarithmic spiral's energy density follows a power law on a log–log plot. Steady-state systems (depicted as circles) move on closed orbits. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

are rarely arbitrary because they result from natural processes. For example, rainfall and other erosive processes carve landscapes just like a species and other dissipative mechanisms shape their respective environments by free energy consumption. The natural processes will balance the energy differences and result in natural terrains whose characteristics largely comply with power laws. For example, when an ecosystem or an economic system is struck by a natural disaster, it does not display a maximum entropy partition but it will begin a recovery toward the natural distribution [71].

3.5. Spirals and circles

A scale-invariant spiral pattern can be understood as a quasi-stationary distribution of energy just like the skewed distribution was understood above as a maximum entropy partition. The spiral form of the distribution is obtained when the approximate equiv-partition (Eq. (2.7)) of energy densities according to Eq. (3.3b) is rewritten in polar coordinates

$$\phi_j = N_j e^{G_j/k_B T} = \phi_1^j e^{ij\Delta Q_1/k_B T} = e^{j\ln\phi_1'} \quad \Rightarrow \quad \rho_j = \alpha_j e^{i\beta_j\varphi_j} = \alpha_1^j e^{ij\beta_1\varphi_1}, \tag{3.4}$$

where ϕ_j accumulates from an increasing number of basic constituents N_1 associated with the density ϕ_1 indexed with increasing *j*. The parametric form $\alpha_j \exp(i\beta_j\varphi_j) = \alpha_j[\cos(\beta_j\varphi_j) + i\sin(\beta_j\varphi_j)]$ shows that the density ϕ_j at a radius ρ_j is a spiral function of the phase $\varphi_j = j\varphi_1$ whose evolution results from the accumulating energy flux $\Delta Q_{jk} = j\Delta Q_j$. The spiral winds out when the system's scalar potential is decreasing from μ_j to $\sum \mu_k$ due to the efflux to the energy-sparse surroundings (Fig. 8). Conversely, the spiral winds in, when the scalar potential is increasing due to the influx from the energy-dense surroundings. High and low pressure weather patterns are familiar examples of point-like sources and sinks. Thus the spiral pattern is recognized, like the other natural patterns, as transduction machinery that conducts energy from one density to another. In other words, the spirals live in a force field, also referred to as a curvature. For example, high and low pressure weather patterns and tornados whirl by consuming atmospheric temperature gradients [114], and galaxies rotate by transforming matter to radiation to attain balance in the respective surroundings [63].

A spiral shape, like other natural distributions, limits itself at the low end where its characteristic mechanisms fail to consume free energy, and at the high end where its most superior mechanism fails to acquire and disperse even more. For example when the atmospheric pressure difference becomes small, turbulence will settle to laminar flow. When net dissipation vanishes, the open curve limits to a closed orbit which is the characteristic of the steady-state balance of the free energy minimum (Fig. 8).

Consistently with scale-free properties of natural patterns, the self-similar logarithmic spirals are self-congruent under all similarity transformations. Spira mirabilis in Eq. (3.4) has the form of Euler spiral, known also as Cornu spiral, whose curvature $1/\rho = d\varphi/d\lambda \propto \lambda$ decreases linearly with its length λ . This identity is recognized by taking inverse of the differential $d\rho/d\varphi \propto \rho$ of Eq. (3.4) since $d\rho \propto d\lambda$. Moreover, partial sums of the Riemann zeta function that have been computed along the critical line have been recognized to form a swirling array of connected Cornu spirals [115]. The overall array of increasingly larger partial sums describes the track transition curve as a sequence of states from a potential to another. Each symmetry relates to a free-energy minimum state where the energy landscape is flat with Euclidean norm so that a stationary solution 2K + U = 0 can be found [73]. Thus the mathematical spiral functions with a series of zeros can be understood as models of evolutionary processes that proceed in steps from one state to another rather than being continuous transformations.

3.6. Standards

Although life on Earth is amazingly diverse, it is perhaps perplexing why it is not even more diverse. For example, biota employs only a minute fraction of all conceivable organic compounds. The standard set of metabolites appears meaningful though, e.g. ATP as the common currency seems a 'sensible' way to supply energy to any of a cell's activities without further conversions. Likewise, natural amino acids are a very limited set of all conceivable polypeptide building blocks. Yet the standard set of basic building blocks, thanks to their distinct physio-chemical properties, allows assembly of proteins for diverse functions. Also the common genetic code appears as a highly effective standard for information exchange within the entire biosphere.

It has been suggested that some of these natural standards, in particular the ubiquitous chirality consensus of natural amino acids and the specific handedness of ribose-units in nucleic acids, have been adopted, perhaps by chance, at the emergence of life and stayed ever since. However, the physical portrayal of natural processes provides another view [116,117]. Primordial standards, just like present-day standards, can be understood to follow from the second law of thermodynamics. When using standardized components and procedures, the molecular assembly is highly effective in outputing a diversity of proteins with distinct properties just like industrial processes will rapidly produce a family of products with discernable features from a standardized set of semi-finished products. The standardized production requires fewer steps of assembly than a customized handicraft. Likewise when the assembly is standardized, there is fewer steps to be improved to speed up the overall throughput. Moreover, the gain in the rate of entropy production due to standardization is larger in larger systems. Therefore, the high degree of standardization at the molecular level reflects not merely a common origin of life [70] but that the biosphere is a large, highly integrated system. Likewise, a fragmented economic system has fewer standards than an integrated system [71]. The on-going globalization in entropy production enforces world-wide standards to facilitate spread of goods, i.e. to disperse energy.

In the case of mirror-image standards it is not apparent which one of the two options would bring in larger gains in reduction of free energy, at least when the environment is achiral. However, the natural process will inevitably exclude one or the other symmetry alternatives. According to the Lyapunov criterion, a growing system that employs both mirror-image standards is labile [55]. When any one of the two standardized assembly lines happens to become ahead, it may yield even a faster autocatalytic mechanism and in this way it will get even further ahead in drawing from the common pool of basic constituents. Thus the evolutionary sequence that converges to a single pure-hand standard follows from the imperative to consume free energy in the least time. In ecology the convergent thermodynamic scenario is known as the competitive exclusion principle [1]. One of the two similar species will inevitably exclude the other when they compete for common resources. The very same motivation of fastest energy dispersal drives fusions of companies and rationalization of economic activities.

Moreover, the common genetic code can be understood by the same argument as a means to facilitate energy dispersal. Genetic information is coded in three-letter words using a four-base alphabet. It translates redundantly its 64 triplet-codons to twenty natural amino acids. Since most of the redundancy is at the third position, also referred to as the wobbling base, it has been suggested that a primordial code would have been limited to only 16 non-redundant doublet-codons for 16 amino acids. However, the physical portrayal of information processing and communication as natural processes provides another view [118–120]. The unambiguous genetic code, like other natural languages, is redundant to ensure effective communication in the presence of noise, i.e. fluctuations in surrounding energy densities. The most frequently used residues are the most copiously coded. The degenerate code is particularly robust for transition mutations (purine to purine or pyrimidine to pyrimidine). Also many amino acid point mutations retain the basic physio-chemical properties – most notably hydrophilicity or hydrophobicity is preserved. Likewise, a change of a vowel to another or a change of a consonant to another does not often obscure the meaning of a message altogether. Intriguingly, small variants of the standard genetic code, i.e. distinct dialects, are found in mitochondria as well as in Mycoplasma and Candida species which are all symbiotic or parasitic organisms [121]. A specific way of communicating is an effective way of distinguishing oneself from others in the surroundings. To cultivate an identity is important to gain access to specific resources rather that to continue in competing for common resources with others that are alike.

4. Discussion

Diversity does not spread out randomly and complexity does not develop arbitrarily but order and regularity in space and time are reflected in ubiquitous self-similar and scale-free patterns. This implies that there is an underlying universal law. Indeed the second law of thermodynamics has been held responsible for the natural patterns for a long time but only recently, when the law was formulated as an evolutionary equation of motion, the association became unambiguous. The equation of evolution, when derived from statistical physics of open systems, proves that the principle of increasing entropy is equivalent to the principle of least action [38,84]. The quest to consume free energy in the least time is also emphasized by the maximum entropy production principle. The profound principle, either in its differential or integral form, simply states that differences in energy will diminish in least time. According to this imperative the flows of energy will search and naturally select and shape the steepest directional descents. The natural patterns are manifestations of these geodesics. This conclusion, however, is neither new nor unexpected but this study serves to show that many mathematical formula that are used to model natural processes and patterns are well-motivated approximations of the evolutionary equation. More importantly, the analysis of evolving systems reconciles thoughts that the natural processes, despite generating order and regularity, are inherently intractable. Thus it is easy to understand that natural patterns are rarely perfected according to some exact formula. This non-deterministic character, while vital for the energy dispersal in the least time, may for some seem a serious setback, perhaps even disqualifying the natural law as an explanation for natural patterns. Indeed, it is very natural for man to aim at predicting precisely and controlling correctly because such a rationale contributes to his survival. The natural law does not satisfy this desire. Instead its mathematical analysis reveals the basic reasons why the strive for determinism and reduction is hopeless. The obstacle is not the complexity of the system as such rather it is the non-conserved nature of an evolving non-Hamiltonian system that makes it impossible to predict future courses of dissipative processes when there are two or alternatives paths to consume free energy. Since evolution itself changes the circumstances where it progresses, the path-dependent course is intractable.

Since natural patterns are ubiquitous, it is relevant to ask, does the natural law of maximal energy dispersal account for all processes? Specifically, do microscopic systems also follow the universal law? In other words, is the indeterminism found in quantum systems similar or dissimilar to the non-determinism described by the evolutionary equation? It is important to realize that quantum mechanics in its basic form is limited to stationary systems, i.e. dP/dt = 0 [58]. However, a measurement is an energy transduction process that forces upon a microscopic just as a macroscopic system in evolution, i.e. dP/dt > 0. It is precisely due to the non-conserved nature of evolution why quantum mechanics as a theory for closed systems fails to describe measurement properly. When the relative phase between the system and its observer is arbitrary, measurement is not predetermined to attain any one of the available states. The indeterminism due to phase dispersal yields a symmetric distribution of observables, whereas non-determinism due to energy dispersal yields a skewed distribution of observables. The evolutionary equation (Eq. (2.4)) employed here is designated for incoherent statistical systems, however, it has also been derived for coherent systems. It then includes the phase-dependence of energy transduction between the system and its surroundings [47]. Likewise, when a macroscopic system such as an ecosystem is sampled it will inevitably be perturbed. Moreover the phase of sampling, for example a day or night time, will influence the outcome.

Considering the central role that has been attributed to information in guiding biological processes as well as economic activities, it may at first sight seem strange why information in our account does not reveal itself as a cause of natural patterns. In fact it does, but since information itself is physical [122] due to its representations, information processing is also a natural process [123] that leads to the natural distributions [124,125]. In the thermodynamic sense information has no special status but it is defined via free energy [126]. Free energy powers an instructed execution

just as it drives any other natural process. According to the holistic thermodynamic tenet, the receiver system values the meaning of a message by the entropy increase produced by the informed free energy consumption [118].

The proposition that the natural patterns in space and time reflect energy dispersal in the least time is conceivable. After all, the principle maximum entropy production and the principle of least action are recognized as the same fundamental law of nature. It is perhaps not so obvious why the underlying principle is simple since many natural processes are mechanistically complicated. The form of evolutionary equation appears very simple in relation to many mathematical models of natural processes. However the simplicity is superficial. The evolutionary equation, when expanded to numerous constituents, is an extremely detailed description of nature but in many cases it would be an impractical model. Thus the thermodynamic description does not in any way undermine the value of many established mathematical models. The formalism for open systems is not a refined model, but it aims at being an accurate description of nature. The description of evolution distinguishes from the traditional focus of physics on Hamiltonian systems that are limited to stationary systems. Despite this insight to the natural processes the intractable evolutionary equation of motion may appear to some unattractive because it does not provide precise predictions. However, nature is recognized to process without prior plans or detailed control yet all trajectories are attracted spontaneously [28] toward free energy minima. Although these least action paths of evolving energy landscape are intricate and intractably open and thus defy deterministic calculations, the thermodynamic thinking is motivated by the observation that the stationary-state trajectories, while comfortably computable, do not account for nature in evolution.

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References

- [1] Rosenzweig ML. Species diversity in space and time. Cambridge: Cambridge University Press; 1995.
- [2] Kleiber M. Body size and metabolism. Hilgardia 1932;6:315-51.
- [3] Zipf GK. Human behaviour and the principle of least effort. Reading, MA: Addison-Wesley; 1949.
- [4] Pareto V. Manuale di economia politica (Manual of political economy). Milano: Società Editrice Libraria; 1906 [1971, translation by Page AN, Kelley AM].
- [5] Newman MEJ. Power laws, Pareto distributions and Zipf's law. Contemp Phys 2005;46:323-51.
- [6] Hutchinson GE, MacArthur RH. A theoretical ecological model of size distributions among species of animals. Am Naturalist 1959;93:117– 25.
- [7] Kapteyn JC. Skew frequency curves in biology and statistics. Groningen: Astronomical Laboratory, Noordhoff; 1903.
- [8] Gaddum JH. Lognormal distributions. Nature 1945;156:463-6.
- [9] Limpert E, Stahel WA, Abbt M. Log-normal distributions across the sciences: keys and clues. Bioscience 2001;51:341-52.
- [10] Bejan A, Marden JH. The constructal unification of biological and geophysical design. Phys Life Rev 2009;6:85–102.
- [11] Turcotte DL, Pelletier JD, Newman WI. Networkswith side branching in biology. J Theoret Biol 1998;193:577–92.
- [12] Cook TA. The curves of life, being an account of spiral formations and their application to growth in nature, to science and to art. New York: Dover; 1979.
- [13] Gielis J. A generic geometric transformation that unifies a wide range of natural and abstract shapes. Am J Bot 2003;90:333-8.
- [14] Eldredge N, Gould SJ. In: Schopf TJM, editor. Models in paleobiology. San Francisco: Freeman, Cooper; 1972. p. 82–115.
- [15] Utterback J. Mastering the dynamics of innovation. Boston, MA: Harvard Business Press; 1996.
- [16] Volterra V. Variations and fluctuations of the number of individuals in animal species living together. Animal ecology. McGraw-Hill; 1931 [Translated from 1928 edition by Chapman RN].
- [17] Belousov BP. A periodic reaction and its mechanism. Sbornik Referatov po Radiatsionni Meditsine. Moscow: Medgiz; 1958. p. 145 [Translated in Field and Burger, op. cit.].
- [18] Briggs TS, Rauscher WC. An oscillating iodine clock. J Chem Educ 1973;50:496.
- [19] Junji Ohtsubo. Semiconductor lasers: stability, instability and chaos. Springer series in optical sciences, vol. 111. Berlin: Springer-Verlag; 2008.
- [20] Snell O. Die Abhängigkeit des Hirngewichts von dem Körpergewicht und den geistigen Fähigkeiten. Arch Psychiatr 1892;23:436-46.
- [21] West GB, Brown JH, Enquist BJ. A general model for the origin of allometric scaling laws in biology. Science 1997;276:122–6.
- [22] Paltridge GW. Global dynamics and climate a system of minimum entropy exchange. Q J R Meteorol Soc 1975;101:475-84.
- [23] Schneider ED, Kay JJ. Life as a manifestation of the second law of thermodynamics. Math Comput Model 1994;19:25–48.
- [24] Dewar R. Information theory explanation of the fluctuation theorem, maximum entropy production and self-organized criticality in nonequilibrium stationary state. J Phys A Math Gen 2003;36:631–41.
- [25] Kleidon A, Lorenz R, editors. Non-equilibrium thermodynamics and the production of entropy in life, Earth, and beyond. Heidelberg, Germany: Springer; 2004.

- [26] Whitfield J. Order out of chaos. Nature 2005;436:905-7.
- [27] Martyushev LM. The maximum entropy production principle: two basic questions. Philos Trans Roy Soc London Ser B 2010;365:1333-4.
- [28] Jaynes ET. Probability theory. The logic of science. Cambridge: Cambridge University Press; 2003.
- [29] Bak P. How nature works: the science of self-organized criticality. New York: Copernicus; 1996.
- [30] Atkins PW. The 2nd law: energy, chaos, and form. New York: WH Freeman; 1994.
- [31] Bejan A. Shape and structure, from engineering to nature. Cambridge, UK: Cambridge University Press; 2000.
- [32] Lineweaver CH, Egan CA. Life, gravity and the second law of thermodynamics. Phys Life Rev 2008;5:225-42.
- [33] De Maupertuis PLM. Les loix du mouvement et du repos déduites d'un principe metaphysique. Hist Acad Roy Sci Belleslett 1746:267-94.
- [34] Georgiev G, Georgiev I. The least action and the metric of an organized system. Open Syst Inf Dyn 2002;9:371-80.
- [35] Hamilton WR. On a general method in dynamics, by which the study of the motions of all free systems of attracting or repelling points is reduced to the search and differentiation of one central relation or characteristic function. Philos Trans Roy Soc (Part II) 1834:247–308; Second essay on a general method in dynamics. Philos Trans Roy Soc (Part I) 1835:95–144.
- [36] Boltzmann L. Populäre Schriften. Leipzig: Barth; 1905; partially translated in: In: McGuinness B, editor. Theoretical physics and philosophical problems. Dordrecht: Reidel; 1974.
- [37] Stöltzner M. The principle of least action as the logical empiricist's Shibboleth. Stud. Hist. Philos. Mod. Phys. 2003;34:285-318.
- [38] Kaila VRI, Annila A. Natural selection for least action. Proc Roy Soc Ser A 2008;464:3055–70.
- [39] Schroeder M. Fractals, chaos, power laws. New York: Freeman; 1991.
- [40] Strogatz SH. Nonlinear dynamics and chaos with applications to physics, biology, chemistry and engineering. Cambridge, MA: Westview; 2000.
- [41] Badii R, Politi A. Complexity: hierarchical structures and scaling physics. Cambridge University Press; 1997.
- [42] Eddington AS. The nature of physical world. New York, NY: Macmillan; 1928.
- [43] Carnot S. Reflexions sur la puissance motrice du feu et sur les machines propres a developper cette puissance. Paris, France: Bachelier; 1824.
- [44] Gibbs JW. The scientific papers of J Willard Gibbs. Connecticut: Ox Bow Press; 1993–1994.
- [45] Annila A, Kuismanen E. Natural hierarchy emerges from energy dispersal. BioSystems 2008;95:227-33.
- [46] Sharma V, Annila A. Natural process natural selection. Biophys Chem 2007;127:123-8.
- [47] Tuisku P, Pernu TK, Annila A. In the light of time. Proc Roy Soc Ser A 2009;465:1173–98.
- [48] Atkins PW, de Paula J. Physical chemistry. New York: Oxford University Press; 2006.
- [49] Alonso M, Finn EJ. Fundamental university physics. Quantum and statistical physics, vol. 3. London: Addison-Wesley; 1983.
- [50] Prigogine I. Laws of nature, probability and time symmetry breaking. Physica A 1999;263:528–39.
- [51] Salthe SN. Evolving hierarchical systems: their structure and representation. New York: Columbia University Press; 1985.
- [52] Gouy LG. Sur l'energie utilizable. J Physique 1889;8:501-18.
- [53] Stodola A. Steam and gas turbines. New York, NY: McGraw-Hill; 1910.
- [54] Kullback S. Information theory and statistics. New York, NY: Wiley; 1959.
- [55] Kondepudi D, Prigogine I. Modern thermodynamics. New York, NY: Wiley; 1998.
- [56] Schrödinger E. What is life? Mind and matter. Cambridge, UK: Cambridge University Press; 1944.
- [57] Garcia-Ojalvo J, Elowitz M, Strogatz S. Modeling a synthetic multicellular clock: Repressilators coupled by quorum sensing. PNAS 2004;101:10955–60.
- [58] Griffiths D. Introduction to quantum mechanics. Upper Saddle River, NJ: Prentice-Hall; 1995.
- [59] Bayes T. A letter to John Canton. Philos Trans Roy Soc 1763;53:269-71.
- [60] Poincaré JH. Sur le problème des trois corps et les équations de la dynamique. Divergence des séries de M. Lindstedt. Acta Math 1890;13:1– 270.
- [61] Sipser M. Introduction to the theory of computation. New York, NY: PWS Publishing; 2001.
- [62] Fraenkel AS. Complexity of protein folding. Bull Math Biol 1993;55:1199–210.
- [63] Annila A. Space, time and machines. arXiv:0910.2629, 2009.
- [64] Bak P, Sneppen K. Punctuated equilibrium and criticality in a simple model of evolution. Phys Rev Lett 1993;71:4083-6.
- [65] Verhulst PF. Recherches mathématiques sur la loi d'accroissement de la population. Nouv Mém Acad Roy Sci Belleslett Bruxelles 1845;18:1–38.
- [66] Kellert SH. In the wake of chaos: unpredictable order in dynamical systems. Chicago, IL: University of Chicago Press; 1993.
- [67] Waage P, Guldberg CM. Studies concerning affinity. Forhandlinger, vol. 35. Videnskabs-Selskabet i Christiana; 1864.
- [68] Sharma V, Kaila VRI, Annila A. Protein folding as an evolutionary process. Physica A 2009;388:851-62.
- [69] Darwin C. On the origin of species. London: John Murray; 1859.
- [70] Annila A, Annila E. Why did life emerge?, Int J Astrobiol 2008;7:293-300.
- [71] Annila A, Salthe S. Physical foundations of evolutionary theory. J Non-Equil Thermodyn 2010;35.
- [72] Bak P, Tang C, Wiesenfeld K. Self-organized criticality: an explanation of 1/f noise. Phys Rev Lett 1987;59:381-4.
- [73] Noether E. Invariante variationprobleme. Nach vd Ges d Wiss zu Goettingen, Mathphys Klasse 1918:235–57; English translation: Tavel MA. Invariant variation problem. Transport Theory Statist Phys 1971;1:183–207.
- [74] Mizushima N. Autophagy: process and function. Genes Dev 2007;21:2861–73.
- [75] Lovelock JE. Gaia as seen through the atmosphere. Atmos Environ 1972;6:579–80.
- [76] Karnani M, Annila A. Gaia again. BioSystems 2009;95:82-7.
- [77] Grönholm T, Annila A. Natural distribution. Math Biosci 2007;210:659-67.
- [78] Knight CB. Basic concepts of ecology. New York, NY: Macmillan; 1965.
- [79] Würtz P, Annila A. Ecological succession as an energy dispersal process. BioSystems 2010;100:70-8.

- [80] Sundrum RM. Income distribution in less developed countries. London, UK: Routledge; 1992.
- [81] Annila A, Salthe S. Economies evolve by energy dispersal. Entropy 2009;11:606-33.
- [82] Harris M. Cultural materialism the struggle for a science of culture. New York, NY: Random House; 1979.
- [83] Annila A, Salthe S. Cultural naturalism. Entropy 2010;12:1325-43.
- [84] Annila A. The 2nd law delineates dispersal of energy. Int Rev Phys 2010;4:29-34.
- [85] Du Châtelet E. Institutions de physique. Paris: Prault; 1740. Facsimile of 1759 edition: Principies mathématiques de la philosophie naturelle I–II. Paris, France: Éditions Jacques Gabay; 1759.
- [86] Gravesande W. Physices elementa mathematica, experimentis confirmata, sive introductio ad philosophiam Newtonianam. Leiden, The Netherlands, 1720.
- [87] Waddington CH. The epigenetics of birds. Cambridge, MA: Cambridge University Press; 1953.
- [88] Griffiths D. Introduction to electrodynamics. Englewood Cliffs, NJ: Prentice-Hall; 1999.
- [89] McCray FA. Embryo development in Nicotiana species hybrids. Genetics 1933;13:95-110.
- [90] May RM. Simple mathematical models with very complicated dynamics. Nature 1976;261:459-67.
- [91] Ulanowicz RE. The dual nature of ecosystem dynamics. Ecol Model 2009;220:1886-92.
- [92] Knight CB. Basic concepts of ecology. New York, NY: Macmillan; 1965.
- [93] MacArthur RH, Wilson EO. The theory of islands biogeography. Princeton, NJ: Princeton University Press; 1967.
- [94] Arrhenius O. Species and area. J Ecol 1921;9:95-9.
- [95] Preston FW. Time and space and the variation of species. Ecology 1960;41:785-90.
- [96] Würtz P, Annila A. Roots of diversity relations. J Biophys 2008;doi:10.1155/2008/654672; arXiv:0906.0251. http://www.hindawi.com/ journals/jbp/2008/654672.html.
- [97] Preston FW. The canonical distribution of commonness and rarity: Part I. Ecology 1962;43:185-215.
- [98] Kilburn PD. Exponential values for the species-area relation. Science 1963;141:1276.
- [99] McGuiness KA. Equations and explanations in the study of species-area curves. Biol Rev 1984;59:423-40.
- [100] Gleason HA. On the relation between species and area. Ecology 1992;3:158-62.
- [101] Williams CB. Area and number of species. Nature 1943;152:264-7.
- [102] Whitehead DR, Jones CE. Small islands and the equilibrium theory of insular biogeography. Evolution 1969;23:171–9.
- [103] May RM. Patterns of species abundance and diversity. In: Cody ML, Diamond JM, editors. Ecology and evolution of communities. Cambridge, MA: Belknap Press of Harvard University Press; 1975. p. 81–120.
- [104] Simon HA. On a class of skew distribution functions. Biometrika 1955;42:425-40.
- [105] Yule GU. A mathematical theory of evolution, based on the conclusions of Dr Willis JC, FRS. Philos Trans Roy Soc London Ser B 1925;213:21–87.
- [106] Gutenberg B, Richter CF. Seismicity of the Earth and associated phenomena. Princeton, NJ: Princeton University Press; 1954.
- [107] Fisher ME, Barber MN. Scaling theory for finite-size effects in the critical region. Phys Rev Lett 1972;28:1516-9.
- [108] Barabási A-L, Albert R. Emergence of scaling in random networks. Science 1999;286:509-12.
- [109] Kim JS, Goh K-I, Kahng B, Kim D. Fractality and self-similarity in scale-free networks. New J Phys 2007;9:177-88.
- [110] Albert R, Barabási A-L. Statistical mechanics of complex networks. Rev Modern Phys 2002;74:47–97.
- [111] Zupanović P, Juretić D, Botrić S. Kirchhoff's loop law and the maximum entropy production principle. Phys Rev E Stat Nonlin Soft Matter Phys 2004;70:056108.
- [112] De Rham G. Sur un exemple de fonction continue sans dérivée. Enseign Math 1957;3:71–2 [On some curves defined by functional equations; 1957];
 - reprinted in: Edgar GA, editor. Classics on fractals. Addison-Wesley; 1993. p. 285-98.
- [113] Morgan BW. An introduction to Bayesian statistical decision processes. Englewood Cliffs, NJ: Prentice-Hall Inc.; 1968.
- [114] Emanuel KA. Atmospheric convection. New York, NY: Oxford University Press; 1994.
- [115] Erickson C. A geometric perspective on the Riemann zeta function's partial sums. Mathematics 2005:22-31.
- [116] Gol'danskii VI, Kuz'min VV. Spontaneous breaking of mirror symmetry in nature and the origin of life. Sov Phys Usp 1989;32:1-29.
- [117] Jaakkola S, Sharma V, Annila A. Cause of chirality consensus. Curr Chem Biol 2008;2:53-8. arXiv:0906.0254.
- [118] Landauer R. Irreversibility and heat generation in the computing process. IBM J Res Dev 1961;5:183–91.
- [119] Landauer R. Minimal energy requirements in communication. Science 1996;272:1914-8.
- [120] Karnani M, Pääkkönen K, Annila A. The physical character of information. Proc Roy Soc Ser A 2009;465:2155–75.
- [121] Jukes TH, Osawa S. The genetic code in mitochondria and chloroplasts. Experientia 1990;46:1117–26.
- [122] Landauer R. The physical nature of information. Phys Lett A 1996;217:188–93.
- [123] Annila A. Physical portrayal of computational complexity. arXiv:0906.1084, 2009.
- [124] Zhang J. Protein-length distributions for the three domains of life. Trends Genet 2000;16:107-9.
- [125] Jaakkola S, El-Showk S, Annila A. The driving force behind genomic diversity. arXiv:0807.0892.
- [126] Feynman R. Lectures on computation. New York, NY: Westview; 2000.