Natural selection for least action

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The second law of thermodynamics is a powerful imperative that has acquired several expressions during the past centuries. Connections between two of its most prominent forms, i.e. the evolutionary principle by natural selection and the principle of least action, are examined. Although no fundamentally new findings are provided, it is illuminating to see how the two principles rationalizing natural motions reconcile to one law. The second law, when written as a differential equation of motion, describes evolution along the steepest descents in energy and, when it is given in its integral form, the motion is pictured to take place along the shortest paths in energy. In general, evolution is a non-Euclidian energy density landscape in flattening motion.

Keywords: coordinate; energy transfer; entropy; evolution; metric; natural process

1. Introduction

The principle of least action (de Maupertuis 1744, 1746; Euler 1744; Lagrange 1788) and *the evolutionary principle by natural selection* (Darwin 1859) account for many motions in nature. The calculus of variation, i.e. 'take the shortest path', explains diverse physical phenomena (Feynman & Hibbs 1965; Landau & Lifshitz 1975; Taylor & Wheeler 2000; Hanc & Taylor 2004). Likewise, the theory of evolution by natural selection, i.e. 'take the fittest unit', rationalizes various biological courses. Although the two old principles both describe natural motions, they seem to be far apart from each other, not least because still today the formalism of physics and the language of biology differ from each other. However, it is reasonable to suspect that the two principles are in fact one and the same, since for a long time science has failed to recognize any demarcation line between the animate and the inanimate.

In order to reconcile the two principles to one law, the recent formulation of the second law of thermodynamics as an equation of motion (Sharma & Annila 2007) is used. Evolution, when stated in terms of statistical physics, is a probable motion. The *natural process* directs along the steepest descents of an energy landscape by equalizing differences in energy via various transport and transformation processes, e.g. diffusion, heat flows, electric currents and chemical reactions (Kondepudi & Prigogine 1998). These flows of energy, as they channel down along various paths, propel evolution. In a large and complicated

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system, the flows are viewed to explore diverse evolutionary paths, e.g. by random variation, and those that lead to a faster entropy increase, equivalent to a more rapid decrease in the free energy, become, in terms of physics, *naturally selected* (Sharma & Annila 2007). The abstract formalism has been applied to rationalize diverse evolutionary courses as energy transfer processes (Grönholm & Annila 2007; Jaakkola *et al.* 2008*a,b*; Karnani & Annila in press).

The theory of evolution by natural selection, when formulated in terms of chemical thermodynamics, is easy to connect with the principle of least action, which also is well established in terms of energy (Maslov 1991). In accordance with Hamilton's principle (Hamilton 1834, 1835), the equivalence of the differential equation of evolution and the integral equation of dissipative motion is provided here, starting from the second law of thermodynamics (Boltzmann 1905; Stöltzner 2003). In this way, the similarity of the fitness criterion ('take the steepest gradient in energy') and the ubiquitous imperative ('take the shortest path in energy') becomes evident. The two formulations are equivalent ways of picturing the energy landscape in flattening motion. Thus, there are no fundamentally new results. However, as once pointed out by Feynman (1948), there is a pleasure in recognizing old things from a new point of view.

2. The probable motion

Probability is the concise concept to denote a state of a system. Forces, i.e. potential energy gradients and differences, drive the system towards more probable states via flows of energy that diminish the differences. The principle is general but it depends on the particular potentials and mechanisms of energy transfer of how the differences are abolished. A small system may evolve rapidly by equalizing its potentials with its surroundings, whereas a large system may evolve over the aeons in the quest for a stationary state in its surroundings.

Usually, motions are described by differential equations. Examples are Newton's equation of motion, the time-dependent Schrödinger and the Liouville–von Neumann equations. Alternatively, motion may be described by integral equations, e.g. as a Lagrangian or an action. For example, Newtonian mechanics and Maxwell's equations (Landau & Lifshitz 1975) can be derived from the principle of least action, which can also be used in the theory of relativity (Taylor & Wheeler 2000).

Recently, the second law of thermodynamics was expressed as a differential equation of motion (Sharma & Annila 2007) for the probability P,

$$\frac{\mathrm{d}P}{\mathrm{d}t} = LP, \qquad (2.1)$$

where the propagator,

$$L = \frac{1}{k_\mathrm{B} T} \sum_{j,k} \frac{\mathrm{d}x_k}{\mathrm{d}t} \left(\frac{\partial \mu_k}{\partial x_j} - \frac{\partial Q_k}{\partial x_j} \right), \qquad (2.2a)$$

drives the transport ($\mathrm{d}x_k/\mathrm{d}t = -\Sigma \mathrm{d}x_j/\mathrm{d}t$) between general coordinates x_k and x_j, e.g. as diffusion and currents, by draining the potential energy gradients $\partial \mu_k/\partial x_j$ and the fields $\partial Q_k/\partial x_j$ that couple to the jk-transport process. The notation $k_\mathrm{B} T$ for the average energy per particle implies that there is a sufficiently statistic
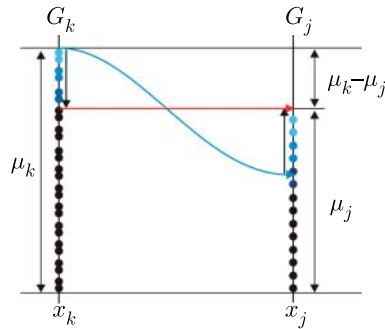
Figure 1. An energy-level diagram depicts schematically transitions between two energy densities ϕ_k and ϕ_j at the position x_k and x_j that are characterized by the entity numbers N_k and N_j and the Gibbs free energy G_k and G_j, respectively. In the quest for a stationary state, the partition evolves by equalizing the potential energy difference $\mu_k - \mu_j$, indicated by the black vertical arrow. The resulting motion appears as kinetic and dissipated flows of energy. The flow of the kinetic energy is depicted by the blue arrow. The dissipated (emitted or absorbed) quanta, indicated by the red arrow, bridge the jk-transformation from N_k to N_j. The dissipation stems from the changes in the interaction energy $dQ = v_k^2 dm_k$ when m_k transform to m_j. The invariant part of the mass is presented by blue circles that are the constituents of j and k densities. Note that the potentials are in relation to each other and the line at the bottom is drawn only for illustrative purposes.

system (Kullback 1959), i.e. a set of repositories of energy where lost and acquired quanta are rapidly dispersed within. After each dissipative event, i.e. an emission or absorption, the system settles via interactions to a new partition corresponding to a new value of $k_B T$, the common reference. The system evolves by dissipation, i.e. by energy efflux or influx, in the quest to reduce the gradients in equation (2.2a) and to attain a stationary state in its surroundings.

Similarly to transport processes, diverse transformation processes, e.g. chemical reactions converting N_k substrates to N_j products or vice versa, are driven by the propagator (Sharma & Annila 2007)

$$L = \frac{1}{RT} \sum_{j,k} \frac{dN_k}{dt} \left(\frac{\partial \mu_k}{\partial N_j} - \frac{\partial Q_k}{\partial N_j} \right). \tag{2.2b}$$

The chemical potential difference between μ_k and μ_j is for convenience denoted as a gradient $\partial \mu_k / \partial N_j$, although this field is not spatially resolved by the observer. When the surrounding density-in-energy couples to the jk-transformation, it contributes by $\partial Q_k / \partial N_j$. For chemical reactions, the average energy $RT = N_A k_B T$ is, as usual, given per mole via Avogadro's number N_A and Boltzmann's constant k_B. The chemical potential (Atkins & de Paula 2006), written as $\mu_k = k_B T \ln \phi_k$, where the density-in-energy (Gibbs 1993–1994) is defined as $\phi_k = N_k \exp(G_k / k_B T)$ for discrete entities k, serves to compare the levels of diverse repositories of energy with each other (figure 1). The Gibbs free energy G_k contains internal and surrounding potential gradients, e.g. in the form of the Coulomb force or electromagnetic radiation field.

The evolution, as given by equation (2.2b), is essentially a restatement of the Gibbs–Duhem equation (Atkins & de Paula 2006) that relates a decrease in the chemical potential of one substance to an increase in the chemical potentials of

the other substances. In accordance with Le Chatelier's principle, the system will evolve towards a stationary state by acquiring from or emitting quanta to its surroundings (figure 1). In the dynamic equilibrium, gradients vanish but diverse pools of energy, indexed by j and k, continuously convert to one and another without net dissipation. These stationary motions along isergonic trajectories are conserved.

In chemical reactions, substrates N_k are distinguished from products N_j when the reaction coordinates differ, i.e. energies $G_k(x_k) \neq G_j(x_j)$. A chemical reaction, which is a movement along the reaction coordinate, is dissipative if it is endergonic $\mu_k < \mu_j$ or exergonic $\mu_k > \mu_j$. Thus, when $\partial \mu_k/\partial N_j - \partial Q_k/\partial N_j \neq 0$, a transformation process $dN_k/dt = -dN_j/dt$ may proceed, whereas when the densities-in-energy ϕ_k and $\phi_{k'}$ and associated gradients are equal, then the entities are indistinguishable from each other.

Likewise, a spatial position x_k differs from another position x_j, i.e. $x_k \neq x_j$ when the motion from one coordinate to another is dissipative. Thus, when $\partial \mu_k/\partial x_j - \partial Q_k/\partial x_j \neq 0$, a transport process $dx_k/dt = -dx_j/dt$ may advance. The dissipative detection itself may impose the energy gradient, i.e. a field with a sufficient resolution to distinguish one compound from another, just as one coordinate from another. On the other hand, when densities-in-energy and their gradients are equal at x_k and $x_{j'}$, then the two coordinates are indistinguishable from each other. They may, nevertheless, differ by a relative phase φ along an isergonic contour. The strength of the potential μ_k determines the invariant rate $\omega = d\varphi/dt$ of conserved motion. Then, a coordinate transformation may be found which renders the precession time independent. Conversely, a change in phase serves to determine μ_k or N_k when G_k is known, subjected to the uncertainty condition $\Delta N_k \Delta \phi$ (Aharonov & Bohm 1959; Gleyzes *et al.* 2007).

The essential difference between equations (2.2a) and (2.2b) is the ability versus inability, respectively, of an observer to resolve an energy transfer process. When distinct entities within the system are resolved, e.g. by a spatial energy gradient, equation (2.2a) can be used, whereas when not, equation (2.2b) is the appropriate form. For example, chemical reactions are customarily monitored only at the level of ensembles but trajectories of individual reactants, if resolved, are expected to be similar to those tracked during simulations or calculations. In the same way, processes in distant stellar objects couple to the observer only via dissipated quanta. Therefore, even if the kinetic energy of the whole ensemble vanishes, the dissipation informs us about internal motions that devour the potential energy gradients in transformations between distinguishable entities within the unresolved system.

For the resolved (equation (2.2a)) as well as for the unresolved systems (equation (2.2b)), the shortest path of motion along the steepest descent in energy will be obtained by minimizing the kinetic energy $(2K)$ or the Lagrangian, i.e. the combination of the kinetic and potential energies $(K - U)$, or dissipation (Q) because the three measures of energy, as will be described in the following sections, are interdependent due to the conservation of the total energy $2K + U = Q$.

Evolution as an energy transfer process aims at an equilibrium where gradients and differences have vanished (figure 2). The process is described from the observer's viewpoint so that the densities-in-energy are given by partitions whereas surroundings are denoted cursorily as fields. The open system evolves
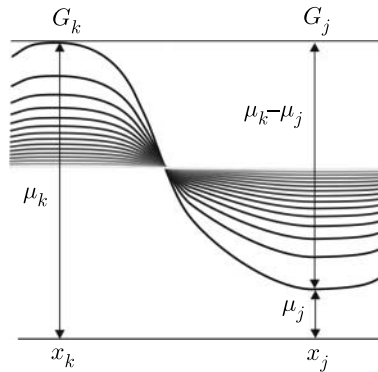
Figure 2. Evolving energy landscape is depicted schematically by a series of grey lines as it is levelling due to the flows of energy towards the stationary state. The flows of energy are driven by the potential energy difference $\mu_k - \mu_j$ or gradient $\partial \mu_k / \partial x_j$ between the sites k and j down along the steepest descents. During the energy transfer, the directed arc s between x_k and x_j is shortening at the rate ds/dt. At the equilibrium, net dissipation vanishes and subsequent stationary motions are conserved.

via the energy transfer from a partition to another more probable one until a stationary state in its surroundings is attained. Although transitions within the system are often of interest, it is the surrounding forces that drive the evolution. Specifically, a closed or stationary system is not subjected to the evolutionary forces. It does not evolve and hence time does not advance either. In a historical perspective, it seems that the concept of a closed system appeared when Lagrange multipliers, corresponding to a fixed entity number and total energy, were employed to determine the maximum entropy state where $L=0$. By contrast, the equation of motion (equation (2.1)) that is derived directly from the probability calculation (Sharma & Annila 2007) elucidates explicitly the driving forces of evolution by $L \neq 0$.

3. The second law as an equation of motion

The second law of thermodynamics given by equation (2.1) is the view by the system. When the surroundings are lower in energy density, the system undergoes dissipative jk-transitions from μ_k to μ_j by emitting quanta that are then no longer part of the system. Hence, the energy content of the system is decreasing. Likewise, when the surroundings are higher in energy density, the system undergoes jk-transitions from μ_j to μ_k by absorbing quanta that become an integral part of the system. Hence, the energy content of the system is increasing. Thus, the inequality $dS/dt \geq 0$ in the second law, i.e. the principle of increasing entropy S means that the open system is evolving towards a more probable partition.

The equation of motion, in terms of the logarithmic probability, i.e. entropy $dS = k_B d(\ln P)$, is for the resolved transformations

$$\frac{dS}{dt} = \frac{k_B}{P} \frac{dP}{dt} = k_B L = \frac{1}{T} \sum_{j,k} v_k \left(\frac{\partial \mu_k}{\partial x_j} - \frac{\partial Q_k}{\partial x_j} \right) \geq 0, \qquad (3.1a)$$

where the flow $v_k = \mathrm{d}x_k/\mathrm{d}t$. When the potential μ_k at x_k is higher (lower) than μ_j at x_j, including the surrounding energy density that couples to the jk-transformation, then the gradient and the flow will be negative (positive), i.e. $\partial\mu_k/\partial x_j - \partial Q_k/\partial x_j < 0 \; (>0)$ and $v_k < 0 \; (>0)$. Thus, $\mathrm{d}S/\mathrm{d}t > 0$ until the gradients have vanished and a stationary state $\mathrm{d}S/\mathrm{d}t = 0$ has been reached. Likewise, for the unresolved transformations, the entropy increases at the rate

$$\frac{\mathrm{d}S}{\mathrm{d}t} = \frac{R}{P}\frac{\mathrm{d}P}{\mathrm{d}t} = RL = \frac{1}{T}\sum_{j,k}\dot{N}_k\left(\frac{\partial\mu_k}{\partial N_j} - \frac{\partial Q_k}{\partial N_j}\right) \geq 0, \qquad (3.1b)$$

where $\dot{N}_k = \mathrm{d}N_k/\mathrm{d}t = -\sum \mathrm{d}N_j/\mathrm{d}t$.

During evolution, given by equations $(3.1a)$ and $(3.1b)$, energy is not conserved *within* an open system, hence $\mathrm{d}S/\mathrm{d}t > 0$. The change in the average energy $k_B T$ resulting from the dissipation is communicated within the system via its interactions. The net dissipation renders the process irreversible and gives the direction of time (Boltzmann 1905; Eddington 1928; Sharma & Annila 2007). When the energy flows affect the driving forces $\partial\mu_k/\partial x_j - \partial Q_k/\partial x_j$, the forces, in turn, redirect the flows v_k. In the absence of invariants of motion, there is no transformation that would make the evolution time independent. In general, trajectories of non-conserved motions cannot be traced (Sharma & Annila 2007) but for symmetrical systems (Noether 1918) analytical solutions (Schwarzschild 1916) can be found. Although the equation of motion (equation (2.1)) is non-integrable for any non-trivial system, the energy transfer can be simulated step by step and the evolving energy landscape can be examined in a piecewise manner.

The probability associates via equation (2.1), and hence also entropy via equations $(3.1a)$ and $(3.1b)$, with energy but not with other attributes, e.g. a disorder that is often, but one-sidedly, linked with entropy (Schrödinger 1948). Obviously, the disorder increases by isergonic phase dispersal due to the sporadic exchange of quanta with incoherent surroundings. Nevertheless, the probability $P_k = \langle\psi_k|\psi_k\rangle$ of the wave function ψ_k remains the same in the coherent and decoherent configurations.

4. The differential equation of motion

An increase in entropy (equations $(3.1a)$ and $(3.1b)$) corresponds to a decrease in the free energy for both the resolved and unresolved energy transfer processes. For the resolved transformations, the flows between distinct potentials μ_k and μ_j result in a decrease in the free energy

$$\frac{\mathrm{d}}{\mathrm{d}t}TS = -\sum_{j,k}v_j\left(\frac{\partial\mu_k}{\partial x_j} - \frac{\partial Q_k}{\partial x_j}\right) = -\sum_{j,k}D_j(\mu_k - Q_k). \qquad (4.1a)$$

The equation states that a flow of the kinetic energy from x_k to x_j stems from the decreasing potential μ_k ($\partial\mu_k/\partial x_j < 0$) concurrent with the dissipation $\partial Q_k/\partial t = -\Sigma v_j \partial Q_k/\partial x_j$ when interactions, defining m_k, break apart and yield m_j (figure 1). Likewise, the kinetic energy flow directs from x_j to x_k and increases μ_k when the influx of energy from the surroundings is bound in interactions and yields m_k from m_j.
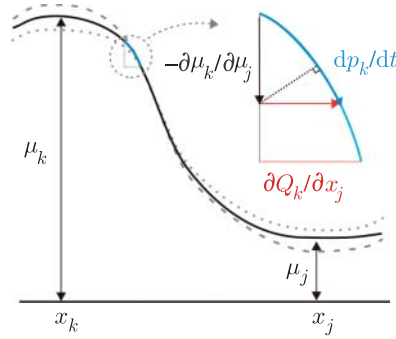
Figure 3. Energy landscape is depicted schematically at time t (solid line) and a moment dt earlier (dashed line) and a moment dt later (dotted line) when an energy flow directs from the high potential μ_k at x_k down along the steepest gradient (blue arrow) towards the low potential μ_j at x_j. The expansion illustrates the differential form of the equation of motion: the potential gradient $-\partial\mu_k/\partial x_j$ (black vertical arrow) translates the mass m_k into the acceleration a_k along a curved path due to the concurrent dissipation $\partial Q_k/\partial x_j$ (red horizontal arrow). During evolution, the potential energy gradient is diminishing and the dissipation stems from the changes in interactions that show up as a decrease in mass $v_k dm_k/dt$. The curvilinear motion adds up, according to equation (4.2a) and (4.2b), from the projection of the potential gradient and the dissipation, indicated by the normal (dotted) of the arc (blue).

The directional derivatives $D = \boldsymbol{v}\cdot\boldsymbol{\nabla}$ in equation (4.1a) describe a manifold of energy by time-dependent tangent vectors (Lee 2003). The landscape is levelling when the flows direct down from the convex regions along the steepest gradients down along the concave regions. The change in the free energy amounts from the projection of potential $-\boldsymbol{v}\cdot\boldsymbol{\nabla}\mu_k$ and the projection of dissipation $\boldsymbol{v}\cdot\boldsymbol{\nabla}Q_k$ (figure 3). Specifically, when there is no dissipative flow $d(TS)/dt = 0$, the parallel transport $D_j\mu_k = 0$ (Carroll 2004) does not change the free energy between the densities-in-energy indexed by j and k.

Likewise, for the unresolved densities-in-energy that appear as point sources and sinks of the manifold, transformations equalize differences in energy according to

$$\frac{d}{dt} TS = -\sum_{j,k} \dot{N}_j \left(\frac{\partial\mu_k}{\partial N_j} - \frac{\partial Q_k}{\partial N_j} \right) = -\sum_j D_j(\mu_k - Q_k), \qquad (4.1b)$$

but as was pointed out earlier, the kinetic trajectories remain unresolved and only dissipation is detected.

The gradient $\partial Q_k/\partial x_j$ is the dissipative force that corresponds to the second term of the time derivative of the momentum $p_k = m_k v_k$ (Newton 1687),

$$\sum_k \frac{dp_k}{dt} = \sum_k \left(m_k a_k + v_k \frac{dm_k}{dt} \right) = -\sum_{j,k} \left(\frac{\partial\mu_k}{\partial x_j} - \frac{\partial Q_k}{\partial x_j} \right), \qquad (4.2a)$$

where $a_k = d^2 x_k/dt^2$ is the acceleration and the energy released from interactions is denoted by the mass loss $dm_k = -dQ_k/v_k^2$. In nuclear reactions, the mass change is apparent, whereas in chemical reactions it is almost negligible. During many transport processes, the potential energy remains nearly constant. Consequently, the dissipation is extremely small but non-zero, i.e. the landscape

is almost flat. Owing to the dissipation, energy is transferred from μ_k at x_k towards μ_j at x_j along a curved path. The dissipative force is pictured orthogonal to the potential gradient (figures 1 and 3). When the two are combined into one, the orthogonality of the components in $-\nabla V = -\nabla(U - iQ)$ is best denoted by i.

When equation (4.2a) is multiplied by velocities dx/dt and integrated over time, the familiar conservation $2K = -U + Q$ for energy in the forms of kinetic (K), attractive potential (U) and dissipation (Q) is obtained. Its time derivative $d(2K)/dt = -v \cdot \nabla(U - Q)$, when written using the continuity $\partial/\partial t = v \cdot \nabla$, is the flow equation (equations (4.1a) and (4.1b)). The energy flow is expelled from the open system to its surroundings as the matter dm_k at the velocity v_k and/or radiated at the speed of light c.

A conserved system that complies with the integrated condition $2K + U = 0$ is without the net dissipation $\langle Q \rangle = 0$. In other words, the mass is invariant $dm_k/dt = 0$ and the forces balance as $\Sigma m_k a_k = -\Sigma \partial \mu_k/\partial x_j$. Then, it is, at least in principle, possible to find a solution to the equation of motion (the Liouville equation) by a transformation that renders the Hamiltonian time independent.

Likewise, for the unresolved transformations, the forces due to the unresolved spatial potential gradient and the detected energy flux add to each other as vectors,

$$\sum_k \left(m_k \ddot{N}_k + \dot{N}_k \frac{dm_k}{dt} \right) = -\sum_{j,k} \left(\frac{\partial \mu_k}{\partial N_j} - \frac{\partial Q_k}{\partial N_j} \right), \qquad (4.2b)$$

where m_k denotes the mass in motion from compounds N_k to N_j. For example, in chemical reactions, the mass change dm_k relates to electronic restructuring, whereas nuclear masses m_k remain intact. The flow rate $\ddot{N}_k = d^2 N_k/dt^2$ is proportional to the potential energy gradient and to the mechanisms of energy transduction (Sharma & Annila 2007).

Although motions are not resolved, the notion of the kinetic energy is not meaningless (Gyarmati 1970). The observed dissipation discloses that energy does flow from higher to lower potentials within the system in the quest for a stationary state with its surroundings (figure 3). The dissipated quanta may, on their way, be influenced by new gradients before being absorbed $|1\rangle \rightarrow |0\rangle$ in a detecting potential where the particular energy transfer process ends. The equation of motion for the electromagnetic energy transfer, corresponding to equation (4.1a) and (4.1b), is due to Poynting (1920). It can be used to picture the propagation of light analogously to figure 3 but will not be digressed into.

Customarily, non-dissipative motions are described by the Euler–Lagrange equation that can be derived by varying the point (x, t) in the middle of an infinitesimal space–time interval (Hanc *et al.* 2004) to determine the stationary trajectory (figure 4). The dissipative motions are described by the dissipative Euler–Lagrange equation (Nesbet 2003)

$$\sum_{j,k} \left(\frac{d}{dt} \frac{\partial L_k}{\partial v_j} - \frac{\partial L_k}{\partial x_j} \right) = \sum_{j,k} \frac{\partial Q_k}{\partial x_j}, \qquad (4.3)$$

where the Lagrangian $L_k = K_k - U_k$ for the transport processes contains the kinetic $K_k = 1/2 m_k v_k^2$ and potential $U_k = \mu_k$ energy terms. The emitted or absorbed quanta $\Sigma_k Q_k \neq 0$ in the $k \neq j$ transitions are included. However, equation (4.3) does not explicitly identify the changes in interactions as the emission

sources or sinks of absorption, unlike equation $(4.2a)$ that shows the mass changes. When identities are created or destroyed, the dissipation is invariably accompanied. Owing to the finite transformation rates $(c, v_k \text{ or } \dot{N}_k)$, it takes time to distinguish x_k from x_j (N_k from N_j) on the basis of an energy difference ($G_k \neq G_j$) by a dissipative process (Brillouin 1963). The dissipative flow of energy $\langle Q \rangle \neq 0$ manifests itself as the flow of time.

Both the resolved and unresolved transformations direct from high potentials down to low potentials along the steepest gradients in energy in terms of both $\partial \mu_k / \partial x_j$ and $\partial Q_k / \partial x_j$. In the following, it is argued that these paths, also known as the geodesics, are the shortest in energy, i.e. in space and time.

5. The integral equation of motion

The integral form of the differential equation (equation $(4.2a)$) for the resolved processes is known as the abbreviated action. The r.h.s.

$$A_0 = -\iint \sum_{j,k} \left(\frac{\partial \mu_k}{\partial x_j} - \frac{\partial Q_k}{\partial x_j} \right) dx_j \, dt = -(U - Q)t \qquad (5.1a)$$

amounts from the potential energy U and the dissipation Q, when the energy flows down along the gradients during the time period dt and over the spatial distance dx. Likewise, for the unresolved transformations (equation $(4.2b)$), the integral form is

$$A_0 = -\iint \sum_{j,k} \left(\frac{\partial \mu_k}{\partial N_j} - \frac{\partial Q_k}{\partial N_j} \right) dN_j \, dt = -(U - Q)t, \qquad (5.1b)$$

where the free energy is consumed in dissipative transformations during dt. The l.h.s. of equation $(4.2a)$ is the form proposed by Maupertuis,

$$A_0 = \int \sum_k p_k \, dx_k = \int \sum_k p_k v_k \, dt = 2Kt, \qquad (5.2a)$$

that amounts from the kinetic energy $2K = \sum m_k v_k^2$ during t. When equations $(5.1a)$ and $(5.2a)$ are equated, the integral form of continuity, *actio est reactio* (the interaction principle), is obtained. The integrands sum as $2K + U = Q$. For the non-dissipative motions along isergonic trajectories $\langle Q \rangle = 0$, the familiar condition of a stationary state $2K + U = 0$ is recovered.

In general, the integral equation of motions just as the differential form cannot be solved because the driving forces, i.e. the potential gradients, are consumed by the flows. There is no invariant of motion and evolution may redirect its course. Therefore, to allow for a changed destination, the integrals are left indefinite.

It is of interest to examine a short stretch of the path where energy is in motion from μ_k to μ_j. The directed arc s that is interconnecting the two repositories on the energy landscape is shortened by ds during dt (figure 5). When the short arc ds is approximated by a straight chord, the dissipative directional step can be carried out by complex numbers so that the differential $d\sigma$, associated with the potential energy change, adds with the dissipation-associated differential $ic \, dt$ along the orthogonal direction, indicated by i, to
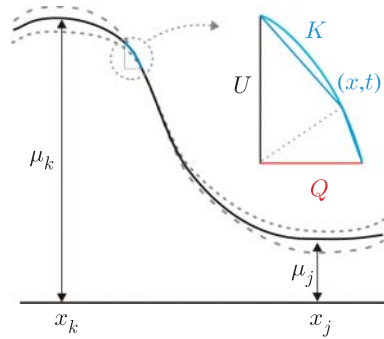
Figure 4. Expanded fraction of an energy landscape illustrates the Euler–Lagrange differential form of the integral equation of motion. The shortest path is found by minimizing the distance $L = K - U$ (dotted line) to the point (x, t) on the infinitesimally short path. Along this optimal path of energy dispersal, the change in the potential U transfers into the kinetic energy K and the dissipation Q.
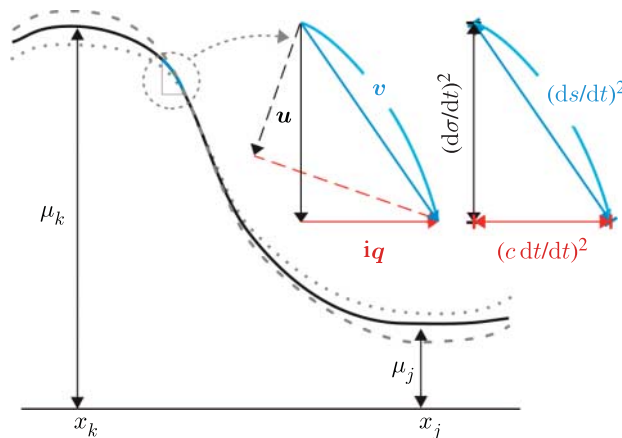

Figure 5. When the energy flows from the high potential μ_k down along the shortest path (solid line) towards the low potential μ_j, the directed path s between x_k and x_j is shortening at the rate ds/dt. The expansions describe the local metric of the curved landscape. (a) The momentum vector $v = u + iq$ is a sum of the momentum due to the potential energy change $u = -\int(\partial \mu_k/\partial x_j)dt$ and the concurrent dissipation $q = \int(dQ_k/dx_j)dt$ along the orthogonal direction. The metric $u^2 = v^2 - q^2$ of the landscape is the Lorentz covariant with respect to a change in the frame of reference (dashed line). (b) When a short local path ds on the non-Euclidian manifold is approximated by a straight chord, the kinetic energy $(ds/dt)^2$ (blue line) amounts from the change in the potential $(d\sigma/dt)^2$ (black vertical line) and the dissipation $(c\,dt/dt)^2$ (red horizontal line) according to Pythagoras' theorem.

result in the differential $ds = -d\sigma + ic\,dt$ that associates with the kinetic energy. When multiplying with the complex conjugate ds^*, the familiar expression $d\sigma^2 = ds^2 - c^2\,dt^2$ for the local metric is obtained (Taylor & Wheeler 2000; Berry 2001). The squared differentials associate with the attractive potential energy $U = -m(d\sigma/dt)^2$, the kinetic energy $2K = m(ds/dt)^2 = mv^2$ and the dissipated energy $Q = mc^2(dt/dt)^2$. Thus, after multiplying with dt^2/mc^2, it is observed that it is the conservation of energy $U = Q - 2K$ that defines the Lorentzian manifold with the familiar metric $d\tau^2 = dt^2 - ds^2/c^2$, where the proper distance σ is related to the proper time τ by $c^2 d\tau^2 = -d\sigma^2$.

The unresolved jk-transformations $\dot{N}_k = -\sum \dot{N}_j$ convert the energy associated with m_k to $\sum m_j$ with concomitant dissipation. When interactions break apart, some mass Δm_k is dissipated, most apparent in nuclear reactions but also non-zero in other evolutionary processes. Since the system as a whole is not observed to move, only the dissipation associated momentum $\Delta p_k = m_k \dot{N}_k - \sum m_j \dot{N}_j = \Delta m_k \dot{N}_k = \sum_j Q_k / \dot{N}_k$ is detected. Integration over $\mathrm{d}t$,

$$A_0 = \int \sum_k \Delta p_k \, \mathrm{d}N_k = \int \sum_{j,k} \frac{Q_k}{\dot{N}_k} \dot{N}_k \, \mathrm{d}t = Qt, \qquad (5.2b)$$

gives the net dissipation due to the flows of energy between distinct potentials during t. An efflux will consume a high potential, whereas an influx will build up a low potential until the stationary state in the surroundings is attained. When the net energy flow from and to the system has vanished $\langle Q \rangle = 0$, the through-flux supporting the stationary state is at maximum. This is the maximum power principle (Lotka 1922). The principle of minimum (net) dissipation (Moiseev 1987) refers to the state of minimum free energy. In this sense, it is also re-expressing the second law.

Customarily, the dissipative Lagrange form of action

$$A = \int L \, \mathrm{d}t = \int \sum_{j,k} \left(\frac{1}{2} m_k v_k^2 - \mu_k - Q_{jk} \right) \mathrm{d}t \qquad (5.3)$$

is preferred over the Maupertuis form (equation $(5.2a)$). However, since $2K$, $L = K - U$ and Q are interdependent by the conservation of energy (figure 4), identical results are obtained either by minimizing A_0 for $2K$ (or Q) or A for L. The shortest path in energy is the one where the kinetic energy $2K$ as the integrand of the abbreviated action or the Lagrangian $L = K - U$ or the dissipation Q is at minimum.

6. Manifold in motion

The thermodynamic description of an energy landscape in motion, as outlined previously, expresses the basic conservation laws for energy and its differential, i.e. force, as well as for the energy integral, i.e. action, and its differential momentum. These equations of evolution state that the time-dependent manifold of energy densities is continuous. The flows of energy are most voluminous between the well-connected reservoirs. The connected densities-in-energy make an affine manifold (Lee 2003; Carroll 2004), i.e. a system, where a flow from a high density necessarily passes through the neighbouring coordinates on its way towards a low density.

The evolving landscape is described by the calculus of variations that is equipped with powerful mathematical machinery conceived by Gauss and elaborated further by Riemann (Weinberg 1972; Carroll 2004). The mathematical counterpart for the thermodynamic evolution is the geometric evolution $\partial_t g_{jk} = -2R_{jk}$ (Chow & Knopf 2004). The Riemannian manifold deforms via the Ricci flows that are driven by the curvature tensor R_{jk}. In analogy to the surrounding fields that are included along with the thermodynamic potential gradients, the Ricci flows may also be powered by additional vector fields. The negative sign signifies that the Ricci flows contract the positively curved regions and expand the negatively curved regions of the manifold, in accordance with the

thermodynamic evolution that flattens heights and fills depths of energy densities (figures 2–5), as well as stretches the saddle regions. Since our description provides mathematically nothing new, we will not make excursions to rephrase the well-established results. Rather, we will picture an evolving space–time as an energy transfer process at a formal level without reference to the explicit forms of diverse potentials and their gradients, i.e. fields.

According to thermodynamics, the space is not empty but energized. If there is no energy in a form of U and no radiation Q, the space–time is empty (does not exist), i.e. $2K = 0$ (Foster & Nightingale 1994). The manifold, given above as a tangential vector field, is customarily given by elements g_{jk} of the metric tensor $\mathsf{G} = J^{\mathrm{T}}J$, which is obtained from the Jacobian J. Since the jk-path is directional, the Jacobian element $J_{jk} < 0$ means that the density at x_k (or N_k) is decreasing during evolution in favour of x_j (or N_j) until the energy gradients (or differences) have vanished. The corresponding transposed element $J_{kj} > 0$ is illustrative in identifying the coordinate x_j as the site of μ_j in the same way as the coordinate x_k associates with μ_k. Thus, the transposition literally means a change in the viewpoint on the common landscape. As usual, the trace, determinant and discriminant of J disclose motional modes of the manifold (Strogatz 2000).

At the stationary state, there is no dissipation and there is no directionality of time and no evolution of the metric either. The space is flat without net forces and all dynamics are conserved during the period of integration. Along an isergonic contour where $\langle Q \rangle = 0$, $\mathrm{d}S/\mathrm{d}t = 0$ and $\mathrm{Tr}(J) = 0$. The dynamics of the manifold about a local point is revealed by the discriminant of the characteristic equation. The conserved motions retain all energies at $x_k(N_k)$ or return to it without net dissipation after t has elapsed in cyclic or sporadic excursions about x_k. Hence, the potential $(\mathrm{d}\sigma/\mathrm{d}t)^2$ equals the energy in motion $(\mathrm{d}s/\mathrm{d}t)^2$ in accordance with the familiar condition $U + 2K = \langle Q \rangle = 0$. For example, the constant curvature, i.e. a fixed radius r, means that $2K = m(\mathrm{d}s/\mathrm{d}t)^2 = mr^2(\mathrm{d}\varphi/\mathrm{d}t)^2 = mr^2\omega^2 = -U$, where the characteristic frequency ω is determined by the strength of the potential. Likewise, the basic wave equation is an expression for the geodesic in a constant potential.

According to thermodynamics, time is only a convenient way to compare the relative rates of dissipative processes that are flattening the energy landscape. The manifold is levelled by the flows that may also be viewed as motions that dilute energy density. The famous invariant of motion $\mathrm{d}t/\mathrm{d}\tau = (1 - v^2/c^2)^{-1/2} = E/mc^2$ relates, for example, the source of quanta to the sink that is receding with high velocity v. Thus, the general coordinates, customarily given by space and time, intermingle with each other in dissipative motions that unfold the manifold of energy densities. Since the rate of dissipation depends on the surrounding energy densities that may differ radically from those which we are accustomed to on Earth, some observations may appear peculiar and counter-intuitive to us.

7. Discussion

Ludwig Boltzmann expressed his unrelenting desire to connect the second law with the principle of least action, as late as 1899 when closing his lectures at Clark University by saying 'It turns out that the analogies with the second law are neither simply identical to the principle of least action, nor to Hamilton's

principle, but that they are closely related to each of them.' (Boltzmann 1905). Apparently, Boltzmann yearned also to express Darwin's theory of evolution by natural selection in terms of statistical mechanics when saying that the existence of animate beings is a struggle for entropy (Boltzmann 1974).

In retrospect, it seems that both the objectives of Boltzmann were somehow concealed already early on. Apparently, the primary objective at that time was to find the equilibrium state partition that is characterized by the well-known Boltzmann factors. Since the equilibrium per definition has zero free energy, the driving force of evolution that led to the stationary state remained obscure. Therefore, in many cases, the Boltzmann factors still today are imposed *ad hoc* to command the system to a stationary state, rather than allowing the system on its own to find the way via natural motions to the equilibrium with its surroundings. Perhaps the elegant mathematical machinery due to Joseph-Louis Lagrange, which is also employed today to determine the equilibrium partition, disguised the physics of evolution, i.e. the probabilities are not invariant but relate to the free energy (Sharma & Annila 2007). Thus, the irreversibility is exclusively based on reasons of probability (Ritz & Einstein 1909; Zeh 2007).

The contemporary obsession to predefine the steady state appears also in the desire for normalized probabilities. A norm associates with symmetry and facilitates calculus. However, probabilities keep changing with a changing energy landscape. This is also the basic idea of Bayesian inference (Bayes 1763), yet another early and conceptually sound realization of evolution, in particular when augmented with the steepest ascent imperative (Jaynes 2003). In general, all paths are explored (Feynman & Hibbs 1965) to distribute energy flows through them according to the principle of least action. Excursions on the energy manifold, e.g. by random variation, will sooner or later naturally converge on the most probable, the shortest paths that follow the steepest gradients in energy.

The principle of increasing entropy, equivalent to the decreasing free energy, is pure and austere but its mechanical manifestations can be complex and intricate. The energy transfer involving the coherent motions between a small system and its surroundings may display complicated phenomena (Sudarshan & Misra 1977; Schieve *et al.* 1989), whereas energy transduction in a large hierarchical system, channelling via numerous paths, becomes easily intractable. For example, numerous enzymes that constitute metabolic machinery of a cell are viewed here as mechanisms that transform chemical energy from one compound pool to another. Likewise, species of an ecosystem form a chain of energy transduction mechanisms that distribute solar energy acquired by photosynthesis. Since the mechanisms of energy transduction are also themselves repositories of energy, other mechanisms may, in turn, tap into and draw from them. Therefore, evolutionary courses and responses to environmental changes of many ecosystems are difficult to predict precisely. Technically speaking, although the equation of motion is known, it is non-integrable.

Particularly, intriguing phenomena may emerge when a high-energy source, such as the Sun, is powering a large energy transduction network, such as that on Earth. When a steady stream of external energy is falling on an open system, there is a driving force to assemble mechanisms from the available ingredients and to improve on them in order to acquire more energy in the quest for a stationary state. The driving force makes no difference between abiotic and biotic mechanisms of energy transduction but favours all those that are dispersing

energy more and more effectively. Therefore, the large global system is, in the language of thermodynamics, an energy manifold in myriad motional modes, most of which are referred to as life. For the large global system that apparently has a suitable mixture of ingredients to couple to the high-energy influx, it has taken aeons to evolve in energy transduction. Although the abstract description of evolution provided by the statistical physics results in a holistic view of nature, it is unarmed to say specifically how energy transduction mechanisms, i.e. species, have emerged. These questions can be addressed by appropriate models. The present formalism emphasizes the imperatives in evolution.

The role of (genetic) information is undoubtedly important in evolution but it has not been elaborated in this study. However, considering the close connection between mathematical communication theory (Shannon 1948) and statistical physics (Kullback 1959), it is not surprising that a piece of information, due to its physical representation (Landauer 1961), is identified by thermodynamics to a deviation from the average energy density. Since deviations are consumed during the probable motion, thermodynamics sheds light on the origin of (genetic) information as a powerful mechanism to increase energy transduction. Thus, life has not only emerged on Earth but also the globe has evolved to a living planet (Lovelock 1988). To extend the thermodynamic description to biotic systems is not new (Lotka 1925) but consistent with many earlier studies that are based on the principle of increasing entropy or reduction of gradients (Ulanowicz & Hannon 1987; Brooks & Wiley 1988; Salthe 1993; Schneider & Kay 1994; Chaisson 1998; Lorenz 2002).

The established connections between the differential and integral equations of evolutionary motions may appear naive and the conclusions may seem simple by modern standards. On the other hand, the presentation, using the basic concepts of physics, is in accord with the inspiring ideas about the evolving nature that appeared in various forms during the past centuries. In summary, tracks of evolution are non-deterministic because the energy flows will affect potentials that, in turn, will alter the flows. The trajectories are integrable only when a stationary state without net dissipation is reached. The contrast between the non-conserved dissipative motions and the conserved stationary-state stance has been phrased so that the subjective non-Euclidian world, i.e. a curved landscape, *happens* (evolves), whereas the objective Euclidian world, i.e. a flat landscape, simply *is* (stationary; Weyl 1949).

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