



Ecological succession as an energy dispersal process

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ABSTRACT

Ecological succession is described by the 2nd law of thermodynamics. According to the universal law of the maximal energy dispersal, an ecosystem evolves toward a stationary state in its surroundings by consuming free energy via diverse mechanisms. Species are the mechanisms that conduct energy down along gradients between repositories of energy which consist of populations at various thermodynamic levels. The salient characteristics of succession, growing biomass production, increasing species richness and shifting distributions of species are found as consequences of the universal quest to diminish energy density differences in least time. The analysis reveals that during succession the ecosystem's energy transduction network, *i.e.*, the food web organizes increasingly more effective in the free energy reduction by acquiring new, more effective and abandoning old, less effective species of energy transduction. The number of species does not necessarily peak at the climax state that corresponds to the maximum-entropy partition of species maximizing consumption of free energy. According to the theory of evolution by natural selection founded on statistical physics of open systems, ecological succession is one among many other evolutionary processes.

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1. Introduction

A well-known case of succession (Odum, 1963) is the rise of the Krakatau island ecosystem from the ground erased practically of all life after the volcanic explosion in 1883 (Verbeek, 1885; Whittaker et al., 1989). The characteristic sequential changes referred to as succession are documented also in many other cases when ecosystems are expanding on unoccupied habitats as well as when existing communities are recovering from disturbances (Beardsley and Cannon, 1930; Fridriksson, 1989). Succession is defined in ecology as the process by which species successively accumulate and eventually also replace each other when the ecosystem in its entirety is evolving toward a climax state. In general, succession displays growing biomass production and increasing species richness, stratification and complexity as well as skewed distributions of species that shift toward higher trophic levels (Knight, 1965; Margalef, 1968; McIntosh, 1985; Rosenzweig, 1995). The typical temporal phases of succession may also present themselves as characteristic stationary stages as was reported first for vegetation stages on sand dunes (Cowles, 1899). In the broader context

of biology ecological succession can be considered as an archetypal evolutionary process.

For a long time it has been understood that the ecological succession is powered by the energy flow from the surroundings into the ecosystem. In general, the reduction of free energy powers diverse processes that drive matter in diverse functional entities (Jørgensen and Svirezhev, 2004; Lindeman, 1942; Lotka, 1925; Morowitz, 1968; Odum, 1969). These are molecules, cells, organisms, populations at increasingly high levels of trophic hierarchy (Salthe, 1985). Specifically, it has been pointed out that succession is a physical process along the direction of decreasing the rate of dissipation per biomass (Margalef, 1968). The ubiquitous law of the maximal energy dispersal (Lambert, 1999) has been understood by the maximum entropy production principle (Jaynes, 1957; Ziegler, 1983; Mahulikar and Harwig, 2004; Martyushev and Seleznev, 2006) to account for a number of natural phenomena (Brooks and Wiley, 1988; Brooks, 2000; Dewar, 2003; Hoelzer et al., 2006; Lorenz, 2002; Matsuno and Swenson, 1999; Salthe, 1993; Schneider and Kay, 1994; Swenson, 1989; Ulanowicz and Hannon, 1987; Vogel, 1988; Weber et al., 1989; Whitfield, 2007). Also the ecological succession can be understood to follow the same universal principle when the 2nd law of thermodynamics is formulated as an equation of motion derived from statistical physics of open systems. The formalism applicable to biological systems can be regarded as the physical foundation of the evolutionary theory based on natural selection (Darwin, 1859). It is consistent with the basic maxim of

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thermodynamics: the increasing entropy results from the decreasing free energy (Sharma and Annala, 2007).

The thermodynamics derived from statistical physics of open systems has recently been useful in clarifying why biological life emerged (Annala and Annala, 2008), what imposed chirality consensus on natural amino acids and nucleic acid residues and gave rise to other standards of life (Jaakkola et al., 2008a) as well as why eukaryote genomes have evolved to diversity including vast amounts of non-phenotypic sequences (Jaakkola et al., 2008b). Also information-guided processes have been shown to follow the laws of thermodynamics (Karnani et al., 2009). Moreover protein folding has been recognized as a non-deterministic evolutionary process (Sharma et al., 2009). Furthermore, the skewed character of plant and animal population and gene length distributions (Grönholm and Annala, 2007) and their cumulative curves, e.g., species–area relationships have been understood to follow from the universal principle of maximal energy dispersal (Würtz and Annala, 2008). Also the nature of global homeostasis (Karnani and Annala, 2008), the rise of hierarchical organizations (Annala and Kuismanen, 2008) and the foundation of economic laws (Annala and Salthe, 2009) have been associated with the principle of the maximal free energy reduction. The description of ecological succession is another corollary of the supreme law of nature that can be expressed also by the principle of least action (Kaila and Annala, 2008) and Newton's 2nd law (Tuisku et al., 2009). To communicate the role of thermodynamics clearly, only the principle characteristics of succession are examined in this study.

2. Ecosystem as an Energy Transduction System

Many motions in nature follow the 2nd law of thermodynamics (Kondepudi and Prigogine, 1998). For example, molecular diffusion, heat flows, ion currents and chemical reactions, abolish concentration, temperature, electric and chemical potential gradients. These transport and transformation processes diminish energy density differences. The resulting decrease in the free energy is equivalent to the increase in entropy as stated by the basic maxim of thermodynamics. Even intricate biological processes involving numerous flows of energy can be formulated concisely and rationalized using the 2nd law. Fundamentally, biological and ecological systems are physical systems (Margalef, 1996). Therefore ecological succession, as will be shown below, can be described as any other natural process that progresses by flows of energy toward a thermodynamic stationary state where all energy density differences have vanished.

To apply the general law of the maximal energy dispersal each and every population N_j in the system is associated with energy density $\phi_j = N_j \exp(G_j/k_B T)$ where the Gibbs energy G_j is relative to average energy $k_B T$ (Gibbs, 1993). According to the scale-independent hierarchical description of nature (Salthe, 2002) each j -entity, e.g., an individual in a species, is a system composed of diverse k -entities each available in numbers N_k . Each population N_k is, in turn, associated with energy density $\phi_k = N_k \exp(G_k/k_B T)$. To express concisely this self-similar organization of nature, statistical physics of open systems defines the probability (Sharma and Annala, 2007; Tuisku et al., 2009)

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

as a measure for the j -system. The formula expresses factors that determine the population of j -entities. The product $\prod N_k$ in the nominator ensures that if any of the k -ingredients, e.g., food supplies, is missing, no j -species may appear in the ecosystem ($P_j = 0$). The degeneracy g_{jk} numbers the k -ingredients that remain indistinguishable in the assembled j -species. The intrinsic energy difference $\Delta G_{jk} = G_j - G_k$ between the j -species and its surround-

ings containing the k -species is bridged by the external influx ΔQ_{jk} that couples to the jk -transformation process. The notation by i emphasizes that the stream of energy along a vector potential gradient couples to the jk -transformation process orthogonal respect to the system's scalar potential energy differences between j - and k -repository (Tuisku et al., 2009). The nominator is raised to the power of N_j because the process may combine the vital k -ingredients into any of the indistinguishable j -individuals in the population N_j . As usual, the division by the factorial $N_j!$ means that the combinatorial configurations of the j -entities in the ecosystem are indistinguishable.

The logarithm of the total probability of the system, defined as $P = \prod P_j$, is the additive measure that takes into account all energy densities and transformation paths (Sharma and Annala, 2007)

$$\ln P = \sum_j \ln P_j \approx \sum_j N_j \left(1 - \sum_k A_{jk}/k_B T \right) \quad (2.2)$$

where Stirling's approximation $\ln N_j \approx N_j \ln N_j - N_j$ has been used. The energy difference, known as the free energy or exergy,

$$A_{jk} = \Delta \mu_{jk} - i \Delta Q_{jk} \quad (2.3)$$

is the motive force (Carnot, 1824) that directs the transformations from N_k to N_j . The concept of free energy applies to chemical systems of molecules just as to ecosystems of organisms that assemble from numerous chemical reactions. According to the definition of P_j (Eq. (2.1)) any two species j and k are distinguishable from each other when their mutual interactions are dissipative ($\Delta Q_{jk} \neq 0$). Conversely, any two individuals belong to the same species, i.e., are indistinguishable, when their mutual interactions are not dissipative ($\Delta Q_{jj} = 0$). The scalar potential difference

$$\Delta \mu_{jk} = \mu_j - \sum_k \mu_k = k_B T (\ln \phi_j - \sum_k g_{jk} \ln \phi_k / g_{jk}!) \quad (2.4)$$

is defined by the logarithm of the energy densities. The chemical potential μ_j denotes the energy content of the j -population and μ_k that of the k -population. The potential difference is a convenient way to relate diverse repositories of energy, i.e., populations to each other to deduce directions of energy flows. All flows direct from high-energy densities to lower energy densities. On Earth the primary source of energy is the high-energy radiation from the Sun that disperses from the base production to the rest of the transduction system (Karnani and Annala, 2008). For example, a steady-state population of a species at a high trophic level is maintained by a dissipative chain of energy transduction from species at lower levels of hierarchical organization. A species j distinguishes from other species k through its characteristic energy conduction mechanisms. In ecological field studies it is obviously hardly possible to distinguish a species from another to a precision of a quantum of energy hence the functional structure of the ecosystem is preferably presented by trophic level organization rather than by a detailed energy level diagram. However, in laboratory environment, molecular species in metabolic and genomic systems are routinely distinguished from each other up to a quantum's precision.

According to the 2nd law of thermodynamics the overall structure of the energy transduction network, commonly known as the food web, results from the energy flows that naturally channel along the most voluminous directional gradients to consume the various sources of free energy A_{jk} as soon as possible. The Stirling's approximation used in Eq. (2.2) implies that the system is well-defined by being able to absorb or emit quanta without a marked change in its average energy content $k_B T$, i.e., $A_{jk}/k_B T \ll 1$. In other words, $\ln P$ is a sufficient statistic for $k_B T$ (Kullback, 1959). However, it is not unusual that the approximation does not hold on a particular level of hierarchical organization of energy transduction. For

example, a rapidly disintegrating ecosystem is not a sufficiently statistical system to be described by a common average energy. Then the energy transduction processes involving an ensemble of sufficiently statistical subsystems is described at a lower level of hierarchy using the same self-similar formalism (Salthe, 2002, 2007).

In general, all life forms acquire high-energy influx from their surroundings, e.g., as sunlight and food as well as discard low-energy efflux such as heat and excrement. When high-energy radiation from the Sun couples to chemical reactions on Earth, chemical potentials of matter are amounting to attain balance with the high-energy radiation density. Thus the energy transduction between an ecosystem and its surroundings is similar to the process when a cold substance is warming up when placed in contact to a hot body. According to thermodynamics there is no demarcation line between animate and inanimate processes since both types are given by the same equation of motion.

A thermodynamic process will commence when there is an energy density difference between the system and its surroundings. The energy density gradient is the force that drives motion. When the system is lower in energy density than its surroundings, the flows of energy will direct to the system. Conversely when the system is higher in energy density than its surroundings, the flows of energy will direct from the system. During the thermodynamic processes the flows of energy naturally select the paths, i.e., the series of transformations facilitated by diverse mechanisms known as species that will level off the energy density differences as soon as possible. Therefore entropy is not only increasing but it is increasing in least time. This maximum entropy production principle manifests itself when more and more effective mechanisms of energy transduction, i.e., the new, succeeding species are gaining ground from the pioneering species. This thermodynamic imperative results in evolution of an ecosystem toward a climax state. At the dynamic steady state of free energy minimum the total influx to the system balances the total efflux from the system. Thus the net dissipation in the flow-through system has vanished and also the net evolutionary force has extinguished. The climax state is customarily referred to as a singular point or a limit cycle (Strogatz, 2000). In an ecosystem, just as in any other system, the steady-state balance between kinetic and potential energy manifests itself as myriad motions (Tuisku et al., 2009) that correspond to conserved currents (Noether, 1918).

3. Succession by Consumption of the Free Energy

To exemplify the use of the general formalism presented above in understanding ecological succession, let us consider a barren island that is open to fluxes. Debris from the surroundings, carried down along concentration gradients by winds will amount on the island due to diffusion. The gradients A_{jk} are the driving forces of transport and also transformation processes that move the emerging ecosystem from one state to another. The transforming flow $v_j = dN_j/dt$ of diverse substances j in amounts N_j takes the direction of increasing entropy. The equation of motion is obtained from the definition for entropy $S = \sum_j S_j = k_B \ln \prod_j P_j$ via the logarithmic probability measure (Eq. (2.2)) when using the chain rule $\sum (\partial S_j / \partial N_j) (dN_j/dt)$ in differentiating S with respect to time t (Lavenda, 1985; Sharma and Annala, 2007; Tuisku et al., 2009)

$$\frac{dS}{dt} = k_B \frac{d(\ln P)}{dt} = \frac{k_B}{P} \frac{dP}{dt} = k_B L = - \sum_{j,k} v_j \frac{A_{jk}}{T} \geq 0 \quad (3.1)$$

The powerful imperative of increasing entropy given by Eq. (3.1) means that the energy density differences, i.e., the free energy con-

tained in the numerous driving forces A_{jk} between j - and k -species tend to equalize by diverse processes that transport and transform k -species to j -species. The species are said to interact with each other via these transformations of energy. The thermodynamic principle account does not explicitly determine the mechanisms of interactions but the law states that when more effective mechanisms appear, they will be naturally selected to consume the free energy as soon as possible. Passive diffusion is among the simplest transport phenomena. Also diverse organisms tend to 'flow' by various active mechanisms from the more abundant surroundings on the island. The transport processes affect concentrations and population densities and chemical reactions consume the free energy by transforming species k to species j . This is customarily referred to as metabolism. Primary production transforms substrate species k and k' , e.g., carbon dioxide and water, to high-energy product species j , e.g., glucose. The resulting high chemical potential is in turn consumed by some subsequent species j' in raising populations N_j corresponding to the potential μ_j' toward a steady-state balance.

The conservation of energy requires that the influx to the system equals the outflow from the surroundings, i.e., $v_j = - \sum v_k$. To satisfy the continuity at each moment of time diffusion $v_j = dx_j/dt = - \sum_k \sigma_{jk} / k_B T (\partial A_k / \partial x_j)$ and kinetics (Lavenda, 1985; Kondepudi and Prigogine, 1998; Sharma and Annala, 2007)

$$v_j = \frac{dN_j}{dt} = - \sum_k \sigma_{jk} \frac{A_{jk}}{k_B T} \quad (3.2)$$

are proportional to the free energy by a coefficient σ_{jk} that depends on the mechanism of energy transduction, e.g., diffusion or catalysis. The overall flow v_j is simply a sum of flows via various paths. When Eq. (3.2) is inserted in Eq. (3.1), dS/dt is in accordance with the principle of increasing entropy found non-negative. However, often kinetics is not described being proportional to the free energy but modeled by the law of mass action so that population changes are driven by population differences, not by the energy density differences denoted in Eq. (3.2). When using the imprecise model, kinetics and thermodynamics appear as incompatible with each other. This misconception promotes thinking that kinetics could possibly override thermodynamics but that would imply violation in the conservation of energy.

According to the self-similar formalism a closer inspection of any mechanism will reveal that it is also a result of natural processes. For example, an enzyme is a result of a protein folding process, just as an individual is a result of myriad of chemical reactions. Thus, when the coefficient σ_{jk} is a constant in Eq. (3.2), the conducting mechanism itself is at a stationary state (Lavenda, 1985). However, it is not unusual that the conduction system itself is evolving. This is no obstacle for the presented formalism since the underlying evolutionary course at a lower level of hierarchical organization can be rationalized by the same self-similar formalism given by Eqs. (2.1)–(3.2) (Annala and Kuismanen, 2008). In practice an extensive tree of recursive formula can be tedious to formulate explicitly for a practical computation. Therefore the coefficient σ_{jk} at a chosen level of hierarchy is often modeled by some analytical form that aims to mimic responses due to changes in the energy gradients. An insightful functional form of σ_{jk} is, e.g., a skewed distribution to acknowledge that the population of transformation mechanism itself forms a partition.

When a j -species at a high trophic level, denoted by G_j , arrives on a barren island, it is susceptible to break down into low-energy k -compounds when $\mu_j > \mu_k$. The available energy sources in numbers N_k are insufficient to fuel the invaders in numbers N_j . The free energy between k and j -species might be so large that not a single j -entity is able to survive on the island. In plain language the immigrant population N_j is starving to death as there is not enough food

accessible to them. Consequently reactions will take the direction of breakdown of the j -immigrants to more basic k -compounds to narrow their mutual chemical potential difference.

The high-energy j -species will survive first when abundant sources have accumulated on the island. Then the individuals of j -species are able to tap into, e.g., high-energy radiation ΔQ_{jk} from the Sun or to devour high potentials of other species that had arrived earlier. Obviously free energy, essentially food at a lower level G_k , must be available in larger numbers N_k than is required to sustain the newly immigrated foragers N_j at a higher level G_j , so that $\mu_k > \mu_j$. Then the flows are in favor of the j -species that will proliferate $dN_j/dt > 0$. In short, the principle of increasing entropy equivalent to the principle of decreasing free energy is found sufficient to account for the basic ecological processes of succession.

The 2nd law clarifies *why* nature is in motion. Evidently it is also important to know *how* all this is happening, e.g., by elucidating molecular mechanisms, behavior of organisms and interspecies relations. However, irrespective of the mechanistic details there is no choice about the direction of succession and evolution in general. The high-energy compounds, species, etc. are forming because the high-energy surroundings, e.g., radiation is forcing the natural process to raise the energy density of the ecosystem toward that of its surroundings. The kinetic courses are driven by thermodynamic forces according to Eq. (3.2). The flow equation is not the law of mass action or its variant or the logistic model (May, 1976; Kot, 2001; Otto et al., 2007) in which only the sizes of populations N_j constitute the driving force, not the free energy. Despite the conceptual inaccuracy in these commonly applied models it is possible to obtain a good agreement with data when the rate constants σ_{jk} are allowed to vary during the process. However, then kinetics and thermodynamics appear incompatible with each other.

The species that are more and more effective in leveling energy density differences are naturally selected by the flows of energy (Annala and Salthe, 2010; Darwin, 1859; Sharma and Annala, 2007). They provide the shortest available paths, i.e., geodesics for the most voluminous energy flows down along the gradients to level a curved non-Euclidian energy landscape toward the stationary state (Kaila and Annala, 2008). In other words, the species at higher and higher trophic levels may exist only due to their more and more effective mechanisms to access and draw from larger and larger potentials and thus diminish free energy. The species, at molecular, cellular, organism or any other level of hierarchy acquire their definitions, identities or phenotypes, in mutual interactions that generate the numerous flows of energy. The ways of interacting are many but the objective is the same, to diminish energy density differences in least time.

The self-similar and holistic thermodynamic description of open systems is consistent with the common consent about the role of energy transduction in ecosystems (Lotka, 1925; Morowitz, 1968). The solar-powered primary production by autotrophs generates increasing μ_j as long as $A_j > 0$. The resulting primary potential μ_j is, in turn, a source of chemical potential μ_k for other species j' , primary consumers to tap into. Thus these may also appear and survive on the ground and raise their potentials $\mu_{j'}$ as long as the corresponding thermodynamic gradient remains positive ($A_{j'} > 0$). Likewise, species j'' predators and parasitoids will succeed species j' to inhabit the island as long as each of them will find the corresponding supplies ($A_{j''} > 0$). In this way, species at higher and higher trophic levels, defined by increasing G_j , the thermodynamic 'price', will succeed each other and populate the initially barren island. The more recent species will establish themselves only when they possess more effective mechanisms to find and tap into free energy. Eventually, when no new mechanisms and no more matter and no more energy is recruited to the natural process, all species will settle to the steady-state populations governed by the condition

$\mu_k + \Delta Q_{jk} \approx \mu_j$ that yields the size of j -population

$$N_j = \prod_k N_k e^{(-\Delta G_{jk} + i\Delta Q_{jk})/k_B T} \quad (3.3)$$

which is the familiar stationary-state condition of a reaction in the presence of an energy flux (Sharma and Annala, 2007). The succession has reached the steady state known as the climax. It is the most probable state since all energy density differences, i.e., forces have vanished. Frequent interactions at the steady state are the rapid to-and-fro flows of energy that maintain the balance. Thus thermodynamics is re-expressing the basic notion that biomass is maintained by an incessant influx of external energy.

Eqs. (3.1) and (3.2) reveal that kinetics of energy transduction takes the *downward* direction to diminish the free energy. Nevertheless, it may appear as if the species at high trophic levels are extracting the energy from their environments *upward*. This incorrect view results when narrowing the perspective to the immediate surroundings of an organism that do not contain sufficient energy to support it. Then the high-energy individual indeed appears improbable, i.e., low in entropy. However, when including the entire surroundings that the individual is interacting with, the energy flow is *downward* to the high-energy individuals that are then indeed probable to exist ($A_{jk} > 0$). The 2nd law of thermodynamics, given by Eq. (3.1), expresses interdependence among species, i.e., the ecological integrity where no species is detached from its surroundings.

4. On the Definition of Diversity

When the ecosystem evolves by acquiring new mechanisms of energy transduction to consume more and more free energy, more and more distinct pools of energy densities will amount. These are the populations of diverse species. Thus diversity grows on diversity. Customarily the number of species is taken as the ecosystem's status measure. However, according to the 2nd law, entropy

$$S = k_B \sum_{j=1} N_j \left(1 - \sum_k \frac{A_{jk}}{k_B T} \right) \quad (4.1)$$

which is available from Eq. (2.2) (Sharma and Annala, 2007) is the self-consistent measure of the status. Its maximum $S_{\max} = k_B \sum_j N_j^{\text{ss}}$ at the steady-state populations N_j^{ss} means that there are no more energy density differences to be consumed, i.e., $A_{jk} = 0$ for all j - and k -species. During succession the net dissipation per average energy of the system is decreasing as S is increasing toward S_{\max} . Earlier this relationship has been phrased qualitatively so that the rate of dissipation per biomass is decreasing toward the climax (Margalef, 1968).

The thermodynamic definition of a species covers all levels of hierarchy with no difference between abiotic and biotic; no particular mechanism of reproduction is defined either. The highest value of class index j in the summations of Eqs. (2.2), (3.1) and (4.1) is the species richness which is left unbound. There is certainly an ultimate limit for a given amount of basic constituents and energy input, but *a priori* the maximum is unknown. It cannot be predicted either. The natural processes are inherently non-deterministic because the density differences as driving forces are inseparable from the energy flows that in turn affect the forces (Eq. (3.1)) (Sharma and Annala, 2007). In plain language this means that a flock of a species is a stock of another.

Importantly, the number of species does not need to be at the maximum at the climax state. The maximum species richness does not have to correspond to the maximal energy transduction because a fewer number of highly effective species may reach higher entropy than a larger number of less effective energy

transformers. This is in contrast with the diversity definition by Shannon (information entropy) which is frequently used in ecology (Demetrius, 2000; Wagensberg and Valls, 1987). However, Shannon's definition only counts the number of species but omits their mutual relations imposed by the imperative of gradient reduction in the energy transduction. Therefore, information entropy misses the free energy as the driving force to diversity and comes up with a maximum where populations of all species, irrespective of their trophic levels, are equal. This seemingly unnatural outcome has been corrected *ad hoc* by introducing constraints to reproduce the skewed distributions of species (Pueyo et al., 2007; Dewar and Porté, 2008). The procedure is analogous to that when the total energy and particle number are held invariant when the equilibrium distribution of a physical system is determined using Lagrange's multipliers. However, normalization of probabilities and using preset constraints are not physically motivated because the open ecosystem is naturally evolving toward the steady state by redirecting its course as it works forward by consuming the free energy. The process that acquires energy from the surroundings is without invariants of motion and inherently non-deterministic. Relationships between thermodynamic entropy and other diversity indexes are more elaborate and approximate to establish. Admittedly, the entropy given by Eq. (4.1) as the self-consistent measure of the ecosystem may not be all that practical for data collection purposes but it nevertheless reveals that the free energy is the source of succession and evolution in general.

It is insightful to rearrange Eq. (4.1) by multiplying entropy S with T (assuming a sufficiently statistical system for which T is nearly constant during each transition) to obtain the energy balance

$$TS = T \sum_{j=1} S_j = \sum_{j=1} N_j k_B T - \sum_{j=1} N_j A_{jk} \quad (4.2)$$

for the system of diverse species j . The first term on right counts the members of a species j but among the indistinguishable there are no density differences to draw from. The second term contains interactions between j and other species k including external energy. As long as $A_{jk} > 0$, there are still density differences for j to benefit from and to increase N_j . If $A_{jk} < 0$, N_j is overpopulating the system. Thus N_j will be soon decreasing and the associated energy will be released for the benefit of others N_k in the ecosystem as well as dissipated into the cold space.

The equations for S (Eq. (4.1)) and dS/dt (Eq. (3.1)) can be used to show that the mature ecosystem is Lyapunov stable (Kondepudi and Prigogine, 1998; Strogatz, 2000) against population fluctuations δN_j about the maximum entropy distribution. These characteristics of system dynamics are available only when entropy and its change are known, not via phenomenological mathematical models (Kot, 2001; May, 1973; Murray, 1989) but without physical correspondence. A particular steady-state system, e.g., prey-predator populations and substrate-product concentrations (Kondepudi and Prigogine, 1998), may also oscillate when the flows of energy repeatedly over-exhaust a local maximum on the energy landscape and thus turning it to a local minimum. Such pendulum motions are familiar from simple closed conserved physical systems. The steady-state dynamics of an ecosystem can be intricate but the principle is simple. Often fluctuations are driven by variations in the surrounding supplies to which the ecosystem has to adapt to. In particular, annual and circadian successions follow from the regular variation in the radiation density ΔQ_{jk} . Also sporadic external perturbations command the ecosystem.

5. Simulated Succession

The salient features of succession, *i.e.*, accumulation of biomass, increasing consumption of energy, increasing stratification and

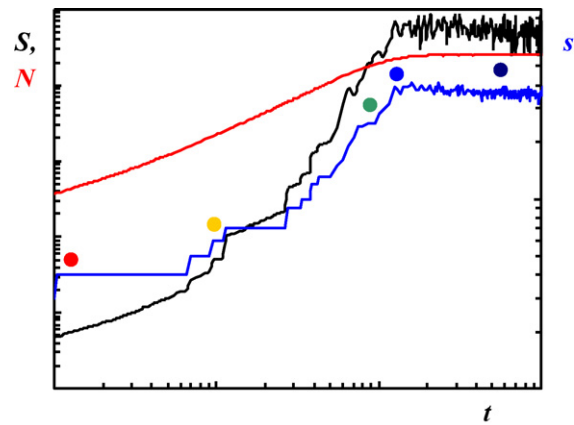


Fig. 1. Simulation of ecological succession (see Appendix for detailed description). Entropy as the ecosystem's status measure (S , black), the total amount of biomass (N , red) and number of species (s , blue) (on logarithmic scales), as a function of time t (on logarithmic scale) were obtained from a simulation. The succession was simulated as series of time steps according to the flow equation (Eq. (3.2)). A species j was able to survive in the ecosystem when its chemical potential μ_j was below the chemical potential of its ingredients (food) μ_k including external energy ΔQ_{jk} that coupled to the syntheses (proliferation). In the thermodynamic sense a species is a mechanism of energy transduction. Every time a new mechanism appeared in the ecosystem, entropy increased rapidly as more matter and energy were recruited to the natural process. The succession continued as long as more external energy could be recruited to the process and as long as there were internal energy density differences to be leveled within the ecosystem. The common characteristics of energy dispersal processes are independent of scale and therefore the monitored variables are given in arbitrary units. Distributions for species were sampled for Fig. 2 at the time points indicated by colored symbols. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

diversity as well as skewed species distributions that shift toward higher trophic levels, are identical for simple and complex systems. These scale-independent characteristics follow from the 2nd law given as the equation of motion (Eq. (3.1)). The simple equation cannot be solved analytically because forces and flows are inseparable. Nevertheless the course of succession can be demonstrated by a simulation.

The succession was simulated according to the flow equation (Eq. (3.2)) as described in Appendix. During the simulated succession (Fig. 1) the appearance of diverse j -species in the ecosystem is modeled so that at each time step some are drawn randomly from the distribution of species representing the surroundings. In terms of ecology, during the initial period of colonization when competition is low, the chance arrival determines the composition of pioneering communities (Margalef, 1963, 1968). In our simulation abiotic, stable ($G_1 = 0$) substances are abundant, *i.e.*, in high concentration (N_1). Therefore these basic constituents are often chosen by the random selection as immigrant species. These abiotic species, representing dust and dirt carried by winds on the barren island, will obviously "survive". Sporadically also metastable ($G_j > 0$) species, corresponding to biotic species, will arrive at the system. However, when the corresponding free energy is negative ($A_{jk} < 0$) on the island system, the particular species remain improbable, *i.e.*, Eq. (3.2) will direct these species toward degradation. In other words, the high-energy species cannot survive at the early stages of succession.

The high-energy species will survive at later stages of succession when enough other species at lower levels have already accumulated in large enough numbers and in high enough energy content during the transport processes from the surroundings and endogenous syntheses powered by external energy (ΔQ_{jk}). The external energy input is the vital gradient that will drive the ecosystem from the equilibrium toward the more probable non-equilibrium states.

In nature high-energy species result from a series of chemical reactions. Many reproduction stoichiometries are evidently more elaborate to specify than the simple assemble rule used in our simulations, however the principle is the same. Even the simple linear stoichiometry means that the j -species at high trophic levels are able to proliferate first when lower levels of energy transduction system, *i.e.*, diverse k -species are abundantly present.

The simple model system with its specific functional forms for the rates and thermodynamic level structuring was not intended to reproduce the succession of any particular natural system but to expose the common principal characteristics. It is emphasized that the simulation was based on the flow equation (Eq. (3.2)) and entropy was only monitored. When simulating succession, it is only essential that the flows are proportional to the free energy. Then the system, irrespective of its size and rates of syntheses and degradations, will evolve without further guidance toward a climax—how fast and how far the course will advance depends on the amount and properties of available ingredients. In other words, not every ground and influx of energy will be able to support a rich ecosystem.

Entropy (S), external energy consumption, total biomass ($N = \sum jN_j$) and the number of levels as well as the number of species (s) were found to increase during the simulations of succession (Fig. 1). Every time a new mechanism of energy transduction appeared in the system, the otherwise approaching stasis was punctuated by a rapid growth phase (Eldredge and Gould, 1972). A new mechanism, *i.e.*, a species gained ground only when it was able to contribute further to the increase of entropy by tapping into potentials. This corresponds to finding a habitant in the thermodynamic sense. The invaders that were not able to contribute to entropy remained improbable. In plain language they had not found food. They perished by degradation to lower level entities. On the other hand, when the species in succession were able to profit from their effective and sophisticated mechanisms, the early pioneers with their primitive and robust mechanisms of energy transduction lost ground and eventually vanished altogether. In thermodynamic terms, the early pioneers were too ineffective by their rates σ_{jk} to reduce free energy in comparison with their recent rivalries.

The total biomass $N = \sum jN_j$ is increasing during the course of succession as the ecosystem is acquiring more and more energy from its surroundings with its more and more effective mechanisms (Fig. 1). Thus energy contained in the system's biomass and interactions is increasing. When approaching the climax, the free energy resources narrow and the net dissipation per the system's energy is decreasing. Thus, the thermodynamic formalism presented here motivates the reasoning that dissipation per biomass is decreasing during succession (Margalef, 1968).

During succession the thermodynamic level restructuring is inevitable. The whole ecosystem dynamics changes during the stages of succession because all species are interdependent and share, by the continual cycles powered by external energy, common ingredients. In other words, the potentials amount when the system acquires more and more energy from its surroundings. The overall course of succession is sigmoid but unpredictable in the detailed trajectories, *i.e.*, non-deterministic (Sharma and Annala, 2007) (Fig. 1). The condition of *ceteris paribus* is characteristic for systems with conserved currents (Noether, 1918), but it does not hold among interdependent energy densities of an open system. Small early changes affect later courses. This chaotic nature of the process is seen already in the simple simulations that are sensitive to the initial conditions. The initial courses are even chaotic because the small system is not sufficiently statistical, *i.e.*, $A_{jk} > k_B T$. The new species that appear sporadically result in rapid changes in a small system but later when the system increases its size and diversifies in composition, the course of succession becomes statistically more and more predictable. There-

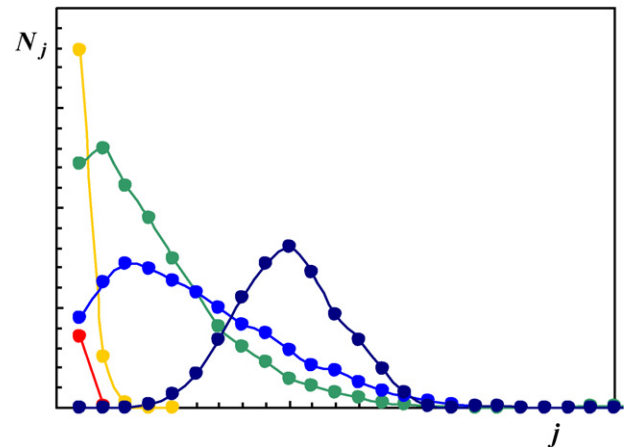


Fig. 2. Simulated trophic level distributions. Populations N_j of species at levels j were sampled from the simulated succession at the colored points marked in Fig. 1. The distributions shifted toward higher levels as the ecosystem grew. The maximum-entropy partition, the climax housed the mechanisms of energy transduction that contributed most to entropy. The particular form of distribution depended on the trophic level spacing as well as on the rates that the species consume the free energy. Early distributions were abundant in pioneer mechanisms, however later these lost ground to more effective mechanisms of energy transduction.

fore an outcome of re-run succession, *e.g.*, growth of a forest after a fire, is somewhat different, not in its overall distribution of chemical energy among species and general organization of energy transduction network, but in its mechanistic and trophic details. Convergence of succession due to driving gradients has been proven also using physico-chemical parameters (Christensen and Peet, 1984). The specific mechanistic and energetic details of a particular ecosystem can be incorporated in models based on the aforementioned equations by denoting more and more species by G_j and annotating mutual jk -interactions more and more specifically.

When more matter and energy are recruited to the open system by its mechanisms of energy transduction, the distribution of species is shifting from the initially abundant low- j -species to peak later at intermediate- j -species (Fig. 2). The increasingly larger integrated distribution becomes more and more skewed toward rarity, *i.e.*, high- j -species when the ecosystem continues to increase in entropy. The skew is characteristic of distributions resulting from natural processes (Grönholm and Annala, 2007; Jaakkola et al., 2008b; Würtz and Annala, 2008). The distinct shift in the trophic level occupancy is usually stated in reference to the logistic model as an r -selection for the developmental stages and a K -selection for the mature stages. This makes sense since the logistic model $dN_j/dt = r_j N_j (1 - N_j/K_j)$, despite being deterministic by the fixed capacity K_j , is often an excellent approximation of the non-deterministic flow dN_j/dt (Eq. (3.2)).

Finally, when no new mechanisms are able to extract more energy and matter to the natural process, the dissipation will attain its maximum. Energy cannot be dispersed any further at the free-energy minimum state. In mathematical terms of non-linear dynamics (Strogatz, 2000), the total attraction of the free energy landscape will not grow any bigger and no new fixed points, *i.e.*, species, will appear. There are no more density differences, *i.e.*, ecological niches available for new species to habit. The attained stationary state is conserved in energy and, in accordance with Poincaré recurrence theorem, reversible in time. Closed orbits, *e.g.*, steady and fluctuating populations as well as cyclic variations might be found. When these transient phenomena are averaged, *i.e.*, integrated over the characteristic times, the distribution of species corresponds to the most probable partition of energy among all thermodynamic levels. This partition uses opti-

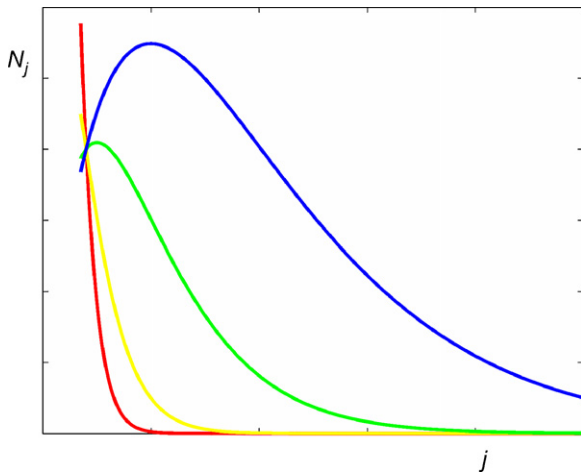


Fig. 3. Calculated distributions of species. Populations N_j of species at increasingly high thermodynamic level j were obtained from the average thermodynamic relation of Eq. (6.1) for ecosystems whose succession had stalled due to external perturbations at increasingly high-entropy (diversity) states (red, yellow, green and blue). The early pioneers were capable of increasing entropy from scant resources and were abundant in numerous small primitive systems but low in the fewer larger sophisticated systems where species equipped with more effective but demanding mechanisms of energy transduction proliferated. The particular form of distribution depends on the thermodynamic level spacing and on the rates of energy transduction specific to the species. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

mally all available free energy to sustain the maximum-entropy non-equilibrium state.

From time to time the climax system may fail to replenish its energy transduction mechanisms swiftly enough to maintain constantly the high-entropy state. Consequently a post-climax fall will follow because the stationary state supplies are not sufficient to restore the vital but metastable mechanisms that emerged during the natural process. Per definition there are no gradients to power restorations at the climax. Thus individual agents at each hierarchical level from molecules to ecosystem will subsequently tend to senesce and become recycled (Salthe, 1993), but the population of them will replenish its individuals by reproduction. For example, an old forest with its deteriorating mechanisms is declining in energy transduction but unable to revive until fallen down for the sunlight to reach down on the forest floor and power a new growth to towards the climax.

6. Distribution of Energy in Climax Systems

Temporal course of succession may be perturbed from time to time by shifting external conditions, *i.e.*, varying thermodynamic gradients. Recurrent interference, *e.g.*, imposed by shifting sand dunes (Cowles, 1899) or forest fires (Westman, 1981), may result in a variety of ecosystems. These systems are stalled at the various stages of succession depending on the amplitude and frequency of external perturbations. The systems will not be able to evolve to the climax of the unperturbed system by acquiring new j -species because corresponding free energy terms A_{jk} fluctuate and remain too low over the characteristic time that would be required to raise a population N_j .

A series of distributions were calculated for stalled ecosystems at different stages of succession when the total amount of matter N and energy in each system was distributed optimally, *i.e.*, when all gradients had vanished at the entropy maximum $S = k_B \sum N_j$ (Fig. 3). The species richness s and distributions of species at thermodynamic levels j were obtained from the average relation, *i.e.*, the

condition of stationary state (Würtz and Annala, 2008)

$$N = \sum_{j=1}^s j N_j = \sum_{j=1}^s j N_1^j e^{(-\Delta G_{j1} + i \Delta Q_{j1}) / k_B T} = \sum_{j=1}^s j e^{\gamma(j-1)} \quad (6.1)$$

that expresses the amount of basic substances N_1 and energy ΔQ_{j1} in the populations N_j at equidistantly spaced trophic levels. For simplicity the series was terminated so that each ecosystem housed only one individual $N_s = 1$ at the top of the food web. These approximations served only to calculate distributions but the actual process that results them is intractable (Sharma and Annala, 2007; Annala, 2009).

The calculated distributions are as expected (Fig. 3). A severely and frequently disturbed terrain houses numerous loosely connected small and ineffective systems whereas a mildly perturbed environment may constitute one large and mostly integrated energy transduction system. The corresponding trophic distributions for larger and larger systems display the characteristic increase of species richness as well as the typical shift toward higher levels. The detailed forms of distributions depend once again on the mechanisms of energy transduction and level spacing. In all cases the steady-state distributions of species report from their contributions to the overall energy transduction in the ecosystem.

Fluctuations that halt succession and result in a fragmented energy landscape of loosely connected ecosystems can be viewed also to result from exploitations by man (Margalef, 1968). Survival of species in the fragmented landscape is of current interest to provide guidelines for environmental projection (Hanski, 1998).

7. Discussion

The view of succession as a thermodynamic scenario is not new but follows from the maximum entropy production principle that has been used earlier to account for numerous natural phenomena. The additional value of this study is that it employs the connection between the principle of increasing entropy and decreasing free energy based on statistical physics of open systems (Sharma and Annala, 2007; Kaila and Annala, 2008). Using the universal law of energy dispersal the formalism shows that the salient characteristics of ecosystem succession are thermodynamic consequences, not results of specific kinetic processes.

The ecological succession is an intricate phenomenon. Therefore it is useful to know that its salient features, growing biomass production and increasing stratification measured by number of thermodynamic levels and accumulation of diversity measured by entropy as well as skewed distributions of species that shift toward higher trophic levels, are thermodynamic outcomes, not results of particular mechanisms. Of course, this is no news because for a long time it has been understood that the early view of initial conditions having an impact on the final organization of an ecosystem (Egler, 1954) does not hold true for any sufficiently statistical system. The thermodynamic analysis shows that the succession advances by bursts, *i.e.*, punctuations (Eldredge and Gould, 1972) when a new species appears. Initially the system enjoys from a new source of free energy but when the supply begins to diminish, the course turns itself toward a stasis. Finally, it can be shown that the climax is stable with respect to random fluctuations in the established populations but the ecosystem is sensitive to new invaders and other external changes. Importantly, the climax does not have to coincide with the maximal species richness. The maximum entropy state is most effective, but not necessarily most diverse, in the free energy reduction.

Notably the succession can be described by the same theoretical framework of evolution by natural selection based here on statistical physics of open systems as other evolutionary phenomena. Nevertheless, the description may at first appear unfamiliar and

inconceivably concise to account for anything as complex as the evolution of an ecosystem. However, Eqs. (2.2), (3.1) and (4.1) enumerate all species and all interactions in a self-similar manner. In other words, the energy transduction network from abiotic via the primary production to the top of food web is described including every quantum of energy and every entity of matter. The holistic and hierarchical account is extremely detailed despite being concise in its notation.

It may appear that the statistical physics description of succession as a natural process would overlook the role of inheritance (information). On the contrary, the natural process advances in steps that are based on previous steps. Hereditary mechanisms conserve and propagate the information about the previous steps for the process to take the next step in consuming free energy. Thus the hereditary mechanisms have been selected during evolution due to their high functional value in increasing entropy. Also the genetic information owing to its physical representation is subject to the same thermodynamic imperative of maximal energy dispersal (Jaakkola et al., 2008b; Karnani et al., 2009).

The equation of motion for evolution (Eq. (3.1)) clarifies concepts about entropy and energy. Also in biological processes entropy is increasing when energy density differences are decreasing. Often but erroneously the biological structures are seen to imply that processes of life would be decreasing entropy at the expense of its surroundings. Such a thought does in fact violate the conservation of energy (Tuisku et al., 2009). The orderly structures are mechanisms of energy transduction for the system to reach high-entropy non-equilibrium states. The agents, despite being orderly structures, are not unlikely. On the contrary, they are likely when supported by the free energy. The principle of increasing entropy by decreasing free energy accounts for the structure-functional organization of matter from atoms to biosphere. The entire global system works to diminish the huge thermodynamic gradient between the Sun and the cold space (Annala and Kuismanen, 2008; Karnani and Annala, 2008; Vogel, 1988).

The succession described in thermodynamic terms rephrases the very idea brought up already in 1860 by Henry David Thoreau in his essay “The Succession of Forest Trees”, an accurate analysis by eloquent words of the intricate interplay among the many biotic and abiotic constituents that make and shape our environment. In the large global ecosystem restructuring and reorganization processes in response to external and internal changes may take eons. The use of non-renewable resources is irreversibly affecting the scope of future states. Therefore evolution, anchored to the principle of increasing entropy, bears importantly on the relationship between man and nature (Odum, 1969).

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Appendix A.

Simulation of ecological succession demonstrates the basic principles and scale-independent characteristics of thermodynamic processes. The course of succession is simulated so that the ecosystem evolves step by step according to the flow equation (Eq. (3.2)). The series of steps is programmed as a for-loop. We require that the system is sufficiently statistical by choosing the step size sufficiently small so that the change in energy in each step remains small in comparison with the total energy of the system. At each step the chemical potential $\mu_j = k_B T \ln(N_j \exp(G_j/k_B T))$ of each species j is calculated from its current population N_j and designated energy

level value G_j that is given relative to the average energy $k_B T$ per species. The energy levels are spaced exponentially to signify that increasingly more matter and energy go to assemble more and more effective species. At each time step a k -species and a k' -species are randomly chosen from the distribution of currently existing species for an endergonic (absorbing energy ΔQ_{jk} from the surroundings) synthesis to yield a j -species according to the simple stoichiometry $k + k' \rightarrow j$. When the corresponding free energy term $A_{jk} = \sum \mu_k - \mu_j + \Delta Q_{jk}$ that includes the external energy ΔQ_{jk} is >0 , couples to the jk -synthesis, N_j will increase and N_k and $N_{k'}$ will decrease. Conversely, when $A_{jk} < 0$, the N_j population will breakdown in an exoergonic process and yield increasing populations N_k and $N_{k'}$ according to the flow Eq. (3.2). The rate of energy transduction is modeled by $\sigma_{jk} \propto \sum \mu_n \exp(-\mu_n)$, $n < j$, including random variation (up to 10%). The particular functional form of σ_{jk} mimics the skewed, nearly log-normal distributions of species (Grönholm and Annala, 2007; Rosenzweig, 1995) and assigns more and more effective mechanisms for the species at higher and higher thermodynamic levels. Likewise, at each time step a j -species is randomly chosen from the distribution of currently existing species for an exergonic (emitting energy ΔQ_{jk} to the surroundings) degradation to yield k and k' -species according to the simple stoichiometry $j \rightarrow k + k'$. Thus, at the thermodynamic steady state, the syntheses requiring influxes and the degradations yield effluxes of energy to and from the ecosystem are equal.

The simulation is not predestined to the free energy minimum of the climax state but the flow equation itself redirects the course over and over again by diminishing free energy. No *ad hoc* terms are used to guarantee the “memory” of the previous state, such as used in Markovian models, because the chemical potentials of large populations themselves hold sufficient capacity so that the overall course of succession is smooth. Only at the times when a new immigrant species is able to proliferate rapidly the succession punctuates. These sporadic events are inherently non-deterministic but the overall rate of succession and the climax state depend only on the size of the system given in terms of N_j and parameter values G_j and ΔQ_{jk} . In our simulation the initial monotrophic state of the simulated ecosystem contained only the basic (abiotic $G_j = 0$) species N_1 . At each time step entropy is calculated according to Eq. (4.1). All populations ($j > 1$) that incorporate energy ΔQ_{jk} from the surroundings in their syntheses are included in the calculation of the total biomass according to the $N = \sum j N_j$. The number of species s present at each time step is the sum of j 's for which $N_j > 0$.

Population distributions of natural processes are skewed, nearly log-normal whose cumulative curves on log-log plot are mostly straight lines, i.e., power-laws (Grönholm and Annala, 2007). Familiar examples of natural distributions are also Maxwell-Boltzmann velocity distribution and Planck radiation law. The steady-state partitions of these energy densities sum up as convergent series. In the same way, the distribution of species in the ecosystem is limited by the total amount of energy, i.e., ingredients as denoted by Eq. (6.1). The steady-state partitions for increasingly larger systems were calculated as before (Würtz and Annala, 2008) symbolically and numerically using Maple software (<http://www.maplesoft.com/>).

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