

Thermodynamic stability of ecosystems

K. Michaelian*

Instituto de Física, Universidad Nacional Autónoma de México, A.P. 20-364, 01000 México D.F., Mexico

Received 14 May 2004; received in revised form 29 March 2005; accepted 25 April 2005

Available online 22 June 2005

Abstract

The stability of ecosystems during periods of stasis in their macro-evolutionary trajectory is studied from a non-equilibrium thermodynamic perspective. Individuals of the species are considered as units of entropy production and entropy exchange in an open thermodynamic system. Within the framework of the classical theory of irreversible thermodynamics, and under the condition of constant external constraints, such a system will naturally evolve toward a globally stable thermodynamic *stationary* state. It is thus suggested that the ecological steady state, or stasis, is a particular case of the thermodynamic stationary state, and that the evolution of community stability through natural selection is a manifestation of non-equilibrium thermodynamic directives. Furthermore, it is argued that punctuation of stasis leading to ecosystem succession, may be a manifestation of non-equilibrium “phase transitions” brought on by a change of external constraints through a thermodynamic critical point.

© 2005 Elsevier Ltd. All rights reserved.

Keywords: Ecosystem stability; Stasis; Punctuated equilibrium; Classical irreversible thermodynamics; Diversity–stability debate; Ecosystem succession

1. Introduction

Our understanding of the evolutionary dynamics of living systems on all scales has lately developed from one based solely on gradualist Darwinian evolution through natural selection at the individual level to one embracing *punctuated equilibrium* (Eldredge and Gould, 1972), a scenario of large periods of stasis punctuated by episodic evolutionary change, with selection acting not only at the individual, but also at gene, species, and possibly higher levels (Gould, 2002). Stasis, once considered as an uninteresting triviality, now forms an important focus of evolutionary study at all levels of the hierarchy of life on Earth (Jackson and Cheetham, 1994; Cheetham and Jackson, 1995). In fact, paleontologists and ecologists, impressed by the ubiquity of stasis (Williamson, 1981; Wake et al., 1983; Gould, 2002) have argued for the search of an active force of stabilization (Paul, 1985).

Stasis and punctuation of stasis is perhaps no better apparent than at the level of ecosystems. It is known that from their inception ecosystems go through a series of successional stages (Goldsmith, 1985), each stage generally being more diverse, complex, and more stable than the previous one (Odum, 1963, 1969, 1983; Margalef, 1963). We also know that the jump between successional stages occurs in a relatively short time span, and that most of the time, most ecosystems may be found in stasis, or in what is generally referred to as ecological *steady states*. In these states, species populations are either fixed or oscillate regularly, or perhaps even chaotically, but always about some fixed point in population space which is surprisingly stable to external perturbations. Every so often, however, rapid extinctions and speciations give rise to succession, instigated perhaps by either a critical change in the external conditions or by intrusion of a new species into the ecosystem. The lack of “missing links” between species, and between successive ecosystems, in the fossil record is an empirical fact, now taken as evidence of stasis punctuated by episodic change, prevalent at all levels of

*Tel.: +52 55 5622 5165; fax: +52 55 5616 1535.

E-mail address: karo@fisica.unam.mx.

living systems and to the earliest times of life on Earth (Gould, 2002).

At the species level, punctuated equilibrium may be described (Gould, 2002) from within Darwinian theory of selection of the individual by allowing for Mayr's (1963, 1971) theory of allopatric speciation. Small populations of a particular species which become isolated geographically or otherwise from the main population are no longer subjected to dilution of their gene pool by the larger parent population and thus have an opportunity to evolve rapidly, perhaps forming new species. If such a new species becomes repatriated with the parent species and has some particular advantage over it in the same environment, then the new species may competitively cause the extinction of the parent species. Links between the two species are missing in the fossil record simply because rapid evolution occurred on a small population which was also geographically limited.

Going up the hierarchy of living systems however, it becomes increasingly difficult to explain the macro-evolutionary dynamics of stasis and punctuation from within Darwinian theory. This because the individual units become further and further removed from the traditional Darwinian objects of selection and reproduction, their numbers dwindle so competition loses significance, and an appropriate target of selection becomes elusive. This limitation of the traditional theory has since been emphasized by Swenson (1997) who has labeled it *the problem of the evolution of a population of one*. At these scales, the macro-evolutionary dynamics of living systems is thus an enigma, indicating a need for a more encompassing theory, one which might be effective at all levels of the hierarchy of living systems.

A more encompassing framework might be grounded in non-equilibrium thermodynamic theory for a number of reasons: (1) Thermodynamic laws are the most universal of all laws and they work on all scales in similar ways, allowing for a unified hierarchical description. (2) The study of the macroscopic behavior of whatever complex system benefits from a reduction in the number of variables to a smaller number of effective variables. Such a reduction is missing in traditional ecological theory and has led to an impasse in accounting for macro-evolutionary patterns. Thermodynamics, on the other hand, was developed in the physical sciences specifically out of this need to find a reduced number of relevant variables to describe macroscopic phenomena. (3) *Stasis* and *punctuation* have intriguing analogues in the form of non-equilibrium thermodynamic *stationary states* and *phase transitions*. (4) The problem of an elusive target of selection at higher than the species level, or, more specifically, the problem of the evolution of a system of a population of one, is solved because it can be reduced to a number of thermodynamic directives involving the entropy production.

A shift in ecosystem analysis from a descriptive paradigm to one based on physical laws began with the seminal work of Lotka (1922) concerning the flow of energy through an ecosystem. The possibility of framing ecology within a quantitative non-equilibrium thermodynamic paradigm, however, was first recognized by Schrödinger (1944) who pointed out that living systems were under the dictates of thermodynamic law and that biological structure and processes were maintained by a continual in-flow of negative entropy, at the expense of an entropy increase of the environment. Apart from developing the physical and mathematical ground work for the description of non-equilibrium phenomena, Prigogine (1967) has emphasized the remarkable similarity in characteristics that living systems share with thermodynamic stationary, non-equilibrium states. Schneider and Kay (1994) have argued, in a qualitative but convincing manner, for the description of ecosystem characteristics in terms of non-equilibrium thermodynamic theory. Zotin (1990), Chakrabarti et al. (1995), Svirezhev (2000), and Zotin et al. (2001) have advanced the use of non-equilibrium thermodynamic concepts to living systems on a number of levels, including ecosystems, while Swenson (1989, 2000) has addressed more general evolutionary principles in living systems from the thermodynamic viewpoint.

The present article may be considered as a continuation of previous work in incorporating living systems, specifically ecosystems, into a non-equilibrium thermodynamic framework. In particular, we consider the possibility that thermodynamic directives may be the basis of the active agent promoting stasis in ecosystems. In the following section, it is shown that stasis is a non-trivial problem in the traditional ecological framework since a simple mathematical analysis shows that any complex interacting system, whether mechanical, chemical, or biological, will have little chance of being stable unless the interaction strengths between its component parts are very carefully chosen and continually maintained. A biological cause of such stabilization, for example through natural selection at the ecosystem level, however, remains elusive, leading to a stubborn complexity–stability paradox (May, 1972, 1974; Pimm, 1991; McCann, 2000).

In this article, ecosystems are considered as open thermodynamic systems subjected to a number of external constraints imposed by the external environment. For certain periods, these abiotic constraints may be considered as being relatively constant and, according to classical irreversible thermodynamic theory, such an ecosystem will necessarily evolve toward a globally stable thermodynamic stationary state. The irreversible evolution toward the stationary state is an empirical fact for all abiotic systems under constant external constraints. This must arguably also be the case for biotic systems if indeed biological processes are under the

dominion of the same physical laws as chemical, transport, and mechanical processes. It is thus suggested that the ecological steady state, or periods of stasis in ecosystems, is a particular manifestation of the thermodynamic stationary state. Furthermore, it will be shown that evolution of the species interaction coefficients leading up to this period is driven necessarily in the direction of securing and maintaining global stability by thermodynamic restrictions on the entropy production and on the rate of change of the entropy production, independent of the size or complexity of the ecosystem. The resolution of the complexity–stability paradox in terms of these non-equilibrium thermodynamic directions constitutes the basic result of this paper.

The present work on ecosystem stasis can be seen to fit in well with more general macro-evolutionary dynamics of ecosystems in the punctuated equilibrium paradigm. For example, from the thermodynamic viewpoint, and in the more general case of variable external constraints, a change in these constraints through a critical point could cause the ecosystem to leave its stationary state and rapidly evolve toward a new, and possibly more stable, stationary state with a greater internal production of entropy. That this dynamics does indeed occur in the macro-evolution of ecosystems is manifest, for example, in the eventual succession of clear-cut overgrowth to an established deciduous forest with an undeniable increase in stability (Odum, 1963) and entropy production, in apparent agreement with Swenson’s (2000) principle of maximum entropy production. Such a phenomena is indeed also observed in the thermodynamics out of equilibrium of abiotic processes as recognized early on by Prigogine (1967). A simple example being the Bénard phenomena of the sudden transformation to convective cooling from conductive cooling as the gradient of temperature across a fluid under the force of gravity is increased beyond some critical value. These non-equilibrium “phase transitions”, induced by changes through a critical point in the external conditions, may play an important part in episodic punctuation which, together with stasis, define the macro-evolutionary dynamics of the ecosystems toward larger, more complex and apparently more stable systems. In fact, empirical evidence for a correlation of punctuation of stasis with environmental variability, particularly through a critical point, has accumulated (Sheldon, 1996).

The general goal of this article is thus to argue for the utility of a quantitative non-equilibrium thermodynamic framework for the description of the stability and dynamics of ecosystems, while the principle objective is to offer an explanation of stasis in thermodynamic terms and thus hopefully provide a convincing resolution of the complexity–stability paradox.

In the following section, the traditional ecological framework based on the empirical Lotka–Volterra-type

equations is reviewed and the complexity–stability paradox is presented. In Section 3, justification for the application of classical irreversible thermodynamics to some ecosystems during periods of constant external constraints is presented. Section 4 presents a thermodynamic framework for ecosystems and compares results with the empirical approach of classical ecological theory based on Lotka–Volterra-type equations. Section 5 briefly considers those ecosystems far from equilibrium in the nonlinear regime, providing a logical alternative to ad hoc nonlinear extensions of Lotka–Volterra approaches. Finally, Section 6 presents a discussion of the results and the conclusions.

2. The traditional ecological framework

Population modeling in the traditional ecological framework is based on (May, 1974),

$$\frac{dp_\gamma(t)}{dt} = F_\gamma(p_1(t), p_2(t), \dots, p_n(t)), \quad (1)$$

where F_γ is, in general, some empirically inspired, nonlinear function of the populations p_γ of the n species γ . For example, for the popular Lotka–Volterra equations (which have the stability characteristics of a much wider class of ecological models employed in the literature (May, 1974)), F takes the following form:

$$F_\gamma = p_\gamma \left(b_\gamma + \sum_{\gamma'=1}^n p_{\gamma'} c_{\gamma\gamma'} \right), \quad (2)$$

where b_γ represents the inherent growth rate of species γ in the absence of all other species, and $c_{\gamma\gamma'}$ represents the effect of species γ' on the population growth rate of species γ . Of interest in ecology, because of its frequent occurrence in nature, is the so-called ecological *steady state* in which all growth rates are zero, giving the fixed point, or steady state, populations p_γ^* ,

$$\frac{dp_\gamma^*(t)}{dt} = F_\gamma(p_1^*(t), p_2^*(t), \dots, p_n^*(t)) = 0. \quad (3)$$

The population dynamics and stability in the neighborhood of the fixed point can be determined by expanding Eq. (1) in a Taylor series about the steady state populations

$$\begin{aligned} \frac{dx_\gamma(t)}{dt} = F_\gamma|_* + \sum_{\gamma'=1}^n \left[\frac{\partial F_\gamma}{\partial p_{\gamma'}} \right]_* x_{\gamma'}(t) \\ + \frac{1}{2} \sum_{\gamma''=1}^n \left[\frac{\partial^2 F_\gamma}{\partial p_{\gamma'} \partial p_{\gamma''}} \right]_* x_{\gamma'} x_{\gamma''} + \dots, \end{aligned} \quad (4)$$

where $x_\gamma(t) = p_\gamma(t) - p_\gamma^*$ and the $*$ denotes evaluation at the steady state. Since $F_\gamma|_* = 0$, and close to the steady

state the x_γ are small, only the second term in expansion (4) need be considered. In matrix notation, this gives,

$$\dot{\mathbf{x}}(t) = \mathbf{A}\mathbf{x}(t), \quad (5)$$

where $\mathbf{x}(t)$ is a $n \times 1$ column vector of the population deviations from steady state values, and the so-called “community matrix” \mathbf{A} has the components

$$a_{\gamma\gamma'} = \left. \frac{\partial F_\gamma}{\partial p_{\gamma'}} \right|_* \quad (6)$$

which represent the effect of species γ' on the rate of change of population γ near the steady state.

The solution of Eq. (5) is

$$x_\gamma(t) = \sum_{\gamma'=1}^n D_{\gamma\gamma'} \exp(\lambda_{\gamma'} t), \quad (7)$$

where $\lambda_{\gamma'}$ are the eigenvalues of the matrix \mathbf{A} and the integration constants $D_{\gamma\gamma'}$ are determined from the initial conditions.

From Eq. (7) it is obvious that asymptotic stability near the steady state requires that the real parts of all the eigenvalues of \mathbf{A} must be negative. This condition gives rise to very restrictive relations among the components $a_{\gamma\gamma'}$ of the community matrix \mathbf{A} (May, 1974). For example, it is easily shown that for an unrealistic but demonstrative $n = 2$ species community the following restrictions are required:

$$a_{11} + a_{22} < 0 \quad (8)$$

and

$$a_{11}a_{22} > a_{12}a_{21}. \quad (9)$$

For the Lotka–Volterra equations, Eqs. (2), this implies

$$p_1^*c_{11} + p_2^*c_{22} < 0 \quad (10)$$

and

$$c_{11}c_{22} > c_{12}c_{21}. \quad (11)$$

For a community of an arbitrary number n of species, it can be shown that the requirement that the $n \times n$ matrix \mathbf{A} have all real parts of its eigenvalues negative is equivalent to the demonstration of the existence of some positive definite function $\mathcal{P} = \mathcal{P}(\mathbf{x})$ (Lyapunov function) having its derivative with respect to time negative definite (Barnett, 1990).

The relations between the components of the community matrix needed for ensuring stability of the ecosystem are thus specific. These relations are in fact more specific the more complex¹ the system (May, 1974). Consequently, the probability that a randomly

constructed community will be stable decreases rapidly with the size of the ecosystem, becoming practically zero at an ecosystem size of only about 10 strongly interacting species (Gardner and Ashby, 1970; May, 1972; Yodzis, 1980). This leads to the *complexity–stability paradox*²: Without a mechanism for “fine tuning” and maintaining the community matrix (for example in the sense of Eqs. (10) and (11) for an $n = 2$ species community) there should be little probability of finding stable complex ecosystems in nature. However, most ecosystems are very complex and most are observed in conditions of stability or stasis (Goldwasser and Roughgarden, 1993; Polis, 1991).

The most plausible mechanism from within the ecological framework thus far offered for tuning the parameters of the community matrix is *natural selection* (May, 1974). However, this explanation remains incomplete until the question of how a stable ecosystem could be the target of evolution through natural selection is addressed. In other words, it is a version of the conceptual problem of natural selection working on the evolution of a system of a population of one (the ecosystem) (Swenson, 1997).

3. On the applicability of CIT to ecosystems

Before applying classical irreversible thermodynamic (CIT) formalism to ecosystems, in this section we acknowledge the general conditions under which CIT theory is valid and thus identify which ecosystems may be justifiably treated through CIT theory.

The classical theory of irreversible thermodynamics is the non-equilibrium thermodynamic theory which has been the most empirically tested and universally accepted. The limitations of the theory have been discussed by Prigogine (1967). Generally, the classical theory can be applied to any system for which it can be shown that the Gibbs relation holds locally. For transport processes it has been demonstrated, through a statistical-mechanics approach, that this corresponds to the requirement of linear phenomenological laws between the generalized forces and flows. However, the phenomenological coefficients may still be functions of the state variables. For chemical reactions, it is only required that the reaction rates are low enough to maintain a Maxwellian distribution of the velocities of each reacting component (Prigogine, 1967). Although these conditions may appear restrictive, they have, in fact, been shown, both experimentally and theoretically, to apply to a wide range of real phenomena, particularly to those to be considered here involving transport processes (Vavruch, 2002).

¹Complexity in this ecological context refers to the size and connectance of the ecosystem. Size is defined as the number of participating species and connectance as the percentage of non-zero elements in the community matrix.

²Sometimes, less accurately, referred to as the *diversity–stability debate*.

At the hierarchical level chosen for the analysis here, at which the unit of entropy production and transport within the ecosystem is the individual, the justification for the applicability of linear CIT is shown in the appendix to be obtained by limiting the analysis to interactions between individuals of the one- and two-body form only. In this case, the relations between the generalized forces and the generalized flows (the species populations and the entropy flows, respectively, see below) are indeed linear. By considering the individual as the basic unit of entropy production and exchange within the ecosystem, the details of all “lower” level processes can thus be avoided and ecosystem dynamics, at least to second order in the species interactions, falls under the dominion of CIT no matter how “far” from equilibrium the lower level processes may be.

Limiting species interactions to the one- and two-body terms has in fact been the norm in most ecological studies, as witnessed by the almost exclusive use of a *two-dimensional* community matrix. There is in fact a conspicuous lack of consideration of three-body and higher-order interaction terms in the literature, with few exceptions (de Oliveira and Fontanari, 2000). This may be somewhat justified on the grounds that higher n -body interactions are increasingly unlikely since they require n -body localization in space and time. This lack of consideration of higher n -body terms is certainly not valid however for social species where many-body interactions surely play an important, if not defining, role. In these cases, specific results from linear CIT can no longer be used, but we can however invoke a more general result concerning the negative definiteness of the sign of the change in the entropy production rate due to changes in the generalized forces (Prigogine, 1967).

While the limitation to the two-body interactions gives rise to only fixed-point attractor dynamics in both the traditional ecological Lotka–Volterra framework and the proposed thermodynamic framework,³ limit cycles and even chaotic attractor population dynamics is allowed through the coupling of irreversible processes in this more general n -body, approach. This will be briefly considered in Section 5 while the full development will be left to a forthcoming article.

Coupling of irreversible processes occurring within an ecosystem requires that the processes occur within the same “macroscopic” region. The scale of the macroscopic region being determined by the range of the forces of interaction between ecosystem components. Since, for example, metabolic rates of herbivores can be influenced by the mere sight or smell of a predator at distances of up to kilometers, or days after passage, it is reasonable to presume that the macroscopic space–time

region available for coupling of irreversible processes within an ecosystem can be quite large. Stationary state coupling of irreversible processes (Prigogine, 1967) is a further possibility.

The importance of ascertaining the validity of CIT theory for ecosystems is that it contains an inherent evolutionary principle, valid under constant external constraints; the natural evolution of an open system toward a stable thermodynamic stationary state. Such a principle is obviously a candidate for an active agent promoting stasis in ecosystems. The condition of constant external constraints, however, is certainly not valid for all ecosystems and requires justification for the rest. Such a condition implies that all thermodynamic forces over the ecosystem (principally the energy difference between the incident sunlight and the light re-emitted by the ecosystem at a lower frequency)⁴ are constant in time. This situation may at first consideration not appear to apply to ecosystems which are subject to short term but pronounced variations, for example, diurnal variations of the Sun’s photon intensity, or seasonal variations, such as those experienced at the very northern or southern latitudes. However, it is noted that species responsible for bringing energy and material into the ecosystem, the photosynthesizing plants and bacteria, have developed characteristic survival times⁵ which are long compared with the diurnal variations (that is, plants and cyanobacteria survive day and night variations) such that the thermodynamic force due to the energy and materials gradient provided by the primary producers to the community at large may in fact be considered to be constant to a good approximation.

Seasonal variations of the Sun’s photon intensity, especially at the very northern and southern latitudes, poses a greater impediment to the applicability of CIT. It is thus an intriguing possibility that the markedly different stability characteristics found between tropical and high-latitude ecosystems may have a thermodynamic origin (tropical ecosystems with more constant external constraints are significantly more stable than high latitude systems with more variable external constraints, just as would be expected under the dominion of CIT theory).

Ecosystems recently subjected to a large external perturbation are very likely to be far from equilibrium and a linear relation between the flows and forces (see appendix) cannot be expected. In this case, some results from CIT in the linear regime cannot be justified. However, here again we can invoke the more general

³Neutral cycles are also allowed in the traditional Lotka–Volterra framework but, as argued below, these are not representative of real cyclical phenomena occurring in nature

⁴Other thermodynamic forces, for example the chemical affinities depending on the external concentrations of the compounds, and temperature gradients, can also be argued to be constant for many ecosystems.

⁵The robustness of individuals to perturbations of the external constraints contributes to ecosystem *resilience*.

result of the work of Prigogine (1967) which shows that the change in entropy production due to changes in the generalized forces is always negative, independent of the systems closeness to equilibrium. This, along with the second law of thermodynamics, provides the necessary and sufficient conditions for the evolution toward stability. This will be briefly studied in Section 5.

4. The proposed thermodynamic framework

We define the *ecosystem* as comprising all organisms usually considered as being alive and having a causal link to at least one other organism in the system. Everything else is considered as composing the *external environment*. The ecosystem is thus an open thermodynamic system receiving a constant negative entropy flow derived from the primary producers utilizing sunlight to produce usable energy through photosynthesis. One-body interactions between the individuals and their external abiotic environment, including the transport of energy and material into, or out of, the system, and two-body and higher-order interactions internal to the ecosystem, between the individuals of the species, are the sources of entropy change and exchange within the system. Within the framework of classical irreversible thermodynamics (CIT), and under the condition of constant external constraints, and if indeed biological processes are under the dominion of the same physical laws as chemical, transport, and mechanical processes, CIT predicts (Prigogine, 1967) that the ecosystem will evolve toward a thermodynamic *stationary state* in which the total entropy S is constant in time. In this section it will be shown that this generates equations for the species populations in the neighborhood of the stationary state which are more general than, but include, those of Lotka–Volterra.

Additionally, the second law of thermodynamics and a result from CIT concerning the negative definiteness of the rate of change of the entropy production, dictate specific relations among the elements of the two-body species interaction matrix. These relations give stability in the thermodynamic framework and are shown here to be equivalent to those required on the community matrix for stability in the ecological framework. Under the conditions enumerated above, the ecosystem is thus shown to be asymptotically stable and the ecological steady state (community stability) is suggested to be a special case of the more general thermodynamic stationary state.

For ecosystems in which higher n -body (three-body and higher order) interactions are important, or which have been significantly perturbed such that the generalized thermodynamic flows are no longer linearly proportional to the generalized forces (see below), it will be shown that the second law of thermodynamics

and a more general result from nonlinear CIT theory, concerning the time change of the entropy production due to the changes in the generalized forces, dictate the population dynamics and the evolution toward stability of the system, as long as the external constraints over the ecosystem remain constant.

The total time change of entropy of the ecosystem (as for any open system) is a sum of an external term of no definite sign, and an internal production term of positive definite sign as required by the second law of thermodynamics,

$$\frac{dS}{dt} = \frac{d_e S}{dt} + \frac{d_i S}{dt}, \tag{12}$$

$$\frac{d_i S}{dt} > 0. \tag{13}$$

In the spirit of the *virial expansion* for a thermodynamic system communicating through n -body interactions, the total change of entropy of the ecosystem can be written as a many-body expansion of entropy changes due to interactions among individuals and among individuals and their external environment. Such a many-body expansion is obviously in complete accord with the *extensivity* property of entropy.

The entropy brought into the ecosystem or carried out of it through one-body transport processes can thus be written as

$$\frac{d_e S}{dt} = \sum_{\gamma=1}^n p_{\gamma} \Gamma_{\gamma}^e, \tag{14}$$

where the sum is over all n species and p_{γ} is the population of species γ . Γ_{γ}^e represents the average rate of exchange, or flow, of entropy with the external environment per individual of species γ . For example, the energy per individual per unit time taken in through photo-synthesis de_{γ} , or the heat dq_{γ} per individual transported to the external environment, and the components (e.g. nutrients) of type α taken in or given out by species γ , $dn_{\gamma\alpha}$, of chemical potential $\mu_{\gamma\alpha}$, give for the rate of entropy exchange per individual,

$$\Gamma_{\gamma}^e = \frac{1}{T} \frac{de_{\gamma} + dq_{\gamma}}{dt} - \frac{1}{T} \sum_{\alpha} \mu_{\gamma\alpha} \frac{dn_{\gamma\alpha}}{dt}. \tag{15}$$

Assuming constant external constraints over the ecosystem, CIT theory predicts that the system will naturally evolve toward a thermodynamic stationary state. The thermodynamic stationary state is characterized by time-independent thermodynamic variables, in particular $dS/dt = 0$, and therefore (since $d_i S/dt > 0$),

$$\frac{d_e S}{dt} = \sum_{\gamma=1}^n p_{\gamma} \Gamma_{\gamma}^e < 0, \tag{16}$$

implying that at least one of the species must bring negative entropy into the ecosystem, and that the amount of entropy introduced per unit time must be of more negative value than that transported back into the environment by all other species. This crucial role is of course usually played by the photo-synthesizing species (the primary producers).

Employing again the spirit of the virial expansion, the entropy production *within* the ecosystem itself may be written in the many-body form

$$\frac{d_i S}{dt} = \sum_{\gamma=1}^n p_{\gamma} \left[\Gamma_{\gamma}^i + \sum_{\gamma'=1}^n p_{\gamma'} \Gamma_{\gamma\gamma'} + \sum_{\gamma',\gamma''=1}^n p_{\gamma'} p_{\gamma''} \Gamma_{\gamma\gamma'\gamma''} + O(4) \right] > 0. \tag{17}$$

The Γ_{γ}^i represent the entropy production due to one-body irreversible processes occurring within the individual such as; photo-synthesis, evapotranspiration, respiration, metabolism, etc. The $\Gamma_{\gamma\gamma'}$ represent the entropy production and exchange due to two-body interactions between individuals (e.g. those involved in predator–prey, competition, symbiosis, mutualism, etc.); $\Gamma_{\gamma\gamma'\gamma''}$ correspond to similar but three-body interactions, and $O(4)$ represents the entropy production due to four-body and higher-order interactions (for example, those required for the functioning of societies).

In this section, Eq. (17) will be truncated at the two-body terms,

$$\frac{d_i S}{dt} = \sum_{\gamma} p_{\gamma} \left[\Gamma_{\gamma}^i + \sum_{\gamma'} p_{\gamma'} \Gamma_{\gamma\gamma'} \right] > 0 \tag{18}$$

$$= \sum_{\gamma} p_{\gamma} \left[\Gamma_{\gamma}^i + \sum_{\gamma'} p_{\gamma'} \left(\frac{\Gamma_{\gamma\gamma'} + \Gamma_{\gamma'\gamma}}{2} \right) \right] > 0 \tag{19}$$

(where the last expression emphasizes the dependence of the entropy production on only the symmetric part of the two-body entropy production matrix $\Gamma_{\gamma\gamma'}$). As mentioned in Section 3, the justification for this truncation is that, for most ecosystems, higher-order n -body interactions will be less probable since they require n -body localization within a limited space–time volume. The more general dynamical equations and stability relations obtained by including the higher-order terms of Eq. (17) will be briefly considered in Section 5.

Eq. (19) can be shown to be an *equivalent representation* (Katchalsky and Curran, 1975) of the usual formulation of the entropy production. To see this we assume that the entropy of the ecosystem is a function of the populations p_{γ} (the state

variables),⁶ $S = S(p_{\gamma})$, then,

$$\frac{dS}{dt} = \sum_{\gamma} \left(\frac{\partial S}{\partial p_{\gamma}} \right)_{(p_{\gamma})} \frac{dp_{\gamma}}{dt} = - \sum_{\gamma} \frac{v_{\gamma}}{T} \frac{dp_{\gamma}}{dt}, \tag{20}$$

where

$$v_{\gamma} \equiv -T \left(\frac{\partial S}{\partial p_{\gamma}} \right)_{(p_{\gamma})} \tag{21}$$

is analogous to the chemical potential μ_{γ} and will be called the *biological potential* of species γ . The ‘ (p_{γ}) ’ implies that all populations other than γ are held constant. The generalized flows in this representation are the population changes in time dp_{γ}/dt and the generalized forces are $-v_{\gamma}/T$.

Again invoking the spirit of the virial expansion to second order, but this time for the population change dp_{γ}/dt (in fact just the Lotka–Volterra Eqs. (1) with (2)), Eq. (20) becomes

$$\frac{dS}{dt} = - \sum_{\gamma} \frac{v_{\gamma}}{T} \left[p_{\gamma} \left(b_{\gamma} + \sum_{\gamma'} p_{\gamma'} c_{\gamma\gamma'} \right) \right] \tag{22}$$

$$= \sum_{\gamma} p_{\gamma} \left[\Gamma_{\gamma} + \sum_{\gamma'} p_{\gamma'} \left(\frac{\Gamma_{\gamma\gamma'} + \Gamma_{\gamma'\gamma}}{2} \right) \right] \tag{23}$$

with

$$\Gamma_{\gamma} \equiv \Gamma_{\gamma}^e + \Gamma_{\gamma}^i = -b_{\gamma} \frac{v_{\gamma}}{T},$$

$$\frac{\Gamma_{\gamma\gamma'} + \Gamma_{\gamma'\gamma}}{2} = -c_{\gamma\gamma'} \frac{v_{\gamma}}{T} = -c_{\gamma'\gamma} \frac{v_{\gamma'}}{T}. \tag{24}$$

Thus, given relations (24), our representation of the internal entropy production, Eq. (19), is an *equivalent* representation of the internal entropy production in its more usual form of Eq. (20).

In our representation, Eq. (19), the generalized internal flows are chosen as

$$\Gamma_{\gamma}^i + \sum_{\gamma'} p_{\gamma'} \left(\frac{\Gamma_{\gamma\gamma'} + \Gamma_{\gamma'\gamma}}{2} \right), \tag{25}$$

describing the net entropy flow to an individual of species γ due to internal irreversible processes and to its interaction with all other species γ' . The generalized forces are simply the populations p_{γ} of the n species ($\gamma = 1, n$).

The advantage of our equivalent representation is that the flows are specifically divided into the entropy production due to the one-body processes and to the

⁶It is argued that the state variables p_{γ} are sufficient to describe the ecosystem as we have defined it since other state variables such as the total internal energy and the total volume are just sums over the populations of the respective individual quantities. The average individual internal energies and volumes can be considered constant in time.

two-body production and exchange processes. The one-body transport terms with the external environment Γ_γ^e can, in principle, be determined using Eq. (15) by measuring the heat flow from an individual to the environment and by accounting for the entropy content, through the chemical potentials, of nutrients taken in, and of waste products given back to the environment. The one-body internal entropy production terms Γ_γ^i can be obtained by measuring individual rates of entropy production of specific irreversible processes necessary for auto-maintenance (e.g. respiration). The two-body terms could be determined by measuring the excess entropy production per unit time due to the species interactions including the transport and exchange of matter, energy and heat (e.g. increases in basal metabolic rates). The generalized forces, the species populations, can of course also be determined empirically. Thus, our particular choice of the flows and forces facilitates the analysis by allowing identification with empirically measurable quantities. As required for equivalent representations, the entropy production remains invariant.

Once the ecosystem arrives at the thermodynamic stationary state, CIT theory says that all net flows will go to zero

$$\Gamma_\gamma + \sum_{\gamma'} p_{\gamma'}^* \left(\frac{\Gamma_{\gamma\gamma'} + \Gamma_{\gamma'\gamma}}{2} \right) = 0. \tag{26}$$

The * now denotes evaluation at the *thermodynamic stationary state* populations. The simple change of variable, Eq. (24), makes Eq. (26) recognizable as equivalents of those defining the steady state populations in the ecological framework obtained with the Lotka–Volterra equations, Eq. (2) with conditions (3).

The second law of thermodynamics requires that the internal entropy production must be always greater than zero

$$\mathcal{P} \equiv \frac{d_i S}{dt} = \sum_\gamma p_\gamma \Gamma_\gamma^i + \sum_{\gamma\gamma'} p_\gamma p_{\gamma'} \left(\frac{\Gamma_{\gamma\gamma'} + \Gamma_{\gamma'\gamma}}{2} \right) > 0. \tag{27}$$

Since the two-body interaction terms can be assumed to not be directly coupled to the one-body internal processes, we must also have that

$$\sum_{\gamma\gamma'} p_\gamma p_{\gamma'} \left(\frac{\Gamma_{\gamma\gamma'} + \Gamma_{\gamma'\gamma}}{2} \right) > 0. \tag{28}$$

As an example, for an unrealistic but demonstrative two species ecosystem ($n = 2$), Eq. (28) implies that

$$\Gamma_{11} p_1^2 + (\Gamma_{12} + \Gamma_{21}) p_1 p_2 + \Gamma_{22} p_2^2 > 0. \tag{29}$$

Since the second law must hold for whatever values of the populations, this implies that

$$\Gamma_{11} > 0 \text{ and } \Gamma_{22} > 0, \tag{30}$$

and

$$4\Gamma_{11}\Gamma_{22} > (\Gamma_{12} + \Gamma_{21})^2. \tag{31}$$

To see how these conditions can be connected to the parameters of the Lotka–Volterra equation in the ecological framework, $c_{\gamma\gamma'}$, through relations (24), consider first the internal entropy production as obtained from Eq. (20)

$$\mathcal{P} = \frac{d_i S}{dt} = - \sum_\gamma \frac{v_\gamma}{T} \frac{dp_\gamma}{dt} - \frac{d_e S}{dt}. \tag{32}$$

Using a most general result of CIT, that the time change of the entropy production due to a change in the generalized forces X (recall that in this representation the generalized forces are $-v_\gamma/T$) is always negative except at the stationary state at which it is zero (Prigogine, 1967), gives

$$\frac{d_X \mathcal{P}}{dt} = - \frac{1}{T} \sum_{\gamma\gamma'} \left(\frac{\partial v_\gamma}{\partial p_{\gamma'}} \right)_{(p_\gamma)} \frac{dp_{\gamma'}}{dt} \frac{dp_\gamma}{dt} \leq 0. \tag{33}$$

Therefore,

$$\sum_{\gamma\gamma'} \left(\frac{\partial v_\gamma}{\partial p_{\gamma'}} \right)_{(p_\gamma)} \frac{dp_{\gamma'}}{dt} \frac{dp_\gamma}{dt} \geq 0. \tag{34}$$

Eq. (34) is analogous to the equilibrium stability conditions against diffusion which involve the chemical potentials μ_γ (Glansdorff and Prigogine, 1971).⁷ Because of its positive semi-definite quadratic form, this equation implies that

$$v_{\gamma\gamma} > 0 \text{ and } \det |v_{\gamma\gamma'}| \geq 0, \tag{35}$$

where $v_{\gamma\gamma'} \equiv \partial v_\gamma / \partial p_{\gamma'}$. Therefore, the following quadratic form must also hold for whatever values of the populations

$$\sum_{\gamma\gamma'} \frac{\partial v_\gamma}{\partial p_{\gamma'}} p_\gamma p_{\gamma'} > 0. \tag{36}$$

Assuming (at least up to second order in the species interactions) that the biological potentials v_γ are homogeneous functions of m th order ($m > 0$) in the populations p_γ we can use Euler’s theorem (Glansdorff and Prigogine, 1971) to convert Eq. (36) into

$$\sum_\gamma p_\gamma v_\gamma > 0. \tag{37}$$

⁷This is also an analogous relation to the positive definiteness of the specific heat at constant volume C_v , ensuring thermal stability, and to the positive definiteness of the isothermal compressibility χ , ensuring mechanical stability. Under the local equilibrium hypothesis on which CIT is based, these relations also hold out of equilibrium since the specific heat, isothermal compressibility and the chemical potential are supposed to depend in the same way on the same variables as in equilibrium (Prigogine, 1967).

For example, for the two species ecosystem, using the substitution of variables (24) this gives

$$-T \left[\frac{c_{11}p_1\Gamma_{11} + c_{22}p_2\Gamma_{22}}{c_{11}c_{22}} \right] > 0. \tag{38}$$

Since this must hold for whatever positive values of the populations, this condition, along with condition (30) implies that

$$c_{11} < 0, \quad c_{22} < 0. \tag{39}$$

With the variable substitutions (24), Eq. (31) give also that

$$c_{11}c_{22} \geq c_{12}c_{21}. \tag{40}$$

These relations can be recognized as sufficient conditions for stability of the steady state populations in the ecological framework, Eqs. (10) and (11).⁸ However, the important point is that these conditions obtained in this proposed thermodynamic framework are the result of non-equilibrium thermodynamic theory and therefore have a clear physical basis. In the ecological framework they are required ad hoc for stability and therefore give rise to the complexity–stability paradox.

The results obtained above may also be derived from a somewhat different perspective. In the stationary state, assuming linear phenomenological laws and Onsager’s reciprocity relations (see Appendix A), the internal production of entropy \mathcal{P} is a minimum with respect to the generalized forces which are not fixed (Prigogine, 1967). In general, if \mathcal{P} is a function of n populations, the condition for it to be a minimum is that the Hessian matrix,

$$h_{\gamma\gamma'} = \left. \frac{\partial^2 \mathcal{P}}{\partial p_\gamma \partial p_{\gamma'}} \right|_{p_\gamma^* p_{\gamma'}^*} \tag{41}$$

is positive definite (Barnett, 1990). As an example, for $n = 2$ species, \mathcal{P} is a function of two variables, p_1 and p_2 , and the following two conditions must be satisfied (Swokowski, 1975):

$$\left. \frac{\partial^2 \mathcal{P}}{\partial p_1^2} \right|_{p_1^* p_2^*} > 0, \tag{42}$$

$$\left. \frac{\partial^2 \mathcal{P}}{\partial p_1^2} \frac{\partial^2 \mathcal{P}}{\partial p_2^2} \right|_{p_1^* p_2^*} - \left[\left. \frac{\partial^2 \mathcal{P}}{\partial p_1 \partial p_2} \right|_{p_1^* p_2^*} \right]^2 > 0.$$

This leads to the following conditions on the interaction parameters:

$$\Gamma_{\gamma\gamma} > 0, \tag{43}$$

$$4\Gamma_{11}\Gamma_{22} > (\Gamma_{12} + \Gamma_{21})^2. \tag{44}$$

⁸Note that restriction (39) is in fact stronger than restriction (10). This is due to the fact that in this thermodynamic analysis the populations were restricted to positive values while no such restriction was enforced in obtaining Eq. (10) (Roberts, 1974).

With the variable substitutions introduced above (Eq. (24)), this leads again to restrictions (39) and (40) on the Lotka–Volterra parameters of the ecological framework.

For an arbitrary ecosystem size of n species, we now show that results from linear irreversible thermodynamics guarantee the stability of the stationary state populations \mathbf{p}^* . Consider the internal entropy production

$$\mathcal{P} = \frac{d_i S}{dt} > 0. \tag{45}$$

This must always be greater than zero by the second law. Assuming again linear phenomenological laws and Onsager’s reciprocity relations (see Appendix A), it can be shown that the changes in the entropy production due to changes in the generalized forces X and that due to changes in the generalized flows J are equal (Prigogine, 1967)

$$\frac{d_X \mathcal{P}}{dt} = \frac{d_J \mathcal{P}}{dt}. \tag{46}$$

Therefore, with Eq. (33), we have also that

$$\frac{d\mathcal{P}}{dt} = \frac{d_X \mathcal{P}}{dt} + \frac{d_J \mathcal{P}}{dt} \leq 0, \tag{47}$$

where the equality holds at the stationary state (populations \mathbf{p}^*). We have thus found the Lyapunov function \mathcal{P} (the internal entropy production) which establishes the asymptotic stability of the stationary state populations \mathbf{p}^* . As mentioned in Section 2, the existence of a Lyapunov function is equivalent to the requirement on the ecological community matrix that the real parts of all eigenvalues are negative definite for stability. *An ecological steady state thus has the dynamic and stability characteristics of a thermodynamic stationary state and it is tempting to consider the former as a particular case of the latter.*

5. Nonlinear ecosystems

In this section, we briefly consider the analysis of ecosystem dynamics and stability beyond the two-body interactions. A more detailed analysis will be provided in a forthcoming article.

The two-body community matrix of the Lotka–Volterra formalism admits solutions for the dynamics of the populations which are either stable points or neutral cycles (neutral cycles can be observed to be allowed by Eq. (7) by considering a community matrix with purely imaginary eigenvalues). As pointed out by Glansdorff and Prigogine (1971) for chemical reactions and later by May (1974) for ecological systems, such neutral stability, in which the amplitude of oscillation depends on the initial conditions or on a subsequent perturbation (see Eq. (7)) is not representative of robust cyclical processes occurring in nature (for example, the almost constant

amplitude, 11-year period oscillations observed for over 100 years in the Arctic hare and lynx populations (May, 1974)). The thermodynamic formalism presented here in fact forbids the possibility of neutral cycles since the existence of a Lyapunov function does not admit closed orbits. Our formalism including only up to two-body interactions thus only allows fixed point attractor solutions in population space.

Including higher-order terms in the formalism, however, leads to the possibility of cyclic attractor and even chaotic attractor dynamics (for ecosystems of at least 3 species). Consider the total change of entropy of the ecosystem in the stationary state, including now higher-order terms

$$\frac{dS}{dt} = \sum_{\gamma} p_{\gamma} \left[\Gamma_{\gamma} + \sum_{\gamma'} p_{\gamma'} \Gamma_{\gamma\gamma'} + \sum_{\gamma'\gamma''} p_{\gamma'} p_{\gamma''} \Gamma_{\gamma\gamma'\gamma''} + O(4) \right] = 0. \tag{48}$$

At the stationary state the net flows will go to zero,

$$\Gamma_{\gamma} + \sum_{\gamma'} p_{\gamma'} \Gamma_{\gamma\gamma'} + \sum_{\gamma'\gamma''} p_{\gamma'} p_{\gamma''} \Gamma_{\gamma\gamma'\gamma''} + O(4) = 0. \tag{49}$$

Eq. (49) provides a many-body generalization of Eq. (26) and a logical alternative to ad hoc nonlinear extensions of the two-body Lotka–Volterra equations describing the steady state populations. However, depending on the values of the entropy production and exchange coefficients, $\Gamma_{\gamma}, \Gamma_{\gamma\gamma'}$, etc., it may now happen that the steady state populations defined by Eq. (49) are not stable, or may not even exist. This may happen because the entropy production \mathcal{P} is no longer a Lyapunov function since the generalized flows are no longer linearly proportional to the generalized forces as they were in the truncated two-body case (see Appendix A) and thus Eq. (47) no longer necessarily holds. However, a more general result of CIT requires that the time change in the entropy production due to a change in the generalized forces X (the populations) is always negative, except at the stationary state at which it is zero (Prigogine, 1967),

$$d_X \mathcal{P} = \sum_{\gamma} dp_{\gamma} \left[\Gamma_{\gamma}^i + \sum_{\gamma'} p_{\gamma'} \Gamma_{\gamma\gamma'} + \sum_{\gamma'\gamma''} p_{\gamma'} p_{\gamma''} \Gamma_{\gamma\gamma'\gamma''} + O(4) \right] \leq 0. \tag{50}$$

Since this is not a total differential, the entropy production \mathcal{P} is not a Lyapunov function and closed orbits are therefore allowed. For example, for an $n = 3$ species ecosystem, and considering up to fourth order in the interactions, the entropy production and exchange coefficients given in Appendix B along with Eq. (50) describe the cyclic attractor dynamics shown in Fig. 1.

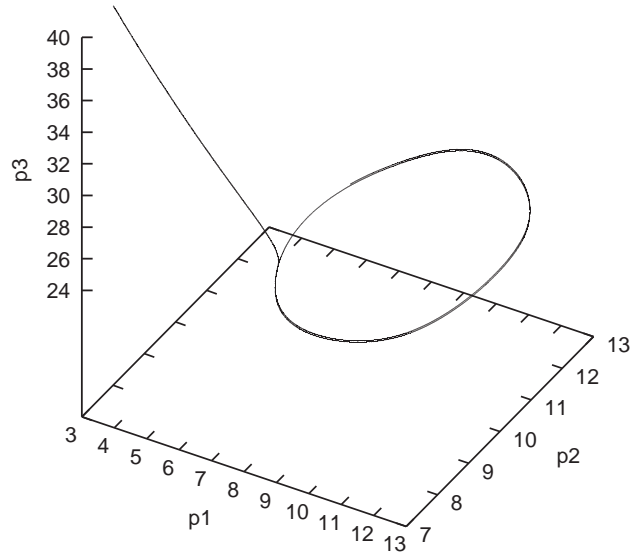


Fig. 1. Cyclic attractor dynamics determined from Eq. (50) using the species interaction coefficients as given in Appendix B.

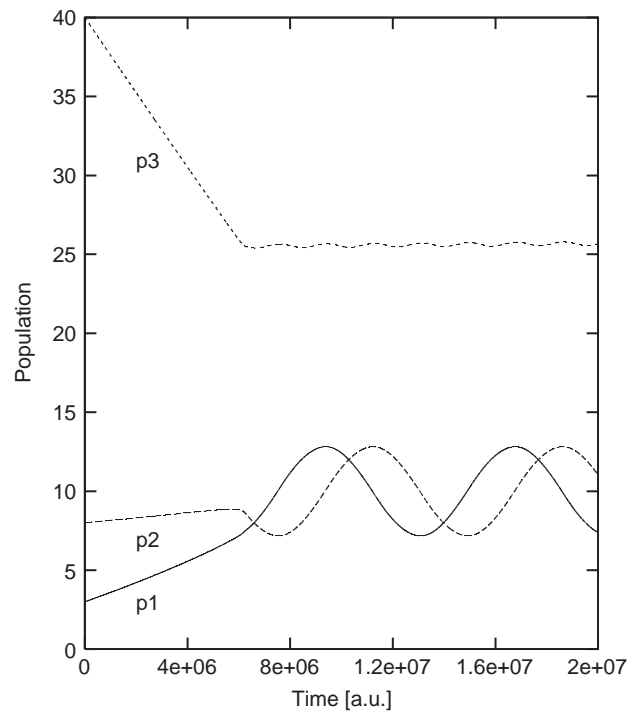


Fig. 2. Population dynamics as a function of time for the attractor given in Fig. 1.

Fig. 2 shows how the populations settle into the attractor as a function of time. The ecosystem always settles into the same attractor from whatever locally confined initial conditions and no local perturbation can change the amplitude nor the position of the attractor. It may thus be that this behavior from nonlinear CIT theory corresponds to the robust cyclical processes observed in real ecosystems.

Note that the requirement that the second law of thermodynamics must be obeyed,

$$\frac{d_i S}{dt} = \sum_{\gamma} p_{\gamma} \left[\Gamma_{\gamma}^i + \sum_{\gamma'} p_{\gamma'} \Gamma_{\gamma\gamma'} + \sum_{\gamma'\gamma''} p_{\gamma'} p_{\gamma''} \Gamma_{\gamma\gamma'\gamma''} + O(4) \right] > 0, \quad (51)$$

limits the spectrum of responses of the ecosystem to external perturbation. How the second law, along with the criterion defined by Eq. (50), determine the evolution of the perturbed ecosystem will be studied in detail in a forthcoming article.

6. Discussion and conclusions

Note that to second order in the species interactions (linear ecosystems) the internal entropy production, and thus the rest of the dynamic and stability analysis, is dependent only on the symmetric part of the entropy production matrix $\Gamma_{\gamma\gamma'}$ (see Eq. (19)). In other words, this thermodynamic framework makes it apparent that the number of independent parameters required to describe the ecosystem dynamics and stability to second order is a little more than one-half (considering the terms on the diagonal) of those usually assumed to be necessary in the traditional ecological framework. This is a testable prediction of the theory.

The parameters of the entropy production matrix are also physically well defined, in contradistinction to the parameters of the community matrix in the ecological framework. For example, the term b_{γ} (Eq. (2)) in the ecological framework represents the inherent growth rate of species γ in the absence of all other species (May, 1972). A direct determination of such a parameter is of course impossible even in principle. Instead, the values of b_{γ} and $c_{\gamma\gamma'}$ (Eq. (2)) can only be determined by fitting to population measurements and will therefore provide little predictive power since the fitting is unlikely to be unique for realistically large ecosystems and restricted field samples. In contrast, in the thermodynamic framework proposed here, the analogous term Γ_{γ} represents the one-body net flow of entropy per unit time per unit individual to species γ , and $\Gamma_{\gamma\gamma'}$ represents the effect of species γ' on the entropy production of species γ , both of which are possible, in principle, to measure directly as outlined in Section 4.

In conclusion, this paper has considered the stability of ecosystems from a non-equilibrium thermodynamic perspective. Although most of the results presented herein apply to a somewhat restricted class of ecosystems (those with constant external constraints), nevertheless the application of CIT to these systems in the linear and nonlinear regimes has provided a number of

important results. In general, it has been shown that ecosystems appear to be amenable to a quantitative physical approach based on non-equilibrium thermodynamic theory. Specific paradoxes and problems from within the ecological framework, for example, the complexity–stability paradox and the problem of the evolution of a system of a population of one, have a natural resolution within the proposed thermodynamic framework. It is simply that the evolution of the interaction parameters in the direction of securing ecosystem stability is a natural thermodynamic consequence for an open system under constant external constraints. The necessary and sufficient conditions, identified in CIT, are the positive definiteness of the internal entropy production and the negative definiteness of the time change of the internal entropy production due to changes in the generalized forces (the species populations). This may be the basis of the active force of stabilization sought after for explaining stasis. This also establishes a clear link between thermodynamics out of equilibrium and natural selection of species interaction strengths.

For nonlinear ecosystems, it was suggested in Section 5 that the proposed thermodynamic framework admits cyclic and chaotic attractor solutions for the dynamics. There is no need to resort to exotic transcendental functions in ad hoc extensions of the Lotka–Volterra-type equations, as often encountered in the literature. Simply extending the interactions to three-body and higher-order terms is sufficient to obtain this flavor in the dynamics. Here again, the second law and the more general result concerning the negative definiteness of the change in entropy production due to changes in the generalized forces drive the interaction parameters into the stability regime. This suggests an interesting relation, hitherto overlooked, between n -body effects and population dynamics. The confinement in space–time of individuals as a precondition to enabling n -body effects, coupled with the resulting flavor in the population dynamics, is the probable generator of the observed complex spatial and temporal structures of species populations (May, 1999).

The time local (at constant interaction coefficient) population dynamics of a locally perturbed ecosystem under constant external constraints can be determined by realizing that any change in the generalized forces (the species populations) must occur in such a manner that the internal entropy production of the ecosystem is reduced.

From a more global non-equilibrium thermodynamic perspective, it is known that biological systems may possess multiple stationary states (Glansdorff and Prigogine, 1971). Ecosystems which have suffered a significant perturbation in their external conditions, through some critical point, may thus in fact lose stability and may evolve rapidly from one stationary

state to another quite different. (Such non-equilibrium phase transitions are well known in abiotic processes, for example at the Bénard transition.) This may correspond to *succession* in ecosystems. New ecological steady states are progressively reached in which the complexity, stability (Odum, 1963), and entropy production are usually higher. There is much evidence for environmental change as a trigger for evolutionary change (Hoffmann and Parsons, 1997). Episodic punctuation of stasis through non-equilibrium phase transitions at a critical point may therefore provide a means for ecosystem growth in both size and complexity by combining it with Swenson’s principle of maximum entropy production. Swenson (1989, 2000) has argued that of all possible paths available to a thermodynamic system after the removal or change of an external constraint, the system will take the path which increases the entropy of the system plus environment at the fastest rate possible given the remaining constraints. Large, complex ecosystems are more efficient at producing entropy than are smaller ones, and thus would be favored by nature if this suggestion were correct.

Finally, a possible thermodynamic explanation for the enhanced stability of tropical over high latitude ecosystems has been offered by relating the observation to the degree of constancy of the respective external constraints.

Since these thermodynamic directives operate on all systems at all scales in similar ways, and since each hierarchical level provides the ecological constraints (and thus the thermodynamical constraints) for the level below (Holling, 1998), this work may provide an explanation for the ubiquity of stasis and episodic change (Gould, 2002) at all hierarchical levels of living, and non-living, systems.

Acknowledgements

The author gratefully acknowledges useful comments on the manuscript by L. García-Colín Scherer, J.A. Heras, J.M. Nieto, J.L. Torres, and numerous anonymous referees. The formation of the ideas expressed in this work began while on sabbatical leave at the Instituto de Física y Matemáticas, Universidad Michoacana, in Morelia, Mexico, with a grant from the Consejo Nacional de Ciencias y Tecnología (CONACYT, 2000).

Appendix A

The employment of the condition of minimal internal entropy production implicitly assumed the linearity of the phenomenological laws and the reciprocity relations of Onsager (Prigogine, 1967). Recalling that for the

internal two-body entropy production the generalized flows and forces can be assigned in the following manner

$$J_\gamma = \sum_{\gamma'} p_{\gamma'} \left(\frac{\Gamma_{\gamma\gamma'} + \Gamma_{\gamma'\gamma}}{2} \right), \quad X_\gamma = p_\gamma \tag{A.1}$$

it is obvious that the phenomenological relations are of the linear form

$$J_\gamma = \sum_{\gamma'} L_{\gamma\gamma'} X_{\gamma'}, \tag{A.2}$$

where the phenomenological coefficients are,

$$L_{\gamma\gamma} = \Gamma_{\gamma\gamma},$$

$$L_{\gamma\gamma'} = \left(\frac{\Gamma_{\gamma\gamma'} + \Gamma_{\gamma'\gamma}}{2} \right). \tag{A.3}$$

From this and Eq. (43), or the condition following from Eq. (29), it follows that,

$$L_{\gamma\gamma'} = L_{\gamma'\gamma} \quad \text{and} \quad L_{\gamma\gamma} > 0. \tag{A.4}$$

The reciprocity relations of Onsager and the positive definite nature of the proper phenomenological coefficients are thus satisfied to second order in the interactions.

Appendix B

Consider, as an example, the following set of species interaction coefficients (see Eq. (50)) for an $n = 3$ species ecosystem and including up to four-body terms;

$$\begin{aligned} \Gamma_{1111} &= 1, & \Gamma_{2222} &= 1, & \Gamma_{3311} &= 1, \\ \Gamma_{1122} &= 1, & \Gamma_{2211} &= 1, & \Gamma_{3322} &= 1, \\ \Gamma_{111} &= -30, & \Gamma_{222} &= -30, & \Gamma_{331} &= -20, \\ \Gamma_{122} &= -10, & \Gamma_{211} &= -10, & \Gamma_{332} &= -20, \\ \Gamma_{112} &= -20, & \Gamma_{221} &= -20, & \Gamma_{311} &= -20, \\ \Gamma_{11} &= 392, & \Gamma_{22} &= 392, & \Gamma_{322} &= -20, \\ \Gamma_{12} &= 201, & \Gamma_{21} &= 199, & \Gamma_{31} &= 400, \\ \Gamma_1 &= -1930, & \Gamma_2 &= -1910, & \Gamma_{32} &= 400, \\ & & & & \Gamma_{33} &= 192, \\ & & & & \Gamma_3 &= -3840. \end{aligned}$$

This set was actually obtained from the following equation for the change in the entropy production due to changes in the generalized forces (Eq. (50)).

$$\begin{aligned} d_X \mathcal{P} &= dp_1 [(p_2 - 10) + (p_1 - 10)(p_1 - 10)^2 \\ &\quad + (p_2 - 10)^2 - 8] \\ &\quad + dp_2 [-(p_1 - 10) + (p_2 - 10) \\ &\quad \times ((p_1 - 10)^2 + (p_2 - 10)^2 - 8)] \\ &\quad + dp_3 [(p_3 - 20)(p_1 - 10)^2 \\ &\quad + (p_2 - 10)^2 - 8] \leq 0. \end{aligned} \tag{B.1}$$

The cyclic attractor given in Figs. 1 and 2 was then obtained by starting from the initial values of $p_1 = 3$, $p_2 = 8$ and $p_3 = 40$, and generating dp_1 , dp_2 and dp_3 at random. Selecting only sets of dp 's which gave a negative value for $d_X \mathcal{P}$, as calculated from Eq. (B.1), the values of p_1 , p_2 and p_3 were updated until various orbits of the attractor had been completed.

References

- Barnett, S., 1990. *Matrices; Methods and Applications*. Clarendon Press, Oxford.
- Chakrabarti, C.G., Ghosh, S., Bhadra, S., 1995. Non-equilibrium thermodynamics of Lotka–Volterra ecosystems: stability and evolution. *J. Biol. Phys.* 21, 273–284.
- Cheetham, A.H., Jackson, J.B.C., 1995. Process from pattern: tests for selection versus random change in punctuated bryozoan speciation. In: Erwin, D.H., Anstey, R.L. (Eds.), *New Approaches to Speciation in the Fossil Record*. Columbia University Press, New York, pp. 184–207.
- de Oliveira, V.M., Fontanari, J.F., 2000. Random replicators with high-order interactions. *Phys. Rev. Lett.* 85, 4984–4987.
- Eldredge, N., Gould, S.J., 1972. Punctuated equilibria: an alternative to phyletic gradualism. In: Schopf, T.J.M. (Ed.), *Models in Paleobiology*. W.H. Freeman, New York, pp. 82–115.
- Gardner, M.R., Ashby, W.R., 1970. Connectance of large dynamical (cybernetic) systems: critical values for stability. *Nature* 228, 784.
- Glansdorff, P., Prigogine, I., 1971. *Thermodynamic Theory of Structure, Stability and Fluctuations*. Wiley, London.
- Goldsmith, E., 1985. Ecological succession rehabilitated. *The Ecologist* 15, 210.
- Goldwasser, L., Roughgarden, J., 1993. Construction and analysis of a large Caribbean food web. *Ecology* 74, 1216–1233.
- Gould, S.J., 2002. *The Structure of Evolutionary Theory*. Harvard University Press, Cambridge, MA and London.
- Hoffmann, A.A., Parsons, P.A., 1997. *Extreme Environmental Change and Evolution*. Cambridge University press, Cambridge.
- Holling, C.S., 1998. The renewal growth birth and death of ecological communities. *Whole Earth Summer* 32.
- Jackson, J.B.C., Cheetham, A.H., 1994. Phylogeny reconstruction and the tempo of speciation in cheilostome Bryozoa. *Paleobiology* 20, 407–423.
- Katchalsky, A., Curran, P.F., 1975. *Nonequilibrium Thermodynamics in Biophysics*, fourth ed. Harvard University Press, Cambridge, MA.
- Lotka, A.J., 1922. Contribution to the energetics of evolution. *Proc. Natl. Acad. Sci.* 8, 147–155.
- Margalef, R., 1963. On certain unifying principles in ecology. *Am. Nat.* 97, 357–374.
- May, R.M., 1972. Will a large complex system be stable? *Nature* 238, 413–414.
- May, R.M., 1974. *Stability and Complexity in Model Ecosystems*. Princeton University Press, Princeton, NJ.
- May, R.M., 1999. Unanswered questions in ecology. *Philos. Trans. R. Soc. Lond. B* 354, 1951–1959.
- Mayr, E., 1963. *Animal Species and Evolution*. Harvard University Press, Cambridge, MA.
- Mayr, E., 1971. *Population Species and Evolution*. Harvard University Press, Cambridge, MA.
- McCann, K.S., 2000. The diversity–stability debate. *Nature* 405, 228–233.
- Odum, E.P., 1963. *Ecology*. Holt Rinehart and Winston, New York.
- Odum, E.P., 1969. The strategy of ecosystem development. *Science* 164, 262–270.
- Odum, H.T., 1983. *System Ecology*. Wiley, New York.
- Paul, C.R.C., 1985. The adequacy of the fossil record reconsidered. In: Cope, J.C.W., Skelton, P.W. (Eds.), *Evolutionary Case Histories from the Fossil Record* (special papers in *Paleontology* 33, 7–15).
- Pimm, S.L., 1991. *The Balance of Nature*. University of Chicago Press.
- Polis, G.A., 1991. Complex trophic interactions in deserts: an empirical critique of food-web theory. *Am. Nat.* 138, 123–155.
- Prigogine, I., 1967. *Thermodynamics of Irreversible Processes*. Wiley, New York.
- Roberts, A., 1974. The stability of a feasible random ecosystem. *Nature* 251, 607–608.
- Schneider, E., Kay, J., 1994. Complexity and thermodynamics: towards a new ecology. *Futures* 24, 626–647.
- Schrödinger, E., 1944. *What is Life?* Cambridge University Press, Cambridge.
- Sheldon, P.R., 1996. Plus ça change—a model for stasis and evolution in different environments. *Palaeogeog. Palaeoclimatol. Palaeoecol.* 127, 209–227.
- Svirezhev, Y.M., 2000. Thermodynamics and ecology. *Ecol. Model.* 132, 11–22.
- Swenson, R., 1989. Emergent attractors and the law of maximum entropy production: foundations to a theory of general evolution. *Syst. Res.* 6, 187–198.
- Swenson, R., 1997. Autocatakinetics, evolution, and the law of maximum entropy production: a principled foundation toward the study of human ecology. *Adv. Hum. Ecol.* 6, 1–46.
- Swenson, R., 2000. Spontaneous order, autocatakinetic closure, and the development of space-time. *Ann. NY Acad. Sci.* 901, 311–319.
- Swokowski, E.W., 1975. *Calculus with Analytic Geometry*. Prindle, Weber & Schmidt, Boston.
- Vavrukh, I., 2002. Conceptual problems of modern irreversible thermodynamics. *Chem. Listy* 96, 271–275.
- Wake, D.B., Roth, G., Wake, M.H., 1983. On the problem of stasis in organismal evolution. *J. Theor. Biol.* 101, 211–224.
- Williamson, P.G., 1981. Palaeontological documentation of speciation in Cenozoic molluscs from the Turkana Basin. *Nature* 293, 437–443.
- Yodzis, P., 1980. The connectance of real ecosystems. *Nature* 284, 544–545.
- Zotin, A.A., Lamprecht, I., Zotin, A.I., 2001. Bioenergetic progress and heat barriers. *J. Non-Equilib. Thermodyn.* 26, 191–202.
- Zotin, A.I., 1990. *Thermodynamic Bases of Biological Processes: Physiological Reactions and Adaptations*. Walter De Gruyter Inc., Berlin.