Thermodynamic stability of ecosystems

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Abstract

The dynamics and stability of ecosystems is studied from the perspective of the linear theory of irreversible thermodynamics. It is argued that if the external constraints are constant, the ecosystem will naturally evolve toward a stable thermodynamic *stationary* state in which the production of entropy within the ecosystem is at a local minimum value. This extremal condition leads to equations for the stationary state population dynamics of interacting species, more general than those of Lotka-Volterra, and to conditions on the parameters of the community interaction matrix guaranteeing stability.

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I. INTRODUCTION

The complexity of a typical ecosystem containing over 3000 species [1] leads to non-trivial questions concerning its stability and dynamics. Such questions are of crucial importance in guiding wildlife management programs, and in forecasting ecological catastrophes. The modeling of ecosystems in the traditional ecological framework is based on *ad hoc* extensions of Lotka-Volterra type equations [2–5]. Apart from providing little theoretical insight or empirical predictive power, such a framework implicitly contains a celebrated paradox contrasting the theoretical improbability of a stable, complex system with ample field evidence of stable, complex ecosystems [2].

This letter looks at ecosystem stability and dynamics from the perspective of the *linear theory of irreversible thermodynamics* (LIT). The ecosystem is modeled as an open thermodynamic system over which a constant free energy flow is impressed, sunlight. Interactions between the individuals of the species and with their external abiotic environment, cause a time change of the total entropy of the system. If the external constraints, energy and nutrient flows, over the system are constant, and if indeed biological processes are under the dominion of the same physical laws as chemical, transport, and mechanical processes, LIT predicts [6] that the system will evolve toward a *stationary state* in which extensive variables such as the total entropy S are constant in time. This generates dynamical equations for the species populations more general than, but including, those of Lotka-Volterra. Further, a LIT condition of minimal entropy production in the stationary state dictates relations among the elements of the community interaction matrix, ensuring stability.

II. THE TRADITIONAL ECOLOGICAL FRAMEWORK

Population modeling in the traditional ecological framework is based on the equations [3],

$$\frac{dp_i(t)}{dt} = F_i(p_1(t), p_2(t), ...p_n(t)), \tag{1}$$

where F_i is, in general, some empirically inspired, nonlinear function of the populations p_i of the n species. For example, for the Lotka-Volterra equations (having the stability characteristics of a much wider class of ecological models employed in the literature [3]), F takes the following form,

$$F_i = p_i(b_i + \sum_{j=1}^{n} p_j c_{ij}). \tag{2}$$

Of much 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_i^*,

$$0 = F_i(p_1^*(t), p_2^*(t), ...p_n^*(t)). \tag{3}$$

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

$$\frac{dx_i(t)}{dt} = F_i|_* + \sum_{j=1}^{n} \left[\frac{\partial F_i}{\partial p_j} \right|_* x_j(t) + \frac{1}{2} \sum_{k=1}^{n} \left[\frac{\partial^2 F_i}{\partial p_j \partial p_k} \right|_* x_j x_k + \ldots , \tag{4}$$

where $x_i(t) = p_i(t) - p_i^*$ and the $*$ denotes evaluation at the steady state. Since $F_i|_* = 0$, and close to the steady state the x_i are small, only the second term in the expansion (4) need be considered. In matrix notation, this gives,

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

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

$$a_{ij} = \left. \frac{\partial F_i}{\partial p_j} \right|_* . \tag{6}$$

which represent the effect of species j on the rate of change of population i near the steady state.

The solution of equation (5) is

$$x_i(t) = \sum_{j=1}^{n} C_{ij} \exp(\lambda_j t) \tag{7}$$

where λ_j are the eigenvalues of the matrix $\mathbf{A}$ and the integration constants C_{ij} are determined from the initial conditions.

From equation (7) it is obvious that local 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_{ij} of the community matrix $\mathbf{A}$ [3]. For example, it can be shown that for a $n = 2$ species community it requires that $a_{11} + a_{22} < 0$, and $a_{11}a_{22} > a_{12}a_{21}$. For the Lotka-Volterra equations, Eqn. (2), this implies

$$p_1^* c_{11} + p_2^* c_{22} < 0, \tag{8}$$

and

$$c_{11}c_{22} > c_{12}c_{21}. \tag{9}$$

For a community of an arbitrary number n of species, 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 a positive definite quadratic function $V = \mathbf{x}^{\mathbf{T}}\mathbf{P}\mathbf{x}$ (Lyapunov function) having its derivative with respect to time negative definite [7].

The relations between the components of the community matrix for ensuring stability of the ecosystem are thus specific, and can be shown to be more specific the more complex the system [3]. This leads to a celebrated paradox: Without a mechanism for fine tuning the community matrix, there should be little probability of finding stable complex ecosystems. However, in nature, most ecosystems are very complex and most are at least locally stable [1,8].

The most plausible mechanism thus far offered for tuning the parameters of the community matrix is *natural selection* [3]. However, this explanation is not complete since it leads to another celebrated problem; that of natural selection working on the evolution of a system of a population of one (the ecosystem) [9].

III. PROPOSED THERMODYNAMIC FRAMEWORK

The linear theory of irreversible thermodynamics provides an interesting framework for accommodating the problem of ecosystem dynamics and stability. We start by writing the total change in time of entropy of the ecosystem as a many-body expansion of entropy changes due to interactions among individuals (allowed by the *extensivity* property of entropy),

$$\frac{dS}{dt} = \sum_{i=1}^{n} \left[p_i\Gamma_i + \sum_{j=1}^{n} p_i p_j \Gamma_{ij} + \sum_{j,k=1}^{n} p_i p_j p_k \Gamma_{ijk} + O(4) \right]. \tag{10}$$

The Γ_i represent the change of entropy in time due to 1-body interactions of individuals with their abiotic environment (eg. evapotranspiration, photo-synthesis, respiration, metabolic heat transfer to environment, etc.); Γ_{ij} represents 2-body interactions between individuals (eg. predator-prey, competition, symbiosis, mutualism, etc.); Γ_{ijk} correspond to the 3-body interactions, and $O(4)$ represents 4-body and higher order interactions (eg. those required for the functioning of societies).

The total time change of entropy can be expressed as a sum of an external term, of no definite sign, and an internal term, of positive definite sign (required by the second law of thermodynamics),

$$\frac{dS}{dt} = \frac{d_eS}{dt} + \frac{d_iS}{dt}. \tag{11}$$

The external part of the change of entropy can be associated with the one body interactions of the individuals with their abiotic environment,

$$\frac{d_eS}{dt} = \sum_{i=1}^{n} p_i\Gamma_i. \tag{12}$$

The internal, dissipative part is then associated with the biotic 2-body and higher order interactions among the participating individuals,

$$\frac{d_iS}{dt} = \sum_{i=1}^{n} \left[\sum_{j=1}^{n} p_i p_j \Gamma_{ij} + \sum_{j,k=1}^{n} p_i p_j p_k \Gamma_{ijk} + O(4) \right] > 0. \tag{13}$$

In the stationary state, $dS/dt = 0$, and since the internal dissipation is positive by the second law, then,

$$\frac{d_eS}{dt} = \sum_{i=1}^{n} p_i\Gamma_i < 0, \tag{14}$$

indicating that in the stationary state, at least one of the species must bring negative entropy into the ecosystem of an amount greater than the positive entropy given back to the environment by the other one-body exchanges. This role is most often played by the photo-synthesizing species.

The inherent stability of the stationary state implies,

$$\frac{\partial}{\partial p_i}\left[\frac{dS}{dt}\right]\Bigg|_{*} = 0, \tag{15}$$

for all species i. The $*$ now denotes evaluation at the stationary state populations.

In the following, equation (10) will be truncated at the two-body terms. The justification for this 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 two-body truncation is in fact the norm in most ecological studies [3,10,11] with few exceptions [12]. This truncation, however, may not be valid for ecosystems with societal species, in which higher n-body interactions probably play an important role. The more general dynamical equations and stability relations obtained from the complete equation (10) employing equation (15) will be developed in a forthcoming article.

Thus, taking equation (10) only to second order in the interactions, Eqn. (15) gives

$$\Gamma_i + \sum_{j=1}^{n} p_j^*(\Gamma_{ij} + \Gamma_{ji}) = 0. \tag{16}$$

A simple change of variable makes these equations recognizable as equivalents of those defining the steady state populations in the ecological framework employing the Lotka-Volterra equations, Eqs. (2) with conditions (3). For example, for the case of $n = 2$, the appropriate substitutions are, $\Gamma_1 \equiv -b_1\sqrt{c_{21}/c_{12}}$, $\Gamma_{12} + \Gamma_{21} \equiv -\sqrt{c_{12}c_{21}}$ and $\Gamma_{11} \equiv -c_{11}\sqrt{c_{21}/c_{12}}/2$, with corresponding definitions for Γ_2 and Γ_{22}.

In the stationary state, assuming linear phenomenological laws (see below), the internal dissipation of entropy, ${}_i\dot{S} \equiv d_iS/dt$ is a minimum [6]. In general, if ${}_i\dot{S}$ is a function of n populations, the condition for it to be a minimum is that the Hessian matrix,

$$h_{ij} = \left(\frac{\partial_i^2 \dot{S}}{\partial p_i \partial p_j}\right)\Bigg|_{*} \tag{17}$$

is positive definite [7]. As an example, for $n = 2$ species, ${}_i\dot{S}$ is a function of two variables, p_1 and p_2, and the following two conditions must be satisfied [13];

$$\left.\frac{\partial^2_i \dot{S}}{\partial {p_1}^2}\right|_{p_1^* p_2^*} > 0,$$

$$\left.\frac{\partial^2_i \dot{S}}{\partial {p_1}^2}\frac{\partial^2_i \dot{S}}{\partial {p_2}^2}\right|_{p_1^* p_2^*} - \left.\left[\frac{\partial^2_i \dot{S}}{\partial p_1 \partial p_2}\right]^2\right|_{p_1^* p_2^*} > 0. \tag{18}$$

To second order in the interactions, this leads to the following conditions on the interaction parameters,

$$\Gamma_{ii} > 0,$$

$$4\Gamma_{11}\Gamma_{22} > (\Gamma_{12} + \Gamma_{21})^2. \tag{19}$$

With the variable substitutions introduced above, these relations can be recognized as sufficient conditions for stability of the steady state populations in the ecological framework, equations (8) and (9).

For arbitrary ecosystem size n, that these conditions are the same as those imposed on the community matrix for stability in the ecological framework can be demonstrated as follows: Consider the quadratic function

$$V = \mathbf{x}^{\mathbf{T}}\mathbf{\Gamma}\mathbf{x} = (\mathbf{p} - \mathbf{p}^*)^{\mathbf{T}}\mathbf{\Gamma}(\mathbf{p} - \mathbf{p}^*), \tag{20}$$

where $\mathbf{\Gamma}$ is the matrix of entropy change due to 2-body interactions Γ_{ij}. The internal entropy production of the ecosystem at arbitrary populations $\mathbf{p}$, i.e. $\mathbf{p}^{\mathbf{T}}\mathbf{\Gamma}\mathbf{p}$, and that at the stationary state populations, $\mathbf{p}^{*\mathbf{T}}\mathbf{\Gamma}\mathbf{p}^*$ are both positive definite by the second law of thermodynamics. Since the internal production of entropy is at a minimum in the stationary state, V is thus also positive definite.

The time derivative of V is

$$\frac{dV}{dt} = \frac{d\left[(\mathbf{p} - \mathbf{p}^*)^{\mathbf{T}}\mathbf{\Gamma}(\mathbf{p} - \mathbf{p}^*)\right]}{dt}. \tag{21}$$

A most general result of linear irreversible thermodynamics is that the time change of the internal production of entropy

$$\frac{d}{dt}\left[\frac{d_iS}{dt}\right] = \frac{d\left[\mathbf{p^T\Gamma p}\right]}{dt} \tag{22}$$

is negative semi-definite if the external constraints are time-independent [6]. Since $d\left[\mathbf{p^T\Gamma p}\right]/dt$ thus has its maximum value of zero at the stationary state populations $\mathbf{p}^*$, it is obvious that dV/dt is negative definite. V is thus the Lyapunov function which establishes the local asymptotic stability of the community matrix for an arbitrary community size. *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.*

These stability conditions can be shown to be somewhat more general. For example, consider the case of a system evolving from one stationary state to another [6]. The second law of thermodynamics requires that always

$$\frac{d_iS}{dt} > 0, \tag{23}$$

or, to second order in the interactions,

$$\sum_{i,j}^{n} p_i p_j \Gamma_{ij} > 0. \tag{24}$$

For example, for $n = 2$ species

$$\Gamma_{11}p_1^2 + (\Gamma_{12} + \Gamma_{21})p_1 p_2 + \Gamma_{22}p_2^2 > 0. \tag{25}$$

Equation (25) can only always be satisfied, for whatever values of the populations, if the first of conditions (19) are met. For ecosystems in which $(\Gamma_{12} + \Gamma_{21})$ is negative, the second of conditions (19) must also be met. The second law of thermodynamics thus places restrictions on the values of the inter- and intra-specific interaction parameters in the direction of securing ecosystem stability during evolution. An association of the second law of thermodynamics with natural selection is thus implied.

IV. PHENOMENOLOGICAL LAWS AND RECIPROCITY RELATIONS

The employment of the condition of minimal internal entropy production and that of the negative definiteness of the time change of the internal entropy production implicitly assumed the linearity of the phenomenological laws and the reciprocity relations of Onsager [6]. To second order in the interactions, the total change of entropy in the ecosystem, Eqn. (10), can be written in the form,

$$\frac{dS}{dt} = \sum_{i=1}^{n} \left[p_i \Gamma_i + \sum_{j=1}^{n} p_i p_j \left(\frac{\Gamma_{ij} + \Gamma_{ji}}{2} \right) \right]. \tag{26}$$

In terms of generalized flows J and forces X [6],

$$\frac{d_i S}{dt} = \sum_i J_i X_i. \tag{27}$$

The flows and forces can thus be assigned as,

$$J_i = \sum_j p_j \left(\frac{\Gamma_{ij} + \Gamma_{ji}}{2} \right), \quad X_i = p_i. \tag{28}$$

The generalized forces are thus the populations of the species and the flows are the total changes of entropy due to the two-body interaction of species i with the rest of the species j. The phenomenological relations are thus of the linear form,

$$J_i = \sum_j L_{ij} X_j \tag{29}$$

where the phenomenological coefficients are,

$$L_{ii} = \Gamma_{ii}, \quad L_{ij} = \left(\frac{\Gamma_{ij} + \Gamma_{ji}}{2} \right). \tag{30}$$

From this and equation (19), or the condition following from equation (25), it follows that,

$$L_{ij} = L_{ji}, \quad L_{ii} > 0. \tag{31}$$

The reciprocity relations of Onsager and the positive definite nature of the proper phenomenological coefficients are thus satisfied to 2nd order in the interactions, within or out of the stationary state.

V. DISCUSSION AND CONCLUSIONS

Including interactions between individuals only to second order was justified on the basis of the smaller probability of higher n-body interactions. This was also useful for comparing our results with the traditional approach based on Lotka-Volterra type equations (in general also of second order). Including higher order interactions means that the phenomenological relations will then no longer be linear, implying that the condition of minimal entropy production no longer strictly applies. However, the more general result found by Prigogine and co-workers [6], concerning the rate of internal entropy production, can still be used in this nonlinear regime. In a forthcoming paper it will be shown that this gives rise to wider spectrum of dynamical behavior for the populations.

In the case of changing external constraints, or more generally an evolving ecosystem, in which the phenomenological coefficients (interaction parameters) cannot be treated as constants, again the linear theory does not apply. However, it is still valid, as shown above, that the universal law of positive internal entropy production places restrictions on the relations between the interaction parameters in the direction of securing ecosystem stability.

In conclusion, non-equilibrium thermodynamics can serve as a useful framework for describing the dynamics and stability of ecosystems. Under the postulates of LIT, the stability of the community matrix is guaranteed, independent of its size, and there is thus no complexity-stability paradox. Under constant external constraints the thermodynamic system evolves naturally toward a stable stationary state characterized by minimal internal entropy production, implying a stable community matrix. The second law of thermodynamics places restrictions on the interaction parameters, maintaining community stability during the evolution of the ecosystem from one stationary state to another. This suggests a connection between natural selection of stable ecosystems and the second law of thermodynamics.

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