A Non-equilibrium Thermodynamic Framework for the Dynamics and Stability of Ecosystems

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The population dynamics and stability of ecosystems of interacting species is studied from the perspective of non-equilibrium thermodynamics by assuming that species, through their biotic and abiotic interactions, are units of entropy production and exchange in an open thermodynamic system with constant external constraints. Within the context of the linear theory of irreversible thermodynamics, such a system will naturally evolve towards a stable stationary state in which the production of entropy within the ecosystem is at a local minimum value. It is shown that this extremal condition leads to equations for the stationary (steady) 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 ecosystem stability. The paradoxical stability of real complex ecosystems thus has a simple explanation within the proposed framework. Furthermore, it is shown that the second law of thermodynamics constrains the inter- and intra-species interaction coefficients in the sense of maintaining stability during evolution from one stationary state to another. A firm connection is thus established between the second law of thermodynamics and natural selection.

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I. INTRODUCTION

Ecosystems are complex. A typical ecosystem contains over 3000 species, from bacteria to insects, plants and higher animals [1]. This size, coupled with strong interactions among species and between species and the abiotic environment, leads to very complex population dynamics. Understanding the dynamics and the inherent stability of ecosystems is, however, of crucial importance in guiding wildlife management programs, and in forecasting ecological catastrophes. Modeling of the population dynamics in the traditional ecological framework has been 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 concerning the improbability of stable, complex ecosystems [2].

This paper presents a new look at the questions of ecosystem stability and dynamics from the perspective of linear irreversible thermodynamics (LIT). The need to frame ecology within a thermodynamic paradigm has been recognized before [6–9]. In the present work, the ecosystem is modeled as an open thermodynamic system over which a constant free energy flow is impressed, sunlight. Free energy also enters the ecosystem in the form of chemical potential, such as nutrients. Interactions internal to the ecosystem, between the individuals of the species, and interactions between the individuals and the external abiotic environment, cause a time change of the total entropy of the system. Assuming that the external constraints, energy and nutrient flows, over the system are constant, the linear theory of irreversible thermodynamics predicts [10], and empirical results suggest, that the system will evolve towards a stationary state in which the local state variables (and hence global, extensive variables such as the entropy $S$) are constant in time. This stationary state is locally stable in the sense that small fluctuations are naturally damped by flows generated in the directions of the perturbing forces [11].

Here, I show that writing the entropy change in time of an ecosystem as a many-body expansion in the interactions between individuals, and between individuals and the abiotic environment, and assuming constant external constraints and the eventual establishment of a thermodynamic stationary state, leads to general dynamical equations for the populations of the interacting species. A LIT condition of minimal entropy production in the stationary state dictates conditions on the interaction parameters which assure the stability of the ecosystem. Furthermore, it is shown that the second law of thermodynamics imposes restrictions on the inter- and
intra-specific interaction parameters, ensuring stability during the evolution of the system from one stationary state to another after the external constraints are changed, or after the system is significantly perturbed.

II. THE TRADITIONAL ECOLOGICAL FRAMEWORK

Population modeling in the traditional ecological framework is based on the equations

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

where $F_i$ is, in general, some empirically inspired, nonlinear function of the populations $p_i$ of the $n$ species. 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), $F$ takes the following form,

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

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 $p_i^*$,

$$0 = F_i(p_1^*(t), p_2^*(t), \ldots p_n^*(t)).$$

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,

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

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 need be considered. In matrix notation, this gives,

$$\dot{x}(t) = Ax(t),$$

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

$$a_{ij} = \frac{\partial F_i}{\partial p_j}|_*.$$

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

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

where $\lambda_j$ are the eigenvalues of the matrix $A$ 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 $A$ must be negative. This condition gives rise to very restrictive relations among the components $a_{ij}$ of the community matrix $A$. For example, it can be shown that for a $n = 2$ species community it requires that
\[ a_{11} + a_{22} < 0, \]  
\text{(8)}

and

\[ a_{11}a_{22} > a_{12}a_{21}. \]  
\text{(9)}

For the Lotka-Volterra equations, Eqn. (3) this implies

\[ p_1c_{11} + p_2c_{22} < 0, \]  
\text{(10)}

and

\[ c_{11}c_{22} > c_{12}c_{21}. \]  
\text{(11)}

For a community of arbitrary \( n \) species, it can be shown that the requirement that the \( n \times n \) matrix \( A \) have all real parts of its eigenvalues negative is equivalent to the demonstration of the existence of a positive definite quadratic function \( V = x^TPx \) (Lyapunov function) having its derivative with respect to time negative definite [11].

The restrictions on the components of the community matrix for ensuring stability are thus specific, and are more specific the more complex the ecosystem [3]. 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 [3,2,12,13]. 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 stable [1,14].

There have been many attempts to reconcile the theory with the field data [3,5,15–20]. The most plausible of these has been to invoke natural selection as the mechanism for tuning the parameters of the community matrix [3]. This explanation, however, may be criticized as being tautological since there is no physical reason postulated for the selection of interaction coefficients leading to stability. Or, from another perspective, it leads to the celebrated problem of natural selection working on the evolution of a system of a population of one [21].

A scenario in which the elements of the community matrix are fortuitously chosen at random can be discarded on the basis of statistical improbability of achieving stability for these large systems containing upwards of 3000 species.

III. A PROPOSED THERMODYNAMIC FRAMEWORK

The linear theory of irreversible thermodynamics provides an interesting framework for accommodating the problem of ecosystem dynamics and stability. The objective of this paper is to demonstrate this by showing that steady state ecosystems have the signatures of thermodynamic stationary states. The starting postulate of this paper is that the total change of entropy of the ecosystem may be written as a many-body expansion of entropy changes due to interactions among individuals. Specifically,

\[
\frac{dS}{dt} = \sum_{i=1}^{n} \left[ p_i \Gamma_i + \sum_{j=1}^{n} p_i p_j \Gamma_{ij} + \sum_{j,k=1}^{n} p_i p_j p_k \Gamma_{ijk} + O(4) \right].
\]  
\text{(12)}

The \( \Gamma_i \) represent the change of entropy due to 1-body interactions of individuals with their abiotic environment (eg. evapotranspiration, photo-synthesis, respiration, metabolic heat transfer to environment, etc.); \( \Gamma_{ij} \) represents 2-body interactions between individuals (eg. predator-prey, competition, symbiosis, mutualism, etc.); \( \Gamma_{ijk} \) correspond to the 3-body interactions, and \( O(4) \) represents 4-body and higher order interactions (eg. those required for the functioning of societies). Although this formulation of the total entropy change is perhaps not the most general imaginable, it is a most common scheme chosen for systems in which the interacting constituents cannot be considered as ideal points in space-time, and in which no singularities are expected. Similar many-body expansion are used, for example, for representing the interactions between extended, deform-able charged objects such as atoms in molecules and clusters [22], and nucleons in nuclei [23].
The total time change of entropy is a sum of an external term of no definite sign, and, as required by the second law of thermodynamics, an internal term of positive definite sign,

\[
\frac{dS}{dt} = \frac{d_e S}{dt} + \frac{d_i S}{dt}.
\]  

(13)

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

\[
\frac{d_e S}{dt} = \sum_{i=1}^{n} p_i \Gamma_i.
\]  

(14)

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

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

(15)

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

\[
\frac{d_e S}{dt} = \sum_{i=1}^{n} p_i \Gamma_i < 0,
\]  

(16)

indicating that at least one of the species must bring negative entropy into the ecosystem, and that this negative entropy is 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 a thermodynamic stationary state implies,

\[
\frac{\partial}{\partial p_i} \left[ \frac{dS}{dt} \right] \bigg|_* = 0,
\]  

(17)

for all species \(i\). The * now denotes evaluation at the stationary state populations. In the following, equation (12) 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 [3,24,25] with few exceptions [26]. This truncation, however, is certainly not valid for ecosystems with societal species, in which higher \(n\)-body interactions play an important role. The more general dynamical equations and stability relations obtained from the complete equation (12) employing equation (17) will be discussed in a forthcoming article. Thus, taking equation (12) only to second order in the interactions, Eqn. (17) gives

\[
\Gamma_i + \sum_{j=1}^{n} p_j^* \left( \Gamma_{ij} + \Gamma_{ji} \right) = 0.
\]  

(18)

A simple change of variable makes these equations recognizable as equivalents of those defining the steady state populations in the ecological framework using the Lotka-Volterra equations, Eqs. (2), and 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 \(\Gamma_2\) and \(\Gamma_{22}\).

In the stationary state, assuming linear phenomenological laws (see below), the internal dissipation of entropy, \(\dot{S}_i = d_i S/dt\), is a minimum [14]. In general, if \(\dot{S}_i\) is a function of \(n\) populations, the condition for it to be a minimum is that the Hessian matrix,

\[
h_{ij} = \left( \frac{\partial^2 \dot{S}_i}{\partial p_i \partial p_j} \right) \bigg|_* \]  

(19)
is positive definite \[11\]. As an example, for \( n = 2 \) species, \( \dot{S} \) is a function of two variables, \( p_1 \) and \( p_2 \), and the following two conditions must be satisfied \[27\]:

\[
\frac{\partial^2 \dot{S}}{\partial p_1^2} \bigg|_{p_1^* p_2^*} > 0,
\]

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

(20)

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

\[
\Gamma_{ii} > 0,
\]

\[
4\Gamma_{11}\Gamma_{22} > (\Gamma_{12} + \Gamma_{21})^2.
\]

(21)

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 (10) and (11). That these conditions for arbitrary ecosystem size \( n \) in this thermodynamic framework 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

\[
V = x^T \Gamma x = (p - p^*)^T \Gamma (p - p^*)
\]

(22)

where \( \Gamma \) is the matrix of entropy change due to 2-body interactions \( \Gamma_{ij} \). The internal entropy production of the ecosystem at arbitrary populations \( p \), i.e. \( p^T \Gamma p \), and that at the stationary state populations, \( p^*^T \Gamma p^* \) 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

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

(23)

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

\[
\frac{dP}{dt} = \frac{d}{dt} \left[ \frac{dS}{dt} \right] = \frac{d}{dt} \left[ p^T \Gamma p \right]
\]

(24)

is negative semi-definite if the external constraints are time-independent \[10\]. Since \( \frac{d}{dt} [p^T \Gamma p] \) has its maximum value of zero at the stationary state populations \( p^* \), it is obvious that \( \frac{dP}{dt} \) is negative definite. We have thus found the Lyapunov function \( V \) which establishes the local asymptotic stability of the community matrix. An ecological steady state thus has the 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 \[10\]. The second law of thermodynamics requires that always

\[
\frac{d_i S}{dt} > 0,
\]

(25)

or, to second order in the interactions,

\[
\sum_{i,j} p_ip_j \Gamma_{ij} > 0.
\]

(26)

For example, for \( n = 2 \) species
\[ \Gamma_{11}p_1^2 + (\Gamma_{12} + \Gamma_{21})p_1p_2 + \Gamma_{22}p_2^2 > 0. \] (27)

Equation (27) can only always be satisfied, for whatever values of the populations, if the first of conditions (21) are met. For ecosystems in which \((\Gamma_{12} + \Gamma_{21})\) is negative, the second of conditions (21) 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. The association of the second law 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 [10]. To second order in the interactions, the total change of entropy in the ecosystem, Eqn. (12), can be written in the form,

\[ \frac{dS}{dt} = \sum_{i=1}^{n} \left[ p_i \Gamma_i + \sum_{j=1}^{n} p_ip_j \left( \frac{\Gamma_{ij} + \Gamma_{ji}}{2} \right) \right]. \] (28)

In terms of generalized flows \(J\) and forces \(X\) [10],

\[ \frac{dS}{dt} = \sum_i J_i X_i. \] (29)

The flows and forces can thus be assigned in the following manner,

\[ J_i = \sum_j p_j \left( \frac{\Gamma_{ij} + \Gamma_{ji}}{2} \right), \quad X_i = p_i. \] (30)

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,

\[ J_i = \sum_j L_{ij} X_j \] (31)

where the phenomenological coefficients are,

\[ L_{ii} = \frac{\Gamma_{ii}}{2}, \quad L_{ij} = \frac{(\Gamma_{ij} + \Gamma_{ji})}{2}. \] (32)

From this and equation (21), or the condition following from equation (27), it follows that,

\[ L_{ij} = L_{ji}, \quad L_{ii} > 0. \] (33)

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

In the work presented here, interactions between the individuals have been taken only to second order. This was justified on the basis of the smaller probability of higher n-body interactions, and was intended for simplicity and for comparing results with traditional ecological approaches based on Lotka-Volterra type equations, which,
in general, are 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 \[10\], 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 a 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 has been shown here, that the universal law of positive internal entropy production places restrictions on the possible values of the interaction parameters in the direction of securing ecosystem stability.

Although we have shown in this paper that large, complex ecosystems are constrained to stability by results from non-equilibrium thermodynamics, we have not argued why such systems might be favored over smaller, less complex ones, as appears to be the case in nature. Although it is not the intention of this paper to suggest a general evolutionary criterion for ecosystems, a possible explanation, not in conflict with the proposed framework, has been presented by Swenson \[21\]. Swenson argues that of all the possible paths available to a system after the removal of an external constraint, a thermodynamic system will take the path which increases the entropy of the system plus environment at the fastest rate 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 theory were correct.

It is interesting that this apparent duality of ecosystems, to move towards stationary states of minimal entropy production over relatively short time scales where the external constraints can be considered constant, and towards stable systems of higher internal entropy production over longer evolutionary time scales, is mirrored within individuals. It appears that an individual advances towards a state of minimal entropy production over development from birth to death \[1\], while there is empirical evidence suggesting that there is an evolutionary trend in individuals towards higher metabolic rates (implying higher individual entropy production) \[28\].

In conclusion, non-equilibrium thermodynamics can serve as a useful framework for describing the dynamics and stability of ecosystems. In this framework, 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 towards a stable stationary state. A stable stationary state, characterized by minimal internal entropy production, implies a stable community matrix if the total change of entropy of the ecosystem can be written as a many-body expansion of interactions between individuals as postulated here. The second law of thermodynamics places restrictions on the interaction parameters in the sense of maintaining community stability during the evolution of the ecosystem from one stationary state to another. This establishes a firm connection between natural selection and non-equilibrium thermodynamics and the second law of thermodynamics.

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