

Editor,
Journal of Theoretical Biology,

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Dear Editor,

I hereby submit a revised version of my manuscript entitled “Thermodynamic Stability of Ecosystems” for consideration for publication in your journal. The revised version incorporates extensive changes in response to the comments and criticisms of the referees. The response to the referees, and a list of changes made to the article are given below.

I thank the editor and the referees for their efforts and for consideration of the revised version of the manuscript.

Sincerely, K. Michaelian

Response to Referee I

I thank the referee for his/her recommendation to publish and for their favorable comments concerning the manuscript. With respect to the possibility of “phase changes” occurring in regimes far from equilibrium, this is certainly an interesting possibility for ecosystems and it may have a connection to what the ecologists refer to as “succession”. In classical irreversible thermodynamics, such a “phase transition” occurs when an external thermodynamic force is increased (or reduced) beyond a certain critical value. In fact, evidence for a correlation between succession and changes in the external environment, especially through a critical point, have accumulated in the ecological literature (see references in the new version of the manuscript). Such an occurrence, a result of a variation of external constraints over the ecosystem, thus belongs to the context of the more general macroevolution of the ecosystem. In the new version of the manuscript I mention the possible role of variable external constraints in macroevolution and the possibility of non-equilibrium “phase changes” occurring in ecosystems in this more general scheme. This is done by relating thermodynamic stability with stasis, and non-equilibrium phase changes with episodic change within the larger framework of ecological succession.

Response to Referee II

I thank the referee for recognizing the importance of the problem concerning the stability of ecosystems which is addressed in the manuscript. The referee, however, is mistaken when they say that I describe the stationary state “as a state where the entropy production is zero”. This is not how the stationary state is depicted in the manuscript. In the manuscript the entropy production is taken as always greater than zero (as it must be for any state which is not the equilibrium state) and this was presented as such in equation (13) ($d_i S/dt > 0$), mentioned as such in the preceding paragraph, and taken consistently as such throughout the manuscript. What does go to zero in the stationary state is the **total change of the entropy** ($dS/dt = d_e S/dt + d_i S/dt = 0$) as expressed by equation (26). This is in fact the definition of the stationary state; all extensive variables (including the total entropy) become time independent.

There are indeed many degrees of freedom (or variables) needed to completely define an ecosystem. Many of these variables will have a spatial dependence as the referee correctly notes. However, the manuscript is only concerned with a particular aspect of ecosystems; the dynamics and stability of the populations of the species. The thesis of the article is that the first and second derivatives of the entropy with respect to time, and as a function of the populations, are the most appropriate thermodynamic variables with which to characterize the population dynamics and population stability of ecosystems. Since these thermodynamic variables are *extensive* variables their spatial dependence may be integrated over.

Energy and work (and in fact chemical potential) from the environment are indeed taken into account in the framework presented in the manuscript. This is expressed clearly in equation (15) which represents the entropy flow to (or from) species γ , from (or to) its external environment (the available resource reservoir);

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

There is in fact a second time derivative in equation (33). This is because $\mathcal{P} \equiv d_i S/dt$ and thus

$$\frac{d\mathcal{P}}{dt} = \frac{d_i^2 S}{dt^2} \quad (2)$$

In response to “some other questions” of the referee:

Sunlight impinges on the plants or cyanobacteria in the ecosystem with a spectrum of wavelengths peaking in the visible. Some of this light is absorbed and the photon energy utilized to promote the formation of glucose using adsorbed CO_2 and absorbed water. The overall reaction being



The energy from the oxidation of glucose, along with other nutrients taken from the soil, is then used in the metabolism of the plant cells to form complex organic molecules and eventually tissues. These molecules and tissues have a negative structural entropy with respect to that of the individual and dispersed molecules of CO_2 , H_2O and the nutrients. This negative entropy amounts to free energy which can then be used by other animals in the ecosystem in building up still more complex systems, and even societies in the case of humans and some other animals. Photosynthesis is indeed an internal process of the ecosystem and the process also produces entropy which is returned to the environment basically through evaporation of water through the leaves. In summary, the negative entropy brought into the ecosystem is related to the difference in free energy between the short wavelength photons absorbed by the plant and the long wavelength photons emitted by the plant. Since this thermodynamic description of the process is relatively well documented elsewhere, I don't think it is appropriate to include it in the article.

An individual of a given species is an open system in which there is a flow into (or out of) of energy, heat, and matter, from (or into) the external environment. This flow for a species γ is represented by the term Γ_γ^e in the manuscript. Therefore, Γ_γ^e must consider all three terms, as in equation (15) of the manuscript (or equation (1) above) and not just the term due to heat flow $1/Tdq_\gamma/dt$.

The terms $c_{\gamma\gamma}$ and b_γ in equation (2) of the manuscript have now been defined in the new version.

The phrase “natural relaxation time” used in the manuscript was meant to indicate the robustness of individuals within the ecosystem to fluctuations of the external constraints. In ecological terms this is sometimes referred to as *resilience*. In thermodynamic terms one can speak of a characteristic time for damping of fluctuations. For example, for an ideal gas in equilibrium it is of the order of the mean time between collisions, about 10^{-15} s. For a simple system out of equilibrium, such as a Bénard cell, it is the characteristic time for recuperation of the cell after perturbation, of the order of a second (of course dependent on various dimensional and physical factors). For still more complex living beings with active homeostasis systems in stationary states, it is reasonable to assume it is much longer. This is important because, for an ecosystem, the flow of photons from the sun is not constant but follows a 24 hour cycle. Plants and cyanobacteria have obviously attained a sufficient resilience to this variability in their external constraints and thus have a characteristic survival time of greater than 12 hours with respect to sunlight variations. In the new version of the manuscript, the term “natural relaxation time” has been replaced by “characteristic survival time” which is related to the ecological concept of resilience.

I thank the referee for pointing out the article by C.G. Chakrabarti et al. I was not aware of this paper but it is now referenced in the new version of the manuscript. Although Chakrabati and I both apply non-equilibrium thermodynamics to ecosystems, our papers are fundamentally different. Chakrabati assumes the Lotka-Volterra equations to describe ecosystems and then studies the stability of solutions to these equations in the neighborhood of the steady state populations. I do not assume the Lotka-Volterra relations but instead postulate a general expression for the entropy production and then show how non-equilibrium thermodynamic directives concerning the entropy production and its time derivative lead to dynamical equations which contain the Lotka-Volterra equations as a subset. Further, I demonstrate that stability is a necessary consequence of these same directives. The other articles mentioned by the referee, although interesting and concerning some of the same phenomena studied here, have little to do with the non-equilibrium thermodynamics of ecosystems and, therefore, in my opinion, are not directly pertinent to the present article.

Response to Referee III

I thank the referee for their recommendation to publish.

The introduction has been completely reworked in the new version, spelling out clearly the main objective of this work as requested by the referee, while at the same time presenting its limitations “up front”, as requested by referee VI, and finally, emphasizing the biological importance of this work in response to the criticisms of referee V.

Since the manuscript refers to the ecosystem as a *whole*, using the *total* entropy, and considering the boundary conditions (in this case fixed conditions), the stability referred to is necessarily *global*. However, this is not to suggest that the stationary state is necessarily unique. The complexity of ecosystems and their external constraints would suggest that many possible stationary states may exist. A perturbation of the external constraints or an internal fluctuation may be sufficient to promote succession from one such state to another. This is now made clear in the revised version of the manuscript.

Section 3, “On the applicability of CIT to ecosystems”, justifies the use of classical irreversible thermodynamics for some ecosystems under certain conditions. The conditions and restrictions are enumerated in this section. As far as I am aware, this analysis on the applicability of CIT to ecosystems has not been considered in this context before. In particular, the conjecture on the differences in stability characteristics between the equatorial and high latitude ecosystems as a result of the differences in the constancy of the external constraints within the CIT framework is, I believe, original and worth pursuing in a following more dedicated article.

Section 4 on the framework has been changed in an attempt to make it more clear. In particular, it now includes a brief introduction, explaining in words what follows in equations.

Equation (20) represents the time change of the total entropy. It is mathematically correct as long as the entropy can be written as a function of the populations, $S = S(p_1, p_2, \dots)$. The difference is that unlike chemical components, individuals of species may bring in, or give out, entropy to the external environment. Thus besides the term due to internal ecosystem interactions, there is also this other part which is related to the exchange of entropy with the external environment. For this reason the left side of equation (20) is the total rate of change of the entropy and not just the internal production of entropy.

The use of the expression “universal evolution criterion” has been avoided in the new version of the manuscript in accordance with the pertinent observations of both referees III and VI.

The simulations in population space of equation (49) have now been described in more detail in the new version of the manuscript. However, the particular mathematical details of the example are still left to an appendix since, in the “Guide for Authors” of the JTB, it is stated

that “detailed mathematical technicalities and experimental procedures may usually be best presented in appendices so as not to impede the exposition of the central ideas.”

I thank the referee for his/her recognition of the necessity of an approach of the type presented in the manuscript to treat non-linear effects in ecosystems.

Response to Referee IV

I thank the referee for pointing out the books related to the theme of the work presented in the manuscript. I have endeavored to obtain these works by contacting the author directly and have read related works by the same author printed in journals. I have now included a reference to a pertinent work in the revised introduction to the manuscript.

Response to Referee V

I appreciate the criticism of the referee concerning the difficulty that a population ecologist might have in assimilating the work presented in this paper. However, I do not believe that this difficulty is due to the math involved (since this is really only basic calculus) but rather due to unfamiliarity with the concepts of thermodynamics out of equilibrium and how these concepts may relate to ecosystem dynamics. In the new version of the paper I have endeavored to provide a more lucid account of the thermodynamic concepts and how they may be related to ecological theory. I believe that the introduction is now more accessible to the non-specialist in thermodynamics and emphasizes more the biological significance of this work.

Although it is a fact that most ecologists and biologists are unfamiliar with the non-equilibrium thermodynamic framework, I believe that there is justification in looking beyond the traditional framework for a satisfying resolution of stubborn paradoxes and problems. Such an approach has historical precedent, for example in the resolution of the problems of; the null result of the Michelson-Morely experiment concerning motion through the Ether, the unexplainable advance of the perihelion of the planet Mercury, or the ultra-violet catastrophe in black-body radiation. All these problems or paradoxes, existent within the traditional classical framework, were eventually solved by analysing the problem in a new (and generally unfamiliar) framework; special relativity, general relativity, and quantum mechanics respectively. For an example from biology, the gradualist framework of traditional evolutionary theory has given way to punctuated equilibrium to resolve a number of paradoxes, including missing links between similar species in the fossil record.

That indeed a problem or paradox exists with respect to ecosystem stability in the traditional “empirical” framework based on the Lotka-Volterra equations and “ad hoc” extensions thereof can be surmized from the large number of papers concerning this problem already published, and which continue to appear in the most prestigious journals. The search for an active force promoting stasis has become a major focus of evolutionary study (see references in the new version of the article). The problem is far from being only “apparent”. In the new version of the manuscript I have included many new references to the original works from within the ecological framework (including those suggested by referee VI). However, the vast number of

subsequent works on this theme are just too numerous to include and, in my opinion, are not pertinent because they have not resulted in a convincing resolution of the problem.

In the “Guide for Authors” of The Journal of Theoretical Biology, it is stated “The aim of the Journal of Theoretical Biology is to publish theoretical papers, which give insight into biological processes. The biological significance should be clearly stated.” I believe that my manuscript is suited to JTB because it fullfills the aim of this journal, notwithstanding its reliance on cross-discipline concepts. In the new version of the manuscript, however, particularly in the introduction, I have paid special attention to clearly formulate the biological significance of this work in a form accessible to the ecologist and biologist.

Response to Referee VI

I thank the referee for a very careful and thoughtful review of the manuscript, and also for recognizing the importance of this work, and their recommendation to publish.

With respect to the three areas of concern expressed by the referee:

1)As mentioned previously, I have completely re-worked the introduction taking into consideration the criticisms of referees III, IV and VI, concerning respectively; a clear statement of the objective, a more lucid explanation for the non-specialist, and an up front admission of the restricted scope of this work. With respect to the latter, the new version of the manuscript makes it clear that I am treating only the aspect of stasis, albeit a most important aspect, in the more general macroevolution of ecosystems, now placed it the context of ecological succession with the dynamics defined by punctuated equilibrium. The “equilibrium” or stasis, an enigma in the ecological framework, is correspondingly placed in the context of non-equilibrium thermodynamic stationary states. An active agent for promoting stasis, conspicuously missing in ecology, is given in terms of non-equilibrium thermodynamic directives concerning the entropy production and its time derivative under constant external constraints.

2)The authors that the referee indicates as being pioneers in the field of ecosystem development are now referenced in the expanded introduction. More appropriate references to both Zotin and Swenson in the sections suggested by the referee are now given.

3)The previous version of the manuscript addressed periods of stability in ecosystems. The more general macroevolutionary dynamics of the ecosystem going to progresively larger and more complex states in ecological terms, or in thermodynamic terms to progressively higher states of internal entropy production, was only considered in passing by referring to Swensons principle. By leaving this more global aspect to only a brief mention in the Discussion, it may have appeared (but certainly was not intended) that I suggest that nature tends to minimize the entropy production, to the obvious absurdity of extinction as the referee notes. The point is that only under *constant* external constraints will the system develop to one of minimal internal entropy production. However, it does not go to zero entropy production (which could only happen in thermodynamic equilibrium, when all constraints go to zero), rather, it is minimal

with respect to the assumed fixed and constant external constraints. In thermodynamic terms it is the end result of inescapable directives. In ecological terms, it leads to the surprising stability of ecosystems against internal fluctuation or external perturbation.

Of course, on a larger time scale, ecosystems evolve by increasing in size, complexity, and stability. As noted above, this was addressed in the old version of the manuscript only through a brief mention to Swenson's principle in this regard. In the new version of the manuscript I have placed this discussion in terms of ecosystem succession, including stasis and episodic change (punctuated equilibrium). Although, as with the old version, the new version deals only with stasis, in response to referee I's observation I have also now provided a discussion of episodic change in terms of non-equilibrium "phase changes" under variable external constraints, especially through a critical point, leaving the discussion of the direction of that change as that governed by Swenson's principle. Of course I do not present this as a definitive theory, only as a means to show a possible way of including the macroevolutionary dynamics of ecosystems within a consistent thermodynamic framework.

Since the article refers basically to explaining the steady state, or stasis, in which there is no ecosystem growth, thermodynamic relations pertaining to the mass specific entropy are identical to those pertaining to the total entropy. In the macroevolutionary process of succession, ecosystems are growing and the referee is correct in that the total entropy production may increase, and, perhaps, the most appropriate variable should then be the mass specific entropy production. However, this is not the theme of the present article. This is now made clear in the new version of the manuscript.