Editor,
Journal of Theoretical Biology, March 29, 2005

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 changes in response to the second round of comments and criticisms by 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 once again for their efforts and for consideration of the revised version of the manuscript.

Sincerely, K. Michaelian

Response to Referee II

It is now clear, after reading the second round of comments, why referee II has problems with understanding the form of equation (33). Equation (33) is NOT a complete differential of the entropy production. It is rather the rate of change of the entropy production due to changes in the forces only (for that reason there appears a subscript $_X$ on the differential $d_X\mathcal{P}/dt$ to specify that the differentiation is only with respect to the forces X). I will remind the referee that the entropy production is a bilinear form of flows times forces. We are only differentiating the forces with respect to time. For that reason, there is not a second differential of the populations on the right hand side of the equation. To make this clear, here I provide all the steps in going from equation (32) to equation (33):
The entropy production is (equation (32))

$$\mathcal{P} = \frac{d_iS}{dt} = -\sum_\gamma \frac{\nu_\gamma}{T}\frac{dp_\gamma}{dt} - \frac{d_eS}{dt}. \tag{1}$$

We now want to determine the time change of the entropy production due to a change in the generalized forces X, that is

$$\frac{d_X\mathcal{P}}{dt}.$$

The generalized flows are (see paragraph below equation (21))

$$J_\gamma = \frac{dp_\gamma}{dt},$$

while the generalized forces are

$$X_\gamma = \frac{-\nu_\gamma}{T}.$$

Therefore, we only differentiate with respect to time X_γ while holding $J_\gamma = dp_\gamma/dt$ constant. In X and J notation, this gives

$$\frac{d_X\mathcal{P}}{dt} = \sum_\gamma \frac{dX_\gamma}{dt} J_\gamma.$$

Substituting for X and J and using the chain rule gives,

$$\frac{d_X\mathcal{P}}{dt} = -\frac{1}{T}\sum_{\gamma\gamma'} \left(\frac{\partial\nu_\gamma}{\partial p_{\gamma'}}\right)_{(p_\gamma)} \frac{dp_{\gamma'}}{dt}\frac{dp_\gamma}{dt}. \tag{2}$$

which is just equation (33).

As a final note to the referee, a total differential, such as that given by equation (47)

$$\frac{d\mathcal{P}}{dt} = \frac{d_X\mathcal{P}}{dt} + \frac{d_J\mathcal{P}}{dt}$$

would indeed have a second time derivative of the populations.

Response to Referee V

1. In the revised version of the manuscript, I have toned down the statement that "Stasis ... now forms a major focus of evolutionary study..." by replacing it with the statement "Stasis... now forms an important focus of evolutionary study ...". I have also removed the entire contents of paragraph 2 in which the work of Elena and Lenski are mentioned. This removal also responds to referee's VI criticism of my inclusion of the homeostasis Gaia hypothesis.

From the thermodynamic viewpoint from which I address ecological issues in the paper, the underlying mechanism of punctuated equilibrium is suggested to be non-equilibrium phase transition. From the biological viewpoint, the manifestation of these phase changes may indeed look quite different, but this is not the viewpoint of the article, and I believe that including this would detract from the thermodynamic viewpoint.

2. I am not in agreement with the referee that "succession is a somewhat outdated view in community ecology...". It is true that since the popularization of the notion by Clements, succession has been repeatedly criticized. However the criticism has usually come in the form of reductionist viewpoints which fail to consider a great quantity of experimental and field data. The criticisms leveled at the concept of succession are not at all universally accepted. For example, E. Goldsmith has severely criticized the critics of succession in his article entitle "Ecological Succession Rehabilitated" (*The Ecologist* **15** (1985) 210). In my article, I use the concept of succession in its modern and most accepted connotation to describe the macro-dynamics of ecosystems; slow development toward stability followed by episodic change and re-initiation of the cycle (Holling CS, *Whole Earth Summer* (1998) 32). In my opinion, there is no other ecological concept which would fit or have better resonance here.

Response to Referee VI

In response to the referee, I have now removed paragraph 2 concerning the homeostasis Gaia hypothesis, including the footnote.

The sentence containing the reference to Raup and Sepkoski concerning a perceived increase in ecosystem stability over time has now been removed.

Concerning the referees general inclination to accentuate the reference to the works by Swenson: I have replaced the reference suggested by the referee to be somewhat inaccessible to a more accessible new reference of Swenson, “Spontaneous order, autocatakinetic closure, and the development of space-time” at the first mention of the problem of the evolution of a system of population of one, in the paragraph giving the historical antecedents, and in the second last paragraph of the introduction which briefly suggests how my paper fits in with more general macro-evolutionary concepts. I have also noted that Swenson has addressed more general evolutionary principles in the historical antecedents paragraph, and refer the reader to Swenson's papers in 5 separate locations in the text.

With regard to the reference to Kay and Schneider in the paragraph containing the historical antecedents, I believe that it is important to give credit to these authors for the following reasons: Although these authors may “simply restate” what has been already said by the “pioneers”, this restatement is in concise non-equilibrium thermodynamic terms. Also, these authors have carried out field experiments to ascertain the validity of principles generally accepted without verification. I would feel uncomfortable with the removal of their reference from my paper. However, to reduce perhaps somewhat the implied emphasis given to these authors, I have reduced the previous two references to only one reference, which, in my opinion, best represents their work.

The second last paragraph of the introduction, concerning more general evolutionary principles, has now been reworked to place the emphasis on a coupling of the work presented in my paper with more general evolutionary principles based on non-equilibrium thermodynamics. The paragraph makes a link between the biological concepts of stasis and punctuation and the thermodynamic concepts of stationary states and non-equilibrium phase transitions. It is suggested that movement through a critical point, either from below or above, of the value of a given constraint or constraints, can lead to abrupt ecosystem evolutionary change, ie. succession. I believe that the view point I take is complementary to but different than Swenson's. It is complementary in the sense that it doesn't contradict Swenson's principle, and Swenson's principle offers a prediction for the most probable direction for evolutionary change in ecosystems. However, it is also different from Swenson's principle in that it suggests that the changes in ecosystems are discontinuous with long periods of intervening stasis. As such, it provides a possible thermodynamic basis for punctuated equilibrium, the fine structure in evolutionary change. In any case, the paragraph is now more modest in its claims and also cites Swenson's work in this context.

Assuming that configurational entropy is not altered much by chemical reactions taking place in an individual, especially after reaching maturity, then metabolic rates can be used as approximate indicators of individual total entropy production (I. Prigogine, “Thermodynamics of

Irreversible Processes", John Wiley and Sons, 1967). As an individual grows, its total entropy production increases, as the referee indicates. However, this increase, as its growth, is not indefinite. The total entropy production reaches a maximum at maturity of the individual, and then the *total* entropy production begins to decline, reaching a minimum steady state value some years before death (see for example "Thermodynamics of Biological Process", Ed. I. Lamprecht and A.I. Zotin, W. de Gruyter, 1978, and R. Glaser, "Biophysics", Springer, 1996). There is evidence that this steady state value for the total entropy production of the individual has increased over the evolutionary history of life on earth (A.A. Zotin et al., *J. Non-Equilib. Thermodyn.*, **26** 191, 2001). This is the duality referred to in my article; decreasing entropy production over the lifetime of the individual after reaching maturity, while increasing entropy production of individuals over evolutionary time.

A young ecosystem (ie. after a successional or catastrophic event) will increase its total entropy production as it grows in size (species immigration under variable external constraints). However, this growth is not indefinite, species invasion will become increasingly difficult as the ecosystem reaches maturity and, given constant external constraints, its total entropy production will decline, reaching a minimum at the steady state. As succession is repeated, the ecosystem generally moves to progressively higher states of internal entropy production. This is evidenced, for example, in the succession of clear cut grass lands to deciduous forest. This is the duality referred to for ecosystems.

I believe that this duality (minimization of entropy production over the short term at constant constraints, while maximization over the long term at variable constraints) is a characteristic of living systems and follows from thermodynamic directives at specific external constraints. However, as the referee rightly states, this detail is not crucial to the main argument of the paper, nor is it developed in the paper. More importantly, the referee has threatened to "change sides" if I stick with it. I have thus eliminated the offending paragraph from the Discussion section.

Other unsolicited changes

I have included a short paragraph in the section "On the applicability of CIT to ecosystems" to justify the assumption of coupling of macroscopic irreversible processes in ecosystems.