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Thermodynamic stability of ecosystems

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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.

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

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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 looses 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 lead 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