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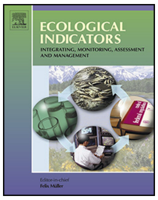

Short communication

Effectiveness of entropy-based functions in the analysis of ecosystem state and development

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ABSTRACT

Following the advances in the field of the thermodynamics of far-from-equilibrium systems, several ecological orientors (indicators able to describe the stage and orientation of ecosystem development) incorporating entropy terms have been proposed. Although most of the proposed functions have a good theoretical basis and have proved to perform adequately as ecological indicators, their suitability as ecological orientors has yet to receive a full confirmation in real case studies. The aim of the present contribution is to examine how several entropy-based indicators (*exergy*, *structural information*, *entropy production*, *specific entropy production* and the *Eco-exergy index*) perform as orientors when applied to a special case of ecological succession, i.e. eutrophication, in a homogeneous set of shallow lakes lying along a trophic gradient, from oligotrophy to hyper-eutrophy. The results show that a coherent pattern of response emerge, which is also consistent with the classical ecological theory. In particular, the maximisation of storage and the minimisation of specific entropy production are confirmed as the most reliable principles of ecosystem development, whereas the maximisation of dissipation (as entropy production) appears as a debatable criterion of development.

1. Introduction

Ecosystem development can be defined as a process in which a succession of biological communities, together with a change in the physical environment, take place until a "final" and more stable state (the climax) is achieved. Thermodynamics appears to possess the crucial features for tracing the path of such a process, as it provides a theoretical framework rooted in physics, useful for describing the state and the direction of development of a system. From a thermodynamic standpoint, ecosystems can be viewed as intrinsically non-isolated systems able to maintain themselves in a far-from-equilibrium condition by exploiting the entropy exchanges with the surrounding environment (Schrödinger, 1944; Nicolis and Prigogine, 1977; Ulanowicz and Hannon, 1987). According to this view, the entropic distance from thermodynamic equilibrium and the entropy exchanges at ecosystem boundary are the key quantities to be taken into account in describing the state of an ecosystem (see the Appendix A for a thermodynamic formulation of these quantities). Based on the above theoretical framework, several entropy-based functions have been proposed as ecological orientors, i.e. indicators able to describe the stage and orientation of ecosystem development (Müller and Leupelt, 1998; Fath et al., 2001). A first type of orientors has been developed by focusing on the entropic distance from equilibrium (Table 1). Among them, exergy is likely the most widely investigated and applied in ecology. As shown by Evans et al. (1966), exergy is strictly related to the change in entropy from the equilibrium and the actual state (see the Appendix). Mejer and Jørgensen (1979) first proposed the following equation for calculating the exergy of ecosystems:

$$Ex = RT\sum_{i=1}^{n} c_i \ \ln \frac{c_i}{c_{i(e)}} - (c_i - c_{i(e)}). \tag{1}$$

In the equation, R is the gas constant, T is the absolute temperature and c_i are the concentrations of the different ecosystem components in suitable units, with the subscript e denoting equilibrium conditions. In itself, the exergy of an ecosystem accounts mostly for the free energy stored in biomass, irrespective of the distribution among ecosystem components. In order to emphasise the structural differences existing among ecosystems having equivalent biomass, Jørgensen (1994, 1995) proposed the Eco-exergy index, in which the number of genes is used for weighting the organisational level of organisms:

$$Eco\text{-}ex = RT\sum_{i=1}^{n} \beta_i c_i, \tag{2}$$

Here, β_i is a weighting factor incorporating the chemical and the informational exergy stored in the unit of biomass of the *i*th

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Table 1
List of some main entropy-based indicators derived in the last decades and associated principles of ecosystem development.

Type	Orientor	Authors	Statement
Distance from equilibrium	Exergy (*Ex*)	Jørgensen (1992a)	"If there are offered more than one pathway to move away from thermodynamic equilibrium, the one yielding the most stored exergy will be selected"
	Structural information (*I*)	Ludovisi (2009)	"Ecological successions proceed towards the maximisation of structural information of organisms and (sub)-communities"
Entropy production	Energy dissipation	Schneider and Kay (1994)	"as ecosystems grow and develop, they should increase their total dissipation, energy flow, cycling activity and develop more complex structures with greater diversity and hierarchical levels"
	Entropy production (S_{prod})	Aoki (1989)	"the entropy production of a living system consists in three or more phases: an early increasing stage, a later decreasing state and an intermediate stage"
Net entropy flow	Net entropy flow (S_{net})	Ludovisi (2012)	"the entropy exchange at a system boundary represents the 'entropy fee' paid by the external environment for sustaining system structure and processes. Such an "entropy fee" becomes increasingly positive as the extent of irreversibilities increase and the entropy of the system decreases"
Combined	Specific dissipation ($T{\cdot}S_{prod}/Ex$)	Ludovisi et al. (2005)	"the ecological design which tends to prevail over time is the one which minimises specific dissipation (or specific entropy production)"

component. On the basis of the hypothesis that the maximisation of exergy represents one of the main criteria for ecosystem development (Jørgensen, 1992a; Jørgensen and Svirezhev, 2004; Jørgensen et al., 2007), exergy and exergy-based indices have been widely used in ecology as indicators of development state (Christensen, 1995; Fath et al., 2004) and ecosystem health (Jørgensen, 1995, 2000; Xu, 1996), as well as goal functions in ecological modelling (Nielsen, 1990; Jørgensen, 1992b; Jørgensen et al., 2002).

Recently, Ludovisi (2009) proposed the following decomposition of the exergy function

$$Ex = RT\left[\underbrace{C}_{\text{Size }(C)}\underbrace{\sum_{i=1}^{n} p_i \ln\frac{p_i}{p_{i(e)}}}_{\text{Structural Information }(I)} + \underbrace{\left(C\ln\frac{C}{C_{(e)}} - (C - C_{(e)})\right)}_{\text{Concentration }(X)}\right] = RT[C\cdot I + X] \tag{3}$$

where $C = \Sigma_i c_i$ is the total concentration of components, $p_i = c_i/C$ is the relative abundance $(0 < p_i < 1)$ of the ith component in the ecosystem and reference state (subscript e). In the above formulation, which is analogous to those proposed by other authors (Herenden, 1990; Aoki, 1993; Svirezhev, 2000), the term I (the Kullback–Leibler information – see the Appendix), expresses the information arising from the change in the matter apportionment from the equilibrium to actual state, and the term X the effect due to the change in the total concentration of components. Ex, C and X are expected to vary (Ex and X increase, C decreases) as a function of the biomass incorporated into the ecosystem, whereas I depends mostly on the difference in the size spectrum of the biotic components between equilibrium and actual state. Since the $c_{i(e)}$'s and thus the $p_{i(e)}$'s of the biotic components are expected to decrease with increasing organism size (see Section 2), I increases with increasing abundance of large and complex species. Since large-sized species typically dominate in late stages of ecological succession, I has been proposed as an indicator of development state, as well as an ecological orientor (Table 1). It is worth stressing that, although Ex and I are linked to each other via Eq. (3), an increase in exergy does not necessarily result in an increase of structural information and vice versa (see Ludovisi, 2009; Ludovisi and Jørgensen, 2009).

A second type of entropy-based orientors focuses on entropy production (S_{prod}, see the Appendix A) and related quantities (Table 1). Among them, we may include the "dissipation" *sensu* Schneider and Kay (1994), in spite of the recalcitrance of the authors to express it in terms of entropy. The idea that ecosystems tend to maximise dissipation (or maximise the entropy production) along their pathway of development is poorly supported by field observations. Rather, Aoki (1987a,b,c, 1989, 1995) has shown that entropy production in living systems ranging from organisms to ecosystems increases in the early stages and decreases in later senescent stages (Table 1). The validity of Aoki's view has been supported by theoretical considerations (Jørgensen et al., 2000; Fath et al., 2004; Holdaway et al., 2010) and by observations in seasonal successions of plankton (Ludovisi et al., 2005; Ludovisi, 2006).

A third type of entropy-based indicator has been defined by considering the net entropy flow across ecosystem boundary (S_{net}, see Appendix and Table 1). This class of indicators has been poorly investigated so far, but a case study (Ludovisi, 2012) suggests that it could include effective orientors, provided that certain methodological issues are properly addressed.

Further, by combining measures of distance from equilibrium and entropy production, Ludovisi et al. (2005) have proposed the ratio:

$$T\frac{S_{prod}}{Ex}, \tag{4}$$

as an ecological orientor, whose minimisation is expected throughout ecosystem development (Table 1). This expectation arises from the fact that the ratio, which has been called the specific entropy