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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

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

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:

$$T\frac{S_{prod}}{Ex}, \qquad (4)$$

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 production, is conceptually coincident with Schrödinger's ratio, or the ratio respiration to biomass proposed by Odum (1983):

$$\frac{\text{Entropy generation rate}}{\text{Entropy of structure}} \approx \frac{\text{Respiration}/T}{\text{Free energy stored}/T} = \frac{\text{Respiration}}{\text{Biomass}}$$

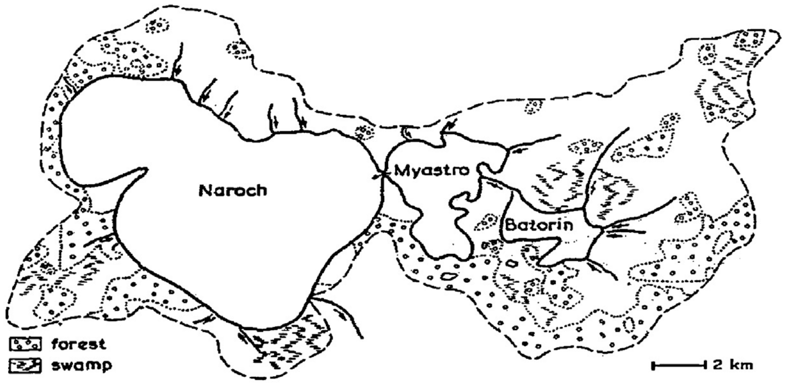
The ratio respiration to biomass is intended to characterise the turnover rate of organisms in ecological systems and has been found to be lower in high-structured and near climax ecosystems (Odum, 1969, 1983; Amblard, 1988; Choi et al., 1999).

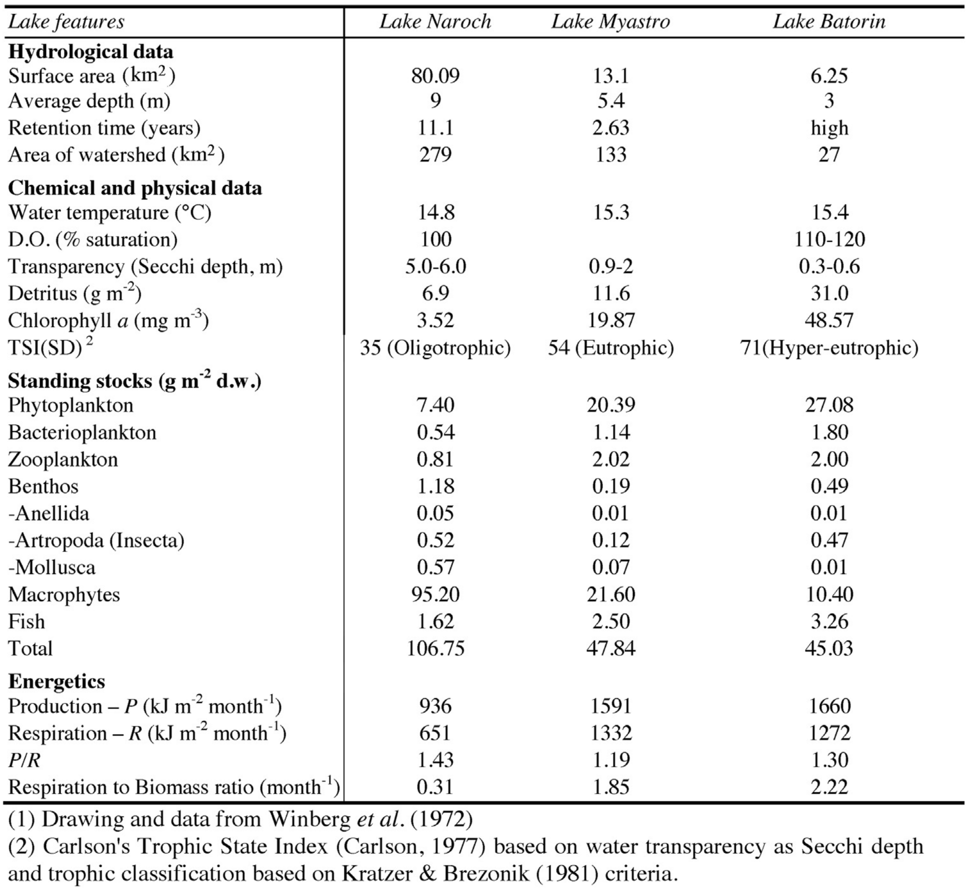
As shown, the above-described functions have a sound theoretical basis and significance as ecological indicators and orientors. However, their suitability as ecological orientors has yet to receive a full confirmation in real case studies. Some of the difficulty in fulfilling this task stems from the intrinsic particularity of ecosystems and from the lack of comprehensive data covering entire communities along successional processes.

The aim of the present contribution is to show how the following entropy-based indicators:

- Exergy (*Ex*, see Eq. (3));
- Structural information (*I*, see Eq. (3));
- Size (*C*, see Eq. (3));
- Concentration (*X*, see Eq. (3));
- Eco-exergy (*Eco-ex*, see Eq. (2));
- Entropy production (S_{prod});
- Specific entropy production ($T{\cdot}S_{prod}/Ex$, see Eq. (4));

perform as indicators of ecosystem development when applied to the analysis of a special case of ecological succession, i.e. eutrophication, in a homogeneous set of small lakes, for which very detailed data about the main standing stocks are available. Further, the available information about ecosystem energetics makes it possible to





Lake features	*Lake Naroch*	*Lake Myastro*	*Lake Batorin*
Hydrological data			
Surface area (km^2)	80.09	13.1	6.25
Average depth (m)	9	5.4	3
Retention time (years)	11.1	2.63	high
Area of watershed (km^2)	279	133	27
Chemical and physical data			
Water temperature (°C)	14.8	15.3	15.4
D.O. (% saturation)	100		110-120
Transparency (Secchi depth, m)	5.0-6.0	0.9-2	0.3-0.6
Detritus (g m^{-2})	6.9	11.6	31.0
Chlorophyll *a* (mg m^{-3})	3.52	19.87	48.57
TSI(SD)^{2}	35 (Oligotrophic)	54 (Eutrophic)	71(Hyper-eutrophic)
Standing stocks (g m^{-2} d.w.)			
Phytoplankton	7.40	20.39	27.08
Bacterioplankton	0.54	1.14	1.80
Zooplankton	0.81	2.02	2.00
Benthos	1.18	0.19	0.49
-Anellida	0.05	0.01	0.01
-Artropoda (Insecta)	0.52	0.12	0.47
-Mollusca	0.57	0.07	0.01
Macrophytes	95.20	21.60	10.40
Fish	1.62	2.50	3.26
Total	106.75	47.84	45.03
Energetics			
Production – *P* (kJ m^{-2} month^{-1})	936	1591	1660
Respiration – *R* (kJ m^{-2} month^{-1})	651	1332	1272
P/*R*	1.43	1.19	1.30
Respiration to Biomass ratio (month^{-1})	0.31	1.85	2.22

(1) Drawing and data from Winberg *et al*. (1972)

(2) Carlson's Trophic State Index (Carlson, 1977) based on water transparency as Secchi depth and trophic classification based on Kratzer & Brezonik (1981) criteria.

Fig. 1. Map of the lakes examined showing the local inlet–outlet system and table reporting the main ecological data averaged over the vegetative season (May–October)^1.

test the effectiveness of the above indicators by comparison with Odum's classical indicators of ecosystem maturity.

2. Materials and methods

The dataset analysed in this study (Fig. 1) was collected by Winberg et al. (1972) in three Bielorussian lakes (Lake Naroch, Lake Myastro and Lake Batorin) during the vegetative season (May–October). The lakes are adjacent, connected to each other and have similar morphology, hydrology and hydro-chemical features, but very different trophic state and community structure.

The exergy and the terms of concentration, size and structural information, were calculated by Eq. (3), after the calculation of the equilibrium concentration for organisms ($c_{i(e)}$). According to the method proposed by Ludovisi (2009), a vanishingly small concentration (the so called virtual equivalent equilibrium concentrations – *VECE*) can be assigned to organisms at equilibrium by applying the equations of classical thermodynamics to the ultimate process that leads a system to thermodynamic equilibrium. If the present composition of the atmosphere is taken, the reference equilibrium (eco)system can be assumed to be composed of inorganic compounds at the highest oxidation state, and the oxidation assumed as the ultimate process leading to equilibrium. By assuming the thermo-chemical properties of *E. coli* as a reference, the *VECE* values for the biological components were calculated as:

$$\log\ c_{i(e)} = \log\ VECE_i = \frac{w_i L}{UCFW} \log\ c_{UCF(e)}, \tag{5}$$

where w_i is the dry mass of the organism (in grams) and L is Avogadro's number = $6.022{\cdot}10^{23}\ \text{mol}^{-1}$, *UCFW* is the molecular weight (25.036 Da) of the "unit carbon formula" (*UCF*) of *E. coli* and $c_{UCF(e)}$ is the *VECE* value of one *UCF* of *E. coli*. The equation must be corrected by an additive term $\ln L$ if the concentration is expressed as Ind. L^{-1}. Under the environmental conditions indicated in Table 2, $c_{UCF(e)}$ is equal to $10^{-102}\ \text{mol L}^{-1}$ (for further details on calculation, see Ludovisi, 2009). Table 2 also shows the values of *VECE* obtained by assigning a representative dry weight to the main ecological components of the lakes examined here. Note that the above calculations are based on concentrations expressed per unit of volume (L^{-1}), whereas the data have been presented per unit of surface (m^{-2}), after conversion.

The Eco-exergy index was calculated by Eq. (2), using the β-values (Table 2) provided by Jørgensen et al. (2005).

The calculation of entropy production was performed by following the empirical method proposed by Ludovisi (2006), which is based on the positive correlation between d' (the entropy production per unit of absorbed solar radiation) and Carlson's (1977) trophic state index *TSI*(*SD*):

$$d' = d'_a + 2 \cdot 10^{-5} \cdot TSI(SD) \tag{6}$$

where the intercept ($d'_a = 2{\cdot}10^{-3}\ \text{K}^{-1}$) can be considered the entropy production per unit of absorbed solar radiation, due to abiotic processes. The biological entropy production was therefore estimated approximately as:

$$S^b_{prod} = (d' - d'_a)Q_s, \tag{7}$$

where Q_s is the solar energy absorbed per surface unit of a lake. The specific entropy production of the biological components was calculated as the ratio $T(S^b_{prod}/Ex)$.

3. Results

The values of the examined indicators, calculated including the biological community only, are shown in Table 3A. Exergy decreases moving from oligotrophy to hyper-eutrophy, as a consequence of the decreasing total biomass incorporated into the standing stocks of the lakes. The exergy terms size (*C*) and concentration (*X*) increase with increasing trophic state, as a consequence of the increasing density of small organisms (mostly bacterioplankton and phytoplankton). In contrast, the structural information (*I*) decreases by one order of magnitude along the trophic gradient, due to the decreasing abundance of large-sized organisms, particularly macrophytes, fish and benthic organisms, which have very low *VECE* values. The Eco-exergy index shows a trend analogous to exergy, although the differences among the three lakes are enhanced, mostly because of the increasing abundance of vascular plants, which possess a very high β-value. The biological entropy production increases along the trophic gradient, and in the hyper-eutrophic Lake Batorin is about twice that in the oligotrophic Lake Naroch. As a ratio between entropy production and exergy, specific entropy production increases along the trophic gradient, reaching the highest value for the hyper-eutrophic Lake Batorin.

When detritus is included in the calculations of exergy and exergy terms (Table 3B), the above described trends are all respected, except for exergy, which shows the minimum values for the eutrophic Lake Myastro. The examination of the value of the exergy terms reveals that the different behaviour of exergy in A and B of Table 3 is due essentially to the higher value of the *X*

Table 2

Virtual equivalent concentration at equilibrium (*VECE*-value) calculated for the main ecological components of Lake Naroch, Lake Myastro and Lake Batorin, assuming $P = 1$ atm and $T = 288$ K (the average temperature of the vegetative season in the three lakes),[a], and Jørgensen's weighting factors.

Organism	Mass	VECE-value ($\log_{10}$)	Weighting factor (β_i)
Escherichia coli (UCF)	25.036 Da	$-102\ \text{mol L}^{-1}$	–
Bacterioplankton (heterotrophic)	$1{\cdot}10^{-12}$ g	$-2{\cdot}10^{12}$ Ind. L^{-1}	8.5
Phytoplankton	$1{\cdot}10^{-9}$ g	$-2{\cdot}10^{15}$	20.0
Zooplankton			
Rotatoria	$1{\cdot}10^{-8}$ g	$-2{\cdot}10^{16}$	148
Cladocera	$1{\cdot}10^{-6}$ g	$-2{\cdot}10^{18}$	232
Copepoda	$5{\cdot}10^{-6}$ g	$-1{\cdot}10^{19}$	232
Benthos			
Insecta	$1{\cdot}10^{-4}$ g	$-2{\cdot}10^{20}$	167
Mollusca	$1{\cdot}10^{-4}$ g	$-2{\cdot}10^{20}$	310
Anellida	$1{\cdot}10^{-3}$ g	$-2{\cdot}10^{21}$	133
Crustacea	$1{\cdot}10^{-3}$ g	$-2{\cdot}10^{21}$	232
Aquatic plants	$5{\cdot}10^{1}$ g	$-1{\cdot}10^{26}$	268
Fish	$1{\cdot}10^{2}$ g	$-2{\cdot}10^{26}$	499
Organic detritus	$1{\cdot}10^{5}$ Da	$-4{\cdot}10^{5}\ \text{mol L}^{-1}$	7.34

[a] The equilibrium concentrations of dissolved gases and ions (mol L^{-1}) are assumed to be: $CO_2 = 1.08{\cdot}10^{-5}$; $O_2 = 2.65{\cdot}10^{-4}$; $H_2O = 55.56$; $NO_3^- = 5.00{\cdot}10^{-5}$; $H^+ = 5.00{\cdot}10^{-9}$; $HPO_4^{2-} = 6.40{\cdot}10^{-8}$; $SO_4^{2-} = 5.70{\cdot}10^{-4}$; $K^+ = 1.50{\cdot}10^{-4}$.

Table 3
Average value of the entropy-based functions examined for Lake Naroch, Lake Myastro and Lake Batorin during the vegetative season (May–October), and emerging trend along the trophic gradient (from oligotrophy to hyper-eutrophy).

	Lake Naroch (oligotrophic)	Lake Myastro (eutrophic)	Lake Batorin (hyper-eutrophic)	Trend
(A) Biological community only				
Exergy (MJ m^{-2})	2.39	1.07	1.01	↘
Size, C (mol m^{-2})	$9.1{\cdot}10^{-13}$	$1.9{\cdot}10^{-12}$	$3.0{\cdot}10^{-12}$	↗
Concentration, X (mol m^{-2})	5.12	10.84	17.07	↗
Structural information, I	$1.1{\cdot}10^{15}$	$2.3{\cdot}10^{14}$	$1.3{\cdot}10^{14}$	↘
Eco-exergy index	64.49	19.07	13.20	↘
Entropy production (MJ m^{-2} $month^{-1}$ K^{-1})[a]	0.28	0.44	0.58	↗
Specific entropy production ($month^{-1}$)[a]	0.12	0.41	0.57	↗
(B) Biological community + detritus				
Exergy (MJ m^{-2})	2.54	1.33	1.70	?
Size, C (mol m^{-2})	$6.9{\cdot}10^{-5}$	$1.2{\cdot}10^{-4}$	$3.1{\cdot}10^{-4}$	↗
Concentration, X (mol m^{-2})	64.39	108.90	289.84	↗
Structural information, I	$1.4{\cdot}10^{7}$	$3.8{\cdot}10^{6}$	$1.4{\cdot}10^{6}$	↘
Eco-exergy index	64.61	19.28	13.75	↘

[a] Revised from Ludovisi (2006).

term, which becomes comparable that of the product $C{\cdot}I$ (see Eq. (3)). This change suggests that the inclusion of the detritus, which is a storage compartment, not an active part of the trophic network, introduces a distortion in the relationships between exergy and the other entropy-based functions.

4. Discussion

The results show that a coherent pattern of response of entropy-based functions emerges when analysing a homogeneous set of shallow lakes lying at different degrees of eutrophication. The exergy carried by the biological compartment decreases along the trophic gradient, reflecting the change in the overall biomass incorporated into the standing stocks considered. On the other hand, the entropy produced by the communities as a whole shows an opposite trend, increasing along the trophic gradient. At first sight, the above response pattern might appear as peculiar, as it implies that a higher distance from equilibrium (or a higher biomass stored) results in a lower entropy production. However, it can be explained by remembering that the extent of biological activity is not straightforwardly linked to the amount of biomass stored in ecosystems (see, e.g., Odum, 1969). In fact, the biological entropy production in ecosystems results from a number of different catabolic and anabolic processes, such as respiration, photosynthesis and anaerobic decomposition. The rate of any single process is generally linked to the overall metabolic rate of organisms, which, in turn, is broadly related to other bionomic characters (Southwood, 1976; Reynolds, 1984):

$$\text{metabolic rate per unit weight} \propto \text{growth rate} \propto \text{turnover rate} \propto \frac{1}{\text{size}} \propto \frac{1}{\text{structural complexity}}$$

If the above series of relationships is respected, the entropy production should be expected to be higher in ecosystems where small-sized organisms dominate, biomass stored being comparable. As a case in point, the biological entropy production in the three Bielorussian lakes has been shown to be mostly due to the photosynthesis, with the contribution due to phytoplankton becoming increasingly dominant along the trophic gradient (Ludovisi, 2006). Therefore, the trend of entropy production can be explained by considering the progressive dominance of small producers (phytoplankton), instead of the large and complex ones (vascular plants).

As a consequence of the opposite trends of exergy and entropy production, the specific entropy production increases with eutrophication, in agreement with the inverse relationships between size and turnover rate of organisms previously illustrated. The decreasing trend of structural information (I) along the trophic gradient is once again in agreement with the reduction in size along the series, as I is strictly dependent on the divergence of the size spectrum of the community with respect to the expected distribution at equilibrium, which is dominated by organisms having smaller size (or higher *VECE* values). On the other hand, the terms size (C) and concentration (X), increase with the trophic state, as a consequence of the increasing density of small organisms in the water column. It is worth emphasising here that, in spite of the increase of both C and X, the total exergy decreases along the trophic gradient, as a direct consequence of the decrease of the information term I, which thus emerges as the "leading" term of exergy into the ecological series examined. The eco-exergy index also shows a decrease with eutrophication, as a consequence of the reduction in the abundance of species of a high complexity, such as macrophytes.

Overall, the emerging pattern supports the use of the entropy-based indicators examined for characterising ecosystem state. However, a thorough discussion is needed in order to evaluate the significance of the results obtained in terms of ecosystem development, i.e. to evaluate the soundness of the examined functions as orientors. First, it must be discussed the meaning of the terms "development" in relation with the eutrophication process. According to its original sense (Hutchinson, 1957), eutrophication is the process of natural ageing of aquatic systems, and thus the most eutrophic state should be regarded as the "final" result of a succession. However, since the eutrophication process moves ecosystems through a continuous succession of different "*prevailing conditions*" in terms of morphology, hydrology and hydrochemistry, the different stages of eutrophication should be regarded not as different states of a given ecosystem, but rather as a succession of different ecosystems. This view is supported by the data at hand (Fig. 1): in the Bielorussian lakes, gross production and respiration are fairly close to balance, but the lakes show very different biomass stored, thus suggesting that their carrying capacities are very different. Therefore, when dealing with eutrophication, we should not expect that ecological or thermodynamic indicators behave as expected in a typical succession. In fact, in our case study, most of Odum's indicators of maturity (total biomass and the ratios R/B or P/B) suggest that the development state decreases with trophic state. This conclusion is widely in harmony with what Odum (1969) stated: “Eutrophication, whether natural or cultural, results when nutrients are imported into the lake from outside – that is, from the watershed. This is equivalent to adding nutrients to the laboratory microsystem or fertilising a field; the system is pushed back, in successional terms, to a younger or ‘bloom’ state”.

Most of the responses obtained here by the entropy-based indicators examined are consistent with the responses of Odum’s classical indicators of maturity. In particular:

- The exergy, the Eco-exergy index and the structural information increase with the total biomass stored in the lakes, supporting Odum’s “maximum biomass principle”, according to which “ecological succession culminates in a stabilised ecosystem in which maximum biomass (or high information content) is maintained per unit of energy flow”. The maximisation of storage (Fath et al., 2001), both in terms of biomass and information, is therefore confirmed as one of the most reliable principle of ecosystem development. However, note that the above indicators focus on different forms of storage: the exergy is essentially related to biomass (irrespective of the distribution among ecosystem components), the structural information is related to community composition (irrespective of the total biomass) and the eco-exergy index is related to both biomass and genetic information. The parallel trend of these indicators suggests that different aspects, not necessarily related to each other (Ludovisi, 2009; Ludovisi and Jørgensen, 2009), dealing with the organisation of individuals and communities co-vary during ecosystem development.
- The exergy terms size (C) and concentration (X) increase with the increasing biomass stored in the investigated lakes. Whereas the trend of C agrees with expectations, that of X is opposite. This incongruence is due to the fact that, because of the incompleteness of water quality data, the calculation of the exergy and exergy terms was made by considering the biogenic components only. This requirement limits the applicability of X as ecological orientor to cases where the main water quality data are available (see, e.g., Ludovisi et al., 2012).
- The entropy production increases with increasing gross production and global respiration in the investigated lakes. This positive correlation supports the reliability of method used for estimating the global biological activity in the lakes. However, the negative correlation found between entropy production and total biomass, as well as the positive correlation between entropy production and the ratio P/B or R/B, confirm that the maximisation of dissipation is a debatable criterion of ecosystem development. In fact, Odum (1969) showed that primary production and respiration in forests or algal cultures attains a maximum during intermediate stages of development, not at the climax stage. I personally agree with Aoki, who predicts entropy production to be higher during the “intermediate” stages, when organisms are accomplishing the colonisation of an unexploited environment (or the “final” step of the growth phase I, as defined by Jørgensen et al., 2000; Fath et al., 2004). Further efforts are therefore needed in order to understand the limit of validity of such a principle and, also, to unify the meaning of the term dissipation, which is often expressed with reference to different thermodynamic quantities (see the discussion in Ludovisi, 2012).
- The specific entropy production decreases with ecosystem development, paralleling the trend of the ratio respiration to biomass (and that of production to biomass), in accordance with Odum’s expectations. Therefore, the minimisation of specific entropy production is confirmed as a creditable principle of development. Furthermore, similarly to structural information, the specific entropy production is an intensive (structural) property of a community, and thus an appropriate indicators for comparing ecosystems having different carrying capacity.

More extended investigations on aquatic, and possibly terrestrial, ecosystems are needed in order to test theories and understand ecological implications. In particular, since most of the entropy-based indicators are correlated to each other, one of the main challenges to be faced is the identification of the prevailing tendency (maximisation of exergy, maximisation of information, minimisation of specific entropy production), and thus the ultimate thermodynamic rule, which drives ecosystem development.

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Appendix A. Theoretical background

In classical thermodynamics, the distance from equilibrium can be expressed in terms of entropy, as (Evans et al., 1966):

$$S_{(e)} - S = \frac{U + P_{(e)}V - \sum_i \mu_{i(e)} N_i - T_{(e)}S}{T_{(e)}}, \tag{A.1}$$

where S is the entropy, U is the energy, P the pressure, V the volume, T the absolute temperature, μ_i the Gibbs chemical potential of the ith component and N_i the corresponding amount in the system, with the subscript e denoting equilibrium conditions. As shown by Brillouin (1956), this distance is related to the information needed to describe the departure from equilibrium:

$$S_{(e)} - S = k \sum_{i=1}^{n} p_i \ \ln \frac{p_i}{p_{i(e)}} \tag{A.2}$$

where $p_1, p_2, \ldots, p_n$ are the probabilities of the n states accessible to the system, k is Boltzmann’s constant and the summation term represents the Kullback–Leibler information (Kullback and Leibler, 1951; Kullback, 1959). Since the entropy in non-equilibrium conditions cannot be higher than the equilibrium value, an information >0 is achieved if the entropy of a system is lower than its equilibrium value, i.e. if the internal order (or organisation, complexity[1]) is higher than that of equilibrium.

The distance from equilibrium can be also expressed in energy units, using the exergy function, which is related to entropy as follows (Evans et al., 1966):

$$Ex = T_{(e)}(S_{(e)} - S) = U + P_{(e)}V - \sum_i \mu_{i(e)} N_i - T_{(e)}S \tag{A.3}$$

Exergy represents the maximum amount of work a system can perform when it is brought to thermodynamic equilibrium with the environment. If a system is hypothesised to be in thermal and mechanical equilibrium with the environment, as is usually done for ecosystems, the departure from equilibrium is only a function of the chemical potential of the species (μ_i) and their variations.

As stated by the second law of thermodynamics, the entropy of an isolated system cannot be indefinitely kept far from the equilibrium value. The entropy can only be kept far from the equilibrium in non-isolated systems, provided that the entropy produced within the system is discharged towards the environment. In fact, the

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[1] The terms order, organisation and complexity are often used as synonyms, although they conceptually refer to different system properties (see Wicken, 1978).

change in entropy (ΔS_t) depends on the entropy balance (Nicolis and Prigogine, 1977), i.e. on the sum of the net incoming entropy flow (S_{net}) and the entropy produced within the system (S_{prod}):

$$DS_t = S_{prod} + S_{net} \tag{A.4}$$

According to the second law of thermodynamics, S_{prod} is ≥ 0, but no constraints are implied on the sign and value of the entropy change, which also depend on S_{net}. Hence, a system can maintain its entropy if $-S_{net} = S_{prod}$ or even reduce it if $-S_{net} > S_{prod}$, as may be expected if dissipative structures (Nicolis and Prigogine, 1977) work within the system.

It is worth emphasising that the different terms of the entropy balance reflect different facets of the phenomenon of the energy degradation (Ludovisi, 2012), dealing respectively with overall degradation (S_{prod}), system degradation (ΔS_t) and environment degradation ($-S_{net}$).

Appendix B. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolind.2013.09.020. These data include Google maps of the most important areas described in this article.

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