

Energy degradation and ecosystem development: Theoretical framing, indicators definition and application to a test case study

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ABSTRACT

During the last few decades, the so-called “maximum dissipation principle” has raised a wide debate as a paradigm governing the development of ecological systems. In the present contribution, after having discussed the meaning of the term *energy degradation* within the framework provided by the entropy and the exergy balance, it is suggested to distinguish three different facets of the phenomenon of the energy degradation, respectively dealing with the overall, system and environmental degradation. In relation with ecological indication, the above classification shows that different types of indicators of energy degradation can be defined, thus emphasising that a clear reference to the specific facet considered should be made in order to avoid ambiguous statements. The behaviour of several thermodynamic indicators, which include previously derived indices and a new set of entropy-based indicators, is examined along the seasonal progression in a lake ecosystem, and the effectiveness of the considered indicators in characterising the development state is evaluated by comparing their responses with the main successional traits of the phytoplankton community. The results show that, although overall degradation and related indices may deserve consideration as indicators of the extent of the degradative (biotic and abiotic) processes acting within an ecosystem, their significance as indicators of development state appears to be limited. On the other hand, indicators related to environmental degradation appear to be more promising as indicators of the development state, provided that some methodological issues dealing with the effect of the abiotic noise are properly addressed. The net radiative entropy exchange shows a significant correlation with phytoplankton successional traits, thus suggesting that the entropy changes in the radiative portion of the entropy budget are the most informative in relation to the development state of aquatic communities. The methodology adopted also lends itself to be used for evaluating the energy quality associated with an energy flow, which is here measured by the energy-to-entropy ratio.

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1. Introduction

During the last century, many efforts were made to identify thermodynamic-based functions possessing specific realisations towards which ecosystem development is supposed to be oriented, the so-called *orientors* (see reviews in: Müller and Leupelt, 1998; Fath et al., 2001; Jørgensen and Svirezhev, 2004; Müller, 2005; Jørgensen et al., 2007). Among them, the so-called “maximum dissipation principle”, stemming from the work of Schneider and Kay (1994), has received wide attention, as well as serious criticisms (see, e.g., Straškraba et al., 1999; Jørgensen et al., 2000; Nielsen, 2000; Fath et al., 2001, 2004; Pykh, 2002; Müller et al., 2006; Meysman and Bruers, 2010). In short, the principle states that ecosystems tend to maximise the dissipation of the incoming energy and develop structural and functional attributes to abet

energy degradation. Although the authors explicitly avoided to formulate the principle in terms of entropy, it is rooted on the second law of thermodynamics and supported by the theoretical framework that has inspired the formulation of several “maximum entropy production principles” (MEPP) in different fields (see a historical review in Martyushev and Seleznev, 2006), including ecology (Ulanowicz and Hannon, 1987; Kleidon and Lorenz, 2005).¹

In their paper, Schneider and Kay start distinguishing between energy dissipation and energy degradation, concepts that have been indifferently used to denote the loss of the work-potential of energy since the appearance of the earlier statements of the second law of thermodynamics (see, e.g., Brunhes, 1908).

¹ The relationship between MEPP and Prigogine's minimum entropy production principle (Prigogine, 1945) has been the subject of long-standing discussions (see, e.g., Jaynes, 1980 and Martyushev and Seleznev, 2006). These principles should not be mutually opposed since they are applicable to different stages of the evolution of a nonequilibrium system (Nicolis and Prigogine, 1977).

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According to Schneider and Kay, dissipation of energy “means to move energy through the system”, thereby reflecting the ability of a system to discharge the absorbed energy towards the environment. As shown by the authors by making reference to the Bénard experiment (Bénard, 1900), the heat transfer rate in a heated container enclosing a fluid increases linearly as a function of the imposed temperature gradient, but the heat transfer becomes faster when convective cells (the Bénard Cells) spontaneously appear within the fluid. This simple phenomenon demonstrates that self-organised structures can emerge in systems subjected to an energy flow, and also that the organisation makes the system more efficient in dissipating the absorbed energy. On the other hand, Schneider and Kay defines energy degradation in terms of loss of work potential of energy, i.e., in terms of exergy loss (Evans et al., 1966), stating that “degradation of energy means to destroy the ability of energy to produce gradients that can accomplish work” and that “energy degradation means exergy destruction”. In the Bénard experiment, the appearance of the convective cells reduces the extent of the overall temperature gradient within the fluid and increases entropy production and exergy destruction. The fact that energy dissipation and exergy destruction do not follow the same trend, the latter increasing more than linearly with respect to the temperature gradient, corroborated the idea that they account for different aspects of the dissipative process.

As a whole, the Bénard experiment was used by Schneider and Kay to support the “restated second law”, according to which any system moved away from equilibrium will utilise all avenues available to counteract the imposed gradient. In order to comply with the principle, a sequence of states of increasing complexity (including chaotic structures) must be expected as the applied gradient increases, with each transition being accompanied by an increasing ability to destroy gradients and degrade energy. By following a heuristic inductive approach, Schneider and Kay extended the above principle to living systems, suggesting that “life exists on earth as another means of dissipating the solar induced gradient and, as such, is a manifestation of the restated second law” and that “as ecosystems grow and develop, they should increase their total dissipation, develop more complex structures with more energy flows, increase their cycling activity, develop greater diversity and generate more hierarchical levels, all to abet energy degradation”. It must be emphasised that the idea that Bénard convection serves as universal template for all self-organising systems, including living matter (see also Schneider and Sagan, 2005 for an updated version of this idea) is controversial matter. Recently, by analysing the thermodynamics of different food web models, Meysman and Bruers (2010) have shown that the analogy holds only to a limited degree, as it breaks down when the food web reaches a certain complexity.

As a tool for testing their principle in real case studies, Schneider and Kay suggested using the ratio R_n/K^* as an indicator of the ability of a system to degrade the incoming solar radiation into lowest-quality energy. In the ratio, R_n is the net radiation flux absorbed at a surface:

$$R_n = K^* - L^* = H + L_c + G, \quad (1)$$

where K^* is the net flux of solar radiation (incoming) and L^* is the net flux of longwave radiation (outgoing), whose difference equates the sum of the energy fluxes associated with low-quality-energy emissions, such as evaporation (H) and sensible heat (L_c), plus the ground storage (G).

The soundness of the ratio R_n/K^* – also known, after Luvall et al. (2001), as the *solar exergy dissipation (SED)* – as an indicator of ecosystem development has been evaluated in several studies focused on terrestrial ecosystems ranging from bare lands to old forests (Schneider and Kay, 1994; Kutsch et al., 2001; Luvall et al., 2001; Dewulf et al., 2008). Most of the studies support the consistency of *SED*, showing that more natural and mature forests exhibit

higher values of *SED* with respect to crop fields and perturbed areas, but some inconclusive or contradictory results also emerged (e.g. Kutsch et al., 2001). Technical limitations related to the low accuracy of the available remote sensing data or calibration issues might help to explain some of the inconclusive results obtained (Dewulf et al., 2008). Kutsch et al. (2001) claim that the energy exchanges due to abiotic phenomena (the abiotic noise), with a particular reference to the sensible heat losses, significantly obfuscates the biotic signal.

However, a part of the limitations of *SED* resides on the fact that it simply expresses the fraction of the absorbed solar radiation that is converted into non-radiative energy losses. Therefore, the significance of *SED* as an indicator of energy degradation relies on the hypotheses that non-radiative releases are the most significant ones in terms of degradation, or that the longwave budget is negligible, which are both questionable assumptions. More importantly, *SED* has the drawback of being based on the energy budget terms of an ecosystem, and, as such, it is unable to account properly for the change in energy quality, because no measure of energy quality is associated with incoming and outgoing energy flows.

In the attempt to take into account the drop of energy quality due to dissipative processes, Svirezhev and Steinborn (2001) derived a method of calculation for the radiation exergy flux across an ecosystem (Ex_f), by following a information-statistical approach:

$$Ex_f = E_l^{out} \ln \left(\frac{E_l^{out}}{E_l^{in}} \right) + E_s^{out} \ln \left(\frac{E_s^{out}}{E_s^{in}} \right) + R_n \quad (2)$$

where E represents the energy flow associated with longwave (subscript l) or shortwave (subscript s) radiation incoming (superscript *in*) or outgoing (superscript *out*) from the system surface. Together with Ex_f , the authors proposed the ratios $\eta_R = R_n/(E_l^{in} + E_s^{in})$ (the radiation efficiency coefficient) and $\eta_{Ex} = Ex_f/(E_l^{in} + E_s^{in})$ (the exergy efficiency coefficient) as useful indicators of the efficiency of the “radiative machine” working at the ecosystem surface. In comparing the seasonal trends of these indicators in a crop field and a 100-year-old beech forest, the authors found that they were slightly higher in the latter case, a result which would indicate that the forest uses the incoming energy more efficiently to perform work.

In order to better clarify the significance of the above described indicators, and to discuss the energy degradation phenomenon in a more comprehensive way, it is convenient to adopt an approach based on the entropy and exergy balance of a system:

Entropy balance (Nicolis and Prigogine, 1977):

$$\Delta S = \Delta_i S + \Delta_e S, \quad (3)$$

where ΔS is the change in the entropy of the system, $\Delta_e S$ is the net incoming entropy flow from the external environment and $\Delta_i S$ is the entropy produced by the processes acting within the system. In compliance with the second law of thermodynamics, $\Delta_i S \geq 0$, with the inequality holding if irreversible internal processes take place. The entropy balance can also be expressed as the difference between the entropy change of the combined system and external environment (ΔS_C) and the entropy change of the external environment (ΔS_E):

$$\Delta S = \Delta S_C - \Delta S_E \quad (4)$$

Exergy balance (Nag, 2002):

$$\Delta Ex = \Delta Ex_t - \Delta Ex_d \quad (5)$$

where ΔEx represents the variation of exergy of the system, ΔEx_t the change of exergy associated with thermodynamic exchanges at system boundary (the exergy transfer) and ΔEx_d is the exergy destroyed by internal irreversibilities (the exergy destruction).

According to the Gouy-Stodola theorem (Nag, 2002), entropy production equates the entropy change of the combined system

($\Delta_i S = \Delta S_C$) and is related to exergy destruction according to the equation:

$$\Delta Ex_d = T_e \cdot \Delta S_C = T_e \cdot \Delta_i S, \quad (6)$$

where T_e is the temperature of the external environment.

Exergy destruction and entropy production are both suitable measures of energy degradation, as they express respectively the loss of work capacity of the combined system and the loss of energy quality that accompanies irreversible processes. In fact, by adopting the neg-entropy ($N = -S$) as a measure of the quality, or grade, of energy (Schrödinger, 1944; Brillouin, 1966), the negative of $\Delta_i S$ can be taken as a measure of the decrease in the energy quality in the combined system.

In isolated system ($\Delta_e S = 0$; $\Delta Ex_t = 0$), energy degradation assumes an unequivocal meaning, as irreversible transformations result in an increase of the entropy of the system, which equates entropy production ($\Delta S = \Delta_i S$), and the decrease of exergy equates exergy destruction ($\Delta Ex = \Delta Ex_d$). In non-isolated systems where thermodynamic exchanges take place at the system boundary ($\Delta_e S \neq 0$; $\Delta Ex_t \neq 0$), ΔEx_d and $\Delta_i S$ still represent suitable measures of the overall energy degradation, but the change in the work capacity (ΔEx), and entropy (ΔS) of the system depend on the balance equations (Eqs. (3) and (5)). In terms of entropy, there are three possible cases:

- (1) $\Delta S = \Delta_i S + \Delta_e S > 0$; $\Delta_i S > -\Delta_e S$
- (2) $\Delta S = \Delta_i S + \Delta_e S = 0$; $\Delta_i S = -\Delta_e S$
- (3) $\Delta S = \Delta_i S + \Delta_e S < 0$; $\Delta_i S < -\Delta_e S$

In case 1, the entropy released towards the external environment is lower than the entropy produced within the system, implying that the system imports entropy ($\Delta_e S > 0$) and/or retains all or a part of the entropy produced by irreversibilities. Cases 2 and 3 represent situations where the system maintains (case 2) or decreases (case 3) its entropy in spite of the internal degrading processes. To be realised, these cases not only require that a net export of entropy is attained ($-\Delta_e S > 0$), but also that the export compensates or exceeds entropy production, which implies a particular configuration of the system that allow the produced entropy to be discharged towards the environment. Since $-\Delta_e S = \Delta S_E$, the entropy exchange at system boundary represents the “entropy fee” paid by the external environment for sustaining system structure and processes, and can be taken as a measure of environmental degradation. Since $-\Delta_e S = \Delta_i S - \Delta S$, such an “entropy fee” becomes increasingly positive as the extent of irreversibilities increase and the entropy of the system decreases, as can be expected, in particular, if dissipative structures work within the system. Prigogine et al. (Nicolis and Prigogine, 1977; Prigogine, 1980) introduced the term “dissipative structures” to denote non-equilibrium systems able to reduce the internal entropy and self-organise by exploiting the thermodynamic exchanges with the external environment. Therefore, the term of entropy exchange at system boundary attains a particular importance in characterising self-organising processes.

An analogous case study can be written in terms of exergy, showing that the “exergy fee” paid by the external environment for the maintenance or the increase of the distance of the system from equilibrium ($\Delta Ex \geq 0$) can be considered to be expressed by the negative of the exergy transfer ($-\Delta Ex_t$).

According to the above framework, three different facets of the phenomenon of the energy degradation can be distinguished, which are respectively described by the terms of the entropy and exergy balance:

Overall degradation (or degradation <i>tout court</i>):	$\Delta_i S, \Delta Ex_d$
System degradation:	$\Delta S, -\Delta Ex$
External environment degradation:	$-\Delta_e S, -\Delta Ex_d$

The examination of all the terms of the entropy and/or exergy balance, as well of their relationships, is therefore needed in order to fully describe the phenomenon of energy degradation in non-isolated systems. It is worth stressing that the entropy and exergy perspectives are not equivalent. In fact, whereas $\Delta_i S$ and ΔEx_d are positively related, the terms ΔS and $-\Delta Ex$, and consequently $-\Delta_e S$ and $-\Delta Ex_d$, can behave very differently, as they express different thermodynamic variations. For example, consider a system that receives a radiative flow from the environment and degrades the absorbed radiation into heat by molecular relaxation: the entropy change (ΔS) associated with the heating is positive, but the exergy change can be positive or negative, depending on the temperature difference between the system and the surrounding environment.

In relation with ecological indication, the above classification shows that different types of indicators of energy degradation can be defined, thus emphasising that a clear reference to the specific facet considered should be made in order to avoid ambiguous statements. Note that, according to the above classification, the previously described indicators (Eqs. (1) and (2)) should be classified as indicators of external environmental degradation, not degradation *tout court*. The distinction between indicators of overall and environment degradation is particularly critical when they are used as indicators of development state, as the steady state condition can be assumed only for particular moments of a seasonal or long-term succession (e.g. the climax stage). These two type of indicators are thus expected to behave very differently along ecosystem development, the difference being due to the changes in the entropy or exergy storage into the system.

In this paper, the behaviour of several thermodynamic indicators, which include previously derived indices and a new set of entropy-based indicators, is examined along the seasonal progression in a lake ecosystem, and their significance and effectiveness in characterising the ecosystem state is evaluated by comparing their responses with the main successional traits of the phytoplankton community.

2. Calculation

The calculations carried out in this work are based on the thermodynamic data reported in Ludovisi and Poletti (2003). In the study, the authors calculated, with a monthly resolution, the energy and the entropy budget of Lake Trasimeno for the period 1988–1996, starting from meteorological and hydrological data.

The monthly energy budget of the lake was calculated as:

$$\Delta E = (E_{dr} + E_{sc} - E_{rf}) + (E_{at} - E_{br}) - (E_e + E_c) + (E_{pl} - E_d - E_a), \quad (7)$$

where ΔE is the monthly change in the energy content of the lake; E_{dr} , E_{sc} , E_{rf} are the energy flows associated with shortwave (solar) radiation to and from the water surface (E_{dr} – direct; E_{sc} – scattered; E_{rf} – reflected); E_{at} and E_{br} are the energy flows associated, respectively, with longwave (thermal) radiation to and from the water surface; E_e is the evaporation–condensation heat loss from the water surface; E_c is the atmosphere–water heat loss by conduction (sensible flow); E_{pl} , E_d , E_a are the heat flows associated with precipitation and water outlet from the lake.

The monthly net entropy flow incoming into the lake was then calculated as:

$$\Delta_e S = (S_{dr} + S_{sc} - S_{rf}) + (S_{at} - S_{br}) - (S_e + S_c) + (S_{pl} - S_d - S_a) \quad (8)$$

A conceptual diagram illustrating the entropy flows associated with the energy flows considered is reported in Fig. 1, whereas the basic relationships used for their calculations can be found in Appendix.

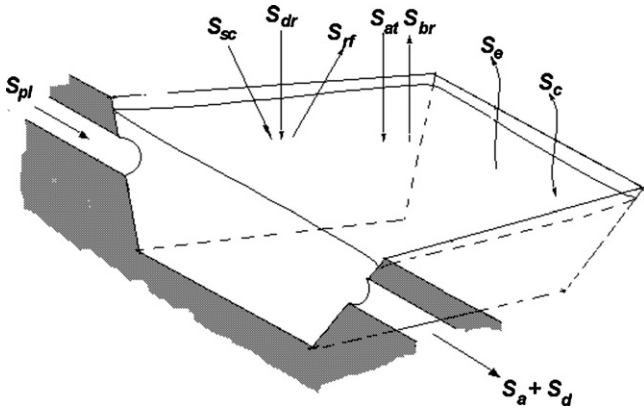


Fig. 1. Conceptual diagram of the entropy flows to and from a lake, considered for the calculation of the monthly entropy budget of Lake Trasimeno. The indicated entropy flows are associated with: S_{dr}, S_{sc}, S_{rf} – the energy flows of shortwave (solar) radiation to and from the water surface (S_{dr} – direct; S_{sc} – scattered; S_{rf} – reflected); S_{br}, S_{at} – the energy flows of the longwave (thermal) radiation to and from the water surface (S_{br} – outgoing; S_{at} – incoming); S_e – evaporation–condensation heat loss from the water surface; S_c – atmosphere–water heat loss by conduction (sensible flow); S_{pl}, S_a, S_d – heat flow associated with precipitation and water inlet–outlet to the lake.

The monthly change in entropy content (ΔS) of the lake was calculated starting from the monthly change in the heat storage (ΔQ), as follows²:

$$\Delta S = \frac{\Delta Q}{T_w}, \tag{9}$$

where T_w is the monthly average temperature of the water. Finally, the monthly total entropy produced by the lake was calculated as the difference between the entropy content and the net incoming entropy flow (see Eq. (3)):

$$\Delta_i S = \Delta S - \Delta_e S \tag{10}$$

For the purposes of the present investigation, the following indicators were calculated starting from the above data:

(I) Net radiation flux absorbed at surface

$$R_n = (E_{dr} + E_{sc} - E_{rf}) - (E_{at} - E_{br}) \\ = (E_e + E_c) - (E_{pl} - E_d - E_a) + \Delta E;$$

(II) Solar exergy dissipation

$$SED = \frac{R_n}{K^*} = \frac{R_n}{(E_{dr} + E_{sc} - E_{rf})};$$

(III) Exergy flux

$$EX_f = E_{br} \ln\left(\frac{E_{br}}{E_{at}}\right) + E_{rf} \ln\left(\frac{E_{rf}}{E_{dr} + E_{sc}}\right) + R_n;$$

(IV) Radiation efficiency coefficient

$$\eta_R = \frac{R_n}{(E_{dr} + E_{sc} + E_{at})};$$

² This calculation provides a rough estimate of the total entropy change. Other contributions (such as those arising from the change in the physical, chemical and biological organisation of the system) should be taken into account for estimating the change of the entropy content. However, these contributions have been neglected, because of the theoretical problems involved in calculations, as well as because they are reasonably minor with respect to that associated with the change in the heat storage.

(V) Exergy efficiency coefficient

$$\eta_{Exf} = \frac{EX_f}{(E_{dr} + E_{sc} + E_{at})};$$

(VI) Exergy destruction

$$EX_d = T_w \cdot \Delta_i S;$$

(VII) Exergy destruction coefficient

$$\eta_{Exd} = \frac{EX_d}{(E_{dr} + E_{sc} - E_{rf} + E_{at})};$$

(VIII) Net entropy flow (outgoing)

$$-\Delta_e S = -[(S_{dr} + S_{sc} - S_{rf}) + (S_{at} - S_{br}) \\ - (S_e + S_c) + (S_{pl} - S_d - S_a)];$$

(IX) Net radiative entropy flow (outgoing)

$$-\Delta_e S = -[(S_{dr} + S_{sc} - S_{rf}) + (S_{at} - S_{br})].$$

According to the theoretical framework here proposed, indicators II–V can be classified as indicators of external environment degradation (see also Eqs. (1) and (2)), together with indicators VIII and IX. On the other hand, exergy destruction (EX_d) and the ratio between EX_d and the radiative energy absorbed by the lake (η_{Exd}) are, respectively, direct and normalised measures of overall degradation.

Finally, the ratio between the energy and entropy of the considered flows ($K_i = E_i/S_i$), is proposed as an energy quality index, and is used to evaluate the seasonal change of the ability of the incoming and outgoing energy flows to do work. As can be seen from the equations reported in Appendix, the ratio energy-to-entropy is proportional to the effective temperature of the emitting grey body (sun, atmosphere, water), or the temperature at which the heat is exchanged by non-radiative flows. Under ordinary conditions, the following scale of energy quality can be derived: $K_{dr} \gg K_{sc}, K_{rf} \gg K_e, K_c, K_{pl}, K_a, K_d > K_{br}, K_{at}$. As an example, the energy quality index associated with the incoming and outgoing energy flows from Lake Trasimeno in August 1990 is reported below:

K_{dr}	K_{sc}	K_{rf}	K_e, K_c, K_a, K_d	K_{pl}	K_{br}	K_{at}
4320	905	837	297	299	218	209
1 ^a	0.209 ^a	0.194 ^a	0.069 ^a	0.069 ^a	0.050 ^a	0.048 ^a

^aRelative to direct solar radiation.

Note that the above ranking of the energy quality index is consistent with the energy grade proposed by Brillouin (1966), who attributes the highest grade to short-wave electromagnetic radiation and the lowest grade to longwave radiation.

3. Results

The seasonal trends of entropy production ($\Delta_i S$) and net entropy flow outgoing from Lake Trasimeno ($-\Delta_e S$) are shown in Fig. 2. As can be seen, the two quantities show an increasing trend from winter to summer, but significantly differ over all the year, as a consequence of the change in the heat storage in the lake, which is positive from February to July and negative in the rest of the year. The seasonal trend of the extensive indicators R_n, EX_f and EX_d is shown in Fig. 3. As can be seen, the net radiation flux absorbed at surface (R_n) increases from winter to summer months, as a function of the incoming solar irradiation. The seasonal progression of the radiative exergy flux (EX_f) parallels that of R_n , but is higher by about

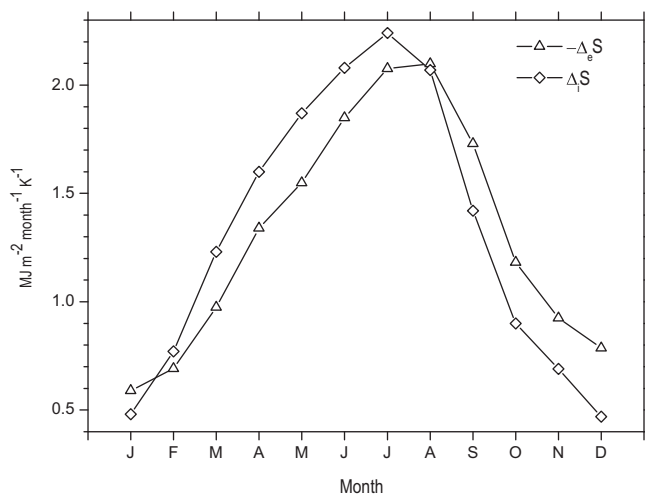


Fig. 2. Seasonal progression of entropy production ($\Delta_i S$) and net entropy flow ($-\Delta_e S$) in Lake Trasimeno. The plotted values represent the monthly averages of the years 1988–1996.

100 MJ m⁻² month⁻¹, this difference being due to the change in the information carried by incoming and outgoing radiations. Exergy destruction (Ex_d) shows a seasonal pattern similar to Ex_f , with some difference in late summer.

The seasonal trends of the normalised indicators (SED , η_R , η_{Ex_f} , η_{Ex_d}) here considered are shown in Fig. 4. The trend of SED indicates that the fraction of the solar energy released by non-radiative flows (plus heat storage) widely varies between 0.05 (December) and 0.73 (July), thus indicating that different (radiative vs non-radiative) processes prevail in dissipating the incoming shortwave radiation during the year. The radiation efficiency coefficient (η_R) and the exergy efficiency coefficient (η_{Ex_f}) show parallel seasonal progressions, with the latter being higher than the former by about 10%. The trend of η indicates that a relatively small fraction (1–30%) of the absorbed radiation (shortwave + longwave) is dissipated by non-radiative processes, the most relevant portion being released as longwave radiation. The exergy destruction coefficient (η_{Ex_d}) shows values comparable to those of η_{Ex_f} , but the seasonal trends significantly diverge during summer, when a more localised maximum of η_{Ex_d} (July–August) can be observed.

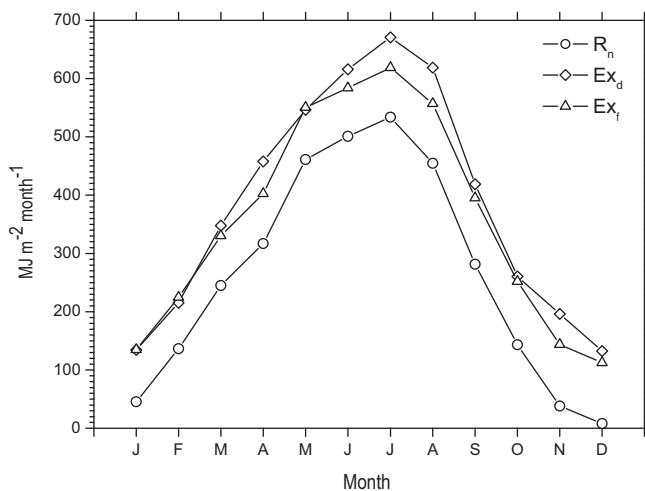


Fig. 3. Seasonal progression of net radiative energy flow (R_n), radiative exergy flux (Ex_f) and exergy destruction (Ex_d) in Lake Trasimeno. The plotted values represent the monthly averages of the years 1988–1996.

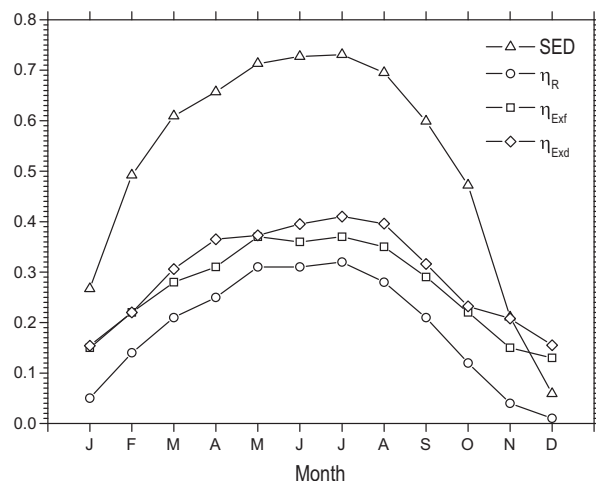


Fig. 4. Seasonal progression of SED , η_R , η_{Ex_f} and η_{Ex_d} in Lake Trasimeno. The plotted values represent the monthly averages of the years 1988–1996.

When compared with the previous indicators, the net radiative entropy flow ($-\Delta_e S_r$) shows quite a different seasonal behaviour (Fig. 5), which identifies a main peak in September and a secondary peak in February–March.

In order to evaluate the relationship between the indicators considered and the development state of the lake community, we compared the above trends with the trend of two basic traits of the phytoplankton community, i.e. the phytoplankton biomass and body size in the years 1990–1992 (Fig. 6a and b). As can be seen, the observed trends follow the typical seasonal dynamics, with the main algal bloom being localised in the late-summer months (August–October), when large-sized colonial Chlorophyceae and Cyanobacteria dominate in the community (Ludovisi et al., 2005). Note also that the phytoplankton biodiversity (as species richness) attains the highest values in late summer-early autumn months (Fig. 6c). From a comparison of the plots shown in Figs. 2–6, there emerges a clear link between $-\Delta_e S_r$ and biomass density, as well as body size of phytoplankton, whereas the other indicators show a poor relationship. A regression analysis (Fig. 7) showed that the correlations are significant at $p < 0.001$. It is worth noting here that, since the exergy stored by phytoplankton is proportional to phytoplankton biomass, a significant positive correlation also holds between $-\Delta_e S_r$ and phytoplankton exergy.

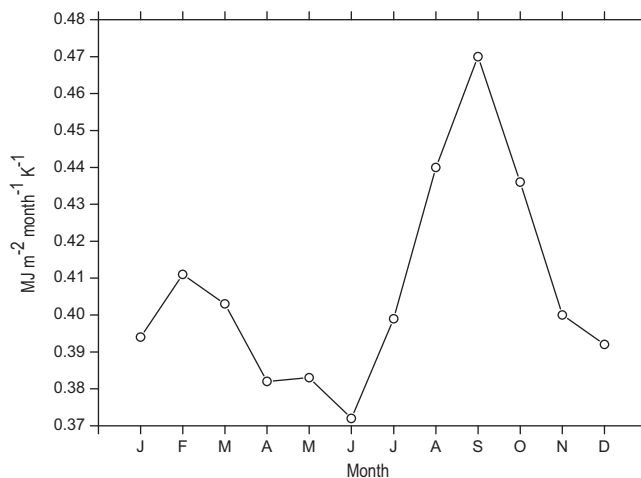


Fig. 5. Seasonal progression of the net radiative entropy flow ($-\Delta_e S_r$) in Lake Trasimeno. The plotted values represent the monthly averages of the years 1988–1996.

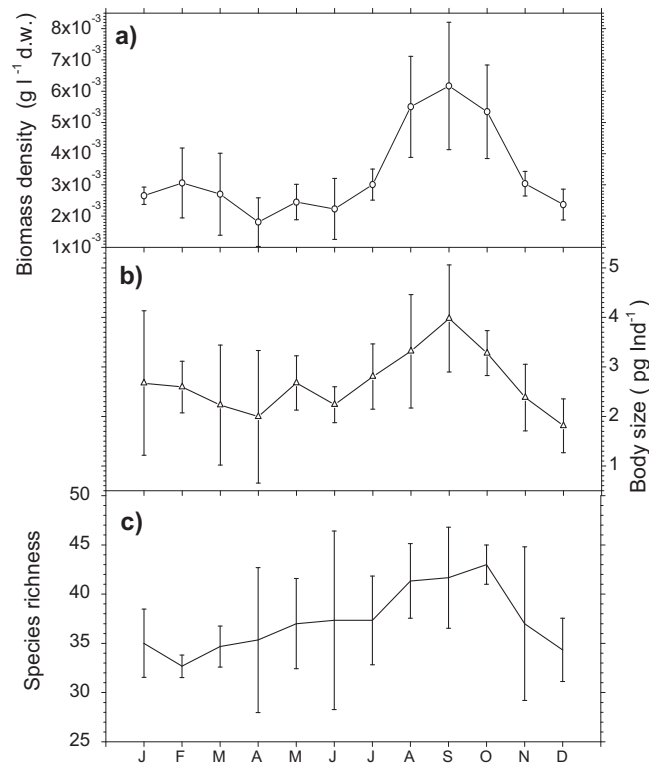


Fig. 6. Seasonal trend of the total density of biomass (a), the average individual body size (b) and the species richness (c) of phytoplankton in Lake Trasimeno. The plotted values represent the monthly averages (with standard deviation) of the years 1990–1992.

4. Discussion

Most of the examined indicators of external environment degradation (SED , η_R , EX_f , η_{EX_f} and $-\Delta_e S$) and overall degradation ($\Delta_i S$, EX_d and η_{EX_d}) showed quite similar seasonal patterns, which identify summer as the period when degradative processes attain their highest extents in Lake Trasimeno, thus suggesting that the nature and/or the strength of degradative processes change in response to the solar input. However, a thorough examination of the relationship between EX_d and the magnitude of energy absorbed by the lake (Fig. 8) reveals that it is strictly linear, thus suggesting that no appreciable transition in the overall ability of the system in destroying exergy takes place in the examined range of variation of the energy input. Does this mean that EX_d and the related indicators of overall degradation are inappropriate or ineffective in revealing significant changes in the biological activity of the lake community examined? As shown by Ludovisi et al. (Ludovisi et al., 2005; Ludovisi, 2006), the entropy production associated with light absorption and photosynthesis by phytoplankton can provide an appreciable contribution to the whole entropy production in lakes. Ludovisi (2004, 2006) also proposed a method for separating abiotic and biotic entropy production in lakes, which is based on the regression between d' (the monthly entropy production per unit of absorbed solar radiation) and Carlson's trophic state index (Carlson, 1977). When applied to Lake Trasimeno, the method led to estimate the biological entropy production as representing about 1/3 of the total, with a seasonal progressions differing slightly from that of the total. These findings suggest that abiotic and biotic entropy production increase almost proportionally with increasing energy forcing, thus explaining the absence of appreciable transitions in the overall ability of the lake to destroy exergy. They also suggest that indicators based on entropy production may deserve consideration as indicators of the extent of the biological activity in a lake.

However, this does not imply that they are adequate indicators of community development, because the magnitude of the biological activity is not straightforwardly related to the development state of a community. As shown by Odum (1969), the extent of the biological activity (as primary production and respiration) in forests or algal cultures attains its maximum value during intermediate stages of ecosystem development, not at the climax stage. Aoki (1987a,b,c, 1995) also showed that entropy production in living systems ranging from organisms to ecosystems follows a unimodal trend, increasing in the early stages and decreasing in later senescent stages. Similar expectations have been hypothesised by Holdaway et al. (2010) in terrestrial successions, and by Jørgensen et al. (Jørgensen et al., 2000; Fath et al., 2004), who suggest that entropy production and exergy dissipation are increasing during the early stages of ecosystem development (Growth Form I) and decreasing in a late senescent stage (Growth Form IV). The mismatch between maximum biological activity and maximum biomass stored is certainly enhanced in real plankton communities, where the standing stocks are continuously eroded by grazing and predation, especially during intermediate stages of development (Amblard and Pinel-Alloul, 1995). Neither should biological activity be expected to increase with the body size of organisms (which can be considered a significant indicators of maturity, according to the r - K model introduced by MacArthur and Wilson (1967)), since the following series of relationships generally holds (Southwood, 1976):

$$\begin{aligned} \text{growth rate} &\propto \text{metabolic rate per unit weight} \\ &\propto \frac{1}{\text{generation time}} \propto \frac{1}{\text{body size}}. \end{aligned}$$

In fact, our results show that no significant correlation exists between the above indicators of exergy destruction and biomass density or body size of phytoplankton in Lake Trasimeno.

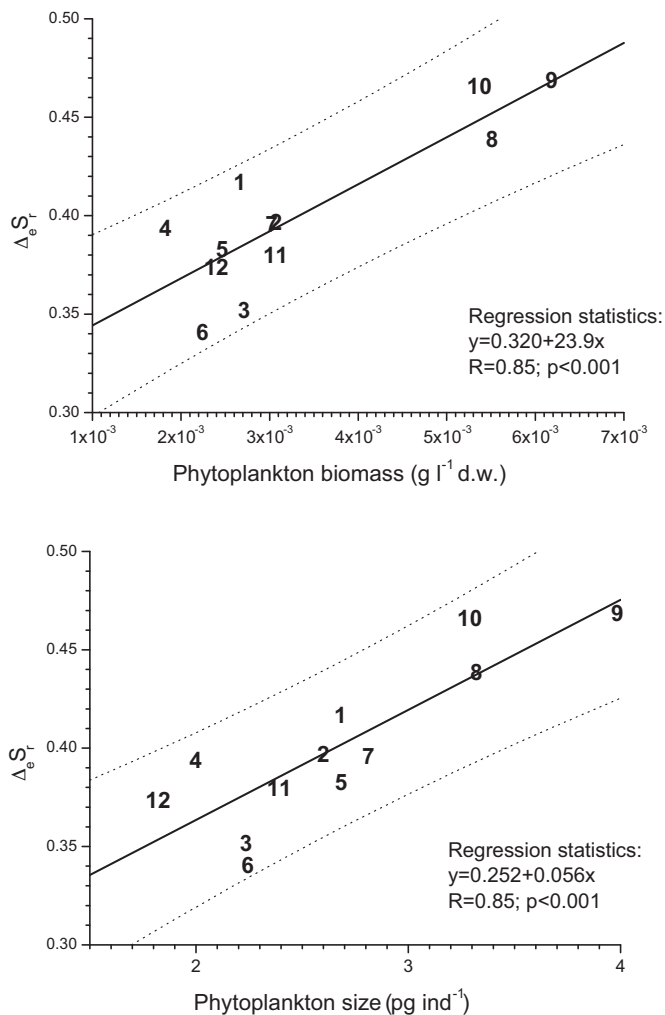


Fig. 7. Linear regression between net radiative entropy flows ($-\Delta_e S_r$) and total density of biomass (top) and average individual body size (bottom) of phytoplankton in Lake Trasimeno. The plotted values represent the monthly averages (labelled as 1–12) of the years 1990–1992.

On the other hand, the net radiative entropy flow outgoing from the system ($-\Delta_e S_r$) exhibits a seasonal progression that parallels that of the phytoplankton successional traits, thus suggesting that the radiative entropy balance is closely related to phytoplankton organisation, both at a global (density of biomass and biodiversity) or individual (body size) level. However, it remains unclear whether this link is controlled by phytoplankton or vice versa. To approach this issue, I have analysed the seasonal trend of the energy quality index (K_i), which is shown in Fig. 9. As can be seen, the energy quality of the total absorbed radiation (K_{ri}) is a maximum during summer, as a consequence of the combined increase of solar irradiation and effective temperature of the atmosphere (K_{li}). The energy quality of the outgoing flows associated with longwave (K_{lo}) and heat losses (K_e) are a maximum in late summer, mostly as a consequence of the increase in temperature of the water. Because of the change in the relative contribution of the direct and diffuse solar radiation, the seasonal progression of the energy quality associated with the absorbed solar radiation (K_{si}) is marked by a quite different pattern, which shows a certain resemblance with that of the net radiative entropy flow (Fig. 5) or phytoplankton traits (Fig. 6), thus suggesting that a higher quality of the absorbed solar radiation promotes the development of the phytoplankton community. Some evidence that direct light could enhance the photosynthetic rate more than diffuse light has been found in the case of some terrestrial plants

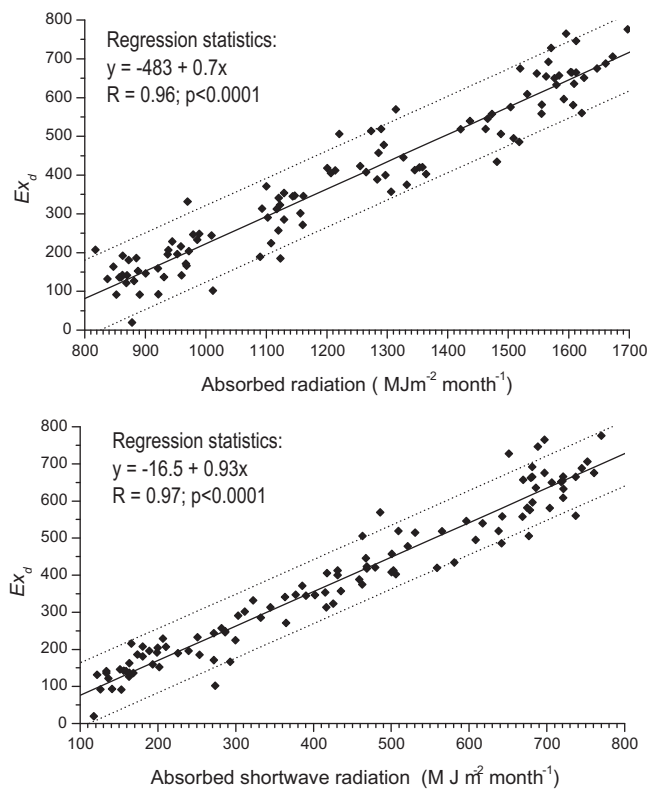


Fig. 8. Monthly exergy destruction vs total (top) and shortwave (bottom) radiation absorbed in Lake Trasimeno the years 1988–1996.

(Brodersen et al., 2008), but this effect seems to be limited to high-light-adapted leaves. Such an anisotropic effect, however, is very unlikely to hold for phytoplankton, which are adapted to an underwater light field dominated by scattered radiation (Kirk, 1994). It must be concluded, therefore, that the relationship between $-\Delta_e S_r$ and phytoplankton traits is driven by phytoplankton, i.e. that phytoplankton blooms significantly affect the drop of energy quality associated with radiation. This is not surprising, if we consider that phytoplankton can contribute greatly to the absorption of the shortwave radiation and to its conversion to heat (Kirk, 1994). Due to photosynthetic pigments, phytoplankton absorbs the PAR

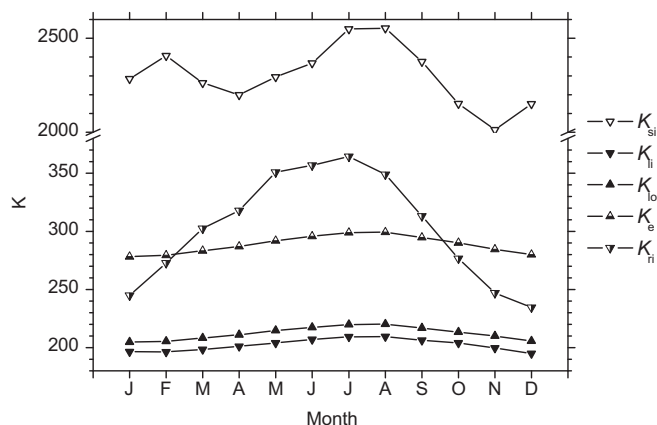


Fig. 9. Seasonal progression of the “energy quality index” for the main incoming and outgoing fluxes from Lake Trasimeno as monthly averages of the years 1988–1996 (K_{si} – shortwave radiation absorbed; K_{li} – incoming longwave radiation; K_{lo} – longwave emissions; K_e – non radiative heat losses; and K_{ri} – total radiation absorbed at the surface).

efficiently, but, because of the low efficiency of the conversion into chemical energy, most of the absorbed energy (>75%) is released as heat. At the same time, phytoplankton cells and colonies, like particulate matter, significantly increase the average pathlength of the photons in water by scattering, thus amplifying the extent of absorption and reducing the amount of light scattered back out of the water. Therefore, an increase in the phytoplankton density can be expected to affect significantly the radiative net entropy balance of a lake by increasing longwave emissions and decreasing the emission of scattered shortwave radiation.

The finding that the development traits of phytoplankton are positively correlated with the net radiative entropy flow ($-\Delta_e S_r$), but not with the total net entropy flow ($-\Delta_e S$), suggests that non-radiative entropy exchanges (such as those associated with evaporation or heat exchange) mask the thermodynamic signal due to the phytoplankton succession. This effect also helps to explain the lack of correlation found between the development traits of phytoplankton and most of the indicators of external environment degradation here investigated (SED , Ex_f , η_R and η_{Ex_f}). In fact, all these indicators are dependent on the net radiation flux absorbed at the lake surface (R_n), which equates the sum of energy flows associated with evaporation and heat exchange, plus heat storage (see Eq. (1)). It is interesting to note that, when Svirezhev's exergy flux (Ex_f) is calculated by neglecting the term R_n , a significant positive correlation ($R=0.75$; $p=0.005$) comes out between Ex_f and phytoplankton biomass.

The above results allow us to approach a discussion concerning the soundness of the hypothesis that the maximisation of external environment degradation represents a criterion of ecosystem development. Although the theoretical foundation of this hypothesis is far from being treatable by using the data at hand, they suggest that such a hypothesis cannot be taken as a general criterion of development for ecosystems as a whole. However, the observed inconsistency seems to arise more from practical than from theoretical issues, because the thermodynamic signal of environmental degradation due to the succession seems to be conserved in the radiative portion of the entropy budget. Among the possible causes able to obfuscate the degradative signal of succession, we can consider the following:

- technical/methodological limitations: the degradative signal is relatively weak in comparison with the magnitude of the flows involved in the computation of the thermodynamic balances. Therefore, the accuracy of data, calibration and modelling stages is crucial for a reliable estimation of the environmental degradation; and
- abiotic noise: although ecosystem development can be regarded as a process along which biotic and abiotic processes vary in an integrated way, some relevant abiotic processes (such as evaporation and heat exchange at water–air interface) are relatively insensitive to the successional process, but affect significantly the thermodynamic balances. This aspect assumes a particular relevance in the case of aquatic ecosystems, where ecosystem/environment exchanges take place at the water–environment interface, not at the organism–environment interface.

Further investigations are therefore needed in order to evaluate the reliability of the current methodologies used for calculating thermodynamic balances in ecosystems, as well as in order to understand the limit of application of energy degradation-based indicators in complex dissipative systems like ecosystems.

5. Conclusion

On the whole, the results here presented emphasise the following aspects:

- Thermodynamic measures of overall degradation (e.g. entropy production and exergy destruction) and related indices may deserve consideration as indicators of the overall extent of the degradative (biotic and abiotic) processes acting within an ecosystem, but their significance as indicators of ecosystem development appear to be limited, as a consequence of the non-monotonic increase of biological activity along ecological successions.
- Thermodynamic measures of external environment degradation (e.g. entropy and exergy transfer) and related indices can deserve consideration as indicators of development state as well as ecological orientors, provided that some methodological/theoretical issues are further clarified. In fact, methodological limitations and/or the abiotic noise can significantly mask the thermodynamic signal due to a succession and, therefore, a significant effort must be paid to identifying thermodynamic indicators able to capture the ecological signal.
- The net radiative entropy exchange emerges as the best candidate for representing an effective indicator of the development state of the phytoplankton community in a meso-eutrophic lake.

In the context of the current pattern of thermodynamic ecosystem theories (Fath et al., 2001; Jørgensen et al., 2007), entropy-based indices of environmental degradation of the kind proposed here represent a specific category of orientors, complementary to those previously established, whose investigation could add a further characterisation of the thermodynamic pattern of ecosystem development. Further investigations on aquatic, as well as terrestrial, ecosystems are needed in order to confirm the results obtained here and develop effective indicators as a function of ecosystem type. On this account, it is worth emphasising that entropy exchanges can be obtained straightforwardly starting from a knowledge of input–output flows, which are currently estimated by well-established methodologies, possibly using remote sensing data. Thus, entropy-based analyses can represent a powerful and relatively easy-to-use tool for testing theories on ecosystem development and building up indicators of environmental quality.

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Appendix A. Appendix

The following list summarises the basic equations proposed by Aoki (1982, 1983, 1987a, 1989, 1990) for the calculation of the entropy associated with radiative and non-radiative incoming and outgoing energy flows from a lake ecosystem:

Entropy flows associated with shortwave radiation

$$\text{Direct solar radiation } S_{dr} = \frac{4}{3} \frac{E_{dr}}{T_0};$$

$$\text{Diffuse solar radiation } S_{sc} = \frac{4}{3} \frac{E_{sc}}{T_0} X(\varepsilon_{sc});$$

$$\text{Reflected solar radiation } S_{rf} = \frac{4}{3} \frac{E_{rf}}{T_0} X(\varepsilon_{rf});$$

where $T_o = 5760\text{K}$ is the temperature of the sun and $X(\varepsilon)$ is a function of the grey body effective emissivity of diffuse (ε_{sc}) and reflected solar radiation (ε_{rf}). Under ordinary conditions, the values of $X(\varepsilon_{sc})$ and $X(\varepsilon_{rf})$ range from 4 to 6, thus showing that the entropy associated with diffuse and reflected radiation is higher than that associated with direct solar radiation.

Entropy flows associated with longwave radiation

Incoming longwave radiation $S_{at} = \frac{4}{3} \frac{E_{at}}{T_{at}} X(\varepsilon_{at});$

Longwave emission $S_{br} = \frac{4}{3} \frac{E_{br}}{T_w} X(\varepsilon_w);$

where ε_{at} and ε_w are the grey-body emissivity of the atmosphere and the water surface having an effective temperature T_{at} and T_w , respectively. Under ordinary conditions, $X(\varepsilon_{at})$ and $X(\varepsilon_w)$ attain values slightly higher than 1.

Entropy flows associated with non-radiative energy exchanges

Evaporation – condensation heat loss $S_e = \frac{E_e}{T_w};$

Sensible heat flow $S_c = \frac{E_c}{T_w};$

Heat flow associated with water inlet – outlet $S_{pl} = \frac{E_{pl}}{T_{at}},$

$$S_a = \frac{E_a}{T_w}, \quad S_d = \frac{E_d}{T_w}.$$

References

- Amblard, C., Pinel-Alloul, B., 1995. In: Pourriot, R., Maybeck, M. (Eds.), Variations saisonnières et interannuelles du plancton. Limnologie générale, Masson, pp. 430–435.
- Aoki, I., 1982. Radiation entropies in diffuse reflection and scattering and application to solar radiation. *J. Phys. Soc. Jpn.* 51, 4003–4010.
- Aoki, I., 1983. Entropy production on the earth and other planets of the solar system. *J. Phys. Soc. Jpn.* 52, 1075–1078.
- Aoki, I., 1987a. Entropy balance in lake Biwa. *Ecol. Model.* 37, 235–248.
- Aoki, I., 1987b. Entropy budgets of deciduous plant leaves and a theorem of oscillating entropy production. *Bull. Math. Biol.* 49, 449–460.
- Aoki, I., 1987c. Entropy balance of White-tailed deer during a winter night. *Bull. Math. Biol.* 49, 321–327.
- Aoki, I., 1989. Hological study of lakes from an entropy viewpoint—lake Mendota. *Ecol. Model.* 45, 81–93.
- Aoki, I., 1990. Monthly variations of entropy production in lake Biwa. *Ecol. Model.* 51, 227–232.
- Aoki, I., 1995. Entropy production in living systems – from organisms to ecosystems. *Thermochim. Acta* 25, 359–370.
- Bénard, H., 1900. Etude expérimentale du mouvement des liquides propagé par convection. *C.R. Acad. Sci. Paris* 130, 1004.
- Brillouin, L., 1966. *Science and Information Theory*. Academic Press, New York.
- Brodersen, C.R., Vogelmann, T.C., Williams, W.E., Gorton, H.L., 2008. A new paradigm in leaf-level photosynthesis: direct and diffuse lights are not equal. *Plant Cell Environ.* 31, 159–164.
- Brunhes, B., 1908. *La Dégradation de l'Energie*. E. Flammarion.
- Carlson, R.E., 1977. A trophic state index for lakes. *Limnol. Oceanogr.* 22, 361–369.
- Dewulf, J., Van Langenhove, H., Muys, B., Bruers, S., Bakshi, B.R., Grubb, G.F., Paulus, D.M., Sciubba, E., 2008. Exergy: its potential and limitations in environmental science and technology. *Environ. Sci. Technol.* 42, 2221–2232.
- Evans, R.B., Crellin, G.L., Tribus, M., 1966. Thermo-economic considerations of sea water demineralisation. In: Spiegler, K.S. (Ed.), *Principles of Desalination*. Academic Press, New York and London, pp. 21–75.
- Fath, B.D., Patten, B.C., Choisis, J.S., 2001. Complementarity of ecological goal functions. *J. Theor. Biol.* 208, 493–506.
- Fath, B.D., Jørgensen, S.E., Patten, B.C., Straškraba, M., 2004. Ecosystem growth and development. *Biosystems* 77, 213–228.
- Holdaway, R.J., Sparrow, A.D., Coomes, D.A., 2010. Trends in entropy production during ecosystem development in the Amazon Basin. *Philos. Trans. R. Soc. B* 365, 1437–1447.
- Kirk, J.T.O., 1994. *Light and Photosynthesis in Aquatic Ecosystems*. Cambridge University Press, Cambridge, 509 pp.
- Kleidon, A., Lorenz, R., 2005. Entropy production by earth system processes. In: Kleidon, A., Lorenz, R.D. (Eds.), *Non-Equilibrium Thermodynamics and the Production of Entropy: Life, Earth, and Beyond*. Springer Verlag, Berlin, pp. 1–20.
- Kutsch, W.L., Steinborn, W., Herbst, M., Baumann, R., Barkmann, J., Kappen, L., 2001. Environmental indication: a field test of an ecosystem approach to quantify biological self organization. *Ecosystems* 4, 49–66.
- Jaynes, E.T., 1980. The minimum entropy production principle. *Annu. Rev. Phys. Chem.* 31, 579–601.
- Jørgensen, S.E., Fath, B.D., Bastianoni, S., Marques, J.C., Müller, F., Nielsen, S.N., Patten, B.C., Tiezzi, E., Ulanowicz, R.E., 2007. *A New Ecology – Systems Perspective*. Elsevier, Amsterdam, 288 pp.
- Jørgensen, S.E., Patten, B.C., Straškraba, M., 2000. Ecosystem emerging: 4. growth. *Ecol. Model.* 126, 249–284.
- Jørgensen, S.E., Svirezhev, Y.M., 2004. *Towards a Thermodynamic Theory for Ecological Systems*. Elsevier, Amsterdam, 366 pp.
- Ludovisi, A., 2004. Biotic and abiotic entropy production in lake ecosystems. *Ecol. Model.* 179, 145–147.
- Ludovisi, A., 2006. Use of thermodynamic indices as ecological indicators of the development state of lake ecosystems: specific dissipation. *Ecol. Indic.* 6, 30–42.
- Ludovisi, A., Pandolfi, P., Taticchi, M.I., 2005. The strategy of ecosystem development: specific dissipation as an indicator of ecosystem maturity. *J. Theor. Biol.* 235, 33–43.
- Ludovisi, A., Poletti, A., 2003. Use of thermodynamic indices as ecological indicators of the development state of lake ecosystems: 1. Entropy production indices. *Ecol. Model.* 159, 203–222.
- Luvall, J.K., Kay, J.J., Fraser, R.F., 2001. Thermal remote sensing and the thermodynamics of ecosystem development. In: Ulgiati, S., Brown, M.T., Giampietro, M., Herenden, R.A., Mayumi, K. (Eds.), *Advances in Energy Studies. Exploring supplies, Constraints and Strategies*. SG Editorial Padova, Italy, pp. 147–158.
- MacArthur, R.H., Wilson, E.O., 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton.
- Martyushev, L.M., Seleznev, V.D., 2006. Maximum entropy production principle in physics, chemistry and biology. *Phys. Rep.* 426, 1–45.
- Meysman, F.J.R., Bruers, S., 2010. Ecosystem functioning and maximum entropy production: a quantitative test of hypotheses. *Phil. Trans. R. Soc. B* 365, 1405–1416.
- Müller, F., 2005. Indicating ecosystem and landscape organisation. *Ecol. Indic.* 5, 280–294.
- Müller, F., Leupelt, M., 1998. *Eco Targets*. In: *Goal Functions and Orientors*. Springer-Verlag, Berlin.
- Müller, F., Schrautzer, J., Reiche, E.W., Rinker, A., 2006. Ecosystem based indicators in retrogressive successions of an agricultural landscape. *Ecol. Indic.* 6, 63–82.
- Nag, P.K., 2002. *Basic and Applied Thermodynamics*. Tata McGraw-Hill, New Delhi.
- Nicolis, G., Prigogine, I., 1977. *Self Organization in Non Equilibrium Systems*. Wiley-Interscience, New York, 491 pp.
- Nielsen, S.N., 2000. Thermodynamics of an ecosystem interpreted as a hierarchy of embedded systems. *Ecol. Model.* 135, 279–289.
- Odum, E.P., 1969. The strategy of ecosystem development. *Science* 164, 262–270.
- Prigogine, I., 1945. Etude thermodynamique des phénomènes irréversibles. *Bull. Cl. Sci. Acad. R. Belg.* 31, 600.
- Prigogine, I., 1980. *From Being to Becoming: Time and Complexity in the Physical Sciences*. Freeman, New York.
- Pykh, Y.A., 2002. Lyapunov functions as a measure of biodiversity: theoretical background. *Original Research Article. Ecol. Indic.* 2, 123–133.
- Schneider, E.D., Kay, J.J., 1994. Life is a manifestation of the second law of thermodynamics. *Math. Comput. Model.* 19, 25–48.
- Schneider, E.D., Sagan, D., 2005. *Into the Cool: Energy Flow, Thermodynamics, and Life*. University of Chicago press, Chicago.
- Schrödinger, E., 1944. *What is Life?* Cambridge University Press, Cambridge.
- Southwood, T.R.E., 1976. Bionomics strategies and population parameters. In: May, R.M. (Ed.), *Theoretical Ecology. Principles and Applications*. Blackwell Scientific Publications, Oxford, pp. 26–49.
- Straškraba, M., Jørgensen, S.E., Patten, B.C., 1999. Ecosystems emerging: 2. Dissipation. *Ecol. Model.* 117, 3–39.
- Svirezhev, Y.M., Steinborn, W.H., 2001. Exergy of solar radiation: information approach. *Ecol. Model.* 145, 101–110.
- Ulanowicz, R.E., Hannon, B.M., 1987. Life and the production of entropy. *Proc. R. Soc. Lond. B* 232, 181–192.