Ecological Modelling, 42 (1988) 289–303
Elsevier Science Publishers B.V., Amsterdam – Printed in The Netherlands

ENTROPY LAWS IN ECOLOGICAL NETWORKS AT STEADY STATE

ICHIRO AOKI

Department of Physics, Osaka Medical School, 2-41 Sawaragi-cho, Takatsuki-shi, Osaka 569 (Japan)

(Accepted 20 January 1988)

ABSTRACT

Aoki, I., 1988. Entropy laws in ecological networks at steady state. *Ecol. Modelling*, 42: 289–303.

Thermodynamical entropy concept is applied to input–output flow analysis of ecological networks at steady state. Entropy versions of the concepts of throughflow, total system throughflow, path length and cycling index are introduced. Throughflow and total system throughflow in entropy versions in irreversible processes are always larger than those in reversible processes. Throughflow and total system throughflow in entropy versions become larger as the extent of irreversibility-activity of the system is enhanced. Increase of irreversibility activity of the system induces any changes (increase, decrease or unchanged) of entropy path length and entropy cycling index, depending upon the structure of ecological networks.

INTRODUCTION

The Second Law of Thermodynamics for open systems states that the change of the entropy content of a system is the sum of the net entropy flow into a system and the entropy production within a system, and that the entropy production should always be non-negative; it is positive when processes occurring in a system are irreversible, and is zero when processes are reversible (e.g., Nicolis and Prigogine, 1977). Hence, when a system is at steady state (the entropy content remains constant with time), the entropy characteristics of a system from a systems-theoretical viewpoint are specified by entropy flows into or out of a system and entropy production within a system. For example, Aoki (1987a) considered a white-tailed deer as one system and characterized it by the entropy inflow into a deer 1.66 J s^{-1} K^{-1}, the entropy outflow from a deer 2.12 J s^{-1} K^{-1}, and the entropy production within a deer 0.46 J s^{-1} K^{-1}. Aoki (1987b) also treated Lake Biwa as a whole from an entropy viewpoint (a "holological" approach to lakes in the jargon of Hutchinson, 1964); the systems-theoretical and entropic character-

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istics of the lake are given by the entropy inflow into the lake 52.2 MJ m^{-2} $year^{-1}$ K^{-1}, the entropy outflow from the lake 63.7 MJ m^{-2} $year^{-1}$ K^{-1}, and the entropy production in the lake 11.5 MJ m^{-2} $year^{-1}$ K^{-1}.

An ecological system is composed of its subsystems or compartments, which are connected with each other by networks of flows among them. As pointed out by Patten and Witkamp (1967), to understand ecosystems ultimately will be to understand networks. Input–output flow analysis of ecological networks has been developed by Hannon (1973), Finn (1976, 1978, 1980), Patten et al. (1976), Patten (1978) and others. They dealt only with flows of the conservative quantities: energy and matter in ecological networks. However, the non-conservative quantity entropy also flows in networks associated with energy and matter, and entropy is always produced within each compartment of an ecological system (the occurrence of production term or source term is just the point that differs from the case of conservative energy and matter).

Thus far, very little is known about thermodynamical entropy in ecological systems, although entropy is as important a concept as energy, as thermodynamics shows (the First Law of Thermodynamics concerns energy, and the Second and the Third Laws, entropy). In the present paper, the thermodynamical entropy concept is applied to the flow analysis of ecological systems at steady state, and entropy laws in ecological networks are presented.

MEASURABILITY PROBLEM

In discussing entropy laws in ecosystems, we should necessarily touch upon the problem of measurability of entropy content or entropy flux in complex organic systems. As textbooks show, thermodynamical variables are divided into two classes: state variables, and process variables. With regard to the entropy concept, the state variable is entropy content and the process variables are entropy flow and entropy production. It has been shown that the quantities entropy flow and entropy production can be calculated, by use of some physical methods from observed energetic data of objects; e.g., the entropy flows and the entropy productions for plant and animal have been computed by Aoki (1987a, c, d), and even those for a whole ecosystem such as a lake have also been calculated (Aoki, 1987b). In these lines of research, it is important to find a quantitative relationship between entropy flow–entropy production and biological characteristics of organisms and ecosystems.

As to the state variable, that is, entropy content, it should be pointed out that no one has yet been able to measure the entropy content of living systems; it is questionable whether it will even be measured in the near future. Hence, at present it is impossible to develop thermodynamical discussions based on measured entropy content of biological systems. Nevertheless, we can consider entropy content of biological objects *in a purely conceptual context* (not as a measured quantity). Biological organisms exist in states far from equilibrium; however, even in such conditions, entropy content of organisms can be defined: Prigogine argued that entropy can be defined if materials are dense and variations of densities with space and time are small; these conditions are fulfilled in biological systems (Nicolis and Prigogine, 1977). Also, Landsberg (1972) asserted that, for a class of non-equilibrium states, extensive variables such as entropy content exist, and called this statement the "fourth law" of thermodynamics. It will be evident that, according to Prigogine, biological systems are in the states for which the extensive variable entropy exists and the "fourth law" holds.

In this paper the existence of entropy content in biological systems is taken for granted, but our discussion does not depend on the measurability of entropy content; we only rely upon the measurability of the process variables (entropy flow and entropy production), which has already been shown by Aoki (1987a, b, c, d) for organisms and ecosystems.

DEFINITION OF TERMS

Let a system H be composed of n compartments H_k, $k = 1, 2, \dots, n$. The compartment H_k has a state variable x_k associated with it, which is, in the present case, the entropy content of the compartment H_k. The compartment H_k may receive entropy inflow $z_{k\text{o}}$ from the environment and donate entropy outflow $y_{\text{o}k}$ to the environment. Within the system H, entropy flows f_{ij} pass from H_j to H_i. Entropy is produced within H_k; the entropy production s_k is non-negative according to the Second Law of Thermodynamics (e.g., Nicolis and Prigogine, 1977). (It is assumed that entropy is kept constant in flowing between compartments; if entropy is increased at some place between compartments, that place should be included as a part of the compartments.) The derivative of x_k with respect to time is equal to the incoming entropy into H_k plus the entropy production within H_k minus the outgoing entropy from H_k:

$$\dot{x}_k = \sum_{j=1}^{n} f_{kj} + z_{k\text{o}} + s_k - \sum_{i=1}^{n} f_{ik} - y_{\text{o}k} \tag{1}$$

where $f_{kk} = 0$ is assumed.

If we put:

$$(\dot{x}_k)_+ = \begin{cases} \dot{x}_k & \text{if} \quad \dot{x}_k > 0 \\ 0 & \text{if} \quad \dot{x}_k \leq 0 \end{cases}$$

and

$$(\dot{x}_k)_- = \begin{cases} 0 & \text{if} \quad \dot{x}_k > 0 \\ \dot{x}_k & \text{if} \quad \dot{x}_k \leq 0 \end{cases} \tag{2}$$

then

$$\dot{x}_k = (\dot{x}_k)_+ + (\dot{x}_k)_-$$

and equation (1) becomes:

$$\sum_{j=1}^{n} f_{kj} + z_{ko} + s_k - (\dot{x}_k)_- = \sum_{i=1}^{n} f_{ik} + y_{ok} + (\dot{x}_k)_+ \tag{3}$$

Each side of (3) defines entropy throughflow T_k at the compartment H_k:

$$\begin{aligned} T_k &= \sum_{j=1}^{n} f_{kj} + z_{ko} + s_k - (\dot{x}_k)_- \\ &= \sum_{i=1}^{n} f_{ik} + y_{ok} + (\dot{x}_k)_+ \end{aligned} \tag{4}$$

The first equation of (4) is the sum of all entropy flows into H_k plus the entropy production within H_k minus the change in x_k (storage) if it is negative (entropy production and decaying storage are treated as inflow). The second equation of (4) is the sum of all entropy flows out of H_k plus the change in x_k if it is positive (increasing storage is treated as outflow). Either expression of entropy throughflow T_k represents the rate at which entropy is moving through H_k. Figure 1 illustrates the definition of the above-mentioned terms.

Total system throughflow in entropy version TST is defined as

$$\text{TST} = \sum_{k=1}^{n} T_k \tag{5}$$

that is

$$\begin{aligned} \text{TST} &= \sum_{k=1}^{n} \sum_{j=1}^{n} f_{kj} + \sum_{k=1}^{n} z_{ko} + \sum_{k=1}^{n} s_k - \sum_{k=1}^{n} (\dot{x}_k)_- \\ &= \sum_{k=1}^{n} \sum_{i=1}^{n} f_{ik} + \sum_{k=1}^{n} y_{ok} + \sum_{k=1}^{n} (\dot{x}_k)_+ \end{aligned} \tag{6}$$

Since the first terms of the above equation are equal:

$$\sum_{k=1}^{n} z_{ko} + \sum_{k=1}^{n} s_k - \sum_{k=1}^{n} (\dot{x}_k)_- = \sum_{k=1}^{n} y_{ok} + \sum_{k=1}^{n} (\dot{x}_k)_+ \tag{7}$$

or

$$Z + S - \dot{X}_- = Y + \dot{X}_+ \tag{8}$$

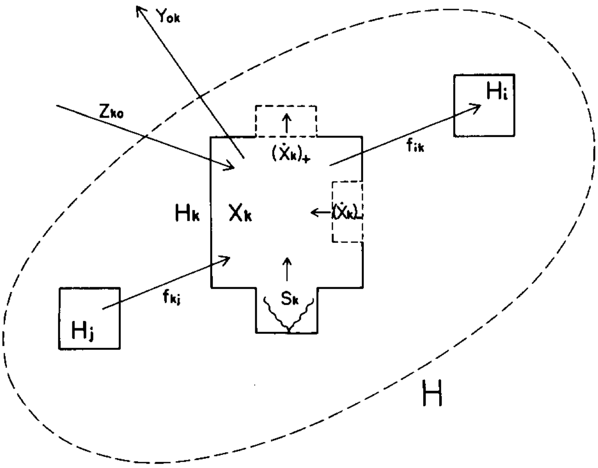

Fig. 1. Illustration of definition of terms. This diagram shows all variables for one particular compartment H_k of a total system H. The compartment H_k has a state variable x_k: the entropy content of H_k. The entropy $z_8 k_o$ is flowing into H_k from the environment (the outside of H) and the entropy y_{ok} is flowing out from H_k to the environment. The variables f_{kj} and f_{ik} are entropy flows from H_j to H_k and from H_k to H_i, respectively. The entropy production in H_k is represented by s_k. The variables $(\dot{x}_k)_+$ and $(\dot{x}_k)_-$ are the increasing and decaying entropy contents of H_k, which are treated as outflow and inflow, respectively.

where $Z = \Sigma_{k=1}^n z_{ko}$ is the total entropy inflow into H; $S = \Sigma_{k=1}^n s_k$ is the total entropy production in H; $\dot{X}_- = \Sigma_{k=1}^n (\dot{x}_k)_-$ is the total decaying storage of entropy in H; $Y = \Sigma_{k=1}^n y_{ok}$ is the total entropy outflow from H; and $\dot{X}_+ = \Sigma_{k=1}^n (\dot{x}_k)_+$ is the total increasing storage of entropy in H.

Following in this paper we only consider the steady state in entropy, in which x_k is constant with time and $\dot{x}_k = (\dot{x}_k)_+ = (\dot{x}_k)_- = 0$. Then, equation (4) is reduced to:

$$T_k = \sum_{j=1}^{n} f_{kj} + z_{ko} + s_k$$
$$= \sum_{i=1}^{n} f_{ik} + y_{ok} \tag{9}$$

and equation (8) to:

$$Z + S = Y \tag{10}$$

ENTROPY STRUCTURE MATRIX

Let the ratio of f_{ik} to T_i be denoted as $q_{ik}^* : f_{ik} = q_{ik}^* T_i$. The second equation of (9) is expressed as:

$$T_k = \sum_{i=1}^{n} q_{ik}^* T_i + y_{ok} \tag{11}$$

or in a matrix form:

$$T^{\mathrm{t}} = T^{\mathrm{t}}Q^* + y^{\mathrm{t}} \tag{12}$$

where $T^{\mathrm{t}} = [T_1 \quad T_2 \quad \cdots \quad T_n]$, $Q^* = [q^*_{ij}]$ and $y^{\mathrm{t}} = [y_{\mathrm{o}1} \quad y_{\mathrm{o}2} \quad \cdots \quad y_{\mathrm{o}n}]$. By solving equation (12) for T, we obtain:

$$T^{\mathrm{t}} = y^{\mathrm{t}}[\mathrm{I} - Q^*]^{-1} = y^{\mathrm{t}}N^*$$

or

$$T_k = \sum_{j=1}^{n} y_{\mathrm{o}j} n^*_{jk} \tag{13}$$

where

$$N^* = \left[n^*_{ij}\right] = [\mathrm{I} - Q^*]^{-1}$$

When $y_{\mathrm{o}j} = \delta_{jl}$, $T_k = n^*_{lk}$. That is, n^*_{lk} is interpreted as the entropy throughflow at H_k when the entropy outflow from H is only $y_{\mathrm{o}l} = 1$ unit. Since throughflow is non-negative, an inequality should hold:

$$n^*_{lk} \geq 0 \tag{14}$$

Similarly, let the ratio of f_{kj} to T_j be denoted as $q^{**}_{kj} : f_{kj} = q^{**}_{kj} T_j$. The first equation of (9) is expressed as:

$$T_k = \sum_{j=1}^{n} q^{**}_{kj} T_j + z_{k\mathrm{o}} + s_k \tag{15}$$

or in a matrix form:

$$T = Q^{**}T + z + s \tag{16}$$

where

$$T = \begin{bmatrix} T_1 \\ \vdots \\ T_n \end{bmatrix}, \quad z = \begin{bmatrix} z_{10} \\ \vdots \\ z_{n\mathrm{o}} \end{bmatrix}, \quad s = \begin{bmatrix} s_1 \\ \vdots \\ s_n \end{bmatrix}$$

and

$$Q^{**} = \left[q^{**}_{ij}\right]$$

Solving for T gives:

$$T = [\mathrm{I} - Q^{**}]^{-1}(z + s) = N^{**}(z + s)$$

or

$$T_k = \sum_{j=1}^{n} n^{**}_{kj}(z_{j\mathrm{o}} + s_j) = T_k^{(Z)} + T_k^{(S)} \tag{17}$$

where

$$N^{**} = [n_{ij}^{**}] = [I - Q^{**}]^{-1}$$

$$T_k^{(Z)} = \sum_{j=1}^{n} n_{kj}^{**} z_{jo}$$

and

$$T_k^{(S)} = \sum_{j=1}^{n} n_{kj}^{**} s_j$$

$T_k^{(Z)}$ is entropy throughflow at H_k due to entropy inflow only, and $T_k^{(S)}$ is entropy throughflow at H_k due to entropy production only. When $z_{jo} + s_j = \delta_{jl}$, $T_k = n_{kl}^{**}$. That is, n_{kl}^{**} is interpreted as the entropy throughflow at H_k due to 1 unit of entropy injection at the compartment H_l. Since throughflow should be non-negative, we have:

$$n_{kl}^{**} \geq 0 \tag{18}$$

The matrix N^* or N^{**} is the structure matrix (Hannon, 1973) or the fundamental matrix (Kemeny and Snell, 1976) or the transitive closure matrix (Patten et al., 1976) in entropy version.

The total system throughflow in entropy version TST is expressed as:

$$\text{TST} = \sum_{k=1}^{n} T_k = \text{TST}^{(Z)} + \text{TST}^{(S)} \tag{19}$$

where

$$\text{TST}^{(Z)} = \sum_{k=1}^{n} T_k^{(Z)} = \sum_{k=1}^{n} \sum_{j=1}^{n} n_{kj}^{**} z_{jo}$$

and

$$\text{TST}^{(S)} = \sum_{k=1}^{n} T_k^{(S)} = \sum_{k=1}^{n} \sum_{j=1}^{n} n_{kj}^{**} s_j$$

SECOND LAW OF THERMODYNAMICS

The Second Law of Thermodynamics claims that entropy production is non-negative; it is positive when the processes are irreversible and is zero when the processes are reversible. If processes occurring in all the compartments are reversible, then $s_j = 0$ for all j and the entropy throughflow T_k at H_k becomes $T_k(\text{rev}) = \sum_{j=1}^{n} n_{kj}^{**} z_{jo}$, which is smaller than the entropy throughflow when the processes are irreversible ($s_j \neq 0$): $T_k(\text{irrev}) = \sum_{j=1}^{n} n_{kj}^{**}(z_{jo} + s_j)$. That is,

$$T_k(\text{irrev}) > T_k(\text{rev}) \tag{20}$$

Thus, when processes occurring in all compartments are irreversible, the entropy throughflow is always larger than that which would be if all the compartments are in reversible processes.

Also for TST, we obtain:

$$\text{TST}(\text{irrev}) > \text{TST}(\text{rev}) \tag{21}$$

where

$$\text{TST}(\text{irrev}) = \sum_{k=1}^{n} T_k(\text{irrev}) = \text{TST}^{(Z)} + \text{TST}^{(S)}$$

and

$$\text{TST}(\text{rev}) = \sum_{k=1}^{n} T_k(\text{rev}) = \text{TST}^{(Z)}$$

The quantity $\text{TST}^{(S)}$ is a measure of irreversibility of the system H. An index $\eta = \text{TST}^{(S)}/\text{TST}$ may be called an irreversibility index showing the extent or the magnitude of irreversibility in the system H. If all compartments are reversible, then $\text{TST}^{(S)} = 0$ and $\eta = 0$.

From equations (17) and (19) it is also clear that the throughflow and the total system throughflow in entropy version become larger as the extent of irreversibility of each compartment of the system is enhanced or, equivalently, as entropy production is increased.

Since all motions and reactions actually occurring in nature are irreversible, irreversibility is also a measure of the extent of violence of processes in nature. Let the extent of violence of processes be called 'activity', which consists of physical activity (associated with heat flow and mass transportation) and chemical activity (associated with chemical reaction). Since irreversibility is a measure of activity as stated above, the word 'irreversibility' can be replaced by 'activity', e.g., the throughflow and the total system throughflow in entropy version become larger as the activity of compartments is enhanced.

In summary, the throughflow and the total system throughflow in entropy version in irreversible processes are always larger than those in reversible processes, and irreversibility–activity of the system induces the increase of the throughflow and the total system throughflow in entropy version. This is a statement of the Second Law of Thermodynamics applied to ecological networks at steady state. It is stated in the terms of the network theory: throughflow and total system throughflow.

Outflow path length $\overline{\text{YPL}}$ in entropy version is the average number of compartments that an average outflow of entropy has passed through (similar to the case of energy and matter), as given by (Patten et al., 1976)

$$\overline{\text{YPL}} = \frac{\text{TST}}{Y} \tag{22}$$

Similarly, inflow path length in entropy version is the average number of compartments that an average inflow of entropy plus an average entropy production will pass through, expressed as:

$$\overline{(ZS)\text{PL}} = \frac{\text{TST}}{Z+S} \tag{23}$$

as easily shown by similar methods described by Patten et al. (1976) (the only difference in derivation is that $z_{k\text{o}}$ is replaced to $z_{k\text{o}} + s_k$). From equation (10):

$$\frac{\text{TST}}{Y} = \frac{\text{TST}}{Z+S} = \frac{\text{TST}^{(Z)} + \text{TST}^{(S)}}{Z+S} \equiv \overline{\text{PL}} \tag{24}$$

which we simply call the entropy path length of the system H.

When processes in all compartments are reversible, $S = 0$, $\text{TST}^{(S)} = 0$, and the entropy path length becomes:

$$\overline{\text{PL}(\text{rev})} = \frac{\text{TST}^{(Z)}}{Z} \tag{25}$$

Entropy path length when processes are irreversible is denoted as $\overline{\text{PL}(\text{irrev})}$, which is given by (24).

Let us introduce two more path lengths here: those due to entropy production and due to entropy inflow. Path length due to entropy production is defined as:

$$\overline{\text{PL}^{(S)}} = \sum_{k=1}^{n} \frac{s_k}{\sum_i s_i} \sum_{j=1}^{n} n_{jk}^{**}$$

$$= \frac{\text{TST}^{(S)}}{S} \tag{26}$$

which is the average number of compartments that an average entropy production will pass through. Also, path length due to entropy inflow is defined as:

$$\overline{\text{PL}^{(Z)}} = \sum_{k=1}^{n} \frac{z_{k\text{o}}}{\sum_i z_{i\text{o}}} \sum_{j=1}^{n} n_{jk}^{**}$$

$$= \frac{\text{TST}^{(Z)}}{Z} \tag{27}$$

which is the average number of compartments that an average entropy inflow will pass through.

If $\overline{\mathrm{PL}^{(S)}} = \overline{\mathrm{PL}^{(Z)}}$, i.e., $\mathrm{TST}^{(S)}/S = \mathrm{TST}^{(Z)}/Z$, then $(\mathrm{TST}^{(Z)} + \mathrm{TST}^{(S)})/(Z+S) = \mathrm{TST}^{(Z)}/Z$, that is:

$$\overline{\mathrm{PL(irrev)}} = \overline{\mathrm{PL(rev)}} \tag{28}$$

Likewise, if $\overline{\mathrm{PL}^{(S)}} \gtrless \overline{\mathrm{PL}^{(Z)}}$, i.e., $\mathrm{TST}^{(S)}/S \gtrless \mathrm{TST}^{(Z)}/Z$, then $(\mathrm{TST}^{(Z)} + \mathrm{TST}^{(S)})/(Z+S) \gtrless \mathrm{TST}^{(Z)}/Z$, that is:

$$\overline{\mathrm{PL(irrev)}} \gtrless \overline{\mathrm{PL(rev)}} \tag{29}$$

Thus, the relations:

$$\overline{\mathrm{PL(irrev)}} \gtreqless \overline{\mathrm{PL(rev)}} \tag{30}$$

hold paralleling to the following relations:

$$\overline{\mathrm{PL}^{(S)}} \gtreqless \overline{\mathrm{PL}^{(Z)}} \tag{31}$$

That is to say, the entropy path length for irreversible processes is equal to (or larger or smaller than) the entropy path length that would be if processes were reversible when the path length due to entropy production is equal to (or larger or smaller than) the path length due to entropy inflow.In general, increase of irreversibility-activity of the system induces any change of entropy path length (increase or decrease or unchanged) depending upon the structure of ecological networks we consider. Simple examples are given below:

Example 1 (Fig. 2a). $T_j = 0.9T_i$, $T_k = 0.7T_j = 0.63T_i$, $T_l = 0.1T_i$, $\mathrm{TST} = 2.63T_i$, $Z + S = z_{io} + s_i = T_i$. Hence, $\overline{\mathrm{PL}} = 2.63$ is independent of T_i. Even if the entropy production s_i in the compartment H_i is changed and hence T_i is changed, $\overline{\mathrm{PL}}$ is kept constant irrespective of any change of s_i.

Example 2 (Fig. 2b). $T_j = 0.1T_i + T_n$, $T_k = 0.4T_j = 0.04T_i + 0.4T_n$, $T_l = 0.3T_k = 0.012T_i + 0.12T_n$, $T_m = 0.9T_i$, $\mathrm{TST} = 2.052T_i + 2.52T_n$; $Z + S = z_{io} + z_{no} + s_i = T_i + T_n$. Hence, $\overline{\mathrm{PL}} = (2.052T_i + 2.52T_n)/(T_i + T_n)$. When $T_i = T_n = 1$ unit, $\overline{\mathrm{PL}}$ is 2.29. If the entropy production in H_i increases and T_i becomes 1.2 unit, then $\overline{\mathrm{PL}} = 2.26$. That is, $\overline{\mathrm{PL}}$ decreases as the entropy production in H_i increases.

Example 3 (Fig. 2c). Similarly as above, $\mathrm{TST} = 3.296T_i + 2.144T_n$ and $Z + S = T_i + T_n$. Hence, $\overline{\mathrm{PL}} = (3.296T_i + 2.144T_n)/(T_i + T_n)$. When $T_i = T_n = 1$ unit, $\overline{\mathrm{PL}}$ is 2.72. If the entropy production in H_i increases and T_i becomes 1.2 unit, then $\overline{\mathrm{PL}} = 2.77$. Thus, $\overline{\mathrm{PL}}$ increases as the entropy production in H_i increases.

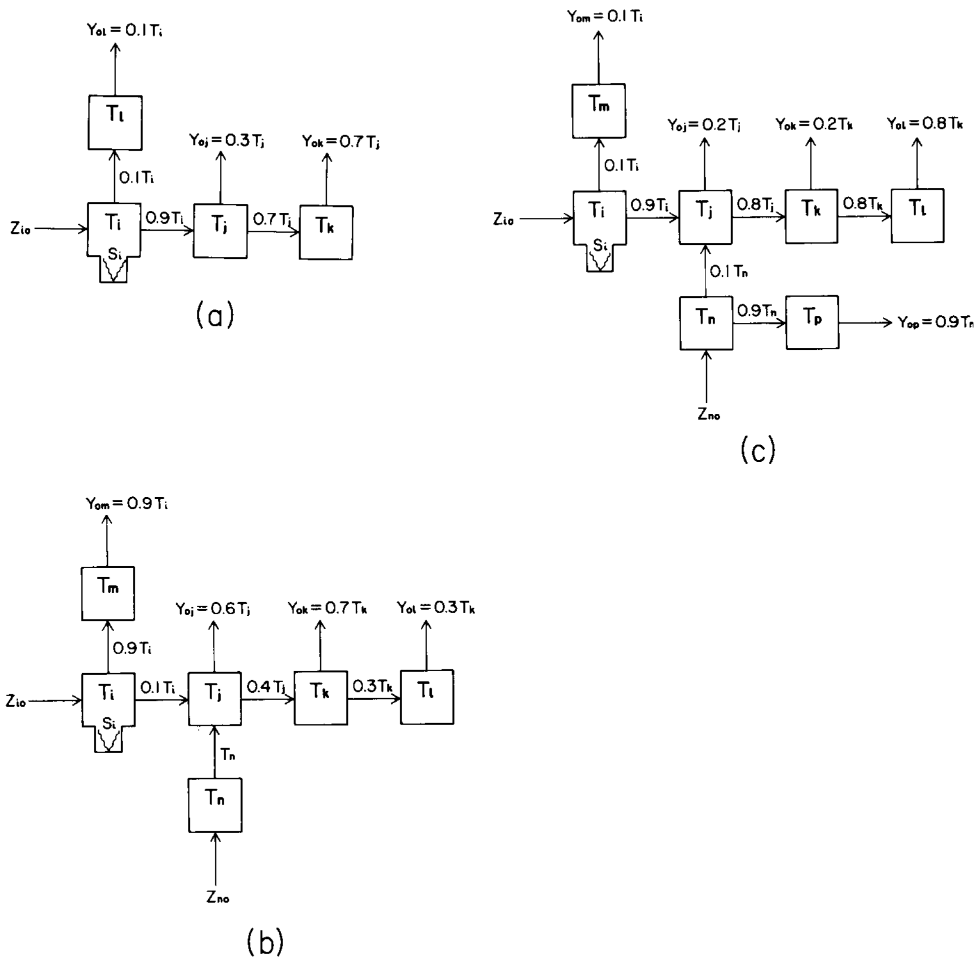

Fig. 2. Hypothetical networks for calculation of entropy path length. T_i is the entropy throughflow at the compartment H_i, which is placed in the symbol for H_i, and so on. Arrow lines represent entropy flows. Processes in H_i are irreversible and the others are reversible. The entropy production in H_i is denoted as s_i.

ENTROPY CYCLING INDEX

As in the case of energy and matter, entropy cycling efficiency at the compartment H_k is defined as the fraction of entropy throughflow T_k that returns to H_k and, as given by Finn (1978):

$$\mathrm{RE}_k = 1 - \frac{1}{n_{kk}^{**}} \tag{32}$$

The cycled portion of total system throughflow in entropy version is expressed as:

$$\mathrm{TST_c} = \sum_{k=1}^{n} \mathrm{RE}_k \, T_k = \sum_{k=1}^{n} \mathrm{RE}_k \left(T_k^{(Z)} + T_k^{(S)} \right)$$
$$= \mathrm{TST_c^{(Z)}} + \mathrm{TST_c^{(S)}} \tag{33}$$

where $\mathrm{TST_c^{(Z)}} = \sum_{k=1}^{n} \mathrm{RE}_k \, T_k^{(Z)}$ and $\mathrm{TST_c^{(S)}} = \sum_{k=1}^{n} \mathrm{RE}_k \, T_k^{(S)}$. The entropy cycling index is the fraction of the total system throughflow in entropy version that is cycled and, as given by Finn (1978):

$$\mathrm{CI} = \frac{\mathrm{TST_c}}{\mathrm{TST}} = \frac{\mathrm{TST_c^{(Z)}} + \mathrm{TST_c^{(S)}}}{\mathrm{TST^{(Z)}} + \mathrm{TST^{(S)}}} \tag{34}$$

When processes in all compartments are reversible, $\mathrm{TST_c^{(S)}} = 0$, $\mathrm{TST^{(S)}} = 0$ and:

$$\mathrm{CI(rev)} = \frac{\mathrm{TST_c^{(Z)}}}{\mathrm{TST^{(Z)}}} \tag{35}$$

Entropy cycling index when processes are irreversible is denoted as CI(irrev), which is given by (34).

Let us introduce two more cycling indices: cycling index due to entropy production:

$$\mathrm{CI^{(S)}} = \frac{\mathrm{TST_c^{(S)}}}{\mathrm{TST^{(S)}}} \tag{36}$$

and cycling index due to entropy inflow:

$$\mathrm{CI^{(Z)}} = \frac{\mathrm{TST_c^{(Z)}}}{\mathrm{TST^{(Z)}}} \tag{37}$$

$\mathrm{CI^{(S)}}$ is the entropy cycling index that would be if there is no entropy inflow in the system, and $\mathrm{CI^{(Z)}}$ is the entropy cycling index that would be if there is no entropy production in the system.

If $\mathrm{CI^{(S)}} = \mathrm{CI^{(Z)}}$, i.e., $\mathrm{TST_c^{(S)}}/\mathrm{TST^{(S)}} = \mathrm{TST_c^{(Z)}}/\mathrm{TST^{(Z)}}$, then $(\mathrm{TST_c^{(S)}} + \mathrm{TST_c^{(Z)}})/(\mathrm{TST^{(S)}} + \mathrm{TST^{(Z)}}) = \mathrm{TST_c^{(Z)}}/\mathrm{TST^{(Z)}}$, i.e.

$$\mathrm{CI(irrev)} = \mathrm{CI(rev)} \tag{38}$$

If $\mathrm{CI^{(S)}} \gtrless \mathrm{CI^{(Z)}}$, i.e., $\mathrm{TST_c^{(S)}}/\mathrm{TST^{(S)}} \gtrless \mathrm{TST_c^{(Z)}}/\mathrm{TST^{(Z)}}$, then $(\mathrm{TST_c^{(S)}} + \mathrm{TST_c^{(Z)}})/(\mathrm{TST^{(S)}} + \mathrm{TST^{(Z)}}) \gtrless \mathrm{TST_c^{(Z)}}/\mathrm{TST^{(Z)}}$, i.e.

$$\mathrm{CI(irrev)} \gtrless \mathrm{CI(rev)} \tag{39}$$

That is, the relations:

$$\mathrm{CI(irrev)} \gtreqless \mathrm{CI(rev)} \tag{40}$$

hold paralleling to the following relations:

$$\mathrm{CI}^{(S)} \gtreqqless \mathrm{CI}^{(Z)} \tag{41}$$

Thus, the entropy cycling index for irreversible processes is equal to (or larger or smaller than) the entropy cycling index that would be if processes were reversible when the cycling index due to entropy production is equal to (or larger or smaller than) the cycling index due to entropy inflow.

In general, increase of irreversibility-activity of the system induces any change of entropy cycling index (increase or decrease or unchanged) depending upon the structure of ecological networks we consider. Simple examples are given in the following:

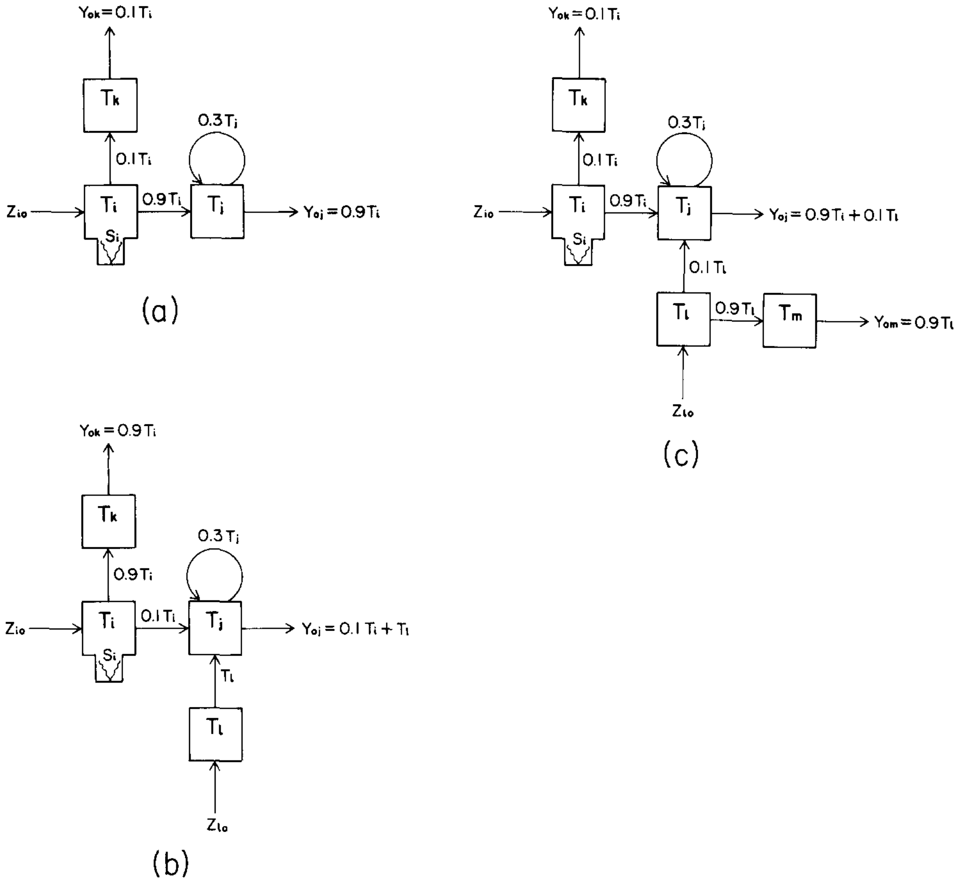

Fig. 3. Hypothetical networks for calculation of entropy cycling index. T_i is the entropy throughflow at the compartment H_i, which is placed in the symbol for H_i, and so on. Arrow lines represent entropy flows. Processes in H_i are irreversible and the others are reversible. The entropy production in H_i is denoted as s_i.

Example 4 (Fig. 3a). $T_j = 0.9T_i + 0.3T_j = 1.286T_i$, $T_k = 0.1T_i$, $\text{TST} = 2.386T_i$, $\text{RE}_j = 0.3$, $\text{TST}_c = \text{RE}_j\ T_j = 0.386T_i$. Hence, $\text{CI} = 0.386T_i/2.386T_i = 0.162$. Thus, CI is independent of T_i. Even if the entropy production s_i in the compartment H_i is changed and hence T_i is changed, CI is kept constant.

Example 5 (Fig. 3b). $T_j = 0.1T_i + 0.3T_j + T_l = 0.143T_i + 1.429T_l$, $T_k = 0.9T_i$, $\text{TST} = 2.043T_i + 2.429T_l$, $\text{RE}_j = 0.3$, $\text{TST}_c = \text{RE}_j\ T_j = 0.0429T_i + 0.429T_l$. Hence, $\text{CI} = (0.0429T_i + 0.429T_l)/(2.043T_i + 2.429T_l)$. When $T_i = T_l = 1$ unit, $\text{CI} = 0.106$. If the entropy production in H_i increases and T_i becomes 1.2 unit, then $\text{CI} = 0.098$. That is, CI decreases as the entropy production in H_i increases.

Example 6 (Fig. 3c). $T_j = 0.9T_i + 0.3T_j + 0.1T_l = 1.286T_i + 0.143T_l$, $T_k = 0.1T_i$, $T_m = 0.9T_l$, $\text{TST} = 2.386T_i + 2.043T_l$, $\text{TST}_c = 0.3T_j = 0.386T_i + 0.043T_l$. Hence, $\text{CI} = (0.386T_i + 0.043T_l)/(2.386T_i + 2.043T_l)$. When $T_i = T_l = 1$ unit, $\text{CI} = 0.097$. If the entropy production in H_i increases and T_i becomes 1.2 unit, then $\text{CI} = 0.103$. Thus, CI increases as the entropy production in H_i increases.

DISCUSSION

As seen above, no assumptions and no approximations are made in our discussion, in which the thermodynamical entropy concept is applied to the flow analysis of ecological networks at steady state. As to the thermodynamical side, the only use is the non-negativity of entropy production, which is just what the Second Law claims (e.g., Nicolis and Prigogine, 1977). As to input–output flow analysis, we have used the 'conventional' theory, which has an origin in economics (Leontief, 1966), applied to ecology by Hannon (1973) and developed by Finn (1976, 1978), Patten et al. (1976) and others – it is a well-established theory. Recently, the input–output flow analysis has been extended, and 'inclusive' throughflow is introduced as a concept that includes both flow and storage (Matis and Patten, 1981; Patten and Higashi, 1984). However, we confine ourselves, for the moment, for the sake of simplicity and clarity, to the use of the conventional input–output flow analysis.

This paper has dealt only with a steady state in entropy (the entropy content of each compartment is kept constant). Dynamical theory of input–output flow analysis has not been fully developed yet, although some progress has been made by Hippe (1983). Application of the entropy concept to the dynamical theory may produce some more new results on entropy laws in ecological networks.

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