Imbalance and Balancing: Development of Ecological Flow Networks

Taichi Haruna [a,*], Yukio-Pegio Gunji [a]

[a] Department of Earth & Planetary Sciences, Faculty of Science, Kobe University
1-1, Rokkodai-cho, Nada, Kobe 657-8501, JAPAN
*Corresponding author. Tel.: +81 78 803 5739; Fax: +81 78 803 5739.
E-mail: tharuna@penguin.kobe-u.ac.jp (T. Haruna).

Abstract

In this paper we address balancing process of ecological flow networks. In existing approaches, macroscopic objectives to which systems organize are assumed. Flow balance provides only constraints for the optimization. Since flow balance and objectives are separated from each other, it is impossible to address how the appearance of objectives is related to flow balance. Therefore we take an alternative approach, in which we directly describe a dynamics of balancing process. We propose a simple mathematical formula for local balancing dynamics and show that it can generate a self-organizing property, which could be seen as a primitive objective.

keywords: ecosystem, imbalance, balancing, objective

1 Introduction

Ecosystems consist of complex networks of energy, materials and services. Various macroscopic indices have been proposed in order to understand complex ecological networks as a whole (Washida, 1995; Salthe, 2005). They can be roughly classified as follows: indices emphasizing productions in ecosystems (Lotka, 1922; Odum and Pinkerton, 1955; Jørgensen and Mejer, 1979), indices emphasizing dissipations in ecosystems (Sweanson, 1989; Schneider, 1994; Aoki, 1998), and indices emphasizing activities of biological communities and their interrelationships (Ulanowicz, 1980; Washida, 1995). They are different in details and have advantages respectively, however, they all assume that macroscopic objectives to which systems self-organize. In recent years, similar attempts emerges in understanding biological networks inside an organism such as metabolic or gene transcription regulation networks (Beard *et al.*, 2002; Ibarra *et al.*, 2002; Kauffman *et al.*, 2003). As in ecology, they assume macroscopic objectives that are to be maximized or minimized.

The idea that biological systems self-organize toward macroscopic objectives may be useful for systems once established. Indeed, flux balance analysis (F-BA) theory makes good predictions on experiments if one can set appropriate objectives (Kauffman *et al.*, 2003). However, appearances of macroscopic objectives cannot be addressed if one assumes them in advance. In order to discuss how macroscopic objectives could emerge we focus on an assumption that the macroscopic objective approach makes. The macroscopic objective approach assumes that a balance between incoming flows to a system and outgoing flows from the system. The flow balance defines constraints under which a macroscopic objective is optimized. The balance and the objective are separated from each other. Here the flow balance is expressed as merely a set of equations that lack the ability of balancing, which can locally regulate flows toward a balance. Macroscopic objectives are introduced in order to compensate for the lack of balancing ability. As an alternative to the macroscopic objective approach, we directly describe the local balancing dynamics by a simple mathematical expression. This alternative approach admits imbalances between incoming and outgoing flows. In this paper we will discuss a possibility that accumulations of imbalances generate a developmental direction of ecological flow networks.

This paper is organized as follows. In section 2, we introduce the notion of balancing. In section 3, we present a mathematical formulation of balancing process. In section 4, we give two examples of balancing process. In section 5, we show balancing process can result in a self-organizing property by computer simulation. In section 6, we analyze the mechanism of balancing. Finally, in section 7, we give conclusions.

2 From Balance to Balancing

The macroscopic objective approach assumes a balance in flows. For example, the sum of incoming flows to a system must be equal to the sum of outgoing flows from the system for each chemical species. Without this assumption, one may not able to find maximal or minimal points of a macroscopic objective since the domain of the objective function is indefinite. This assumption might be plausible for biological systems that can exist persistently. The intuition that this assumption is plausible might come from the imagination that flow balances are self-regulated as a whole at every moment in persistently existing biological systems. However, if this image is described by mathematics then it becomes merely a set of equations. The image of self-regulation at every moment is killed. Macroscopic objectives are introduced in order to compensate for the lack of the image of self-regulation at every moment. Here the image of self-regulation toward a balance as a whole is separated into two parts, balance equations and an objective function.

Since such a way of description assumes a macroscopic objective in advance, we cannot address a question about how macroscopic objectives could appear. An approach that could get in this question is simply describing the image of self-regulation of flows toward a balance. In this approach we admit the existence of an imbalance between incoming and outgoing flows at each node of a flow network (Matsuno, 1989). Flows in a network regulate their size in order to eliminate the imbalances. We call this process *balancing*. However, if balancing works only a local manner then imbalances might be never eliminated. The balancing process would persist indefinitely. We consider the possibility that a local balancing process could induce development of flow networks toward organization. In the next section we introduce a mathematical formulation of this idea.

Imbalance can be seen as a local orientating function of ecosystems, which is not a macroscopic objective but specifies only direction of change of each flow. The idea of orientating function is due to Ulanowicz (1997). At first he propose a quantity called ascendency (which will be reviewed in section 5) as a macroscopic objective of ecosystems (Ulanowicz, 1980; Ulanowicz, 1986). However, he later turned to ascendency as an orientating function of ecosystem, not an objective. This probably arises from internal perspective since ecosystems themselves would never know the global optimums. We enforce the direction of Ulanowicz by focusing on locality (Matsuno, 1989; Salthe, 1993).

We can compare our approach with the existing approach as follows.

Existing Approach Balance+Objective.

Our Approach Balancing.

The same idea as balancing here is proposed in the study of animal learning behaviors such as sexual imprinting and discrimination learning of mimicry (Lynn, 2005; Lynn, 2006; ten Cate *et al.*, 2006; ten Cate and Rowe, 2007). We briefly explain them as an auxiliary line of understanding. Peak shift is known as the following phenomenon. When animals are trained to discriminate between a positively rewarded stimulus (S+) and a negatively or neutrally rewarded stimulus (S-), we might expect that their responses to novel stimuli are the strongest around the training stimuli. In peak shift, however, animals' responses to novel stimuli are stronger away from the S+ in a direction opposite from the S-, and vice versa.

The research group of ten Cate treats sexual imprinting of male children of a zebra finch (ten Cate *et al.*, 2006). Male children are raised by parents that are sexually dimorphic, different in only beak color. Beaks of fathers in the first experimental group are colored red and that of mothers are colored orange. In the second group, the reverse coloring is done. It is known that when a male raised in this way becomes an adult he prefers females with orange beaks if he belongs to the first group. On the other hand, if he belongs to the second group then he prefers females with red beaks. Thus the beak color of mothers works as S+ and that of fathers works as S-. In the experiment of ten Cate *et al.* (2006), the males can choose their mates from eight females whose beaks are colored in different eight stages from more intense red to more yellow orange including two beak colors (i.e. red and orange) of their parents. Males in the first group tend to choose females with more extreme red than their mother on one hand, males in the second group prefer females with more yellow orange than their mother

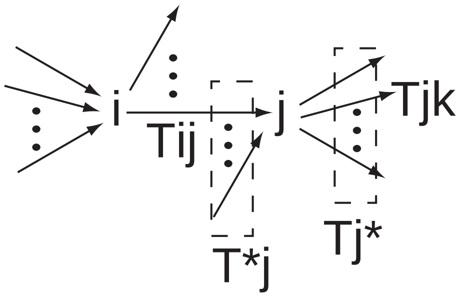

Figure 1: Imbalance of flow $i \to j$ at node j.

on the other hand. In the other articles, the possibility that peak shifts lead to species discrimination is discussed (Lynn, 2006; ten Cate and Rowe, 2007).

In general learning is aimed to an acquisition of a specific performance. However, the experiment of ten Cate *et al.* (2006) shows that if males try to learn a performance of choosing females with a specific color then the performance itself shifts as a result. This implies that there are biases in males' cognitions. It suggests that an accumulation of the biases in animal cognitions could cause species discrimination.

3 Imbalance and Balancing in Flow Networks

Let an ecosystem consist of N nodes (taxa). Let T_{ij} be the size of flow from node i to node j for $1 \leq i, j \leq N$. Total throughput in the system is defined by $T = \sum_{i,j} T_{ij}$. The sum of incoming flows to node i is denoted by $T_{*i} = \sum_k T_{ki}$ and the sum of outgoing flows from node i is denoted by $T_{i*} = \sum_k T_{ik}$. The flow balance at node i is defined by

$$T_{*i} = T_{i*}.$$

As mentioned in section 2, we do not assume flow balance in advance and admit imbalances (Matsuno, 1995). Instead of flow balance condition we assume balancing process at each flow. Each flow in a flow network detects an imbalance locally and changes its size in the direction that decreases the imbalance detected.

The definition of imbalance δ_{ij} for flow $i \to j$ is as follows. One of the simplest way is to define imbalance at each node as the difference between the sum of incoming flows and the sum of outgoing flows. In this definition imbalance is defined associated with a node. However, we would like to define imbalance associated with a flow. This is done by considering how an incoming flow to a node is distributed between outgoing flows from the node and how an outgoing flow from a node is contributed by incoming flows to the node. This consideration can be seen as a generalization of an operation called "decomposition into function" in Haruna and Gunji (2007).

Let us focus on node j (Figure 1). The amount of flow from $i \to j$ to $j \to k$ will be

$$T_{ij} \times \frac{T_{jk}}{T_{j*}}$$

if how obtained materials are utilized is irrelevant to their sources at node j. On the other hand, the contribution of $i \to j$ to T_{jk} will be

$$T_{jk} \times \frac{T_{ij}}{T_{*j}}$$

under the same assumption. Obviously if flow balance is satisfied at node j then these two quantities are equal. So we make use of the absolute value of the difference between them in order to define imbalance associated with a flow. Consider the summation with respect to k :

$$\sum_k T_{ij}T_{jk}|\frac{1}{T_{j*}} - \frac{1}{T_{*j}}| = T_{ij}T_{j*}|\frac{1}{T_{j*}} - \frac{1}{T_{*j}}| = T_{ij}|1 - \frac{T_{j*}}{T_{*j}}|.$$

Moreover we consider imbalance per unit flow by dividing this quantity by T_{ij} :

$$|1 - \frac{T_{j*}}{T_{*j}}|.$$

If we focus on node i then we obtain a quantity

$$|1 - \frac{T_{*i}}{T_{i*}}|$$

by the same manner. Let $0 \leq \alpha \leq 1$ be contribution rate of node i. We define an imbalance associated with flow $i \to j$ by

$$\delta_{ij} = \alpha|1 - \frac{T_{*i}}{T_{i*}}| + (1-\alpha)|1 - \frac{T_{j*}}{T_{*j}}|.$$

Balancing process is defined so that each flow changes its size in the direction in which the imbalance associated with it decreases. That is, if the partial differential with respect to T_{ij}

$$\frac{\partial \delta_{ij}}{\partial T_{ij}} = \mathrm{sgn}(T_{i*} - T_{*i})\alpha\frac{T_{*i}}{T_{i*}^2} + \mathrm{sgn}(T_{*j} - T_{j*})(1-\alpha)\frac{T_{j*}}{T_{*j}^2}$$

is negative then the flow increases and if the partial differential is positive then the flow decreases, where $\mathrm{sgn}(x) = +1 (x > 0), \mathrm{sgn}(x) = -1 (x < 0)$. At present we do not specify precise functional form of flow change but only specify the direction of flow change.

In the next section we analyze two examples by using the above formulation.

4 Examples

The first example is from economics. Let us denote the size of material flow from resources to manufacturers by f_0, from manufacturers to merchants by f_1 and from merchants to consumers by f_2.

$$\text{resources} \xrightarrow{f_0} \text{manufacturers} \xrightarrow{f_1} \text{merchants} \xrightarrow{f_2} \text{consumers}$$

We focus on the flow f_1 from manufacturers to merchants. The imbalance associated with this flow and its partial differential with respect to f_1 are

$$\begin{aligned} \delta_1 &= \alpha|1 - \frac{f_0}{f_1}| + (1-\alpha)|1 - \frac{f_2}{f_1}|, \\ \frac{\partial \delta_1}{\partial f_1} &= \operatorname{sgn}(f_1 - f_0)\alpha\frac{f_0}{f_1^2} + \operatorname{sgn}(f_1 - f_2)(1-\alpha)\frac{f_2}{f_1^2}. \end{aligned}$$

If $f_1 < f_0, f_2$ then $\operatorname{sgn}(f_1 - f_0) = \operatorname{sgn}(f_1 - f_2) = -1$. Since $\partial\delta_1/\partial f_1 < 0$ for any α, f_1 increases by balancing process independent of α. This could be interpreted as follows. If outgoing flow is greater than incoming flow at merchants then they try to increase incoming flow in order to sell more and at the same time if outgoing flow is less than incoming flow at manufacturers then they try to increase outgoing flow in order to decrease stocks.

If $f_1 > f_0, f_2$ then $\operatorname{sgn}(f_1 - f_0) = \operatorname{sgn}(f_1 - f_2) = +1$. In this case we have $\partial\delta_1/\partial f_1 > 0$. Hence f_1 decreases independent of α. Since production and sales of commodities are restrected by both inflow of resources and amount of consumption, this case is also consistent with our intuition about economics.

Next we consider the case $f_0 < f_1 < f_2$. In this case whether f_1 increases or decreases is dependent on α. The condition in which

$$\frac{\partial \delta_1}{\partial f_1} = \frac{\alpha f_0 - (1-\alpha) f_2}{f_1^2}$$

is negative is

$$f_2 > \frac{\alpha}{1-\alpha} f_0.$$

If $\alpha \leq 1/2$ then this condition is always satisfied by the assumption $f_2 > f_0$ and hence f_1 increases. On the other hand, if $\alpha > 1/2$ then f_1 increases only if f_2/f_0 is greater than $\alpha/(1-\alpha)$, that is, f_0 is sufficiently smaller than f_2.

If $f_2 < f_1 < f_0$ then the condition in which

$$\frac{\partial \delta_1}{\partial f_1} = \frac{-\alpha f_0 + (1-\alpha) f_2}{f_1^2}$$

is negative is

$$f_2 < \frac{\alpha}{1-\alpha} f_0.$$

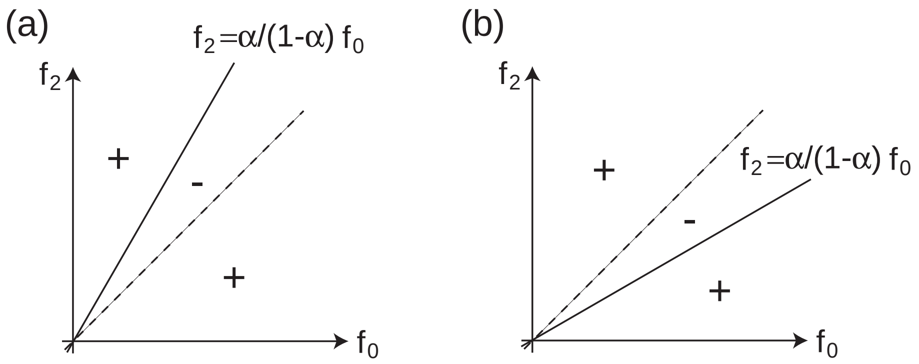

Figure 2: $\min\{f_0, f_2\} < f_1 < \max\{f_0, f_2\}$. + indicates the region in which f_1 increases and $-$ indicates the region in which f_1 decreases. (a)$\alpha > \frac{1}{2}$. (b)$\alpha < \frac{1}{2}$.

If $\alpha \geq 1/2$ then this is always true and hence f_1 increases. If $\alpha < 1/2$ then f_1 increases only if f_2/f_0 is smaller than $\alpha/(1-\alpha)$, that is, f_0 is sufficiently larger than f_2.

Figure 2 summarizes the case $\min\{f_0, f_2\} < f_1 < \max\{f_0, f_2\}$. First note that if $0 < \alpha < 1$ and sizes of f_0 and f_2 are chosen independently in the circle centered at the origin then the probability of increase of f_1 is greater than the probability of decrease. In particular, if $f_0 < f_1 < f_2$ then f_1 increases if f_2/f_0 is sufficiently large for given α. This would mean that manufacturers flow more commodities to merchants in order to fulfill the demand of consumers f_2. In this case f_0 must also increase in order manufacturers to survive. If the demand of consumers increases continually then the flow from resources to manufacturers must increase in order to respond to the demand. This would be possible in the knowledge based industries like software business in which one can expect increasing return, not in the resource based industries like heavy industries (Arthur, 1994). For small α, f_1 can increase easily. On the other hand, if α is large then the possibility of increase in f_1 decreases. Thus roughly it seems that small α corresponds to the knowledge based industries that can be pulled by the demand of consumers and large α corresponds to the resource based industries that are largely restricted by resources. Of course we cannot know all aspects of the economic system in terms of balancing process, however, we can see certain aspects through the proposed formulation.

Next example is a simple tritrophic ecosystem consisting of plants, herbivores and carnivores. We denote material flows between them as follows.

$$\text{environment} \xrightarrow{f_0} \text{plants} \xrightarrow{f_1} \text{herbivores} \xrightarrow{f_2} \text{carnivores}$$

In particular here we suppose a tritrophic ecosystem such as consisting of Lima bean, two-spotted spider mites and predatory mites in which plants emit volatiles that attract carnivores when herbivores eat plants (Shiojiri *et al.*, 2002;

Suzuki *et al.*, 2002). The conditions for increase or decrease in f_1 are the same as in the first example. Carnivores that catch herbivores are bodyguards for plants and carnivores can find their foods by volatiles emitted by plants that attract them. One question arises here. Is there any merit for herbivores in this system? It is known that plants do not emit volatiles that can attract carnivores by physical stimuli only. Plants attract carnivores only if they are subject to chemical stimuli originated from herbivores. Why do herbivores provide chemical stimuli to plants that attract carnivores (Shiojiri *et al.*, 2002)? On the other hand, Suzuki *et al.* (2002) shows that if there is interaction by volatiles then both the number of herbivores and carnivores can increase by computer simulation.

Let us answer the question in terms of balancing process. Since plants do not emit volatiles until the amount of chemical stimuli exceeds a certain level, we can assume that $f_0 < f_1$ when they begin to emit volatiles. On the other hand, since if carnivores begin to catch herbivores then the number of herbivores tends to decrease, we assume that $f_1 < f_2$. Hence the situation $f_0 < f_1 < f_2$ appears. In this case if f_2/f_0 is greater than a constant dependent on α then f_1 increases by balancing process. This could be a merit for herbivores. How is such a consequence possible in reality? We borrow an explanation by Suzuki *et al.* (2002). As mentioned above, there is a time-lag between start of eating by herbivores and emission of volatiles. Therefore a part of herbivores will be able to move to the other leaves before the arrival of carnivores. Such herbivores will make a new colony on the other leaves. Thus in some cases, the number of herbivores could increase.

From the above two examples, one can see that balancing process could have certain explanatory power. In the next section we present the result of computer simulation based on balancing process on more general flow networks and discuss how the distribution of flows develops.

5 Computer Simulation

In this section we discuss balancing process on more general flow networks. We prepare a random network with N nodes. We assume that the number of in-degree is the same as the number of out-degree for every node. We denote the number by m. We also assume that there is no self-loop in the random network. Such a setting is not realistic, however, the purpose of this section is to address the properties of balancing process. This setting is adopted in order to facilitate mathematical analysis. In the computer simulation below, $N = 30$ and $m = 10$. So the total number of flows is 300. Furthermore, we assume that $\alpha = 1/2$ in this section. The behaviors for different values of α is discussed in the next section. When $\alpha = 1/2$ we will show that the flow network has a self-organizing property in the following.

Time evolution of flows is defined by the following stochastic model. Let ϵ

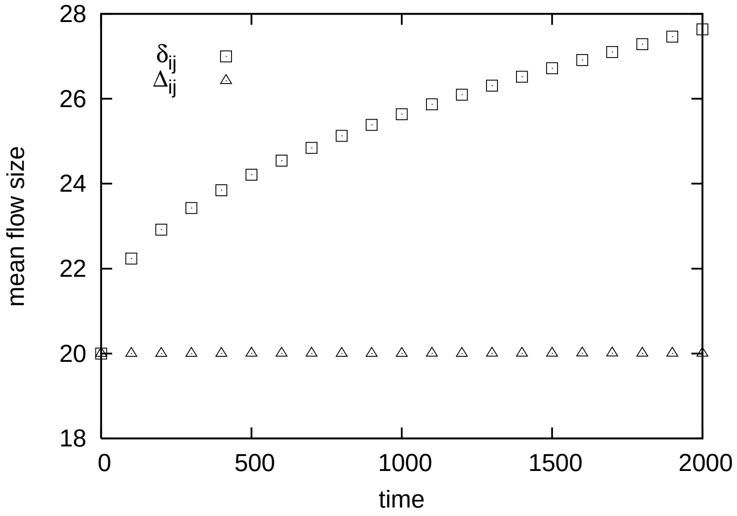

Figure 3: Time evolution of mean flow size.

be a uniform random number in $[0, 2\eta]$. We define

$$T_{ij}^{\tau+1} = \begin{cases} T_{ij}^{\tau} + \epsilon & (\frac{\partial \delta_{ij}^{\tau}}{\partial T_{ij}^{\tau}} < 0) \\ T_{ij}^{\tau} - \epsilon & (\frac{\partial \delta_{ij}^{\tau}}{\partial T_{ij}^{\tau}} > 0). \end{cases}$$

The suffix τ indicates quantities at τth period. As a control experiment, we also show results when imbalance is defined by

$$\Delta_{ij} = |T_{*i} - T_{i*}| + |T_{*j} - T_{j*}|.$$

Initial condition is given by a uniform distribution with mean 20 and width 0.1 in both cases. Moreover, $\eta = 0.1$ for both cases. Figure 3 shows time evolution of mean flow size. Each point is averaged over 1000 trials. Mean flow size increases when imbalance is given by δ_{ij}. In contrast, it does not increase in the case of Δ_{ij}.

Next we calculate ascendency of the system in order to measure degree of development of flow networks. Ascendency is first defined as a macroscopic objective of ecosystem organization, afterward re-defined as an orientating function (Ulanowicz, 1980; Ulanowicz, 1986; Ulanowicz, 1997). It is defined for a flow network by the multiplication of total throughput T and mutual information I of the network. Total throughput T is an index of growth of the system on one hand, mutual information I measures how the system is organized. The re-defined version of ascendency hypothesis says that “any ecosystem has a natural propensity to increase its ascendency if there is no significant perturbations from outside of the system" (Ulanowicz, 1997). Note that this statement is derived from empirical observations. From Figure 3, we already know that total throughput T increases by balancing process with δ_{ij}. Hence we focus on mutual information I in the following. Mutual information I to be defined here is average information gain between incoming flows and outgoing flows at each node. The *a priori* probability to find a flow $i \to j$ and its uncertainty are

$$\frac{T_{i*}}{T} \times \frac{T_{*j}}{T}, \; -\log \frac{T_{i*}T_{*j}}{T^2},$$

respectively. On the other hand, the emprical probability to find a flow $i \to j$ and its uncertainty are

$$\frac{T_{ij}}{T}, \; -\log \frac{T_{ij}}{T},$$

respectively. Therefore average information gain (mutual information) I is

$$\sum_{i,j} \frac{T_{ij}}{T}(-\log \frac{T_{i*}T_{*j}}{T^2} - (-\log \frac{T_{ij}}{T})) = \sum_{i,j} \frac{T_{ij}}{T} \log \frac{TT_{ij}}{T_{i*}T_{*j}}.$$

Ascendency is defined by

$$A = T \times I = \sum_{i,j} T_{ij} \log \frac{TT_{ij}}{T_{i*}T_{*j}}.$$

If a distribution of flows is given by $P(t)$ then mutual information I is approximately given by the following formula (Ulanowicz and Wolff, 1991).

$$I = \langle \frac{t}{\langle t \rangle} \log \frac{t}{\langle t \rangle} \rangle + \log \frac{N}{m},$$

where $\langle \cdots \rangle$ is average with respect to P, N is the number of nodes and m is the number of in-degree or out-degree of each node (they are the same number for every node). Unfortunately, I can increase by isotropic diffusion. We consider that this effect is a superficial organization of flow networks. In order to eliminate the effect we subtract it from I. If each flow increases by ϵ with probability $1/2$ and decreases by ϵ with the same probability independently at each step, where ϵ is a uniform random number in $[0, 2\eta]$, then we can easily show that the expected value of increase in I per one step is approximately

$$\frac{2}{3\langle t \rangle} \langle \frac{1}{t} \rangle \eta^2.$$

We define γ by

$$\gamma(0) = \beta(0), \; \gamma(\tau + 1) = \gamma(\tau) + \frac{2}{3\langle t \rangle_\tau} \langle \frac{1}{t} \rangle_\tau \eta^2$$

where $\beta(\tau) = I_\tau - \log N/m = \langle (t/\langle t \rangle_\tau) \log(t/\langle t \rangle_\tau) \rangle_\tau$ and $\langle \cdots \rangle_\tau$ denotes average with respect to the distribution of flows at τth period. Note that $\log N/m$ is a

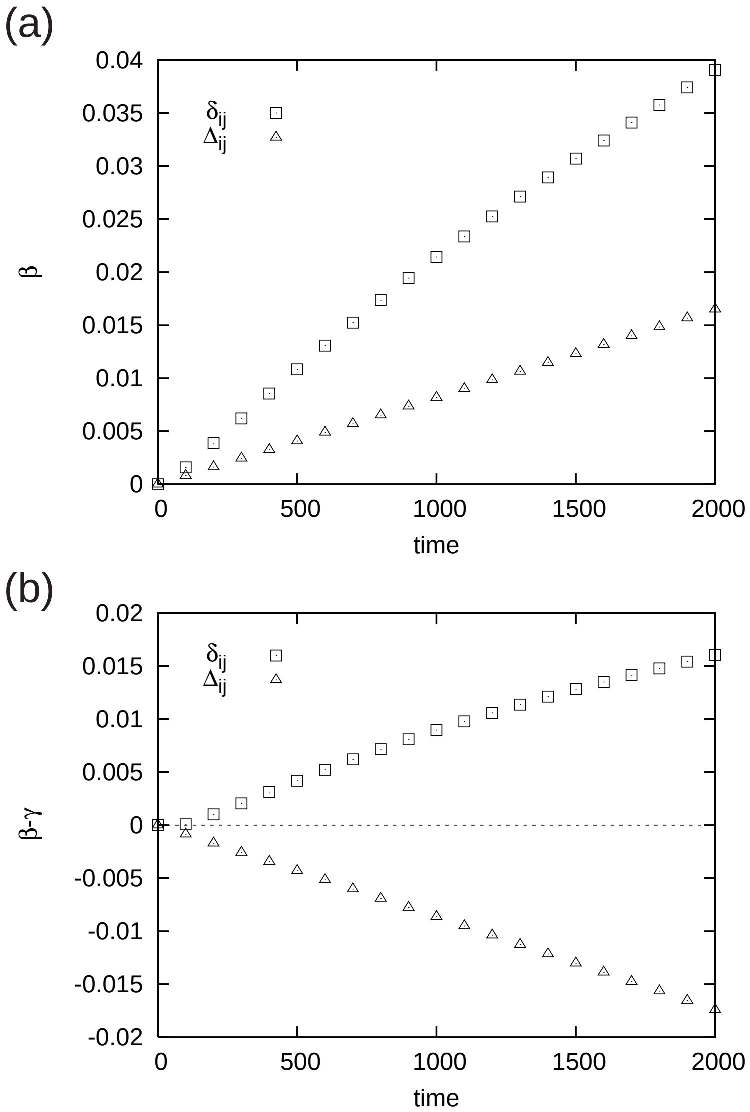

Figure 4: (a)Time evolution of β. (b)Time evolution of $\beta - \gamma$.

constant. Figure 4 shows the result of our computer simulation averaged over 1000 trials. β increases due to the effect of isotropic diffusion even in the case of Δ_{ij} (Figure 4(a)). However, if the expected value of increase by the effect of isotropic diffusion is subtracted from β then $\beta - \gamma$ still increases in the case of δ_{ij} as before on one hand, it now decreases in the case of Δ_{ij} on the other hand (Figure 4(b)). This result suggests that if balancing process proceeds by δ_{ij} then flow networks really develop to more organized direction.

Let us examine how flow networks are organized by balancing process. Figure 5(a) shows frequency distribution of flow size in 100 steps from 1000th period accumulated over 1000 trials. In the case of Δ_{ij} the distribution is bell-shaped. On the other hand, the distribution corresponding to δ_{ij} has a long tail toward large flow size. Figure 5(b) shows probability of increase at each flow size estimated from the same data in Figure 5(a). In the case of Δ_{ij} the smaller flow size is, the larger the probability of increase is below mean flow size and the larger flow size is, the smaller the probability of increase is above mean flow size. On the other hand, in the case of δ_{ij} the larger flow size is, the larger the probability of increase is even above mean flow size. Thus flow networks developing by balancing process with δ_{ij} have a self-organizing property that larger flows tend to increase more frequently, which could be seen as a primitive objective. This self-organizing property can generate a distribution of flow size with longer tail. We note that the distributions of flow size of real ecosystems are close to power law distributions that have long tails (Ulanowicz and Wolff, 1991).

In the next section we analyze the mechanism how the results in this section arises through balancing process. In particular, we will see that the self-organizing property that larger flows tend to increase more frequently remains if α is in a sufficiently small neighborhood of $1/2$. This implies that the self-organizing property is robust under small perturbations to α at $\alpha = 1/2$.

6 Mechanism of Balancing Process

First we see how the behavior of flow networks changes if α is diffrent from $\alpha = 1/2$. Figure 6 shows that how mean flow size after 2000 periods depends on α. All the other conditions in computer simulation are the same as those in the previous section. It takes maximal values as a function of α at two points $\alpha = 0.4984, 0.5016$, slightly displaced from $\alpha = 1/2$. There is a flat region around $\alpha = 1/2$ between the two maximal points. As α becomes close to 0 or 1, increase in mean flow size after 2000 periods tends to become 0. Figure 7(a) shows that flow size distributions for $\alpha = 0.5, 0.499, 0.4984$. The distribution for $\alpha = 0.499$ is similar to that for $\alpha = 0.5$ with a long tail toward larger flow size. On the other hand, the distribution for $\alpha = 0.4984$ is a bimodal distribution. Figure 7(b) shows that probability of increase at each flow size. One might expect that the organizing mechanism at $\alpha = 0.4984$ is totally different from that around $\alpha = 0.5$. In order to explain such behaviors next we investigate the mechanism of balancing process.

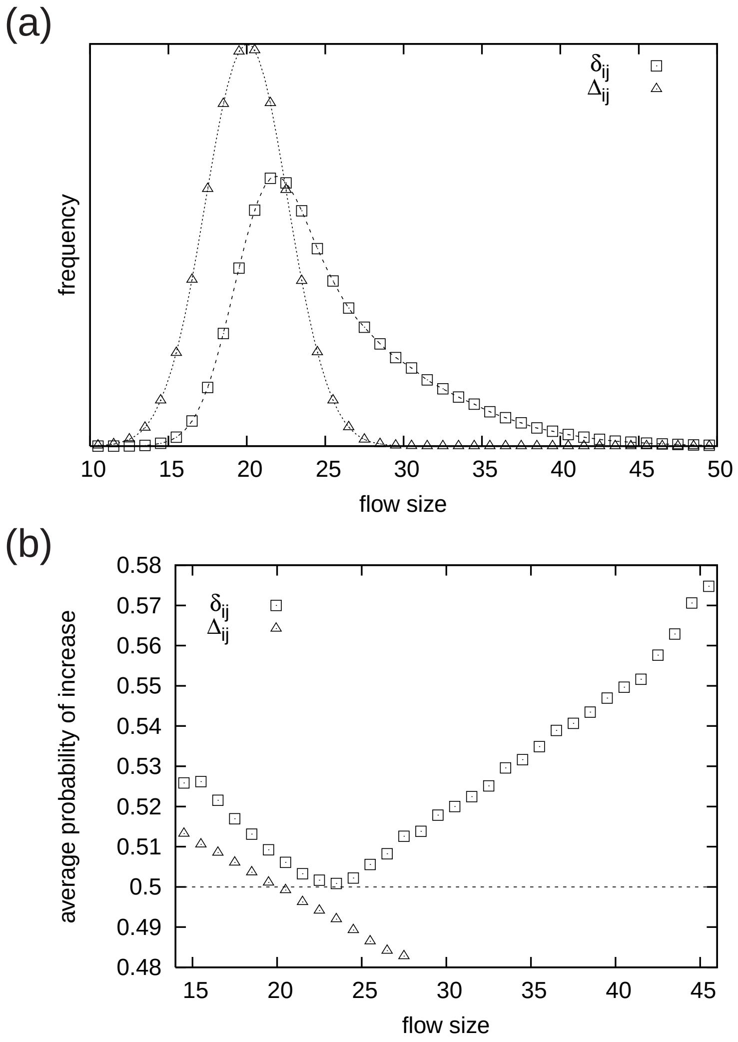

Figure 5: (a)Frequency distribution of flow size in 100 steps from 1000th period. (b)Probability of increase at each flow size estimated from the same data in (a).

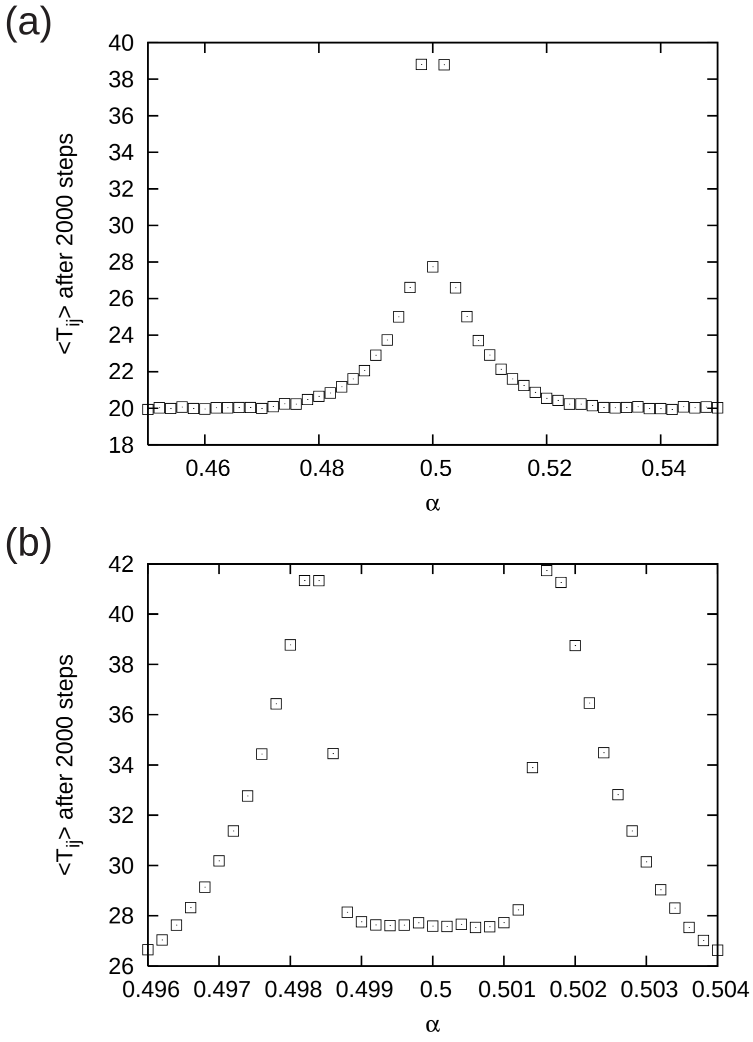

Figure 6: (a)Mean flow size after 2000 periods. (b)A magnified picture of (a) around $\alpha = \frac{1}{2}$.

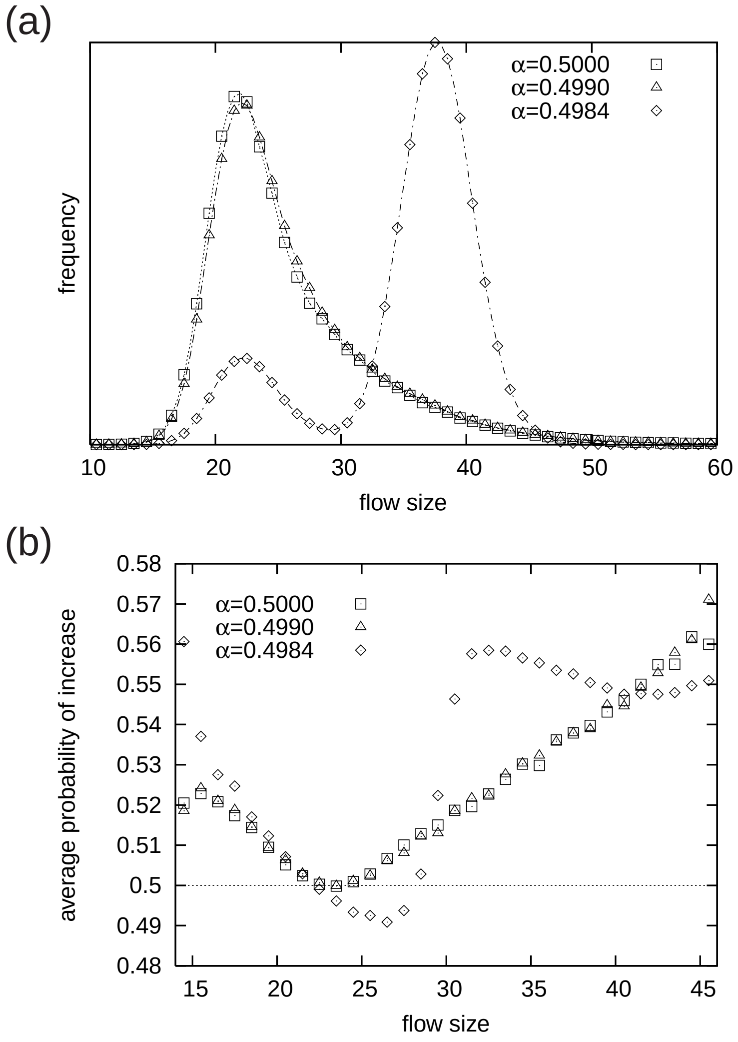

Figure 7: (a)Frequency distribution of flow size in 100 steps from 1000th period for $\alpha = 0.5,\ 0.499,\ 0.4984$. (b)Probability of increase at each flow size estimated from the same data in (a).

Since the direction of change of T_{ij} is dependent on four values T_{*i}, T_{i*}, T_{*j} and T_{j*} we first focus on the relationships between them. We assume that all the four values have different values and all flows with positive sizes also have different values. It is enough to consider $\alpha \leq 1/2$ by symmetry.

(i) $T_{*i} > T_{i*}$ and $T_{*j} < T_{j*}$.

In this case we have

$$\frac{\partial \delta_{ij}}{\partial T_{ij}} = -\alpha \frac{T_{*i}}{T_{i*}^2} - (1-\alpha)\frac{T_{j*}}{T_{*j}^2} < 0.$$

Thus T_{ij} always increases regardless of α.

(ii) $T_{*i} < T_{i*}$ and $T_{*j} > T_{j*}$.

In this case we have

$$\frac{\partial \delta_{ij}}{\partial T_{ij}} = \alpha \frac{T_{*i}}{T_{i*}^2} + (1-\alpha)\frac{T_{j*}}{T_{*j}^2} > 0.$$

Thus T_{ij} always decreases independent of α.

We can prove that the number of pairs (i,j) that satisfy (i) is the same as the number of pairs (i,j) that satisfy (ii). Indeed, we can assume that $T_{*i} > T_{i*}$ for $1 \leq i \leq n$ and $T_{*i} < T_{i*}$ for $n+1 \leq i \leq N$. Suppose the number of pairs (i,j) with $T_{*i} > T_{i*}$, $T_{*j} < T_{j*}$ is k. Then the number of pairs (i,j) with $T_{*i} > T_{i*}$, $T_{*j} > T_{j*}$ is $nm - k$. In order to obtain the number of pairs (i,j) with $T_{*i} < T_{i*}$, $T_{*j} > T_{j*}$ we subtract the number of pairs (i,j) with $T_{*i} > T_{i*}$, $T_{*j} > T_{j*}$ from the number of pairs (i,j) with $T_{*j} > T_{j*}$. That is, the number of pairs (i,j) with $T_{*i} < T_{i*}$, $T_{*j} > T_{j*}$ is $nm - (nm - k) = k$. This implies that if two cases (i) and (ii) are combined together then they do not contribute to increase of mean flow size.

(iii) $T_{*i} > T_{i*}$ and $T_{*j} > T_{j*}$.

Since

$$\frac{\partial \delta_{ij}}{\partial T_{ij}} = -\alpha \frac{T_{*i}}{T_{i*}^2} + (1-\alpha)\frac{T_{j*}}{T_{*j}^2}$$

is a summation of a positive number and a negative number, the sign depends on the relationships between $T_{*i}, T_{i*}, T_{*j}, T_{j*}$ and α.

(iii)-(i) $\frac{T_{i*}}{T_{i*}+T_{*j}} < \alpha$.

Since the condition is equivalent to

$$-\alpha \frac{1}{T_{i*}} + (1-\alpha)\frac{1}{T_{*j}} < 0,$$

we obtain

$$\frac{\partial \delta_{ij}}{\partial T_{ij}} = -\alpha \frac{T_{*i}}{T_{i*}^2} + (1-\alpha)\frac{T_{j*}}{T_{*j}^2} < -\alpha \frac{1}{T_{i*}} + (1-\alpha)\frac{1}{T_{*j}} < 0.$$

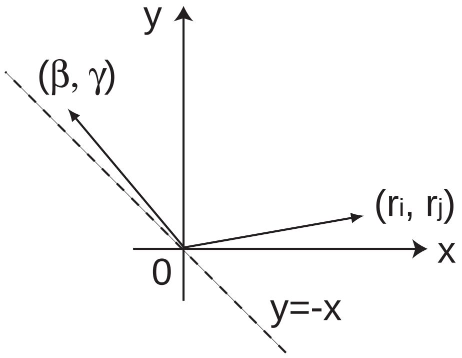

Figure 8: $\langle(\beta,\gamma),(r_i,r_j)\rangle$ is negative if the angle between the two vectors is greater than $\frac{\pi}{2}$.

(iii)-(ii) $\alpha < \frac{T_{i*}}{T_{i*}+T_{*j}}$.

Put $r_i = T_{*i}/T_{i*}, r_j = T_{j*}/T_{*j}$. By the condition of (iii), $r_i > 1$ and $r_j < 1$. We also put $\beta = -\alpha/T_{i*}$ and $\gamma = (1-\alpha)/T_{*j}$. Then $\partial\delta_{ij}/\partial T_{ij}$ can be represented as an inner product of two plane vectors (β,γ) and (r_i,r_j):

$$\frac{\partial\delta_{ij}}{\partial T_{ij}} = \beta r_i + \gamma r_j = \langle(\beta,\gamma),(r_i,r_j)\rangle,$$

where $\langle\cdots,\cdots\rangle$ is the standard inner product in $\mathbb{R}^2$. Since $\beta < 0,\ \gamma > 0$ and $\beta+\gamma > 0$ by the condition of (iii)-(ii), (β,γ) is in $\{(x,y)\in\mathbb{R}^2\,|y > -x,\ x < 0,\ y > 0\}$. On the other hand, since $0 < r_j < 1 < r_i$, (r_i,r_j) is in $\{(x,y)\in\mathbb{R}^2\,|y < x,\ x > 0,\ y > 0\}$. Therefore $\langle(\beta,\gamma),(r_i,r_j)\rangle$ tends to be negative if (a) the angle between (β,γ) and $(-1,1)$ is smaller or (b) the angle between (r_i,r_j) and $(1,0)$ is smaller (Figure 8). Note that the two conditions (a) and (b) are not independent.

First we consider (a). The closer the inner product

$$\langle(-1,1),\frac{1}{\sqrt{\beta^2+\gamma^2}}(\beta,\gamma)\rangle = \frac{1}{\sqrt{\beta^2+\gamma^2}}(-\beta+\gamma)$$

is to $\sqrt{2}$, the smaller the angle between (β,γ) and $(-1,1)$. In order to see how the value of the inner product depends on T_{ij}, let us assume that $a = \sum_{k\neq j} T_{ik}$ and $b = \sum_{k\neq i} T_{kj}$ are constant and consider the following function.

$$f_\alpha(x) = \frac{1}{\sqrt{(\frac{\alpha}{x+a})^2 + (\frac{1-\alpha}{x+b})^2}}(\frac{\alpha}{x+a} + \frac{1-\alpha}{x+b}).$$

The differential of $f_\alpha(x)$ is

$$f'_\alpha(x) = \frac{\alpha(1-\alpha)(a-b)\{(1-\alpha)a - \alpha b + (1-2\alpha)x\}}{\{(1-\alpha)^2(x+a)^2 + \alpha^2(x+b)^2\}^{\frac{3}{2}}}.$$

There is just one point that gives an extreme value of f_α if $\alpha \neq 1/2$. We denote it by

$$x_* = \frac{\alpha b - (1-\alpha)a}{1-2\alpha}.$$

By the condition of (iii)-(ii), we have

$$T_{ij} > \frac{\alpha b - (1-\alpha)a}{1-2\alpha} = x_*.$$

Therefore we only consider the range $x > x_*$. In this range $(1-\alpha)a - \alpha b + (1-2\alpha)x$ is always positive. So the sign of f'_α only depends on $a-b$. If $a > b$ which is equivalent to $T_{i*} > T_{*j}$ then $f_\alpha(x)$ is increasing for $x > x_*$. $f_\alpha(x)$ converges to $1/\sqrt{\alpha^2 + (1-\alpha)^2}$ from below as $x \to \infty$. Note that x_* is negative if $a > b$. If $a < b$ which is equivalent to $T_{i*} < T_{*j}$ then $f_\alpha(x)$ is decreasing for $x > x_*$. $f_\alpha(x)$ converges to $1/\sqrt{\alpha^2 + (1-\alpha)^2}$ from above as $x \to \infty$. If $\alpha = 1/2$ then $f'_\alpha(x)$ has no zero point. Since the condition of (iii)-(ii) becomes $a > b$, $f_\alpha(x)$ is increasing for all $x \in \mathbb{R}$. It converges to $\sqrt{2}$ as $x \to \infty$. However, we can virtually suppose that $f_\alpha(x)$ takes a minimal value at $-\infty$ and treat both cases $\alpha < 1/2$ and $\alpha = 1/2$ at the same time.

Next we consider (b). The closer the inner product

$$\langle (1,0), \frac{1}{\sqrt{r_i^2 + r_j^2}}(r_i, r_j) \rangle = \frac{r_i}{\sqrt{r_i^2 + r_j^2}}$$

is to 1, the smaller the angle between $(1,0)$ and (r_i, r_j) is. Assuming $p = T_{*i}$, $q = T_{j*}$ are constants, we define a function

$$g(x) = \frac{\frac{p}{x+a}}{\sqrt{(\frac{p}{x+a})^2 + (\frac{q}{x+b})^2}}.$$

Since $g(x)$ can be rewritten as

$$g(x) = \frac{1}{\sqrt{1 + (\frac{q}{p})^2 (1 + \frac{a-b}{x+b})^2}},$$

$g(x)$ is increasing if $a > b$ and converges to $1/\sqrt{1 + (\frac{q}{p})^2}$ from below as $x \to \infty$. If $a < b$ then $g(x)$ is decreasing and converges to $1/\sqrt{1 + (\frac{q}{p})^2}$ from above as $x \to \infty$.

Combining both (a) and (b), we can conclude as follows for given $0 \leq \alpha \leq 1/2$. If $T_{i*} > T_{*j}$ then $\partial \delta_{ij} / \partial T_{ij}$ becomes negative more often for larger T_{ij}. If $T_{i*} < T_{*j}$ then $\partial \delta_{ij} / \partial T_{ij}$ becomes negative more often for smaller T_{ij}.

Next we examine how the degrees of the above properties change if α changes. The partial differential of f_α with respect to α is

$$\frac{\partial f_\alpha}{\partial \alpha} = \frac{(x+a)(x+b)\{(1-\alpha)a - \alpha b + (1-2\alpha)x\}}{\{(1-\alpha)^2(x+a)^2 + \alpha^2(x+b)^2\}^{\frac{3}{2}}}.$$

By the condition of (iii)-(ii), $(1-\alpha)a - \alpha b + (1-2\alpha)x$ is always positive hence $\partial f_\alpha / \partial \alpha > 0$. Therefore if α becomes smaller then $f_\alpha(x)$ decreases for a fixed x, which implies that $\partial \delta_{ij} / \partial T_{ij}$ becomes negative less often.

(iv) $T_{*i} < T_{i*}$ and $T_{*j} < T_{j*}$.

In this case we have

$$\frac{\partial \delta_{ij}}{\partial T_{ij}} = -\alpha \frac{T_{*i}}{T_{i*}^2} + (1-\alpha)\frac{T_{j*}}{T_{*j}^2}.$$

So the sign is dependent on $T_{*i}, T_{i*}, T_{*j}, T_{j*}$ and α as in (iii).

(iv)-(i) $\alpha < \frac{T_{i*}}{T_{i*}+T_{*j}}$.

By the condition, we can obtain $\partial \delta_{ij} / \partial T_{ij} < 0$ as in (iii)-(i).

(iv)-(ii) $\frac{T_{i*}}{T_{i*}+T_{*j}} < \alpha$.

As in (iii)-(ii), we represent $\partial \delta_{ij} / \partial T_{ij}$ by an inner product

$$\frac{\partial \delta_{ij}}{\partial T_{ij}} = \langle (\beta', \gamma'), (r_i, r_j) \rangle,$$

where $r_i = T_{*i}/T_{i*}$, $r_j = T_{j*}/T_{*j}$ and $\beta' = \alpha / T_{i*}$, $\gamma' = (1-\alpha)/T_{*j}$. By a similar argument, we can see that the inner product tends to be negative if (c) the angle between (β', γ') and $(1, -1)$ is smaller or (d) the angle between (r_i, r_j) and $(0, 1)$ is smaller. We can obtain the same function $f_\alpha(x)$ as in (iii)-(ii) for (c). By the condition of (iv)-(ii), we always have $a < b$ if $0 < \alpha \leq 1/2$. Therefore, again by the condition of (iv)-(ii), the range of x to be considered is $x < x_*$. In this range $f_\alpha(x)$ is increasing.

For (d), we consider the following inner product

$$\langle (0,1), \frac{1}{\sqrt{r_i^2 + r_j^2}} (r_i, r_j) \rangle = \frac{r_j}{\sqrt{r_i^2 + r_j^2}}.$$

As in (iii)-(ii), we define a function

$$h(x) = \frac{\frac{q}{x+b}}{\sqrt{(\frac{p}{x+a})^2 + (\frac{q}{x+b})^2}} = \frac{1}{\sqrt{1 + (\frac{p}{q})^2 (1 + \frac{b-a}{x+a})^2}}.$$

If $a < b$ then $h(x)$ is increasing and converges to $1/\sqrt{(\frac{p}{q})^2 + 1}$ from below.

Thus one can see that $\partial \delta_{ij} / \partial T_{ij}$ becomes negative more often as T_{ij} becomes large if (c) and (d) are combined together. Moreover, we have $\partial f_\alpha / \partial \alpha < 0$ by the condition of (iv)-(ii). Hence $f_\alpha(x)$ becomes larger as α becomes smaller, which implies that $\partial \delta_{ij} / \partial T_{ij}$ can become negative more often.

So far we argue the non-statistical structures of balancing process. In particular, we find that in the two cases (iii)-(ii) with $T_{i*} > T_{*j}$ and (iv)-(ii) larger T_{ij} can increase more often. Figure 9 shows that these structures are effective to generate longer tail flow size distributions around $\alpha = 0.5$ and a bimodal distribution at $\alpha = 0.4984$. The distributions in the controlled numerical experiments are generated by as follows. First we estimate the probability of increase in the case (iii)-(ii) with $T_{i*} > T_{*j}$, which is denoted by p_1, and the probability of increase in the case (iv)-(ii), which is denoted by p_2, from the uncontrolled numerical experiment for each value of α. Second, in the controlled numerical experiments, if T_{ij} satisfies the conditions of (iii), (iii)-(ii) and $T_{i*} > T_{*j}$ (or the conditions of (iv) and (iv)-(ii)), it increases with probability p_1 (or p_2), regardless of flow size. Thus the structures of balancing process described above which enable larger flows to increase more often are broken.

If α is sufficiently close to $1/2$ then the effect of these structures would not so different from that for $\alpha = 1/2$ by the continuity of conditions with respect to α appeared in the above argument. This suggests that the self-organizing property at $\alpha = 1/2$ observed in the previous section is robust to small perturbations to α.

There are also statistical effects. For example, suppose T_{*i}, T_{i*}, T_{*j} and T_{j*} have values close to mean. If the condition of (iii) $T_{*i} > T_{i*}$ and $T_{*j} > T_{j*}$ is satisfied then the greater T_{ij} is apart from mean flow size toward larger flow size, the smaller $\sum_{k \neq j} T_{ik}$ is in order $T_{*i} > T_{i*}$ to hold. This implies that $T_{i*} < T_{*j}$ is satisfied more often if T_{ij} larger than mean flow size is larger. In addition, the greater T_{ij} is apart from mean flow size toward smaller flow size, the larger $\sum_{k \neq i} T_{kj}$ is in order $T_{*j} > T_{j*}$ to be satisfied. Hence $T_{i*} < T_{*j}$ is satisfied more often if T_{ij} smaller than mean flow size is smaller. Such an effect would be relevant to frequency distribution of flow size within (iii)-(i) if $\alpha \leq 1/2$ is close to $1/2$. The same thing can be said for (iv).

There is another statistical effect what we call the effect of threshold. We see $T_{i*}/(T_{i*} + T_{*j})$ as a function of T_{ij}. That is, we consider a function

$$k(x) = \frac{x+a}{2x+a+b} = \frac{1}{2}(1 + \frac{a-b}{2x+a+b}),$$

where $a = \sum_{k \neq j} T_{ik}$ and $b = \sum_{k \neq i} T_{kj}$ are supposed to be constants. If $a > b$ then $k(x) > 1/2$ for all $x > 0$. If $a < b$ then $k(x)$ is increasing for $x > 0$ and converges to $1/2$ as $x \to \infty$. Therefore $\alpha < T_{i*}/(T_{i*} + T_{*j})$ will be satisfied if T_{ij} is larger than certain threshold value when $\alpha < 1/2$. If α is too close to or too far from $1/2$ then such an effect would not be relevant. However, for some values of α the effect of threshold might be significant. For example, the bimodal distribution without long tail for $\alpha = 0.4984$ shown in Figure 7(a) would be a cooperative effect of the effect of threshold and the mechanism for (iii)-(ii) with $T_{i*} < T_{*j}$.

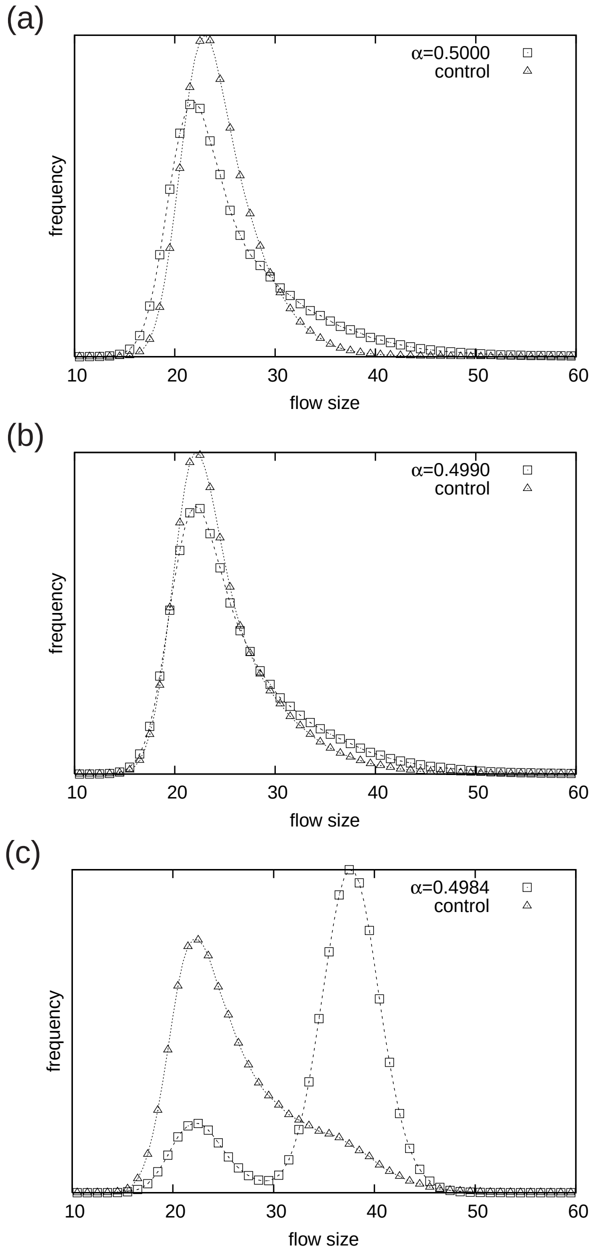

Figure 9: Results of controlled numerical experiments in which the structures of balancing process which enable larger T_{ij} to increase more often are broken. See text for details. (a)For $\alpha = 0.5$, $p_1 = 0.035451$ and $p_2 = 0.035566$. (b)For $\alpha = 0.4990, p_1 = 0.008836$ and $p_2 = 0.033590$. (c)For $\alpha = 0.4984, p_1 = 0.002520$ and $p_2 = 0.004638$.

7 Conclusions

We give up the position where one can assume macroscopic objectives to which ecosystems organize themselves. At this position we cannot address the relationship between flow balance and macroscopic objectives. Instead, in this paper we directly describe a dynamics of balancing process and argue how a self-organizing property can arise from the balancing process. Balancing process we proposed is a process of local elimination of imbalances. Since the process of balancing is local, an effort of eliminating an imbalance can lead to generation of a new imbalance. As a result of such a process, flow networks can have a self-organizing property.

Objectives are related to wholeness of biological systems. Apparently objectives are unique to biological systems since they seem not to be in physical or chemical systems. However, if one can set an objective that can be identified from the outside of a system then he treats the system as a machine. Any machine is made for certain objective. If it is broken then it is not a machine since it does not have functions that are expected. A broken machine is not a machine, however, it is at least some material. If this material could acquire a new function by itself then we might recognize it as a new machine. However one might also feel that it is not appropriate to call it machine anymore. In such a situation one would not find a machine but a life. At this point we focus on a system that comes into existence as the system. When a system is recognized as the system, there is already a wholeness that enable the system to come into existence. We call such a wholeness intrinsic wholeness, which is distinguished from a wholeness specified by a macroscopic objective.

In this paper we attempt to represent intrinsic wholeness as balancing process toward flow balance. Intrinsic wholeness itself does not imply any macroscopic objective, however, balancing process, an effort to maintain intrinsic wholeness, can generates a self-organizing property, which could be seen as a primitive objective.

Our stance in this paper is that of minimalist. We propose a model of balancing process without any consideration on constraints in real ecosystems. Such minimalist stance induces a gap between the behavior of our model and real ecosystems. While our model flow network keeps glowing forever, real ecosystems senesce in their final stage of developmental process (Salthe, 1993; Ulanowicz, 1997). However, such an unrealistic result would be resolved if we introduce constraints to the system from its environment in a suitable manner, which is left as a future work.

Another link to real ecosystems is an application of the idea in our model to data analysis (Ulanowicz, 2004). In the definition of balancing process we consider the flow from node i to node k via node j. The probability that a unit amount of flow from node i goes into node k via node j is

$$\frac{T_{ij}}{T_{*j}} \times \frac{T_{jk}}{T_{j*}}$$

if we assume that the mass action interaction at node j. On the other hand, the probability of interaction among node i, node j and node k will be proportional to

$$\frac{B_i}{B} \times \frac{B_j}{B} \times \frac{B_k}{B}$$

if we assume the mass action law on the whole system, where B_i is the amount of stock at node i and $B = \sum_i B_i$. We define the former probability by considering each node as a collection of relations with other nodes. In contrast, the latter probability is defined by considering each node as a structure-less element. In order to quantify the difference between these two perspectives, we can consider the Kullback-Leibler information of the latter probability $q_{ik} = B_i B_k / B^2$ from the former probability $p_{ik} = T_{ij} T_{jk} / T_{*j} T_{j*}$ (Kullback and Leibler, 1951)

$$I_j = \sum_{i,k} p_{ik} \log \frac{p_{ik}}{q_{ik}}$$

for each node j. Ulanowicz and Abarca-Arenas (1997) considered the Kullback-Leibler information for the whole system in order to define the ascendency including biomass. However, I_j here is not defined for the whole system but for each node j. Hence I_j could be used to measure the degree of organization around node j. The collection of all I_j would characterize the heterogeneity of organization in the whole system. If both flow and stock data are available for real ecosystems, we can readily calculate the quantity I_j. Data analysis on real ecosystems is also left as a future work.

8 Acknowledgements

This work was supported by JSPS Resarch Fellowships for Young Scientists.

References

Aoki, I., 1998. Entropy and energy in the development of living systems: a case study of lake-ecosystems. *J. Phys. Soc. Jpn.* 67, 2132-2139.

Arthur, W. B., 1994. *Increasing Returns and Path Dependence in the Economy.* The University of Michigan Press, Ann Arbor.

Beard, D. A., Liang, S. C. and Qian, H., 2002. Energy balance for analysis of complex metabolic networks. *Biophys. J.* 83, 79-86.

ten Cate, C. Verzijden, M. and Etman, E., 2006. Sexual imprinting can induce sexual preferences for exaggerated parental traits. *Curr. Biol.* 16, 1128-1132.

ten Cate, C. and Rowe, C., 2007. Biases in signal evolution: learning makes a difference. *Trends Ecol. Evol.* 22, 380-387.

Haruna, T. and Gunji, Y.-P., 2007. Duality Between Decomposition and Gluing: A Theoretical Biology via Adjoint Functors. *Biosystems* 90, 716-727.

Ibarra, R. U., Edwards, J. S. and Palsson, B. O., 2002. *Escherichia coli* K-12 undergoes adaptive evolution to achieve *in silico* predicted optimal growth. *Nature* 420, 186-189.

Jørgensen, S. E. and Mejer, H., 1979. A Holistic Approach to Ecological Modelling. *Ecological Modelling* 7, 169-189.

Kauffman, K. J., Prakash, P. and Edwards, J. S., 2003. Advances in flux balance analysis. *Cur. Op. Biotech.* 14, 491-496.

Kullback, S. and Leibler, R. A., 1951. On Information and Sufficiency. *Ann. Math. Stat.* 22, 79-86.

Lotka, A. J., 1922. Contribution to the energetics of evolution. *Proc. Natl. Acad. Sci.* 8, 147-151.

Lynn, S. K., 2005. Learning to avoid aposematic prey. *Anim. Behav.* 70, 1121-1226.

Lynn, S. K., 2006. Cognition and evolution: learning and the evolution of sex traits. *Curr. Biol.* 16, R421-R423.

Matsuno, K., 1989. *Protobiology: Physical Basis of Biology.* CRC Press, Boca Raton, FL.

Matsuno, K., 1995. Consumer Power as the Major Evolutionary Force. *J. Theor. Biol.* 173, 137-145.

Odum, H. T. and Pinkerton, R. C., 1955. Time ’s speed regulator, the optimum efficiency for maximum output in physical and biological systems. *Am. Sci.* 43, 331-343.

Salthe, S. N., 1985. *Evolving Hierarchical Systems: Their Structure and Representation.* Columbia University Press, New York.

Salthe, S.N., 1993. *Development and Evolution: Complexity and Change in Biology.* MIT Press, Cambridge, MA.

Salthe, S. N., 2005. The natural philosophy of ecology: developmental systems ecology. *Ecological Complexity* 2, 1-19.

Schneider, E. D. and Kay, J. J., 1994. Life as a manifestation of the second law of thermodynamics. *Math. Comput. Model.* 19, 25-48.

Shiojiri, K., Maeda, T., Arimura, G., Ozawa, R., Shimoda, T. and Takabayashi, J., 2002. Functions of Plant Infochemicals in Tritrophic Interactions between Plants, Herbivores and Carnivorous Natural Enemies. *Jpn. J. Appl. Entomol. Zool.* 46, 117-133.

Suzuki, Y., Takabayashi, J. and Tanaka, H., 2002. Investigation of tritrophic interactions in an ecosystem using abstract chemistry. *Artificial Life and Robotics* 6, 129-132.

Swenson, R., 1989. Emergent attractors and the law of maximum entropy production: foundations to a theory of general evolution. Syst. Res. 6, 187-198.

Ulanowicz, R. E., 1980. An hypothesis on the development of natural communities. *J. theor. Biol.* 85, 223-245.

Ulanowicz, R. E., 1986. *Growth and Development: Ecosystems Phenomenology.* Springer-Verlag, New York.

Ulanowicz, R. E. and Wolff, W. F., 1991. Ecosystem flow networks: Loaded dice? *Math. Biosci.* 103, 45-68.

Ulanowicz, R. E., 1997. *Ecology, The Ascendant Perspective.* Columbia University Press, New York.

Ulanowicz, R. E. and Abarca-Arenas, L. G., 1997. An informational synthesis of ecosystem structure and function. *Ecological Modelling* 95, 1-10.

Washida, T., 1995. Ecosystem configurations consequent on the maximum respiration hypothesis. *Ecological Modelling* 78, 173-193.