

ENERGY FLOWS IN COMPLEX ECOLOGICAL SYSTEMS: A REVIEW*

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Received: November 20, 2007

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Abstract Energy flow drives the complex systems to evolve. The allometric scaling as the universal energy flow pattern has been found in different scales of ecological systems. It reflects the general power law relationship between flow and store. The underlying mechanisms of energy flow patterns are explained as the branching transportation networks which can be regarded as the result of systematic optimization of a biological target under constraints. Energy flows in the ecological system may be modelled by the food web model and population dynamics on the network. This paper reviews the latest progress on the energy flow patterns, explanatory models for the allometric scaling and modelling approach of flow and network evolution dynamics in ecology. Furthermore, the possibility of generalizing these flow patterns, modelling approaches to other complex systems is discussed.

Key words Energy flow, allometric scaling, food web, flows in complex systems

1 Introduction

Energy flow is an important ingredient for complex systems because the development and evolution of systems must be driven by energy flows. Ecosystem is a good example of open system driven by energy flows^[1]. In the ecological community, each organism is an open system consuming energy and material by metabolism continuously. Some species may be consumed by other species as the prey, therefore, a tangled network of feeding relationships called food web^[2] forms. Energy flows along directed edges are from the prey species nodes to the predator species nodes on the web.

There are some universal patterns of energy flows both in individuals and large scale ecological communities. Allometric scaling relationship between energy flows and stores is one of the most important discoveries in ecology recently^[3]. The underlying branching transportation networks of energy flows may explain the universal scaling relationships of flow systems^[4,5]. Flows are not only determined by the structure of the transportation network but also change the topology of the network simultaneously by the evolution of the system^[6]. This kind of co-evolution can be modelled by the population dynamics on the evolutionary food web models.

However, as complex systems researchers, we care more about the universal properties or principles in various systems. Do ecologists' discoveries help us? Actually, all kinds of complex systems need resource flows including energy flows, material flows or goods flows to survive.

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*This research is supported by Guozhi Xu Post Doctoral Research Foundation and National Natural Science Foundation of China(No.60574068).

Some recent studies found that these flow systems exhibit similar allometric scaling patterns just like ecological systems^[7,8,9]. Furthermore, the branching transportation network which is the underlying mechanism of the particular flow patterns may be universal. And the energy flows on the evolutionary food web model have become a useful tool to study the dynamics of the flow-structure co-evolutionary networks^[10].

This paper reviews the discoveries of flow patterns in ecology from the individual to population level, explanatory models of these patterns and modelling approaches of the dynamical aspects of flows in the ecological community level. The purposes are to discuss the potentialities of generalizing the modelling approach to other systems and to provide insights of the general theory of flows in complex systems.

The organization of this paper is as follow. Section 2.1 introduces the power law flow patterns which are called allometric scaling in metabolic ecology. Section 2.2 reviews explanatory models of these scaling power laws. In the ecological community level, food web as a powerful abstraction of the system also exhibits some universal patterns which are discussed by section 3.1. As a concrete modelling approach of energy flows, the model of population dynamics on the evolutionary food web is presented in section 3.2. At last, section 4.1 suggests that these flow patterns and modelling approaches may be extended to other complex systems which can be regarded as the generalized ecological systems driven by resource flows. In section 4.2, some studies in physics are referred as the perspective of finding out the theoretical foundation of flow phenomena.

2 Energy Flow Patterns

Individual organism, ecological community, ecosystem, and biosphere, as the complex system, must be open to obtain the energy flows from their environments. The dissipation of the energy as the wasteful heat will flow out of the system unavoidably in the same time. These systems store the workable energies (called exergy^[11]) as the biomass which will be used to do works in the future. Therefore, a picture can be drawn to depict this story (See Fig 1). Recently, the studies in the ecology found some universal patterns of this picture, which is called allometric scaling law.

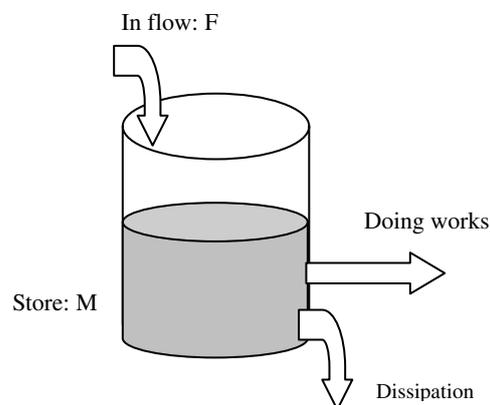


Figure 1 Energy flows in an open system

2.1 Allometric Scaling

2.1.1 3/4 Power Law

Fig1 can be used to describe individual organisms. Here the energy flow of an organism is its metabolism denoted as F . The store of the energy is the organism's body mass or body size proportionally denoted as M . A universal relationship between the average metabolism F and body mass (or size) M of a species was found by biologists^[12] for all species in nature^[13]:

$$F = F_0 M^{3/4}. \quad (1)$$

Here, F_0 is a constant different in various classes of species^[14]. The relationship is not linear but a power law with exponent 3/4. So it is called allometric scaling law^[15]. Although some articles argued that the exponent of equation (1) is 2/3 but not 3/4^[16,17], the equation (1) is supported by the massive empirical data.

Actually, equation (1) is universal because for all species, from mouse to elephant, the equation can describe the relationship between the species' metabolism flux and body size. And we will see in the following sections, even for other complex systems which can be abstracted by Fig 1 follow the similar law with the same form of equation (1):

$$F = F_0 M^b \quad (2)$$

That is, for generalized flow systems, equation (2) is able to describe the universal relationship between flux and store, although the exponent b may be not 3/4 for other systems.

2.1.2 Other Allometric Scaling Relations

Furthermore, equation (1) can not only describe the relationship between metabolism and body size but also derive scaling relationships of other biological variables with the body size^[15]. It is not difficult to calculate the average turn-over time T for an imaginary particle flowing into the system and flowing out^[3]: $T \approx M/F \propto M/M^{3/4} = M^{1/4}$. Lots of time-related variables of individual organisms, such as life span, age of reproductive maturity, circulation of blood volume etc., follow this quarter-law^[18]. So mouse with small body size has shorter life span than the elephant with bigger body size. Biological rates including heart rate, death rate, and the rate of molecule evolution always follow $R \propto M^{-1/4}$. Because they obey the reciprocal relation of rates and turn over time^[3]. Other individual phenomena including the development of the organism^[19], life history^[20], the relationship between biological variables and temperature^[3] can be explained indirectly from equation (1).

Allometric scaling can not only fit for the individual level but also for the larger scale levels from population to community^[15,21]. For example, ecologists found that the population density N of a species in a habitat and its average body size has a power law relation^[22-25]: $N \propto M^{-3/4}$. And the average energy production P of plants is independent to their body sizes because $P \propto NF \propto M^{-3/4} M^{3/4} = 1$. This is called the energetic equivalence hypothesis^[26,27]. More universal energy flow patterns in the ecological community will be discussed in section 3.

Equation (1) becomes very important especially for its power of deriving so many universal patterns in ecology. But what is the underlying mechanism? Theoretical explanations are needed.

2.2 Theoretical Explanations

Three explanatory models of equation (1), which are Rubner's model, West's model and Banavar's model, are mentioned in this section. Banavar's optimized transportation network model is mainly discussed.

2.2.1 Rubner's Model

The first explanation of the allometric relation between metabolism and body size was given by Rubner through the simple geometric analysis^[28]. Assume that the organism absorbs the energy by its surface, therefore: $F \propto S$, here, S is the area of the organism's surface. And its body size is the volume, i.e., $M \propto V$. Because in the 3 dimensional space, the area of the surface scales its volume as: $S \propto V^{2/3}$, so: $F \propto M^{2/3}$. Unfortunately, this relationship is not supported by the empirical equation (1).

This failure explanation made people realize that the organism is not a common geometric body in the 3-d space. The geometry of the organism may be very rough and complicated so that its shape can only be described by fractal geometry.

2.2.2 West's Model

In 1997, G. West gave a successful explanation for the 3/4 power law^[4]. There are three basic assumptions in his model: (i). Organism's entire volume is filled by a hierarchical branching transportation network with nutrient flows (like mammalian circulatory and respiratory systems or plant's vessel-bundle vascular system); (ii). There are size-invariant units in the final branch of the network; (iii). The distribution of flows and the structure of the network are optimized by evolution to minimize the energy consumption of nutrient flows in the network. By some complicated calculations^[4], West yielded equation (1). To simplify his calculation, he found another approach to derive equation (1) which was similar as Rubner's method but assumed that the organism was a fractal object with 4-dimension^[29].

2.2.3 Banavar's Model

We will discuss Banavar's model in details because it is more reasonable and concise. Assume the body of an organism is an object in the Euclidean space with constant density which can be modeled by a nutrient or energy transportation network. This network contains many nodes (called sites in [5]) which are abstract and have no concrete biological meanings. All energy flows on the network originate from a single node called root. The energy must be distributed to all of the nodes by transportation of edges, see Fig 2(a).

For these flow transportation networks, Banavar gave some hypothetical constraints:

(1). Without losing generality, this network is embedded in a d -dimensional Euclidean space and the nodes distributed in the space evenly, i.e., the number of nodes $N \propto l^d$, where l is the radius of the area occupied by the network (see Fig 2(a));

(2). The edge from node i to node j denoted as $i \rightarrow j$ can only be constructed between neighboring nodes in the space where the network embeds. And the energy flux on the edge $i \rightarrow j$ is denoted as $w_{i \rightarrow j}$;

(3). Each node obtains the energy only from the connecting neighbors;

(4). The energy is consumed by each node, and node i 's energy consumption (net flux of i , $f_i = \sum_{j \rightarrow i} w_{ji} - \sum_{i \rightarrow j} w_{ij}$) is within $[f_{min}, f_{max}]$, hence the total influx F from the root must balance the total consuming flux in the steady state such that $F = \sum_i f_i$, and $F \propto l^d$ if f_i is a constant for any i .

Under these constraints, different network topology for a set of fixed nodes has different efficiency. If the total flux of the network is $M = \sum_{i \rightarrow j} w_{ij}$, then the efficiency of the network is $1/M$, i.e., the smaller of the total flux M the more efficient of the network.

Furthermore, the total flux for all edges of the network is treated as the energy store in the system because the nodes are abstract energy consumption sites without biomass. The body mass of the organism is mainly filled by the flowing matters, i.e., the total flux on edges. We will find the relationship between F and M by maximizing the efficiency $1/M$ (minimizing M) in different network structures.

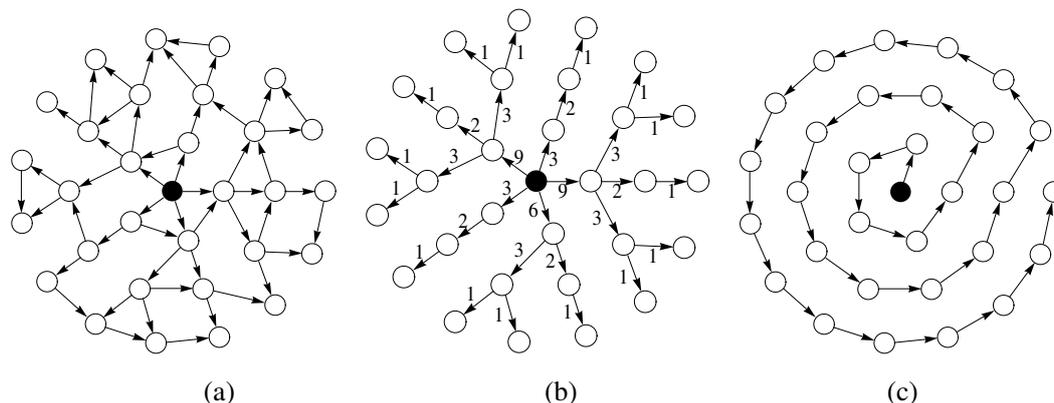


Figure 2 Illustration of Banavar's model to explain the 3/4 power law

(a). A 2 dimensional space filling transportation network which models the body of an individual organism. Nodes are abstract energy consumption sites distributed evenly without concrete biological meaning and biomass. The radius of the network area is l . The directed edge $i \rightarrow j$ denotes the energy flow from i to j , and the flux is w_{ij} . The black node called root is the only node obtaining the energy influx from the environment. The net flux through the node i representing the energy consumption by this node defined as $f_i = \sum_{j \rightarrow i} w_{ji} - \sum_{i \rightarrow j} w_{ij}$, where j is selected from all of neighbors of i . In the steady state, the influx energy F from the root must balance the total energy dissipation for all nodes, i.e., $F = \sum_i f_i$. And the total flux for all edges $M = \sum_{i \rightarrow j} w_{ij}$ reflects the efficiency of the network in different network topology with fixed nodes (see text). (b). The most efficient network under the constraints (see the text) is a spanning tree from the root. The numbers on each edge are the energy flux between nodes when $f_i=1$ for all nodes. In this network, the relation $F \propto M^{d/(d+1)}$ holds (see text), where $d = 2$ is the dimension of the space. (c). The most inefficient network which is a spiral chain. In this network, $F \propto M^{1/2}$

By the mathematical analysis, Banavar proved that the spanning trees from the root node are more efficient than other networks. And these spanning trees share the same feature $M \propto l^d \langle L_X \rangle$, where $\langle L_X \rangle$ is the average distance from the root to every other node (the distance between two nodes is defined as the length of the shortest directed path between them). It is not difficult to proof that $\langle L_X \rangle$ reaches the maximal value when it scales as l^d (A chain-like spiral shown as Fig 2(c)). While it reaches the minimal value when it scales as l (A tree whose nodes only connected to the neighbors under the constraints, shown in Fig 2(b)).

Therefore, for the least efficient network, $F \propto l^d$ and $M \propto l^{2d}$, so $F \propto M^{1/2}$ holds. Whereas for the most efficient network, $F \propto l^d$ and $M \propto l^{d+1}$, so $F \propto M^{d/(d+1)}$ holds. As West's explanation, Banavar treated the organism as a transportation network filling in the 3-dimensional space, hence $F \propto M^{3/4}$.

Furthermore, Banavar gave a more detailed illustration of his model by the supply-demand balance of the transportation network and discussed the situation of 2/3 power law might be correct because of the imbalance of the network^[30].

2.2.4 West's Model V.S. Banavar's Model

Comparing Banavar's model with West's model, there are some significant differences: (1) Banavar's model is more concise by throwing more physical details away; (2) In West's model, the transportation network must be a fractal tree as the model's requirement. But it is just the

result of optimization in Banavar's model.

Some commonalities are shared by these two models: (1) They both assume that the organism is a 3-d space filling flow transportation network. (2) Both models use an assumption that the system has evolved to an optimized state. The optimizing object in West's model is the minimal energy dissipation and it is the minimal total flux of the system in Banavar's model. The common features are important because the branching network and optimization toward flows might be universal systematic properties. Next section will introduce how to generalize Banavar's model to food web analysis.

2.3 Summary

This section reviews the allometric scaling energy flow patterns and explanatory models. Equation (1) is important because it is the foundation of other allometric scaling relations in ecological systems. Additionally, equation (2) is more universal because it reflects the ubiquitous relationships between flow and store in complex systems which will be shown in the next few sections.

There are many other explanatory models for the 3/4 power law besides the models mentioned above. Most of them are reviewed by paper [31]. However, those models always depend on the concrete and detailed biological mechanisms which are disadvantageous for the generality of the model. As equation (2) implies, it is required that the explanatory model must be so abstract that it can be extended to other systems. The models we discussed have the potentiality to become a general approach to analyze the problems related to flows in transportation networks. Firstly, the fractal like branching networks are ubiquitous in nature such as river networks^[5], electrical supply networks in human cities^[9] and so on. Secondly, the optimization to some goal functions is reasonable because the transportation networks in systems are always influenced by natural or artificial ingredients to make them more efficient. For instance, the road network of human cities is optimized by designers to minimize the traffic congestions^[10]. The river network is changed by water flows to maximize the total flux^[32].

Although the models introduced in previous section are successful, there are some criticisms. Makarieva et al. pointed out some unreasonable implicit assumptions are inevitable in both models^[33,34]. For example, in Banavar's model, one of implications is body mass M scales as l^4 which contradicts our observation, $M \propto l^3$ ^[33]. The criticisms imply that all of these models are not perfect and more theories and analysis should be developed.

One of the shortcomings is both models are static because they are invented to explain the static power law patterns. How can we use some modelling techniques to analyze energy flows dynamics in the ecological systems? New research approaches which are food web model and population dynamics on the evolutionary food web will be discussed

3 Energy Flows on Food Webs

Food web represents the prey-predator interactions in a community^[2]. In some food webs, the energy flow can be visualized as the weight of the edge. This section will introduce some patterns of food webs, especially the universal allometric scaling on the un-weighted food web that was found by extending Banavar's transportation network model. Then a modelling approach of energy and network topological dynamics is presented.

3.1 Food Webs

3.1.1 Food Webs and Patterns

A directed graph $\langle V, E \rangle$ is a food web, where $V = \{1, 2, \dots, s\}$ is the set of species, and $E = \{e_{ij} = \langle i, j \rangle\} \subseteq V \times V$ stands for all predator-prey interactions. Any element $e_{ij} \in E$ denotes species j consuming species i .

Another type of food web is a weighted network where its edge is denoted as $e_{ij} = \langle i, j, w \rangle$, and w is the weight of this edge denoting the energy flux from species i to j [35].

Abundant high quality empirical food-web data have been accumulated [36,37]. The studies of the binary food webs are relatively mature because some successful computer models [38,39] have been built to duplicate several statistical properties of the empirical food webs.

For the weighted food webs some prominent features have been presented in recent years [35]. The trivariate relationships among body size, numerically abundant and food web trophic levels of each species on the food web have been investigated in detail for the Tuesday lake by Cohen et al. [36]. As mentioned in section 2.1, body size is a very important trait in ecology [21]. It also plays a significant role in food webs. The energy flux of the edges and the body size distributions of nodes are all integrated in a food web [35]. The ratio of prey and predator body sizes [40,41] determines the energy flux between them. Some researchers even proposed that the body size of a species in a community can be viewed as the niche value which determines the feeding relations, i.e., the structure of the food web [6,42].

But all of these patterns are complicated, so further abstractions and simplifications are needed. Compared to these patterns, another significant feature of food webs is much simpler and clearer. That is the universal allometric scaling of food webs.

3.1.2 Food Webs as Transportation Networks

We can treat the food web as a transportation network of energy flows so that Banavar's transportation network model can be extended here and the universal energy flow patterns (such as the allometric scaling between flow and store) can be revealed. Garlaschelli et al. made the first step in this direction for the binary food web [43].

Fig 3(a) shows a hypothetic food web where the black node is added to represent the environment that provides energy to the whole system. Now, we will find the allometric scaling relationship (equation (2)) in this network. Garlaschelli reduced this network to a spanning tree as shown in Fig 3(b) by deleting the "weak links" at first. Here, "weak links" means the edges between species in trophic levels $L(i)$ and $L(j)$ with $L(i) \geq L(j)$ (trophic level $L(i)$ of species i is defined as the length of the shortest path from the root to i) because the amount of energy flow transported along these links are relatively small. Therefore, it is reasonable for reserving only "strong" links in the spanning tree.

In the tree-form network, each node can be viewed as a source providing energy to all nodes in the sub-tree rooted from this node. That is to say, each sub-tree of the spanning tree from the food web can be regarded as an instance of Banavar's transportation network. If the energy consumption of each node is the same, say 1 unit in each time, then the total number of the sub-tree rooted from i can be viewed as the total influx to this sub-tree. This number of i called A_i is indicated inside the circles in Fig 3(b). It is the corresponding F in Banavar's network (see section 2.2.3). And the summation A_j for every node j in the sub-tree rooted from i can be calculated as $C_i = \sum_{j \in T_i} A_j$, where T_i is the set of nodes inside the sub-tree rooted from i . This value C_i is drawn beside node i in Fig 3(b). Actually, C_i corresponds to M which is the total flux on edges in Banavar's model because each influx of node i equals A_i when the energy consumption of each node is always 1 unit per time (see Fig 2(b)).

We can take the sub-tree of gray nodes in Fig 3(b) as an example to illustrate the calculation of A_i and C_i . This sub-tree is rooted from 2, therefore A_2 is calculated as the total number of nodes in the sub-tree (including node 2), it is 3. And C_2 is the summation for all A_j s in the sub-tree, i.e., $C_2 = A_8 + A_6 + A_2 = 1 + 2 + 3 = 6$.

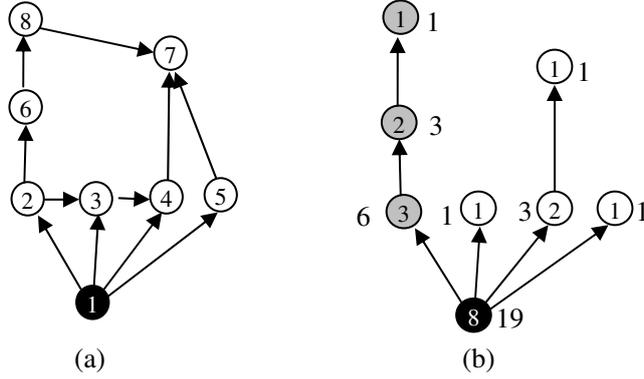


Figure 3 Calculation of allometric scaling of a hypothetical food web

(a). A hypothetical food web with a root node (black) representing the environment. This food web is a binary network which means the edges are un-weighted. The numbers inside the circles are the coding numbers of nodes; (b). The spanning tree reduced from (a) by deleting "weak links" (see text) to calculate the allometric relation. For each node i , we can regard the sub-tree rooted from i as a transportation network. Hence, the A_i (the number of nodes in this sub-tree which is denoted inside the circle) and C_i (the summation of all A_i s for all nodes in this sub-tree, shown beside the circle) for the sub-tree rooted from i can be calculated as the equivalent values of F and M in Banavar's network. For example, the gray nodes (node 2,6,8 in (a)) compose a sub-tree rooted from node 2. Then $A_2 = 3$ is the total number of nodes in this sub-tree, $C_2 = 6$ is the summation of all A_i s in the sub-tree ($C_2 = A_8 + A_6 + A_2$). At last, we can plot all pairs of (A_i, C_i) for the whole spanning tree on the log-log coordinate. The curve can be fitted by a line. That means (A_i, C_i) follows a power law relation (see text).

At last, we can obtain a set of (A_i, C_i) for all of nodes in the spanning-tree (Fig 3(b)). These pairs (A_i, C_i) can be drawn in a log-log coordinators and then a straight line to fit all of these pairs can be obtained (see [43]).

That is to say, A_i and C_i have an allometric scaling relationship as equation (2), $A \propto C^{1/\eta}$. And η is about 1.13 ± 0.03 for all of the seven empirical food-webs investigated in reference [43]. Therefore, Garlaschelli concluded that this scaling relationship is a universal pattern of food webs.

Actually, in [43], η is obtained by averaging for many spanning trees originated from one food web because there are still a large number of possible spanning trees from the original network after deleting the "weak links". And reducing food webs to spanning trees will lose a great deal information. Therefore, Allesina and Bodini found another way to calculate the scaling exponent^[44]. They reduced the food web to a directed acyclic graph, which is the sub-graph without directed cycles. Obviously, directed acyclic graph can keep more information than spanning trees because it retains more edges (Fig 3(a) is the directed acyclic graph itself, so no information lose anymore in this instance). Allesina and Bodini calculated the similar values of A_i and C_i for directed acyclic graph by linear algebra. And the similar power law relation was found, whereas the exponent is around 1.879 for most of food webs^[44].

In fact, the value of η can reflect the efficiency of the transportation networks. The network is more efficient if η is smaller. Frank et al. investigated the relationship of food web topology and transportation efficiency by random generated spanning trees controlled by food chain length and basal species ratio^[45].

Garlaschelli's exponent captures the main feature of food webs from the angle of view of energy flows, but it can only describe one snapshot of the energy flow, i.e., it is a static description. However, energy flows are dynamical phenomena on food webs. Can we study food web and energy flows from a dynamical point of view?

3.2 Modelling Energy Flows on Food webs

3.2.1 Population Dynamics and Energy Flows

Those energy flow patterns need to be explained theoretically^[46]. Population dynamics on the food web is an efficient approach to understand the dynamical aspects of the ecological systems^[47,48]. Differential or difference equations can be used to describe the dynamics of predator and prey's population^[49]. But the conventional population dynamics which is only for two species should be generalized to food webs^[48,50,51]. For species i , we have:

$$\dot{x}_i = e \sum_{\langle j,i \rangle \in E} f(x_i, x_j) - \sum_{\langle i,j \rangle \in E} f(x_j, x_i) - a_i x_i - b_i x_i^2 \quad (3)$$

Here x_i is the population or equivalent energy resource stock, biomass abundance of species i . The first term is the summation of energy flows to the species i by i 's predation per unit time; e is a coefficient to stand for the energy transfer efficiency, and the second term is the summation of energy flows from the species i to its predators. The third term is the loss of energy because of individual death, and the last term is the loss because of the intra-species competition. In some literatures^[51,6], the last term is the summation for all of the species sharing the similar preys of i . Actually, the last two terms can be viewed as the generalized energy dissipation. If there are only two species on the food web, equation (3) becomes the normal population dynamics of prey-predator system.

$f(x_i, x_j)$ is the prey-predator interaction function that has concrete form in different systems. Usually, $f(x_i, x_j)$ has the form of Lotka-Volterra equation^[47], $f(x_i, x_j) = d_{ij} x_i x_j$, where d_{ij} is a coefficient of interaction strength between i and j . Holling^[52], DeAngelis^[53] and other people^[54] studied various forms of f . Actually, the key point that the population dynamics can be used to model energy flows is treating $f(x_i, x_j)$ as the energy flux from j to i ^[42,53].

For the whole food web, the energy input must be considered to maintain the system. Some studies added a special node 0 which represents the environment or the concentration of nutrients in a pool which can be denoted by another equation^[42,53]:

$$\dot{x}_0 = I - \sum_{\langle 0,j \rangle \in E} f(x_j, x_0) - a_0 x_0 \quad (4)$$

Where, I is a constant denoting the energy flux into the whole system. Hence, for any species on a food web, we can use these differential equations to simulate the dynamics of the energy flows and the distribution of the biomass.

Because this set of differential equations are non-linear, obtaining analytic solutions is very difficult. So computer simulation approach is mainly used. After iterations of equations (3) and (4), we can get a numerical solutions for those equations, such that $\dot{x}_i|_{x_i^*} = 0$ for $i = 0, 1, 2, \dots, s$. The vector $\langle x_1^*, x_2^*, \dots, x_s^* \rangle$ is called the steady state of the system. Lots of flow patterns and properties can be calculated in the steady state such as the total system throughflow ($\sum_{\langle i,j \rangle \in E} f(x_i, x_j)$), total biomass of the system ($\sum_{i \in V} x_i$) etc.^[55]

3.2.2 Evolutionary Food Web Models

Energy flows are determined by the food-web structure and also can change the topology of the food-web in the longer time scale by means of evolution. In the model of energy flows on the food web, if a node's population or the equivalent biomass abundance becomes zero or below a given threshold representing the extinction of that species, it will be deleted by the system^[56]. Also some new nodes with new links to the existed nodes can be added, which indicates the invasion of a new species or the natural process of speciation. These processes are food web evolution^[57].

If the new species are added through the speciation from an existing species by means of Darwinian evolution^[58,59], the offsprings will inherit the traits of their mother species. Many evolutionary food-web models use the niche value (a real number or a pair of real numbers) to characterize the species in the system^[6,50,55]. Hence, the new species will inherit the niche value of its mother species with mutation in small possibilities. The new edges will be built by the generalized matching process between niche values of new species and old species^[6,50,55]. Finally, an integral picture of energy flows dynamics determined by the topology of food webs and the evolutionary dynamics of the food-web structure influenced by energy flows can be drawn. Various dynamics of food web evolution and energy flow patterns emerge from the system^[6,42,50,58,60]

3.2.3 Applications

The model of energy flows on the evolutionary food-web is a powerful tool. Some of the pervasive power law patterns of energy flows such as the distribution of energy flux, body size and biomass abundance among different species have been reproduced by the evolutionary food web models^[42]. The results of long time evolution of the food web model can match some statistical properties of the empirical food webs^[6]. Also some controversial theoretical problems, e.g., the maximum power principle^[61,65,66] which will be discussed further by section 4.2 can be studied by this modelling approach^[55].

Actually, the model of energy flows on the evolutionary food-web is not only a theoretical tool for food webs but also a modelling method to study the co-evolution of network structure and dynamics on the network. The nodes on the food web could be generalized to any component in the system which is described by population. And the edges of feeding relationships can be generalized as the material or energy flows which represent the interaction between two nodes. The fast dynamics of flows is modelled as a set of differential equations. Once the rules of updating the network are given, the slow dynamics of network structure is determined. Hence, the co-evolution of dynamics on the network and the dynamics of the network can be modelled.

One of the earliest applications of this modelling approach can be traced to Farmer and Bagley et al.^[62,63] They used the similar method to study the auto-catalytic network in which the nodes are chemical species. They considered two kinds of interactions, catalysis and material flows within chemical reactions, so more complicated differential equations were used in their model. Jain simplified their model by only considering the catalytic relation^[56]. He also pointed out the auto-catalytic network can be applied to more practical problems such as: cooperation, species extinction, origin of life etc^[64]. The phenomenon and modelling method for co-evolution of network structure and the dynamics on the network is paid much attention recently in the community of complex networks^[10].

4 Flows in Other Complex Systems

4.1 Flows in Generalized Ecological Systems

Although most of studies of energy flows are concentrated in ecology, flow as a pervasive phenomenon exists in other complex systems. The resource flow in a complex system may function the similar way as the energy flow in the ecological system. The resource flow provides the basic power to drive the system evolving although the components of these complex systems may be very different from enterprises and human beings to computer programs. Different components in the system will be connected by the mutual resource flow to form a complex entangled network. Therefore, these systems can be studied as a generalized ecological system.

Human cities are generalized ecological systems called urban ecosystems in which human beings and artificial objects interact each other to form a complex system^[67]. Urban ecosystems need energy flows to survive and develop. The similar allometric relationship between the energy flux and the store in the urban ecosystems was found. Kuhnerta et al.^[9] collected the data of population and the electronic supply of several German cities, then they got a similar power law relation between the generalized flux F (electronic supply) and store M (population of the city) like: $F \propto M^b$. However the exponent b is not $3/4$ but around 1.1 that represents urban system is more efficient to transport energy flows. Moses et al. found a power law relation between the per capital consumption F (Generalized energy influx) and fertility rate of human being (R) (See Section 2.1.2) in the human cities which is a deduction and indirect proof of equation (1)^[7].

Industrial systems can also be viewed as a generalized ecosystem in which the enterprises as individual organisms form a complex transportation network for product flows^[68]. The material and energy resource connect all of them as a whole. The model of food web have been used to analyze the interactions between these enterprises and quantify the various fluxes in the industrial system^[68–70]. Using the approach of ecology to study the industrial system forms a new discipline called industrial ecology^[68].

Some economic systems are examples of generalized ecological system in which money and products flow on the trade network. These resource flows function as the energy on the food web so that the structure of the network is changed by flows to deduce the similar statistical patterns. Duan^[8] studied the international weighted trade network by treating them as the transportation networks. He used Garlaschelli's approach to reduce the trade network as a spanning tree and drew the relationship between A_i and C_i to obtain a power law distribution. The exponent is 1.30 for the binary web and it is 1.03 for the weighted web. One more example is the power law distribution of firm sizes well known as Zipf law in the economic system^[71] because this power law is the indirect result of the relationship between N (population density) and M (See section 2.1.2).

Some computer systems or software systems may be viewed as a generalized ecological system in which programs are like organisms that are striving to obtain the generalized energy flow resource (CPU time) and memory space to survive^[72]. The computational ecological systems can provide new horizons to simulate the natural systems^[72] and help us to solve some real problems such as the distribution of various computational resources^[73,74]

4.2 Physical Theory of Flows

In fact, flow as an important phenomenon in nature has been studied by non-equilibrium physics for a long time^[75,76]. Some new studies in this direction have also emerged in recent years.

A principle called maximum entropy production^[77] in far from equilibrium systems functions the similar way as the second thermodynamic law or the principle of maximum entropy in equilibrium systems. Actually, there is a corresponding principle called maximum power in ecology^[65,61,66]. They all predict that a non-equilibrium system will evolve to a state that

maximizes the flux in the system. So Bejan extended these principles as the maximum flux principle. He claimed that various fractal patterns in nature are the spontaneous results of the optimization of the flux^[32]. He called his theory as the construction law which can be used to other subjects.

Dewar has provided a statistical foundation for the maximum entropy production principle^[78] and maximum flux principle^[79]. He used the principle of maximum information entropy to derive the maximum entropy production principle and power law distributions^[78]. Influenced by Jaynes, Dewar believes that the macroscopic phenomenon that we have perceived is the most probable one which can be obtained by maximizing the information entropy as a statistical inference result. The maximum entropy principle is very successful in equilibrium statistical physics. It is plausible to apply it in non-equilibrium systems. The key idea of Dewar's extension of maximum information entropy principle to non-equilibrium systems is treating the flow pathways as the basic statistical objects just like the states in equilibrium systems. In another word, the flow pathway that is observed by us is the most probable path. And Dewar also showed the most probable pathway is just the path of maximum entropy production.

It is plausible that Dewar's work might provide the theoretical foundations of flow phenomena in complex systems. It may be a heuristic for the explanation of general allometric scaling principle. Particularly, Equation (2) for different exponent b in different systems might be predicted by the new statistical mechanics of flows. The physical theory of flows have emerged to be a powerful approach to understand numerous natural phenomena^[80,81].

5 Concluding Remarks

Energy flow is a very important phenomenon of complex systems because the system needs to be open to obtain resource. Allometric scaling is a pervasive pattern found in ecological systems. This law is fundamental because many other relationships between biological variables and body size can be derived from it. This power law is universal since it can be used to describe the very general relationship between flow and store which can be extended not only for the different ecological scales but also other generalized complex ecological systems.

The branching structure of the flow transportation network can provide the reasonable explanation for the allometric scaling law. Also it can be generalized for the other flow systems. Food web is the instance of this transportation network of the ecological community.

The dynamics of flows and the co-evolution of flows and network structure can be modeled by the population dynamics on the evolutionary food web. This method could be used in other systems.

Finally, some fundamental principles of flow system may be discovered by the studies of non-equilibrium physics. The principle of maximum flux and construction theory will play the fundamental role in the study of flows. The statistical mechanics framework of flow systems may be the future direction needed to be studied.

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