

Allometric Scaling of Weighted Food Webs

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Abstract. Allometric scaling is an important universal property of metabolic living systems. It also describes the self-similar branching tree-liked structures in transportation networks. This paper presented a new approach to calculate the allometric scaling power law relations for arbitrary flow networks. This method can not only avoid the shortcoming of losing lots of information in the process of generating spanning trees in the conventional approaches but also can be applied to arbitrary weighted networks. The allometric scaling properties of 20 empirical weighted food webs (weights are energy fluxes) are computed according to the new approach, the power law relationships are derived with the universal exponent $\eta = 1.0298$ which reflects the transportation efficiency of the food webs.

Keywords: allometry, power law relations, energy flow, weighted network.

1 Introduction

Food web is a network to describe the prey-predator interactions in an ecological community or ecosystem. Binary food web only cared about the existence of a given predation interaction. However, energy flows play more important roles on comprehending complex ecological community than the binary networks because every species needs energy to survive. Thereafter, food web is actually an energy transporting network. When a species predate its preys, energy embodied as food transferred from the prey vertices to the predator vertex. Thus, weighted food web whose edges have weights to denote the energy fluxes transferred from a prey to a predator is more comprehensive on describing ecological communities than the binary food web. Recently, more and more empirical weighted food webs data with high quality have been collected [1]. What we need is a good approach to reveal the common features of these networks [2].

Allometric scaling is an important universal pattern for transportation systems. Kleiber [3] found that the metabolism and body size of all species follow a ubiquitous power law relationship, and the exponent is $3/4$. West et al. [4] and Banavar et al. [5] explained these patterns as an emerging property of nutrient and energy transportation networks. This recognition encouraged people to reveal that the allometric scaling may be a universal feature for all transportation systems. Garlaschelli et al. [6] extended Banavar's approach to binary food

webs and found a similar allometric scaling power law relationship. Because Garlaschelli's approach is an abstract algorithm for any network, it can be applied to other systems. Duan [7] used Garlaschelli's approach on international trade network and found similar power law relationship. Herrada et al. [8] applied this method on the tree of life.

Although Garlaschelli's method as an algorithm had been used in various binary networks, there are some shortcomings. Firstly, Garlaschelli's approach loses lots of information to get the result. The first step of his algorithm is obtaining a spanning tree, so lots of edges of the original network must be cut although Garlaschelli had claimed that the cut edges are always "weak" links. Allesina and Bodini [9] improved this method by reducing the original network to a directed acyclic graph. Although less amounts of information will be lost, the problem remains there. The second shortcoming is Garlaschelli's approach and Allesina's improvement can be only applied to binary networks. The allometric scaling power law was found in various transportation systems, thus the flows are more important. That is the reason why Garlaschelli's method should be extended to weighted flow networks.

In this paper, we presented a method to calculate the allometric scaling relationship for weighted transportation networks. This approach avoids the shortcomings of Garlaschelli's method. And then the new algorithm is applied on 20 empirical weighted food webs, the universal allometric scaling relationship is found.

2 Revisiting Allometric Scaling of Food Webs

Before presenting our method, we should revisit Garlaschelli's approach at first. For a given binary food web (See Fig. 1(b) as an example), the spanning tree (Fig. 1(b)) is reduced from the original network (The method of generating the spanning tree is referred to [6]).

In Fig. 1(a), the numbers of each vertex are just indices of nodes. In Fig. 1(b), the number inside the circle of any vertex i is called A_i , and the number outside

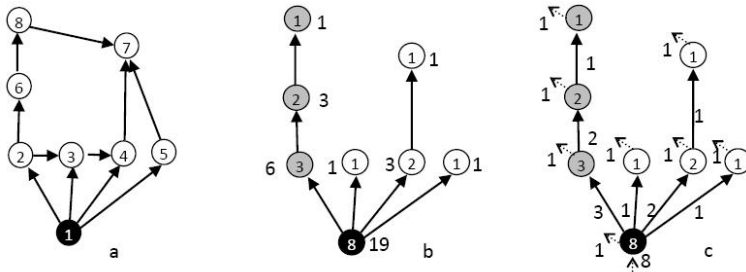


Fig. 1. Calculation of allometric scaling of a hypothetical food web. (a) is a hypothetical food web; (b) is a spanning tree of the original network (a). (c) is the flow network representation of (b) implied by Garlaschelli's approach.

the circle of the vertex i is indicated as C_i . If we denote the sub-tree rooted from the node i as T_i , then A_i is the number of vertices of T_i , and C_i is the summation of all vertices' A_i s in T_i , that is, $C_i = \sum_{i \in T_i} A_i$. For example, the gray vertices in Fig. 1(b) belong to the sub-tree of the whole spanning tree of Fig. 1(a) rooted from vertex 2 (The indices are from Fig. 1(a)). Therefore, $A_2 = 3$ is just the number of vertices in this sub-tree, which is denoted in the circle of vertex 2. We can calculate the A_i s in all of the vertices in the sub-tree T_2 , then C_2 can be calculated as, $C_2 = A_2 + A_6 + A_8 = 6$, which is denoted outside of the circle of vertex 2.

Therefore, we can calculate a set of pairs (A_i, C_i) for any spanning tree, and the allometric scaling can be derived if the plot of pairs (A_i, C_i) on the Log-Log coordinate can be fitted by a line. Garlaschelli applied this method to a set of empirical food webs, the universal allometric scaling relationship and power law exponent was found [6].

Actually, Garaschelli's method was inspired by Banavar's [5] model to explain the Kleiber's law. The spanning tree is just the Banavar's transportation network (See [5]). Thus, the energy flows into the whole system from the root (black vertex) and is delivered along the links of the network to all nodes. Suppose that each node would consume 1 unit of energy in each time step. Then the flux with 1 unit representing the energy consumption by each vertex should be added on the original spanning tree. In Fig. 1(c), the energy dissipation by each vertex is added as a dotted line. And the numbers beside edges are weights representing the energy flux of the edge. As the result, a flow network can be constructed from the original food web. And A_i of each node is just the total influx of this vertex. C_i is the total flux of the sub-tree rooted from i . For example, the sub-tree with gray vertices is just a sub-system of the whole spanning tree. And A_2 is the total influx of this sub-system, and C_2 is the total amount of the energy flowing in this sub-system.

Hence, for any vertex i , the sub-tree T_i rooted from i can be viewed as a sub-system of the whole spanning tree. Then, A_i is the influx from outside of the sub-system. And C_i is the total flux of the T_i (total amount of flowing matters in T_i). Thus, if we treat the sub-system T_i as a living system, then A_i is the metabolism of this organism, and C_i is its biomass. Therefore, if A_i and C_i follow a power law relationship, that means the living system T_i obey Kleiber's law although the exponent may be different. This comprehension is important because it will be extended to general flow network systems.

3 The Method

In this section, we will introduce a new approach which can calculate the values (A_i, C_i) to testify the allometric scaling relationship of any general network flow system. The approach will be given at first, and then be explained further by a simple example. At last, this method is testified by comparing to Garlaschelli's approach.

3.1 Deriving A_i s and C_i s for Any Flow Network

For a network flow system with $N + 1$ vertices (the $(N + 1)$ th vertex is just the environment) and weighted directed edges, we can use an $(N + 1)^2$ entries flux matrix F to represent it. Any entry of F denoted as f_{ij} is the weight representing the flux from vertex i to vertex j . Assume that the system is in the steady state. That means the flux balance condition should be hold,

$$\sum_{j=1}^{N+1} f_{ji} = \sum_{j=1}^{N+1} f_{ij}, \forall i \in [1, N + 1] \tag{1}$$

For defining C_i , two matrices M and U should be defined at first. For any balanced matrix F , we can define an $N \times N$ real matrix M , any entry of it m_{ij} satisfies:

$$m_{ij} = \frac{f_{ij}}{\sum_{k=1}^{N+1} f_{ik}}, \forall i, j \in [1, N] \tag{2}$$

Because the condition (1) is hold for F , the determinant of M is smaller than 1. Therefore, another matrix U can be derived from M :

$$U = I + M + M^2 + \dots = \sum_{i=0}^{\infty} M^i = (I - M)^{-1} \tag{3}$$

According to the discussion in the previous section, A_i representing the influx to the vertex i from outside of the sub-system that i can influence, then it can be defined as (We don't need calculate the A_i value of the vertex $N + 1$):

$$A_i = \sum_{j=1}^N f_{N+1,j} U_{j,i} / U_{i,i}, \forall i \in [1, N] \tag{4}$$

Finally, C_i of any vertex i can be defined as:

$$C_i = A_i \sum_{j=1}^N U_{ij}, \forall i \in [1, N] \tag{5}$$

For any flow network, the condition (1) may not be satisfied, we must balance the fluxes artificially. Suppose condition (1) is not hold for vertex i , which means $\sum_{j=1}^N f_{ji} \neq \sum_{j=1}^N f_{ij}$, then we can add an edge with the weight $|w_{ij}|$, $w_{ij} = \sum_{j=1}^N f_{ji} - \sum_{j=1}^N f_{ij}$ to connect the vertex i and $N + 1$. If $w_{ij} > 0$, the direction of this artificial edge is from i to $N + 1$. If $w_{ij} < 0$, the direction is from $N + 1$ to i . Once the artificial edges are constructed for all vertices, the approach mentioned before can be applied. At last, we locate all pairs of A_i C_i on a Log-Log coordinate, and expect the following equation holds:

$$C_i \propto A_i^\eta \tag{6}$$

Where, η is the exponent of the power law and the slope of the best fit line on the Log-Log coordinate which may reflect the transportation efficiency of the network [6].

3.2 A Simple Example

To understand the method introduced in the previous sub-section, let's take a simple example. See Fig. 2,

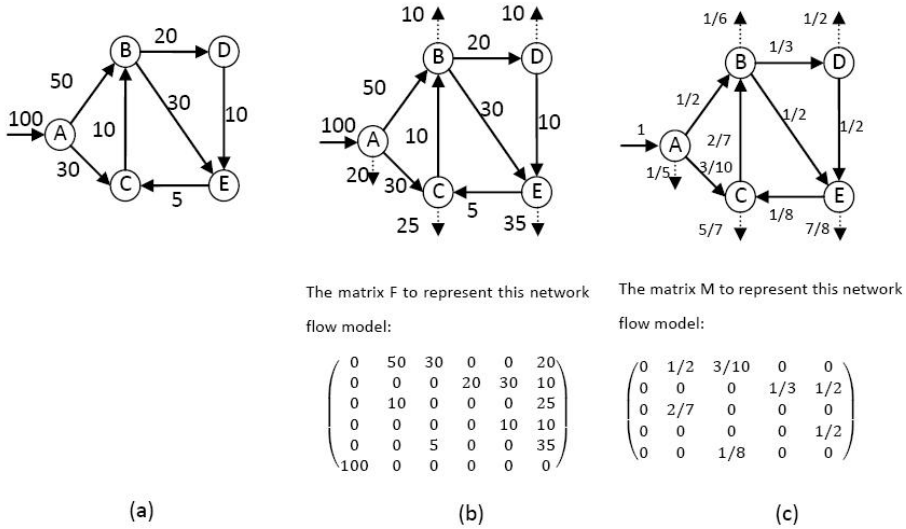


Fig. 2. An example to illustrate our method on deriving A_{is} and C_{is} (a) is the original flow network, (b) is the balanced network from (a), (c) is the probability network represented by M

Fig. 2(a) is the original flow network, and Fig. 2(b) is the balanced network from (a). The matrix representation of Fig. 2(b) is the matrix F listed under the Fig. 2(b). The matrix M derived from F is listed under the Fig. 2(c).

To understand the physical meaning of the matrix M , suppose a particle flows in this network from A . It will have $1/2$ probability to transfer to B , $3/10$ probability to C and $1/5$ probability to the environment. Thus, the matrix M represents the probabilities the particle flows from one vertex to the other after 1 step transfer. $M \cdot M$ represents the probabilities the particle flows from one vertex to the other after 2 steps, i.e., any entry (i, j) in $M \cdot M$ represents the probability of a particle flows from i to j along any paths in 2 steps. And $M \cdot M \cdot M$ represents the probabilities after 3 steps, etc. [10]

When we repeat this experiment again and again, many particles flow along the network randomly, the fluxes can be formed. Then, the flux from A to E after three steps is the number of particles that travel from A to E after three steps. Because the number of particles flowing into A in each step is 100, the flux from A to E after three steps is $100 \cdot (M \cdot M \cdot M)_{1,5} = 25$. The total flux from A to E should be the summation of fluxes with one step, two steps,..., until the infinite steps from A to E along all possible paths. So we can compute the matrix,

$$U = I + M + M^2 + \dots = (I - M)^{-1} = \begin{pmatrix} 1 & \frac{3}{42} & \frac{7}{20} & \frac{1}{5} & \frac{2}{8} \\ 0 & \frac{41}{42} & \frac{82}{42} & \frac{14}{41} & \frac{28}{41} \\ 0 & \frac{41}{42} & \frac{41}{42} & \frac{41}{4} & \frac{41}{8} \\ 0 & \frac{164}{3} & \frac{328}{21} & \frac{164}{1} & \frac{41}{21} \\ 0 & \frac{82}{82} & \frac{164}{164} & \frac{82}{82} & \frac{41}{41} \end{pmatrix} \tag{7}$$

to calculate the total flux from i to j along all possible paths with all possible time steps.

Now, we will show how to calculate the A_i and C_i for vertex B . According to the discussions in the previous sub-section, the A_i value is the metabolism of the sub-tree rooted from i , C_i value is the total flux of the sub-tree. But now, for any flow network, sub-trees can not be obtained. Suppose the particles flowing to B will be colored red. Then all of red particles flowing in the whole network can be viewed as the sub-system rooted from the vertex B although the sub-system is not obvious. Hence, in each time step, the total number of particles which turns from uncolored to red is just the value A_2 . The total number of red particles in the whole network is just C_2 . According to the linear algebra [10], the number of particles turning to red in each step is:

$$A_2 = \sum_{j=1}^5 f_{6,j} U_{j,i} / U_{i,i} = 100 \times \frac{3/5}{42/41} = 410/7 \tag{8}$$

Where, $f_{6,j}$ is the flux from environment to the vertex j . And $\sum_{j=1}^5 f_{6,j} U_{j,i}$ is the total flux of the particles entering the network and getting to the node i along all paths with various lengths. Of course, some of them may have passed the vertex i and reenter this node again. Thus, we should not count this part of flux. That is the reason why dividing by $U_{i,i}$ in equation 8 [10]. In a word, the calculation of A_2 in equation 8 is the total number of particles which turns to red from uncolored state in one step.

The total number of red particles flowing in the whole network is:

$$C_2 = A_2 \sum_{i=1}^5 U_{2,i} = 410/7 \times 175/82 = 125 \tag{9}$$

Hence, we can use this approach to calculate C_i values of all vertices.

3.3 Validation of Our Approach

Our approach can be used to any flow network including the spanning trees. So Garlaschelli's approach is included by our method. Actually, it is not difficult to testify that our approach can get the same values of A_i s and C_i s as Garlaschelli's approach. For example, when we apply our approach to Fig. 1(c), we can get vectors of A_i s and C_i s: $A = (8, 3, 1, 2, 1, 2, 1, 1), C = (19, 6, 1, 3, 1, 3, 1, 1)$. It is exactly same as the values denoted on Fig. 1(c).

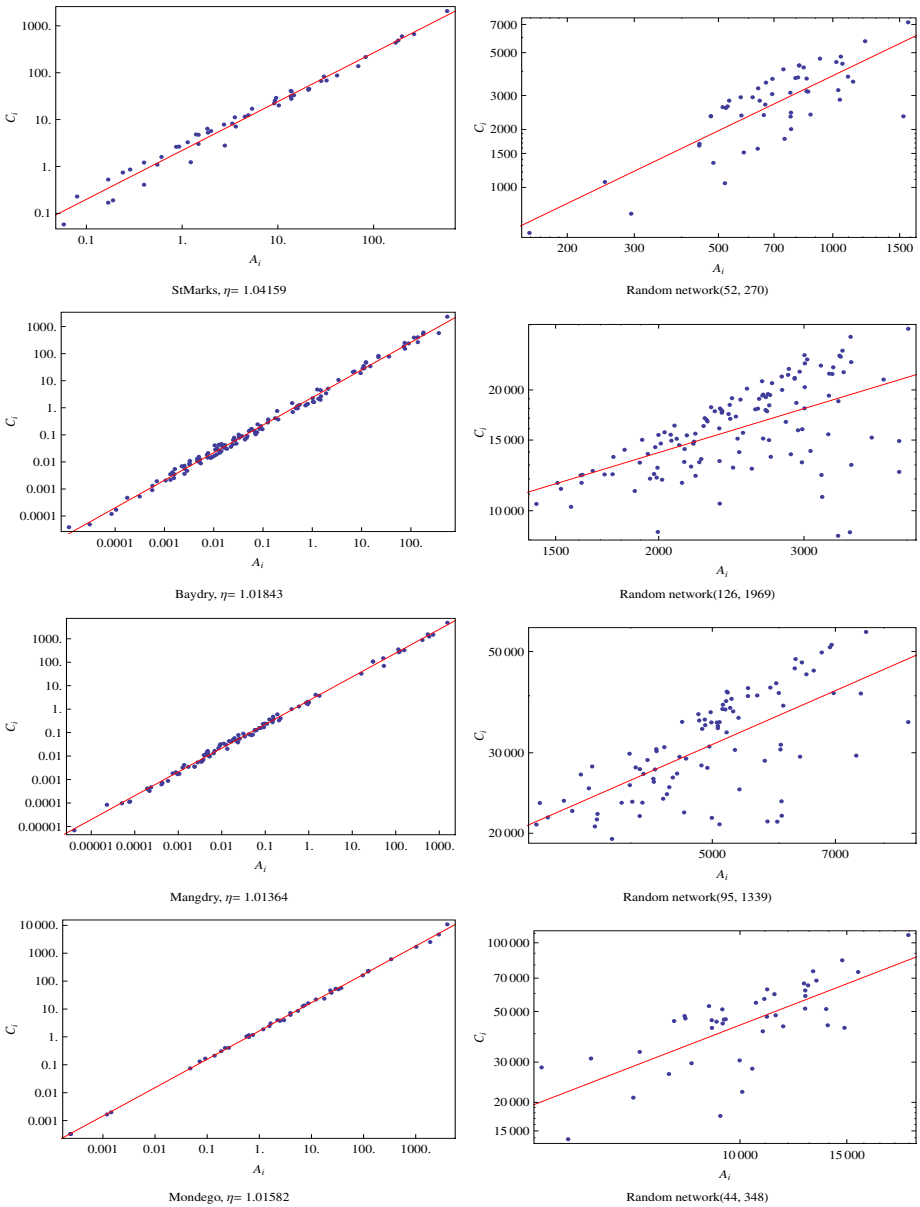


Fig. 3. A_i , C_i plots of 4 selected food webs and the random generated network flow with the same scale (number of vertices and edges) as the corresponding food webs. The plots in the left column are allometric scalings of empirical food webs with best fitting lines. The plots in the right column are A_i s and C_i s of random networks generated with the same scale as the left corresponding food web. The numbers in brackets are the number of vertices and edges respectively. The numbers of vertices of each food web are excluding input,output and respiration nodes which are contained in the original data files.

4 Results

Empirical weighted food webs can be obtained by field experiments. The vertices stand for living species or non-living units such as detritus or respiration. The flux of each edge is obtained by the experiments of tracing the flows of Carbon or Nitrogen isotope in the real food webs. The raw data of 20 weighted food webs is obtained from [11]. (All data of food webs on this web page are obtained from published papers)

The allometric scaling relationships are computed by our approach for 20 food webs, the results are listed in Table. 1. Four food webs are selected to plot their A_i and C_i values on the log-log coordinate with the best fit line. Also, the same approach is applied to the generated random network with the same number of vertices and edges as the food web, and they are plotted on the right side to compare with the original food webs.

From Table. 1, we found that almost all food webs have the allometric power law relationship no matter what size (the number of vertices and edges) it is. One exception is Rhode, it has larger deviation of power law. The reason may be the number of vertices of this food web is too small, so the power law relationship can not emerge. The average exponent (except Rhode) η is 1.0298. This value reflects the average efficiency of the food webs as transportation networks. All of η values fall into the interval [1.00, 1.08], that means the power law relationship and the exponent is a universal feature of food webs.

From Fig. 3, we can observe that allometric power law relationship is a distinct character comparing to the random flow networks with the same size. Thus, our approach may reveal a hidden property of the transportation of energy in food

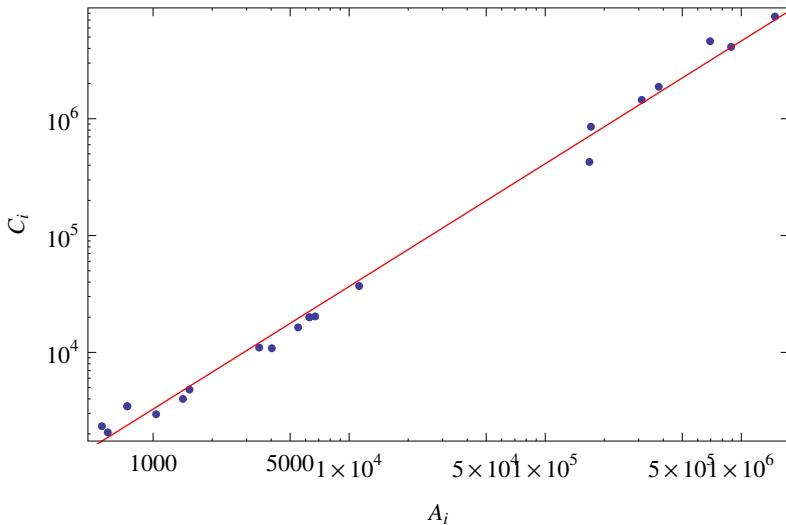


Fig. 4. A_i, C_i plot for root nodes of 20 food webs. The slope η (the power law exponent) in this figure is 1.04998.

Table 1. Allometric scaling of Empirical food webs

Food web	Fitting line equation	η	RSquare
St Marks	0.787904+1.04159 x	1.04159	0.978889
BayDry	0.87144+1.01843 x	1.01843	0.994778
BayWet	0.959133+1.02323 x	1.02323	0.994782
ChesLower	0.567216+1.05332 x	1.05332	0.997818
ChesMiddle	0.797378+1.04472 x	1.04472	0.996428
ChesUpper	0.708627+1.06001 x	1.06001	0.996794
Chesapeake	1.10347+1.00882 x	1.00882	0.996792
CrystalC	0.391906+1.04403 x	1.04403	0.997969
CrystalD	0.412903+1.0448 x	1.0448	0.998158
CypDry	0.787941+1.00028 x	1.00028	0.995786
CypWet	0.807567+0.999697 x	0.999697	0.997128
Everglades	0.554555+1.02117 x	1.02117	0.999203
Florida	0.959133+1.02323 x	1.02323	0.994782
GramDry	0.616884+1.02685 x	1.02685	0.999158
MangDry	0.835557+1.01364 x	1.01364	0.996732
Michigan	0.392247+1.01494 x	1.01494	0.99865
Mondego	0.488492+1.01582 x	1.01582	0.999255
Narragan	0.974056+1.0821 x	1.0821	0.992774
Maspalomas	0.985035+1.02975 x	1.02975	0.98396
Rhode	3.09222+0.775947 x	0.775947	0.803483

webs. And when we plot all root nodes' A_i and C_i values of these food webs, we got another power law relationship which was presented in Fig. 4. (The RSquare of this fitting line is 0.993534).

5 Discussion

Allometric scaling power law relationship between metabolism and body size of the creatures is one of the most important discoveries in ecology. In general systems, this pattern reveals that the universal power law relationship between flows and stores.

Food webs can be regarded as a self-similar flow system that means each sub-system of the food web can be viewed as a dependent metabolic system. Thus the flow of each metabolic system is just the total influx of each node and the store is the total flux of all vertices in this sub-system.

The conventional approach reduced the network as a branching tree structure, and each sub-tree is treated as a sub-system. Although the universal allometric scaling relationship can be found by this approach, lots of information is wasted when the spanning tree is generated. Another disadvantage of the traditional method is it can not be applied to weighted food webs but only binary networks.

In this paper, we presented a new approach to calculate the allometric scaling relationship of the food webs to avoid the two shortcomings. The key idea of our work is realizing that the information about the hierarchical structures is

hidden in the flux distributions on the whole network although sub-systems are invisible from the topological structure. The algorithm based on all flow paths that was put forward in this paper can extract these hidden patterns. Finally, the advantage of this approach is it can be applied to any flow networks but not only limited on tree structures.

The new approach of calculating allometric scaling can not only find the universal power law exponent for empirical food webs, but also provide new theoretical insights. As we have seen, the universal power law exponents of empirical food webs are closed to 1. According to equation (5) which is the definition of C_i , this equation implies the linear relationship between C_i and A_i . If $C_i \propto A_i^\eta$ holds for every vertex, then $\sum_{j=1}^N U_{ij}$ should be a constant (or a Gaussian random variable). That is to say, the allometric scaling relationship can be deduced to a new mathematical judgment. Further mathematical analysis will be done in future works.

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