

EVOLUTION OF COMPLEX FOOD WEB STRUCTURE BASED ON MASS EXTINCTION

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ABSTRACT

We demonstrate that complex food webs may originate from mass extinctions. For this purpose, a minimal computational model for the evolution of food webs is constructed. In the model, food web structure is represented by a kind of dynamic random graph with some biological constraints, and evolves under the condition without fitness, competition among species, nor population dynamics. It is shown that the behavior of the system has three different phases, among which the Class B (mid-phase) exhibits complex nonequilibrium dynamics and can reproduce the empirical observations.

Key words: complex networks, food webs, mass extinction, phase transition, power law, macroevolution

1. INTRODUCTION

Significant advances have been made in the field of complex networks in recent years [1, 6]. Especially the structure and the evolutionary dynamics of food webs are among the central issues under discussion [7, 15, 9, 4]. A food web is represented by a directed graph consisting of vertices (species) and directed edges (trophic links). Several reports have shown that such graphs do not have network topology of classical Erdős-Renyi's random graph, but rather are described as 'small world' or 'scale-free' [7, 15, 4].

Besides empirical analysis, there are theoretical approaches with some different classes of models [5]. The first class is characterized by static models, and suggest that food webs have some universal properties [16, 4]. The second is characterized by dynamic models, which include traditional population dynamics. And the last is concerned with food web properties of longer time scales or macroevolution. While the first two classes lack the combined view of dynamics and structure, this class targets such a combined view. Among them, scientists have taken a new approach based on toy models in recent years, where the patterns of mass extinctions in the fossil record or self-organized critical phenomena are focused [2, 14, 3, 11].

Recently several reports have investigated on the patterns of mass extinctions in the fossil record. Among them,

one of the most striking common features is that mass extinction follows power law distribution:

$$f(s) \propto s^{-\tau}, \quad (1)$$

where s is the size of mass extinctions, and $f(s)$ is frequency, with an exponent $\tau \approx 2$ [10]. Furthermore, quantitative models have been proposed to explain this power law distribution, and some relationships between food webs and mass extinctions are suggested [11, 2]. The essential problem can be summarized by two questions. What is the cause of mass extinction, and what is the mechanism of selecting victims [2]? Specifically, this paper focuses on the question: what mechanisms could generate the non-random but complex topology of food webs in nature?

According to the emerging complex networks theory, such non-random structures can be formed through network growing or some specific rewiring processes [6]. However, it is unlikely that food webs have perpetual growth in size or such specific rewiring mechanisms. Therefore, we investigate another simple mechanism which can reproduce such non-random topology.

Our basic idea is that mass extinctions may bring about non-random topology to food webs, in other words, mass extinctions keep food webs far away from equilibrium state and at the same time complex structure gradually evolves through symmetry breaking. In general, symmetry breaking occurs in a situation where, given a symmetrical equilibrium state, a self-amplifying mechanism of fluctuation exists which can be activated by asymmetric input or flow. Such a self-organized structure in a situation of this type is known as "dissipative structure" [12], where the fluctuation is essential. Therefore, were it not for any constraint in the evolution of species, food web structure would be like random graph. However, living organisms have evolutionary constraints such as natural selection at least at the level of individuals within a population (microevolution). We believe that mass extinctions may function as the amplifying mechanism at the level of stable species (macroevolution).

With these issues in mind, we construct a minimal model of food web evolution which has following two key features.

- The model has an evolutionary mechanism which is represented by random rewiring. Thus food webs are destined to random networks as equilibrium state but for any other mechanisms.
- At the same time, a mass extinction mechanism is adopted, which potentially drives the networks to non-random state through symmetry breaking.

At least in principle, the model could generate non-random network topology and show both the power law distribution of extinction sizes and scale-free degree distribution of networks. The degree distribution is the distribution of number of edges attached to each vertex. These features are based on the idea that fitness or interspecies competition might not be the driving force of macroevolution [8, 13].

This paper is organized as follows. First, we describe a minimal model for macroevolution. Then we investigate its statistical and structural properties based on the computer experiments. Finally we discuss some biological implications and conclude the paper.

2. MODEL

A food web is represented by a directed graph, in which each node expresses a species and each arrow from one node to another indicates a trophic link, in other words, an energy flow from a resource species (prey) to a consumer species (predator). The single root node represents the energy source like the sun.

The dynamics of the system is governed by two mechanisms. The first one represents an evolutionary process realized by random rewiring of edges (addition or removal). This mechanism has a tendency to increase the system's entropy towards a maximum. The second mechanism has the potential to cause mass extinctions. Extinctions occur in two cases. The first case is random accident; a species is selected for extinction randomly. The other is co-extinction; a vertex lost all in-edges becomes also extinct. Note that if all of a species' prey become extinct, then it too becomes extinct (recursively). So, avalanches of extinction (mass extinction) can occur. This mechanism is based on Amaral-Meyer [2]. After these processes, randomly selected species will be duplicated immediately. Thus the size of network N will be kept in constant.

The model is summarized as the following repetition of steps:

1. A random accident occurs with a probability P_{accident} , which means that a vertex is selected randomly and all edges connected to it and itself are deleted. Otherwise, the following rewriting process is executed. First, a pair of vertices is selected randomly. Then addition of the edge is attempted with the probability P_{addE} . Otherwise removal of the edge (if any)

Table 1: Parameters.

N	the size of network
P_{accident}	the rate of random accident at each steps
P_{addE}	the rate at which adding edge is attempted

is attempted. In case of addition, the direction of the new edge is determined based on the trophic level; the edge would be directed from vertex of a lower trophic level to upper one. The trophic level of a vertex is the path length from the root to it.

2. All vertices with no in-edge and all edges connected to them are deleted recursively.
3. The process that randomly selected vertex and all edges connected to it are copied is repeated until the size of the network reaches to the constant value N .

In the case that there is no vertex other than the root, a new vertex is generated, and the root and the vertex are connected by a new edge.

3. RESULTS

3.1. General behavior

First, we focus on the trophic diversity so as to explore the general behavior of the system. The trophic diversity is defined as the number of trophic species. Here, trophic species are the groups of vertices that share the same set of trophic relations.

Figure 1 shows the trophic diversity determined by temporal average at each run with parameter sets. We see that it is steady nearly at the upper limit in the region of low P_{accident} and high P_{addE} . In contrast, the highest P_{accident} or lowest P_{addE} region has the trophic diversity of the lower limit 1. The transition region between them is limited to the narrow area.

A time-series of the trophic diversity is examined in order to investigate the evolutionary activity and the transition process (Figure 2). Note that P_{addE} is increased linearly at a constant rate every time step. Trophic diversity has the value of the lower limit at start-up (Class A), then an explosive growth up to the upper limit occurs as P_{addE} increases. In this phase, intensive fluctuation is seen (Class B). After that, the number of fluctuation comes down (Class C). Considering the way of the extinction and replication mechanisms adopted in the model, it is clear that the fluctuation indicates mass extinction.

Next, we conducted an analysis in order to reveal statistical features of the system. Figure 3 shows the frequency distribution of sizes of extinction (the number of deleted

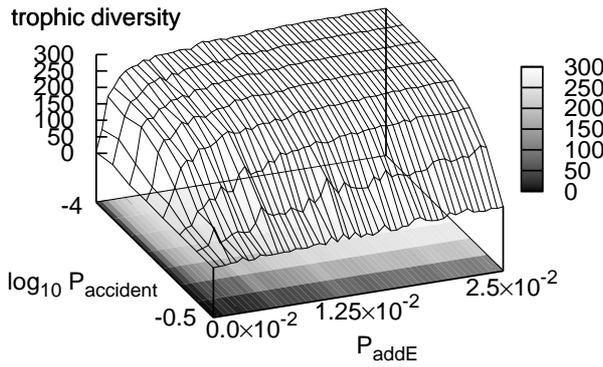


Figure 1: The landscape of trophic diversity; X: P_{addE} , Y: $P_{accident}$ (log scale), Z: trophic diversity. $N = 300$.

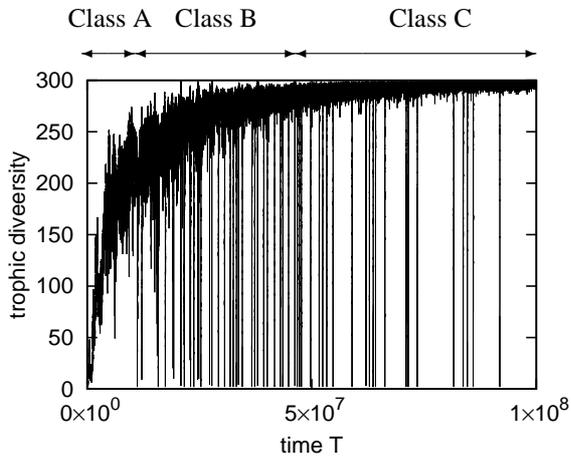


Figure 2: Transition process of trophic diversity. $P_{accident} = 0.001$. P_{addE} follows linear function of time step T ; $P_{addE} = T \times 2.5 \times 10^{-10}$. Network size $N = 300$.

vertices at one step). It is shown that it approximately follows the power law $F(s) \approx s^{-\tau}$ with exponent $\tau = 1.5 \sim 4.0$, in which as P_{addE} increases the exponent τ also increases.

We also examined the network topology by its degree distributions. Figure 4 shows the degree distributions of networks. As we see from the figure, the distribution can be clearly divided into three types: exponential, scale free and poissonian distributions. The terms Class A, B and C used in the above description are defined based on this observation. Exponential distribution arises at very low P_{addE} , which correspond to Class A. It has been also shown that scale free distribution arises in Class B, and poissonian distribution arises in Class C.

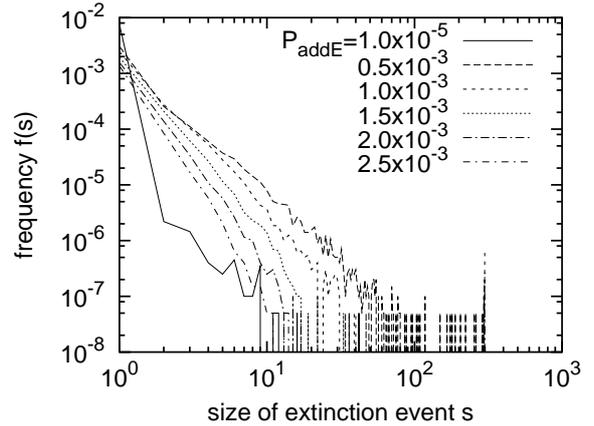


Figure 3: Frequency distributions of size of extinction. $P_{accident} = 0.001$. Network size $N = 300$.

3.2. Behavior in each class

Class A, B and C are investigated individually in order to do more detailed analysis. Firstly, we investigated the relation between parameter sets and the evolutionary behavior. The result is shown in Figure 5. Parameter sets of the area shaded black or dark gray (the left or upper side) produce the behavior classified as class A. White area (the lower right large area) of parameter sets corresponds to class C. Class B corresponds to the parameter sets in the light gray area between class A and class C.

3.2.1. Class A (frozen state)

In this class, the system is in the frozen equilibrium state. It appears when ‘adding of an edge’ is rare, and ‘random accident’ is frequent. In this class, almost all vertices are linked directly to the root vertex at all times. Thus, the networks have always the star network topology. As for the dynamics (Figure 6), trophic diversity is kept around the lower limit 1, and at the same time mass extinction is rare, which is an inevitable corollary. The state in this class is summarized as low diversity, high stability, and high spatial symmetry.

3.2.2. Class B (complex state)

In this class, the system exhibits complex and inhomogeneous behaviors. As shown in Figure 4, the degree distribution follows the power law behavior. However, degree distribution at every step has a significant deviation from that (in Figure 9). In many cases, they seem to be exponential rather than power-law distribution. From the dynamical view point, the networks always fluctuate intensively in contrast to the class A. In conjunction with such network

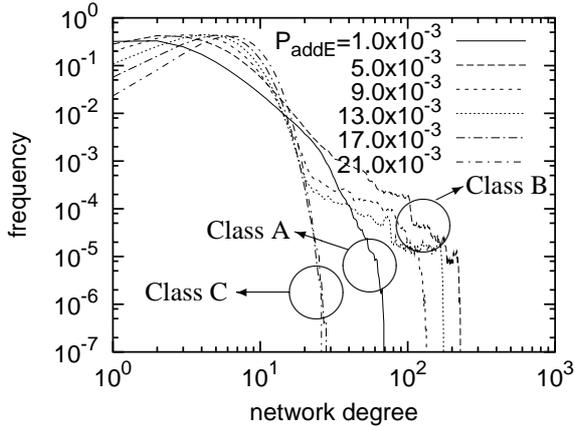


Figure 4: Degree distributions of networks. $P_{\text{accident}} = 1.0 \times 10^{-3}$, Network size $N = 300$.

dynamics, this class has many punctuated mass extinctions with different sizes ($1 \sim N$) as shown in Figure 7.

3.2.3. Class C (chaotic state)

In this class, the system exhibits chaotic or random behavior. In other words, the system is in the homogenous equilibrium state. Networks are random graph at all times. The number of mass extinctions is smaller than that in class B, and the size of mass extinctions are homogenous; small extinction or annihilation as shown in Figure 8. Annihilations occur when the trophic link is removed for some reason, given that it is just one trophic link from the root in the network. After such annihilations occur, the network takes back a random topology swiftly. Thus, in this class the system shows an equilibrium state at almost all times. Dynamics in this class is summarized as an equilibrium homogeneous behavior with exception of annihilations and prompt recovery from it.

4. SUMMARY AND DISCUSSION

This paper has proposed a minimal model for the evolution of food webs using a kind of dynamic random graphs with some biological features, so as to examine the possibility that mass extinctions may originate complex food web structure.

It was shown that the system consists of three phases: frozen, complex and chaotic, one of which emerges according to the parameter sets. The dominant factor here determining the behavior is the balance between the rate of randomization (evolution) and the frequency of accidents (ex-

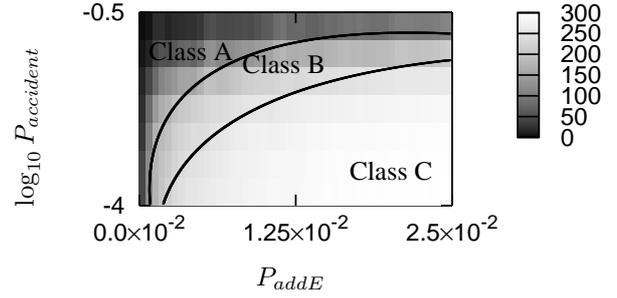


Figure 5: Phase diagram. Gray scale represents trophic diversity. Network size $N = 300$. The border lines are not accurate, but rough sketches.

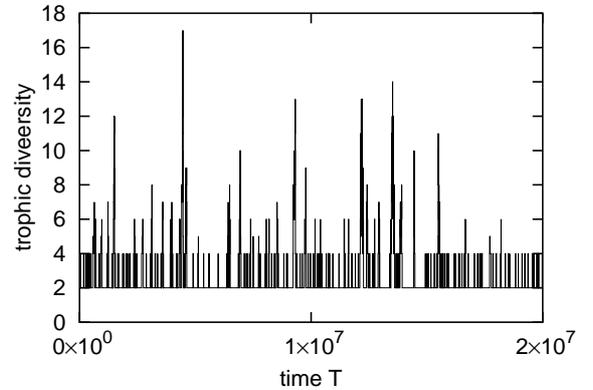


Figure 6: Evolution in Class A. $N = 300$. $P_{\text{addE}} = 1.0 \times 10^{-5}$. $P_{\text{accident}} = 0.01$.

inction). When the rate of randomization is high compared with accidents, in other words evolution of each species is sufficiently quick or ecosystems have few accidents, the food web evolves toward a random graph in which the system is in a chaotic state. On the contrary, in a too risky environment with many accidents, the system could never evolve its diversity and remains in a frozen state which consists of only autotrophic species.

The most suggestive state is the complex state (Class B: mid-state). It is inhomogeneous and in nonequilibrium, and is maintained through a self-amplifying mechanism of fluctuation: 1) mass extinctions cause deviation from equilibrium through replicating process, 2) copied vertices accelerate the growth of deviation after the mass extinctions. Thus, symmetry breaking could occur in this phase through mass extinctions.

With regard to topology in this class, the degree distribution at every time step seems to have an exponential dis-

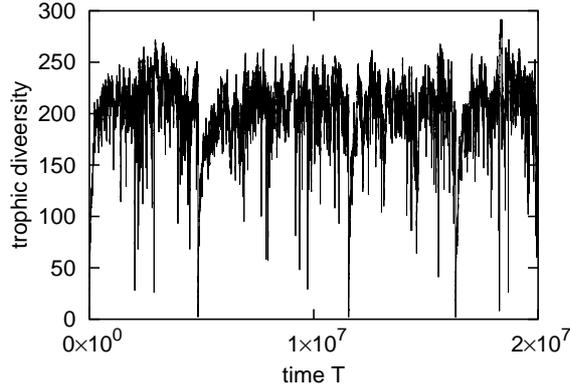


Figure 7: Evolution in Class B. $N = 300$. $P_{addE} = 3.0 \times 10^{-3}$. $P_{accident} = 1.0 \times 10^{-3}$.

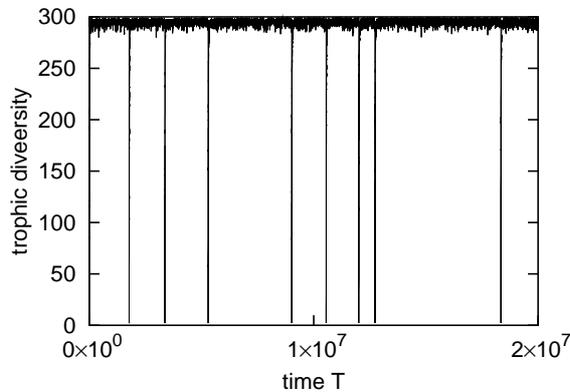


Figure 8: Evolution in Class C. $N = 300$. $P_{addE} = 0.02$. $P_{accident} = 0.001$.

tribution typically rather than power law distribution. This observation corresponds to empirical data [7]. On the other hand, when measuring the degree distribution in a long time scale it seems to have a power law degree distribution as shown in Figure 4. Though it seems very difficult to collect such empirical data in a long time scale, these results suggest that the real food webs might have a power law degree distribution, if longer time scale is in scope. Also, it is worth noting that in this class the exponent τ of power law in mass extinction takes a value in $1.9 \sim 2.5$, which is parallel with the empirical data ($\tau \approx 2$).

These observations lead to the conjecture that real food webs may be an embodiment of this complex class. That is, food webs might have been maintained in a nonequilibrium complex state through mass extinctions. In contrast to the mid-phase, the chaotic state with a topology of random graphs has no empirical data. The chaotic state in this model is realized under the condition with the low extinction rate

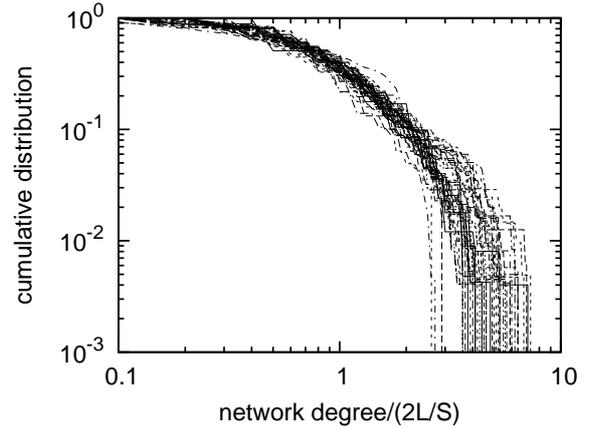


Figure 9: Cumulative degree distribution at each time step. $N = 300$. $P_{addE} = 3.0 \times 10^{-3}$. $P_{accident} = 1.0 \times 10^{-3}$. 50 networks are randomly sampled from 2×10^7 steps. The data are normalized by the number of edges/vertices ($=L/S$) in each network.

compared to the rate of evolution, in other words, under the quiet and stable environment, which seems contrary to the nature of ecological systems on earth.

These results support the idea that the main driving force behind macroevolution might not be the competition among species known as “the survival of the fittest” based on the fitness. Alternatively, another mechanism might be the main driving force: the natural selection or accident, which acts not on individual species but on the segments or clusters in ecological networks, forms the structure of ecosystems. That is, as for macroevolution, the unit exposed to selection might not be individual but the structure of ecological networks.

The discussion can be summarized in the following two hypotheses.

- Real food webs may be an embodiment of the nonequilibrium complex class formed through mass extinctions.
- Degree distribution of the real food webs at longer time scale may follow the power law.

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