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Self-organizing stability of food web that emerges from the evolution of restrictions on speciation

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Abstract

The food chain length has been considered as a key characteristic of food webs, and thus understanding its determinants is becoming increasingly important for ecosystem management and biodiversity conservation. For this purpose, we propose an evolutionary network model of food webs that captures the essential features of the ones in the real-world. The results show some universal features of food webs including the fractions of top, intermediate and basal species in the webs, which are in good agreement with empirical data. We will discuss how this structure can emerge in the simple evolutionary model of food webs.

Keywords: Ecosystem, Evolution, Extinciton, Restriction, Food chain, Scale-free network.

1 introduction

A food web is a highly complex network which defines prey-predator relationships of species. Understanding the structure and functioning of ecosystems by exploring the network topology has long been a central topic of ecological research. Various modeling levels and types of models have been proposed by ecologists, mathematicians and physicists for understanding the mechanisms of ecological dynamics.

Amaral and Meyer's model [1] is a well-known example based on a dynamic growth structure to clarify universal features of food webs. They constructed a network model for large-scale extinction and evolution of species, in which there exists a strong restriction that limits the number of the species on each trophic level and the establishment of prey-predator relationship between distant trophic levels. The results showed a power-law distribution of extinction avalanche sizes, in good agreement with available data from fossil records. However, they did not discuss on the influence of such restriction on the global behavior of the network.

In the previous work, we clarified how the restriction based on the trophic level can affect the evolution and extinction of food webs [8], by expanding their model so that the strength of the trophic level restriction on evolution can be adjusted by a single parameter. We found that the network structure and the stability of the ecosystem strongly depended on the strength of the restrictions, which implies that the evolution of restriction on speciation events itself is a key factor that can affect the self-organization of food webs.

It has been the subject of debates and speculations among ecologists why the food chain length is short [2, 6]. Some researchers ague that they are productivity, system size or their combination [11, 12]. The understanding of its determinants has recently become important for ecosystem management and biodiversity conservation [4].

In this paper, we focus on this subject and investigate it by using an evolutionary network model of food webs in which the restriction of speciation events is evolvable [9].

2 The Model

2.1 Network representation

Figure 1 shows an example of food webs in our model. There is one special node representing the sun in an abstract form, which is the permanent energy source. The other nodes represent species. The directed links represent the energy flow from one species (prey) or the sun to another species (predator). The trophic level of the sun is defined as 0, and the trophic level of each species is defined as the minimum distance from the sun. The species at the level 1 correspond to the autotrophic species, and cannot survive

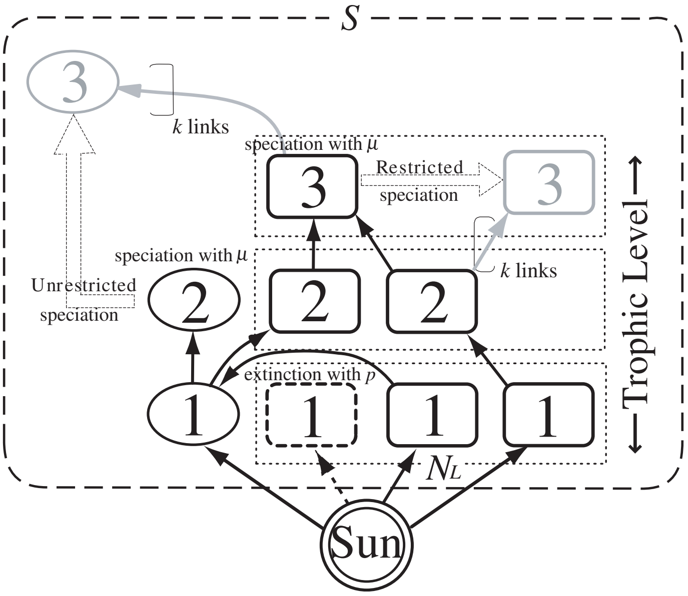

Figure 1: Schematic representation of the model. Circle and square nodes represent omnivorous species and restricted species, respectively.

without the link from the sun. The other species correspond to heterotrophic species, and cannot survive without incoming links from the other species. There are two types of species, which are determined genetically. The first type is a restricted species preying on species at lower trophic levels and speciating at a neighboring trophic level. The second is an omnivorous species preying on any species and speciating at any trophic level.

2.2 Algorithm

The dynamics of the web is driven by the speciation and extinction of species. The model starts with N_0 species at the level 1 and evolves according to the following rules:

1. Speciation.

   Every existing species at the level l tries to speciate with a probability μ.

   - Restricted species: A restricted species creates a new restricted species in an available niche at the same or neighboring levels l-1, l or l+1, and then make K_l links from species at the lower level. This event occurs only when the number of nodes at the speciating level is smaller than the saturation point of each level N_L.
   - Omnivorous species: An omnivorous species creates a new omnivorous in an available niche at any levels, and then make K_l links from randomly-selected species in all levels. This event occurs only when the number of nodes in the system N_S is smaller than the system size S.

   The number of prey links K_l is loosely inherited from the one of the original species $K_{o,l}$. Specifically, K_l is chosen randomly from $K_{o,l-1}$, $K_{o,l}$ or $K_{o,l+1}$. However, the speciation does not happen if K_l is 0.

   In addition, the type of the new species is mutated (flipped) with a probability ϕ.

2. Extinction.

   Only autotrophic species can trigger an avalanche [1] as is the case with Amaral and Meyer 's model. When a species goes extinct, all the links from it to other species are removed. The extinction occurs on all species which have lost all incoming links recursively.

3 Experiments

We used the system size $S = 1000$, the saturation point of each level $N_L = 100$, the the extinction probability $p = 0.01$, the probability of speciation $\mu = 0.02$ and mutates $\phi = 0.01$. Those parameter values are based on the previous studies [5, 7, 10].

We adopted a food web composed of 10 restricted species and 10 omnivorous species at the level 1 that receive a link from the sun as the initial state of this simulation.

3.1 Basic Dynamics

Figure 2a shows a typical result of the experiments. The number of entire species N_S tended to fluctuate around the maximum value 1000 while it often decreased sharply. We observed the extinction of entire species as seen at the 21000th step in the figure. It is also shown that there is a strong correlation between the number of speciation and extinction, which is in good agreement with empirical data [1].

Figure 2b shows the transition of the length of the food chain of restricted and omnivorous species. The

[1] The avalanche means chains of extinction.

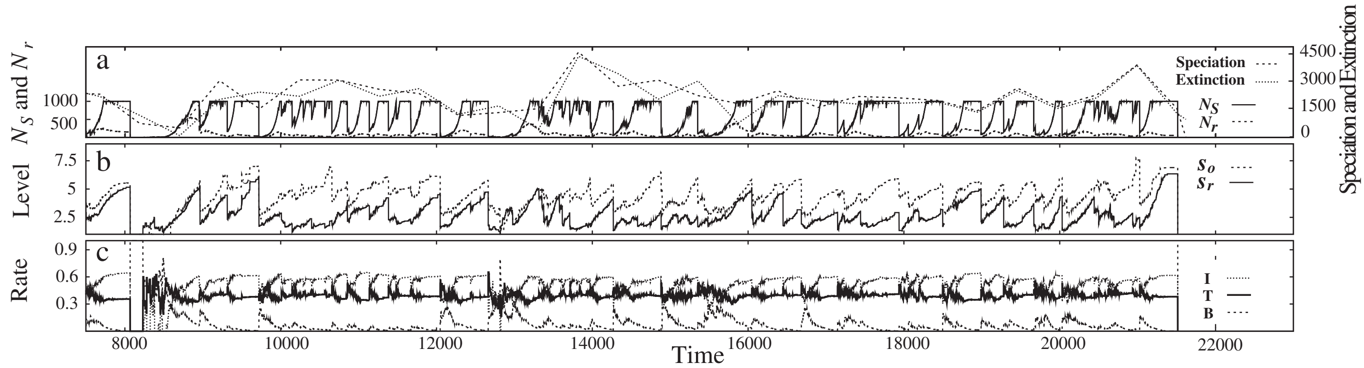

Figure 2: Time sequence of the number of species, speciation and extinctions events. The number of speciation or extinction is the total number of speciation or extinction events during consecutive non-overlapping intervals of 512 time steps.

values of the length was oscillating at around level $1 \sim 7$ with the number of species N_S, and the length of omnivorous species kept longer level than the one of restricted species. This indicates that the system was composed of two layers; lower layer: restricted species, higher layer: omnivorous species, and the food chain length was oscillating around the lower level.

Cohen and Briand [3] found a fundamental property of food webs that the ratio among basal species B (predators without predators), intermediate species I (predators and prey species) and top species T (prey species without prey) is roughly constant: $B : I : T = 0.19 : 0.52 : 0.29$. Figure 2c shows the fraction of the BIT at each step. The average of the fraction in the time sequence for 50 runs is $B : I : T = 0.104 : 0.513 : 0.383$. The fraction shows the same tendency with empirical data [3].

3.2 Effect of the system size

Table 1 summarizes the results of the simulations for 50 runs with the three different size of system $S = 500, 1000$ and 2000. As the system size increased, the survival time[2] and the rate of the number of all species and restrected species decreased. On the other hand, the length of the food chain and the fraction of intermediate species increased. This means that the system has same features of partial sphere which tended to increase the ratio of volume area to surface and to be unstable in larger system.

[2]The elapsed time before all the species went extinct.

The results show that the length of food web does not get longer compared to the increasing of the system size. Here, we explain the reason of the relatively short length of food web.

The system has two tendencies. The length of food web tends to increase with the system size increasing. The system also tends to be unstable as the system size becomes large. This instavility is supposed to derive from the inherent property concerning the ratio: $I > T > B$, which appears when the system size is large. The smaller number of basal species could be the cause of mass extinction.

For these reasons, the length of food web is oscillating around lower level without reaching a higher level.

4 Conclusion

It has long been discussed among ecologists what the determinant factors of the food web length are. Some researchers ague that they are productivity, system size or their combination [11, 12]. However, from the results of the simple constructive food web model, it is strongly suggested that the determinative factor of the short length is the general property cocerning the ratio among basal species B (predators without predators), intermediate species I (predators and prey species) and top species T (prey species without prey): $I > T > B$. This tendency coupled with the basic tendency of the system to grow is supposed to control the high frequency of extinction, which leads to a limited

Table 1: Effects of system size on the behavior which was the averages taken over 50 runs.

S	Survival time	Rate of species			Average chain length			Fraction of BIT		
		s	s_r	s_o	s	s_r	s_o	s	s_r	s_o
500	5677.04	74.67 %	35.74 %	64.26 %	3.75	2.98	4.04	0.112 %	0.494 %	0.394 %
1000	4460.16	66.17 %	22.12 %	77.88 %	4.27	2.92	4.44	0.104 %	0.513 %	0.383 %
2000	3714.26	59.94 %	17.15 %	82.85 %	4.62	2.71	4.76	0.095 %	0.530 %	0.375 %

length of the food-web. It should be noted that the senario presented in this paper is in good agreement with empirical data.

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