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The effects of the trophic level on the stability of food webs

Hirofumi Ochiai Reiji Suzuki Takaya Arita
Graduate School of Information Science, Nagoya University
Furo-cho, Chikusa-ku, Nagoya 464-8601, Japan
E-mail: ochiai@alife.cs.is.nagoya-u.ac.jp, reiji@is.nagoya-u.ac.jp, arita@nagoya-u.jp

Abstract

The study of food webs has long been a central topic of ecological research, but structural effects of a trophic level on their stability are still not clear. The work described here addresses the influence of a restriction arising from the trophic level on the network topology of food webs, which affects their global behaviors. We propose a network model of food webs in which the degree of the effects of the trophic level on speciation can be adjusted continuously by a single parameter. The restriction limits the number of species on each level and the establishment of prey-predator relationships between distant levels. Experimental results show that the restriction contributes to the stability of the ecosystem. It is because the strong restriction kept less robust species at the lower levels abundant by making the distribution of the number of species at each level flat, while the distribution became a inverse-pyramidal structure without restriction. On the other hand, we found that the several features of the network such as the power-law distribution of coextinction sizes and the number of predators do not depend on the degree of restriction. We also show several comparisons of the experimental data with empirical data of fossil records.

Keywords: Food web, trophic level, mass extinction, restriction, power-law, fossil record, artificial life.

1 Introduction

In ecology, the various types of models on food webs have been proposed by ecologists, mathematicians and physicists for understanding the mechanism of ecological dynamics. The models on food webs fall roughly into two categories. The first group of the models has a fixed structure of food webs and the second group of the models has a dynamic growth structure. Amaral and Meyer's model [1] is known as one of the latter ones. They constructed a network model for large scale extinction and evolution of species, in which there exists a strong restriction arising from the trophic level that limits the number of the species on each level and the establishment of prey-predator relationships between distant levels. The results showed a power-law distribution of coextinction sizes, in good agreement with available data from the fossil records [1, 3, 4, 8]. Recently, this model was reconsidered by Pekalski *et al.* [8]. They investigated the dependence of the system behavior on the maximum number of the species at each level and on the maximum number of preys per predator, then showed that the food web may collapse if either or both are too small. However, it is still unclear how the restriction arising from the trophic level can affect the global behaviors of ecological networks.

We clarify how the restriction based on the trophic level can affect the evolution and extinction of food webs. We propose a network model of food webs in which the degree of the effects of trophic level on evolution can be adjusted continuously by a single parameter θ. Amaral and Meyer's model is thus equivalent to our model with a specific setting of this parameter.

Experimental results have shown that the restriction contributes to the stability of the ecosystem, but the several features of the network such as the a power-law distribution of coextinction sizes and the number of predators do not depend on the degree of the restriction. We also show several comparisons of the experimental data with the empirical data of fossil records.

2 Model

Fig. 1 shows an example of food webs in our model. There is one special node termed the sun which is the permanent energy source. The other nodes represent the species. The directed link represents the energy flow from one species or the sun to another species.

The trophic level of the species is defined as the minimum distance from the sun whose trophic level is defined as 0. The species at the level 1 corresponds to the autotrophic species, and the other ones correspond to heterotrophic species. It is because the former cannot exist without incoming links from the sun and the latter cannot exist without incoming links from the other species. 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:

(i) Speciation. — Every existing species tries to speciate with a probability μ. For each speciating species at the trophic level l ($1 \le l \le L$), it performs the following speciation event with a probability θ as shown in Fig. 1 (restricted speciation). In this case, it creates a new node at the level l-1, l or l+1

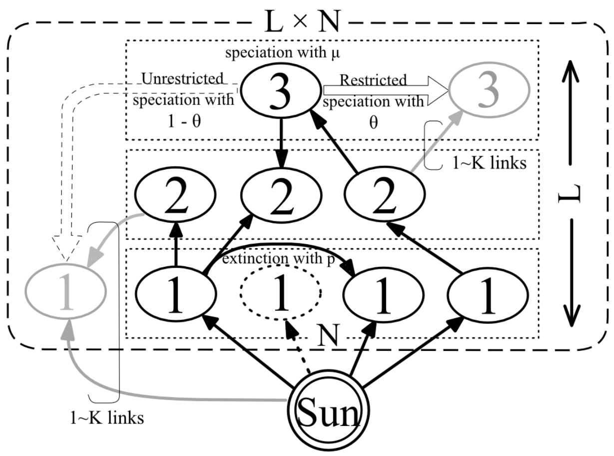

Figure 1: Schematic representation of the model for K=3, L=3 and N=4.

which receives the links from randomly selected number ($1 \le k \le K$) of nodes at the level l-2, l-1, or l respectively. This event occurs only when the level of the new node is from 1 up to L and the number of nodes at the same level l is smaller than N.

Otherwise, with a probability 1-θ, it creates a new node which receives the links from a randomly selected number ($1 \le k \le K$) ones from all species as shown in Fig. 1 (unrestricted speciation). This event occurs only when the number of nodes in the system is smaller than $L \cdot N$.

(*ii*) Extinction. — Only autotrophic species can trigger the avalanche (chains of extinction) 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 use the canonical set of parameters used in [1], namely, the maximum trophic level L=6, the extinction probability p=0.01, the probability of speciation μ=0.02, and the maximum number of preys K=3. These values came from the data of statistical investigation [5]. Although Amaral and Meyer used N=1000 in the simulations, we use N=100 because the total size of the experimentally observed food webs does not have such large number of species according to [8].

We shall investigate how is the system influenced by the parameter θ for the restriction of the choice of level and feeds. The results obtained will be compared to the empirical data coming from investigations of the fossil records [6].

3.1 Basic Dynamics

At the beginning, we discuss the basic dynamics of the system which was commonly observed across the

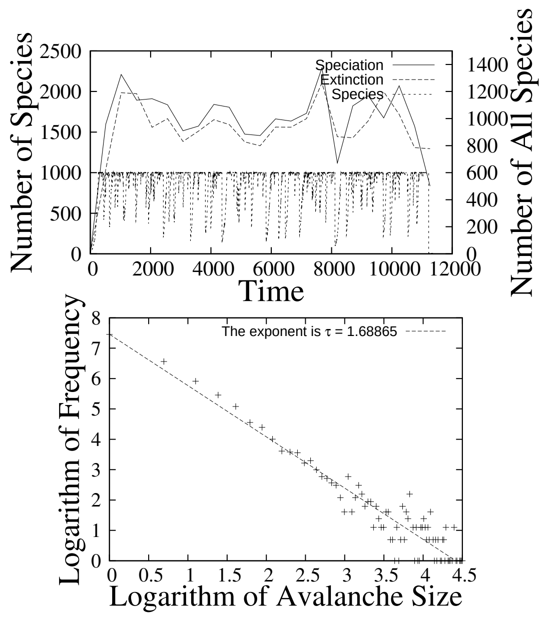

Figure 2: Time sequence of the number of species, speciation and extinctions events for θ= 0.6 (top). The number of speciation or extinction is the total number of speciation or extinction events during consecutive non-overlapping intervals of 512 time steps. Avalanche size for θ=0.6 (bottom). Both axes are in logarithmic scale (to base 10) on the vertical and horizontal axis.

whole range of θ. Amaral and Meyer's model, which is basically equivalent to our model in the case of θ=1.0[1], leads to a power-law (i.e., scale-free) distribution of extinction avalanche sizes which form $p(x) \propto x^{-\tau}$ and a strong correlation between the number of speciation and extinction events [1]. Irrespective of the parameter θ, we observed identical results except for the exponent value of power-law τ. As a typical example, we focus on the results in the case of θ=0.6. Fig. 2 (top) shows the transitions of the number of entire species, speciation and extinction. From the figure, we see the number of entire species fluctuated around the maximum value 600 and its drastic decreases often happened. We also observed the extinction of entire species as seen at the 11,000 step in the figure. It is because we used the lower value of the parameter N in the experiments compared to the original one as explained above, and also used the intermediate value of the parameter θ as described later. We also see that the number of speciation and extinction have a strong correlation. This trends are in good agreement with empirical data [1]. Fig. 2 (bottom) shows the distribution of the frequency of the extinction size in a single run. The extinction size means the number of extinct species at each step. We see that the shape of the distribution is approximately a straight line, which

[1]To be exact, there is a small difference between our model and Amaral and Mayer's in the sense that we adopted the probabilistic occurrence of extinction which was used in [2], and the random choice of the number of preys in a speciation event. But the global behaviors of the system was basically the same.

θ		0.00	0.20	0.40	0.60	0.80	1.00
Survival Time		626	1071	1575	3001	10930	50000
Number of Species		291	320	397	501	537	565
Variance of the Number of Species		218	236	224	163	124	69
Maximum Outdegree		8.79	1.34×10	1.68×10	1.83×10	1.38×10	1.03×10
Exponent of Avalanche size	τ	3.11×10^{-1}	3.50×10^{-1}	1.67	1.69	1.73	1.96
Exponent of Species Lifetime	α	-	-	-	1.30	1.78	1.86
Exponent of Outdegree	β	2.65	3.37	3.32	3.72	3.33	4.41

Table 1: Effects of θ on the system behavior. The first four values were the averages taken over 20 runs and the rest were calculated from a randomly selected run. When $\theta \leq 0.40$, the distribution of the species lifetime did not follow a power-law, which is expected to be due to the short survival time and the small number of species.

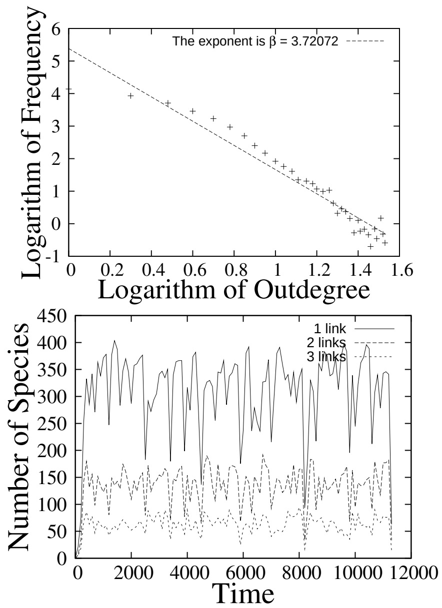

Figure 3: Outdegree distribution for θ=0.6 (top). The axes are in logarithmic scale (to base 10) on the vertical and horizontal axis. Time sequence of the indegree for θ=0.6 (bottom).

means that it is a power-law (i.e., scale-free) distribution which form $p(x) \propto x^{-\tau}$. The result also agreed with the fossil records [6]. Here, we further focus on the topology of the network. Fig. 3 (top) show the distribution of the number of outdegree (predators) for each species. It is approximately a straight line which form $p(t) \propto t^{-\beta}$. It is interesting that the distribution of the number of outdegree follows such a power-law, because it means that the system is composed of a scale-free network [2]. Fig. 3 (bottom) shows the transition of the distribution of indegrees (preys) for each species. The order of the number of links was unchanged, and the species with one indegree held the maximum number. This indicates that most of the species had a single prey.

3.2 Effects of θ on the overall dynamics

Table 1 summarizes the results of the experiments in the various cases of θ. As the parameter θ decreased, the survival time[2] and the average number of species decreased and the variance of the number of species increased. This means that the system tended to be small and unstable, and easily become extinct in the range of lower values of θ. The average maximum outdegree was largest when θ=0.6, which means there were preys predated by larger number of species in the case of intermediate restriction.

Here, we explain the relationship between the stability of the entire system and the restriction of the trophic level from the standpoint of the network structure and the robustness of species. Fig. 4 (top) illustrates the rate of species at each level averaged over 20 runs. In the cases of lower θ, it became the system an inverse-pyramidal structure, which means that the species at higher trophic levels were more populated than the lower ones. On the other hand, in the higher cases of θ, it became a flat structure in the sense that there were almost the same rate of species at every level. The species at the higher level tends to be more robust against the avalanche of extinction as a general trend, because the potential routes from the sun to the target species can become more diverse. Thus, we could see the frequency of species became higher as the level increased in the case of smaller restriction from the Fig. 4 (top). On the other hand, we could also see the constant frequency of species through the whole level in the case of larger restriction. This is clearly due to the restriction of the maximum number of species at each level N.

Fig. 4 (bottom) shows the average robustness of species at each level. The robustness of species is defined as the number of different species at the level 1 which exist in all the routes from the sun to the target species. Basically, there was a trend that the robustness increased with the increasing the level in all the cases of restriction. We observed clearly this trend when the parameter θ was highest. The condition of the system was basically static in that the number of

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

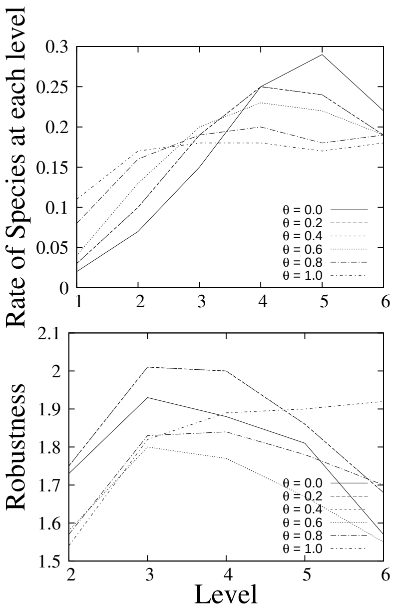

Figure 4: The rate of species at levels (top) and the rate of species robustness at levels (bottom). The averages was taken over 20 runs.

species saturated at any level, because the restriction made less robust species at the lower levels abundant. On the other hand, the robustness had a peak at an intermediate level (3 or 4) in the cases of lower value of the parameter θ. This is because the whole system grows and collapses many times with dynamic change in its system size. In the growth stage, there is a trend that the robustness of the higher level becomes slightly smaller due to a time lag between the appearance of the species at the higher level and the increase in its robustness.

After all, we can say that the restriction of the trophic level contributes to the stability of the whole system because it makes less robust species at the lower levels abundant by making the distribution of the number of species at each level flat.

Also, Table 1 shows the exponent of the distribution of avalanche size and species lifetime were proportional to the parameter θ. The fossil records of marine animals appears to have a power-law distribution of the extinction size with an exponent τ=2.0 $\pm$ 0.2 [9]. We found that the distribution of the extinction sizes in the case of θ=1.0 was in the best agreement with the fossil records among these results. The distribution of the genus lifetime appears to follow a power-law with an exponent α=1.7 $\pm$ 0.3 [9]. Its distribution was in the best agreement with the fossil records when θ=0.8. On the other hand, there were no clear trends in the effect of θ on the exponent of outdegree.

In addition, we observed that the fraction of highly connected species (omnivores) significantly increased just before the extinction of the whole species when $\theta < 0.4$ (not shown). It was reported in [8] that the similar phenomenon can occur when N is very small.

4 Conclusion

We have discussed the influence of the restriction arising from the trophic level on the global behavior of food webs, which were neglected in previous studies. From the experimental results, we found that the network structure and the stability of the ecosystem strongly depended on the degree of the restrictions. With decreasing the degree of the restriction, the distribution of the species at each trophic level changed from flat to inverse-pyramidal, and its stability became more unstable. This is because the restriction maintains the number of less robust species at lower levels in abundance. On the other hand, we found the features that the distribution of the extinction sizes and the outdegrees followed a power-law regardless of the degree of the restrictions.

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