International Symposium on Nonlinear Theory and its Applications
Xi'an, PRC, October 7–11, 2002

Structural Stability of Self-Organizing Complex Food Webs

Takashi Shimada, Hiroyuki Hida† and Hisa-Aki Tanaka†

Department of Applied Physics, School of Engineering
The University of Tokyo,
Bunkyo-ku, Hongo, Tokyo, 113-8656, Japan.
Phone: +81-3-5841-6865, FAX: +81-3-5841-6861
† University of Electro-Communications,
1-5-1, Chofugaoka, Chofu-Shi, Tokyo, 182-8585, Japan.
Phone:+81-424-43-5174, Fax:+81-424-43-5174
Email: shimada@acolyte.t.u-tokyo.ac.jp, htan@ee.uec.ac.jp, hida@synchro2.ee.uec.ac.jp

1. Introduction

Food web, the graph of prey-predator relations between species, is considered to contain an important character of ecosystems since the preying interaction is expected to play the dominant role in the system. A popular way to express the interaction between species has been the population dynamics model represented by the generalized Lotka-Volterra equations. However, it is widely known that self-organizing food webs based on the generalized Lotka-Volterra equations tend to die out totally or tend to collapse to a simple structure.

One of the authors (T.S.) has recently proposed a simple model of self-organizing food webs based on a modified population dynamics, which reproduces important aspects of ecosystems; diversity of species, structural stability, and the distribution of the species life span [1].

Here, we investigate why this simple model leads to a stable, diverse structure, by focusing on the following issues:
(i) stability of the population equilibria; for a given food web, how can we characterize the population equilibria?
(ii) robustness of the network structure; for the mutation (invasion) of a randomly created new species, how is the food web structure altered ?

Moreover, a qualitative characterization of the network topology is made to clarify the following issues;
(iii) self-organizing networks in our model does not have a scale-free structure, and
(iv) they have some order in their structure as opposed to random networks; i.e., they have markedly higher clustering coefficients than those of random networks.

These investigations give an insight into the reason why our simple model reproduces important aspects of ecosystems.

2. Population dynamics models for self-organizing ecosystems

The most popular way to express the interaction between species is to use population dynamics model represented by the generalized Lotka-Volterra equations,

$$\frac{dx_i}{dt} = c_i x_i + \sum_{j=1}^{N} a_{ij} x_i x_j \quad (i = 1, 2, 3, \cdots, N), \qquad (1)$$

where c_i and a_{ij} represent the rate of self-growth and metabolism and the interaction coefficient between species i and j, respectively. Here, we regard x_i as the energy of the species i instead of the generally regarded population density. Since the energy and the population of species are related linearly, the form of the equations is not altered.

Constraint of the energy and nutrition should be introduced to this general equations so that they model ecosystems. Through preying interaction, the energy and nutrition are transfered from the primary producer to other animals. The preying interaction holds under a sub-conservation law of energy and nutrition which can be taken in by introducing the condition $a_{ij} + a_{ji} < 0$ for all interactions. In this study, we consider antisymmetric interaction coefficients (; $a_{ij} = -a_{ji}$) for simplicity.

In addition to the above constraint, extinction and mutation of species should be introduced to the system (see [1] as an example). In conventional studies, extinction is modeled by removing the species whose population becomes small enough. Also, mutation is modeled by adding a new species to the system. Interactions between the new species and the natives are given by the prescribed dynamics. Here we assume this mutation

takes place randomly which may be better interpreted as invasion.

3. Self-organizing food web model with "size-free" interactions

It is widely believed that simply applying the Lotka-Volterra equations(Eq. (1)) to the ecosystem is inexpedient, because in the Lotka-Volterra model, interaction coefficients must cover extremely large range to model a large ecosystem as they have the dimension of $[\text{energy}]^{-1}$ or $[\text{population}]^{-1}$ in addition to the dimension of $[\text{time}]^{-1}$. For example, the interaction coefficient between *rare* species should be far larger than the one between *dominant* species. However, in the real ecosystem, the *rare* species will not keep such a large interaction coefficients if they happen to become dominant. Hence it is hopeless that proper choice of interaction coefficients are obtained by a totally random way. Artificial rules for mutation can be introduced to determine the coefficients [2]. However, Applying some artificial rules for mutation does not satisfy the system to be truly self-organized because this implies some preconceived structure. For a truly self-organized systems, we consider a modification of the interaction term. The interaction term we need here must be simple since a complicated one again implies certain artificiality or preconceived structure. In this study, we modify the interaction term as,

$$a_{ij}x_ix_j \longrightarrow a_{ij}x_i^{\lambda}x_j^{1-\lambda} \quad (\lambda \in (0,1)), \tag{2}$$

where species j is a predator which preys species i. It corresponds to the modification of the preying rate per predator from $a_{ij}x_j$ to predator-dependent form $a_{ij}(x_i/x_j)^{\lambda}$. The predator dependence of preying rate is not unrealistic [3]. The condition that $\lambda \in (0,1)$ corresponds to the saturation of the preying rate when prey is abundant. Although every λ may depend on i and j, like a_{ij}, we set the parameters λ uniformly for simplicity in this study. In this case, we should limit the uniform value λ in $\in (0,1/2]$ to keep the preying rate convex under certain transformation of variables. The metabolism rate c_i is also uniformly chosen to 1 except for the plants which are the sole energy source in the system and have the logistic growth rate. After that, the equations of our model become,

$$\begin{aligned}
&\text{"plants"}: \\
&\frac{dx_1}{dt} = Gx_1(1-x_1) + \sum_j a_{1j}x_1^{\lambda}x_j^{1-\lambda}, \\
&\text{"animals"}: \\
&\frac{dx_i}{dt} = -x_i + \sum_{a_{ij}<0} a_{ij}x_i^{\lambda}x_j^{1-\lambda} + \sum_{a_{ij}>0} a_{ij}x_i^{1-\lambda}x_j^{\lambda}, \\
&(a_{ij} = -a_{ji} \in (-1,1), \lambda \in (0,1/2], \quad G>0)
\end{aligned} \tag{3}$$

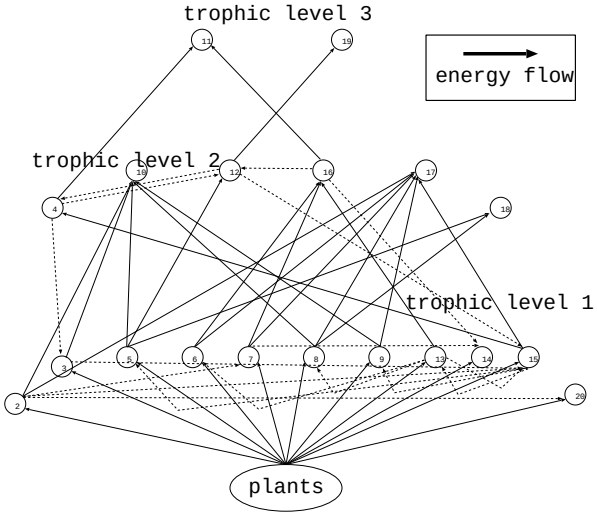

Fig. 1 Generated food web with rich self-organized structure under the model with the size-free interaction. Each circle represents certain species and arrows represents the preying interaction. Number of trophic levels is equal to the one of real ecosystem in a continental shelf.

where G denotes the growth rate of the plants. We call this interaction $a_{ij}x_i^{\lambda}x_j^{1-\lambda}$ as "size-free" because it and the linear metabolism term make the equations of the system invariable to the uniform change of the population size from $\{x_i\}$ to $\{\alpha x_i\}$ with constant α except for the logistic growth term of the plants. Under the size-free form, interaction coefficients have the dimension same as the metabolism rate.

In addition to Eqs.(3) we introduce the following rules of extinction and mutation:

Extinction : If energy of a species i,x_i, becomes 0, the ith degree of the freedom is eliminated. Isolated species are eliminated instantaneously.

Mutation(Invasion) : A new species comes into the system randomly at time. Initial energy of the new comer is chosen to be very small; we takes 10^{-8} for example. Number of the interactions is assigned randomly in the range of $(1, 2m)$, where m is a constant and we take $m = 5$ here. The interaction coefficients are also randomly assigned in $(-1, 1)$.

It is worth stressing that we do not require artificial threshold for the extinction rule in this model. In Lotka-Volterra model, populations of the unmatched species do not become zero in finite time but they approach to zero exponentially in time therefore threshold is necessary to cause extinction [1,4]. In contrast, our size-free interaction causes the algebraic decay of the unmatched species, so the orbits of the unmatched species decrease to 0 in finite time.

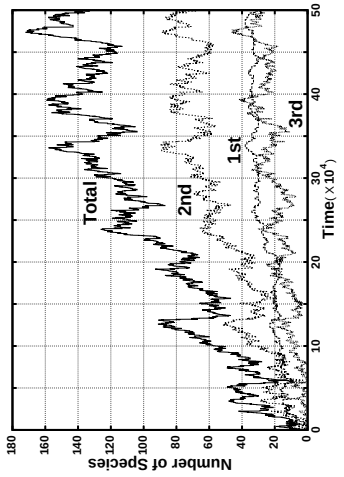

Fig. 2 Time development of the number of the species in the system. Mutation rate is 0.01 per time. Four lines represent the number of; total species, species in the second trophic level, species in the first trophic level, species in the third trophic level, respectively in the order of top to bottom.

Let us see the consequence of this modification. One can find a clear contrast with the Lotka-Volterra model. In the present model(Eqs.(3)), some succeed in adapting although most of the new species fail to survive as same in case of the Lotka-Volterra model. The structure of this self-organized system is not trivial but very rich. In Fig. 1, which shows an example of such self-organized food webs, we can see three trophic levels above the plants. Concerning with real ecosystems in the sea, for example, number of trophic levels varies from 2(up-welling area) to 5(oceanic area) and 3 corresponds to that of continental shelf [5]. Therefore, the obtained food web is realistic at least in vertical direction. Moreover, size of the food web shown in Fig. 1 is not a special one. We can get more complex food web which has more species and trophic levels. It is noted that size-variant form interactions, like $a_{ij}\sqrt{x_i}x_j$, for example [6], can not yield such diverse structure.

One natural question is the relation with the arguments about the stability of interacting systems argued in 1970s (see [7,8] for example). From these arguments, the condition for large systems to have sufficient probability of being stable is written as

$$\sqrt{2m\sigma^2} < 1 \tag{4}$$

where σ is the deviation of the interaction coefficients a_{ij}. It turns out that the condition in our simulation($2m = 10, \sigma^2 \sim 1/12$) satisfies Eq.(4). Concerning about the average number of connections per species, there are some comparable data obtained by analyzing real food webs in resolution of species. For example, the average numbers of connections per species($= 2m$) are 8.7 and 4.75 for Ythan estuary food web(with 134 species) and Silwood park food web(with 154 species), respectively [9]. Hence, we can conclude that the interactions in our model is strong enough comparing with the real food webs and that still satisfies the condition for stability. We should note that the condition of this linear stability is still valid so that systems with stronger interactions can not have monotonous trend to grow and goes on fluctuating. In that case, temporal fluctuation of the number of species forms $1/f$ noise.

4. Patterns observed in our network structure

4.1. stability and robustness of the network

At $\lambda = 1/2$ in Eq. (3), a remarkable simplification becomes possible by setting $x_i^{1/2} \equiv y_i$;

$$\begin{aligned} \frac{dy_1}{dt} &= Gy_1(1-y_1^2) + \sum_j a_{1j}y_j, \\ \frac{dy_i}{dt} &= -y_i + \sum_j a_{ij}y_j, \end{aligned} \tag{5}$$

where the only nonlinear term appears in the first equation. From Eq. (5), it is clear that for large $G \gg 1$, the equiribirum of species is uniquely determined by the matrix equation of $[a_{ij}]$, and the 'feasible' equilibrium defined in Eq. (3) corresponds to the equilibrium of y_i with $y_i > 0$ in Eq. (5).

As for the stability of the equiribrium, it is proved that any 'feasible' equilibrium state is stable if $G \gg 1$ and $a_{ij} = -a_{ij}$. (The proof is simple and omitted here.) This property seems a bit counterintuitive, because any network topology can be realized as far as the equilibrium is feasible. However, if we consider the growth process of the network it is observed that new species in higher trophic levels have less possibilities to survive in the net. Hence, the evolving process of the network itself limits the resulting structure of the network.

4.2. distribution of life span of species

The distribution of life span of species is produced from the time-evolution of Eq. (3). This distribution corresponds to the paleontological data, which is the distribution of life span of families which we evaluated from fossil data [10]. Thus, it is important to compare

the experimentally obtained paleontological data with our data from simulations. The profile of paleontological data is skewed but well fitted by the power-law curve with exponent about -2 while the simplest stochastic extinction process("red queen hypothesis") predicts the exponential decay [11]. In the simulations, we can see that the distribution of the life span of species in the present model also has the power-law tail in long-life region. Moreover, its a little skewed profile and the exponent of the power decay show good agreement with the one of fossil data. While the distribution of life-span of species has power-law tail, the distribution of extinction sizes in our model do not show power-law behavior. It shows exponential decay which is consistent with one of fossil record [11,12]. (In the simulation, to get accurate statistics, we set interactions strong enough so that the number of species goes on fluctuating with no trend to grow. Since almost all new invading species fail to survive, the raw distribution obtained from simulations has sharp peak near at the life span equal 0. We are not concerned with this part because it is expected that the real species corresponding to short-life group in our model can hardly leave their fossil.)

4.3. statistical properties of the network structure

Since the food web generated in the present model is not lattice-like, the distribution of the number of interactions of each species characterizes the statistical properties of the network structure. Our simulations support that the distribution in our model does not have power-law tail and is well fitted by Gaussian distribution. In this sense, the food web constructed in our model is rather random net than scale-free net.

Adding to this, we have calculated the clustering coefficients C for a few instances of generated networks. The clustering coefficient C is given as the averaged ratio of existing links between k neighbors to the possible number of such connections $k(k-1)/2$. The results show that C is always more than 10 times larger than $C_{\rm rand}$ which is the clustering coefficient of the associated random network. We have also calculated the clustering coefficient C' for the network in which all links to 'the plant' are removed. The results show that $C' \sim C_{\rm rand}$ and this characterizes that some order is created around 'the plant' in our networks.

5. Conclusions

A simple self-organizing food web model is presented, in which several advantages over the conventional models (based on the Lotka-Volterra model) are obtained. Further investigations on the network properties will be reported soon.

We thank Profs. N. Ito, S. Yukawa, K. Tokita, and Z. Yoshida for their beneficial comments.

References

[1] Tokita, K. & Yasutomi, A. Phys. Rev. E **60**, 842 (1999).

[2] Drake, J. A. J. Theor. Biol. **147**, 213 (1990).

[3] Abrams, P. A. & Ginzburg, L. R. Trends in Ecology and Evolution **15**, 337 (2000).

[4] Taylor, P. J. J. Theor. Biol. **135**, 569 (1988).

[5] Lalli, C. M. & Persons, T. R. *Biological Oceanography : an Introduction 2nd. ed.* (Butterworth & Hinemann, Oxford, 1997).

[6] Szathmáry,E. & Gladkih, I. J. Theor. Biol. **138**, 55 (1989).

[7] Gardner, M. R. & Ashby, W. R. Nature **228**, 228 (1970).

[8] May, R. M. Nature **238**, 413 (1972).

[9] Montoya, J. M. & Solé, R. V. J. Theor. Biol. **214**, 405 (2002).

[10] Benton, M. J. (ed.) *The Fossil Record Vol. 2* (Chapman & Hall, London, 1993). Data are available at (http://palaeo.gly.bris.ac.uk/frwhole/FR2.html).

[11] Solé, R. V. & Bascompte, J. Proc. R. Soc. Lond. B **263**, 161-168 (1996).

[12] Raup, D. M. Science **231**,1528-1533 (1986).