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Dynamic Stability and Chaotic Multispecies-Coexistence in a Food Web Model

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Abstract: The relationship between stability and complexity of an ecosystem has been one of the main issues in community ecology. In such ecosystems, a food web is one of the most complex biological networks in nature, and has been focused on by field and theoretical ecologists. We consider a food web model represented by the Lotka-Volterra equation with hierarchically ordered random interspecies interactions, and show that the model has a class of dynamic stability, and that an arbitrary number of species can coexist in it.

1. INTRODUCTION

Food webs are among the largest and most complex of biological networks, in which a vast number of species coexist stably. The condition of such coexistence of many species has been a controversial issue [1] since studies of random community models revealed that diversity and complexity tend to destabilize community dynamics [2, 3]. Recent theoretical studies, for example, have clarified the stabilizing factors of random community models: omnivores (higher connectance) [4, 5], weak interactions [6], antisymmetric prey-predator relationships [7, 8], foraging adaptations [9], evolution [10] and network structures [11].

This paper intends to give another example of a stabilizing factor in a random community model: the hierarchical structure of a food web. In Sec.2, general community dynamics will be introduced, together with the concept of dynamic stability (*persistence*). Then, in Sec. 3, we introduce a food web model represented by the Lotka-Volterra equation (LVE) with hierarchically ordered random interactions, and show that they have an *average Lyapunov function*, that their dynamics are *persistent*, and that an arbitrary number of species can coexist after extinctions of at most half of the species.

2. DYNAMIC STABILITY

Let us first consider a widely adopted model of community ecology represented by the so-called N-species generalized Lotka-Volterra equation (LVE) [12]

$$\frac{\mathrm{d}y_i}{\mathrm{d}t} = y_i(r_i + \sum_{j=1}^{N} b_{ij}y_j) \tag{1}$$

for the abundance $y_i(t)(\in [0,\infty])$ of species $i\,(= 1, 2, \ldots, N)$ where b_{ij} and r_i denote the interspecies interaction between species j and i, and the intrinsic growth rate of species i, respectively. One of the main purposes of the present study is to classify the behavior of Eq. (1) depending on the set of parameters $\{b_{ij}\}$ and $\{r_i\}$, and to find a stability condition of the solution.

We then introduce the important concept of the dynamic stability of nonlinear equations such as the LVE. For all species i if there is a positive constant δ which satisfies

$$\delta < \lim_{t\to+\infty} \inf y_i(t), \tag{2}$$

the system is *permanent* [12]. In the case of $\delta = 0$ it is *strongly persistent*. Permanence and persistence are not classical concepts for stability of a fixed point but are concepts for the trajectory of the dynamics neighborhood of the phase space boundary. Eq. (2) denotes that any arbitrary perturbation less than δ never causes extinction of a species, that is, the boundary is a *repeller* type one.

Note that the *evolutionary stable strategy (ESS)* and the *Nash equilibrium* in the context of the dynamical game theory, on the other hand, are concepts for a static stability condition of a fixed point. The ESS implies global stability of a fixed point, which is useful information on the behavior of the dynamics. There are, however, games without an ESS and games with multiple ESSs, where the ESSs are on the boundary (one or more species extinct ($y_i = 0$)). It should be noted that a unique ESS is, in general, not expected for a large system ($N \gg 1$) with complex interactions. This means that more or fewer extinctions are inevitable for the LVE with many species and complex interactions.

Another informative concept is the *saturated* fixed point [12]. A fixed point $\boldsymbol{p}$ is saturated if a function $\alpha_i(\boldsymbol{y}) \equiv r_i + \sum_{j=1}^{N} b_{ij}y_j$ satisfies

$$\alpha_i(\boldsymbol{p}) \begin{cases} = 0 & \text{for} \quad p_i > 0, \\ < 0 & \text{for} \quad p_i = 0. \end{cases} \tag{3}$$

The LVE has at least one saturated fixed point. Let us call a species with positive abundance at a saturated fixed point $p_i > 0$ a *persistent species* and a set of such species $P = \{i|p_i > 0\}$ a *persistent set*. The number of persistent species, i.e., the diversity of the ecosystem, is given by $S \equiv \sum_{i=1}^{N} \theta(y_i)$ where $\theta(z) = 1\,(z > 0);\ = 0\,(z \leq 0)$ is the step function. It is known that the time average of the persistent species converges to the saturated fixed point [12]:

$$\lim_{T\to\infty} \frac{1}{T} \int_0^T y_i(t)\mathrm{d}t = p_i \quad (i \in P). \tag{4}$$

3. MODEL

We here study a general food web model represented by the LVE (1) with hierarchically ordered interspecies interactions:

$$b_{ii} = 0, \tag{5}$$
$$b_{ij} = -b_{ji}, \tag{6}$$
$$b_{ij} < 0 < b_{ji} \quad (i < j), \tag{7}$$

that is, the matrix $B = \{b_{ij}\}$ is antisymmetric and the upper (lower) triangular elements of B take negative (positive) values. In the context of ecology, this type of B denotes that every lower-ranking species i is preyed on by any higher-ranking species $j(> i)$, that is, an omnivorous species.

Flows of the LVE are, in general, uniformly bounded if the diagonal elements b_{ii} are all negative. On the other hand, if $b_{ii} = 0$, they are not always uniformly bounded and one species often explodes. If $b_{ii} = 0$ and $r_i = 0$ for all i, only the top predator N can survive and other species become extinct [13].

Let us consider the replicator equation (RE) [12]

$$\frac{\mathrm{d}x_i}{\mathrm{d}t} = x_i(f_i - \bar{f}) \qquad (i = 1, 2, \cdots, M \equiv N + 1) \tag{8}$$
$$f_i \equiv \sum_{j=1}^{M} a_{ij} x_j \tag{9}$$
$$\bar{f} \equiv \sum_{i=1}^{M} f_i x_i, \tag{10}$$

which is transformed from the LVE (1) with the antisymmetric interactions (5) and (6) by the transformation [12]:

$$y_i = x_i / x_M \quad (i = 1, 2, \cdots, N), \tag{11}$$
$$r_i = a_{iM} - a_{MM}, \tag{12}$$
$$b_{ij} = a_{ij} - a_{Mj}, \tag{13}$$

Since the flows of the LVE and the transformed RE are homeomorphic [12], we can study the transformed RE instead of the LVE. The RE is, moreover, more tractable when we execute numerical simulations because the population density $x_i(t)$ is uniformly bounded ($0 \leq x_i(t) \leq 1$) by definition, while $y_i(t)$ of the LVE sometimes explodes and the simulation breaks down. It is known that the total population density is conserved at all times as $\sum_{i=1}^{M} x_i(t) = 1$, and, therefore, the trajectory of the dynamics (8) is bounded in the simplex $\sum_{i=1}^{M} x_i = 1$.

The interaction matrix $A = (a_{ij})$ of the transformed RE is ”quasi-antisymmetric” (antisymmetric except for the M-th row and the M-th column):

$$a_{ij} = -a_{ij}, \quad a_{ii} = 0 \quad (i, j = 1, 2, \ldots, N) \tag{14}$$
$$a_{iM} = r_i, \quad a_{Mi} = 0, \quad a_{MM} = 0, \tag{15}$$

which is similar to the ”almost” skew-symmetric matrix [14].

Because the species M does not have an intraspecific interaction ($a_{MM} = 0$) nor has interactions from any other species ($a_{Mi} = 0$), its fitness is always zero: $f_M = \sum_{j=1}^{M} a_{Mj} x_j = 0$. The average fitness $\bar{f}$, however, depends on time, and the population density $x_M(t)$ is a variable in time. Let us term the species M an ”environmental” species.

4. RESULT

The main result is the simple extension of the theorem for the RE with antisymmetric interspecies interactions [7].

Theorem 1. *For the LVE (1) with zero infraspecific competition (5) and antisymmetric interspecies interactions (6) and the transformed RE (8) with quasi-antisymmetric interactions (14) and (15), both systems of the persistent species are strongly persistent.*

Proof. Since the average fitness $\bar{f}$ is of the form

$$\begin{aligned} \bar{f} &= \sum_{i=1}^{M}\sum_{j=1}^{M} a_{ij} x_i x_j \\ &= \sum_{i=1}^{N}\sum_{j=1}^{N} a_{ij} x_i x_j + \sum_{i=1}^{M} a_{iM} x_i x_M \\ &\quad + \sum_{j=1}^{M} a_{Mj} x_M x_j \\ &= x_M \sum_{j=1}^{M} r_j x_j = x_M \boldsymbol{r} \cdot \boldsymbol{x}, \end{aligned} \tag{16}$$

where Eqs. (14) and (15) are used for the third equality, the dynamics of the environmental species M is described by

$$\frac{\mathrm{d}x_M}{\mathrm{d}t} = -\bar{f} x_M = -x_M^2 \, \boldsymbol{r} \cdot \boldsymbol{x}, \tag{17}$$

since $f_M = 0$. The vectors $\boldsymbol{x} \equiv (x_1, x_2, \ldots, x_M)$ and $\boldsymbol{r} \equiv (r_1, r_2, \ldots, r_N, r_M)$ denote the sets of the population density and the intrinsic growth rate, respectively. In general, for persistent species of the RE, at the saturated fixed point $\boldsymbol{p}$, the condition

$$\tilde{\alpha}_i(\boldsymbol{p}) \equiv f_i(\boldsymbol{p}) - \bar{f}(\boldsymbol{p}) \begin{cases} = 0 & \text{for} \quad p_i > 0, \\ < 0 & \text{for} \quad p_i = 0. \end{cases} \tag{18}$$

is satisfied in the same way as in (3). Then, if the environmental species is a persistent species ($p_M > 0$) at the saturated fixed point $\boldsymbol{p}$, $\tilde{\alpha}_M(\boldsymbol{p})$ and $\bar{f}(\boldsymbol{p})$ are both zero, and thus, using (16), $\boldsymbol{p}$ fulfills the condition

$$\boldsymbol{r} \cdot \boldsymbol{p} = 0. \tag{19}$$

This means that at least the system of the persistent species of (1), (5) and (6) (or, (8), (14) and (15)) is not permanent because it is proved that $\bar{f}(\boldsymbol{p})$ is positive if the RE with $a_{ii} = 0$ is permanent [12, 15].

If we define a function $L_p(\boldsymbol{x}) \equiv \sum_{i=1}^{M} p_i \log x_i$ which is actually the Lyapunov function for the RE with antisymmetric interactions [7], the derivative of this with respect to time satisfies the inequality:

$$\begin{aligned} \frac{\mathrm{d}L_p(\boldsymbol{x})}{\mathrm{d}t} &= \sum_{i=1}^{M} p_i \frac{\dot{x}_i}{x_i} \\ &= \sum_{i=1}^{M} p_i (\sum_{j=1}^{M} a_{ij} x_j - x_M \boldsymbol{r}\cdot\boldsymbol{x}) \\ &= \sum_{j=1}^{N} x_j \sum_{i=1}^{N} a_{ij} p_i + x_M \sum_{i=1}^{N} a_{iM} p_i \\ &\quad + p_M \sum_{j=1}^{N} a_{Nj} x_j + a_{MM} x_M p_M \\ &\quad - x_M \boldsymbol{r}\cdot\boldsymbol{x} \\ &= -\sum_{j=1}^{N} x_j \sum_{i=1}^{N} a_{ji} p_i - x_M \boldsymbol{r}\cdot\boldsymbol{x} \\ &= -\sum_{i=1}^{M} \tilde{\alpha}_i(\boldsymbol{p}) x_i - \xi_M\, \boldsymbol{r}\cdot\boldsymbol{x} \\ &\geq -\xi_M\, \boldsymbol{r}\cdot\boldsymbol{x}, \end{aligned} \tag{20}$$

where (8), (9) and (16) are used for the second equality, (14), (15), (18) and (19) are used for the fourth equality, (18) is used for the inequality, and $\xi_M \equiv x_M - p_M$. The equality in the last line holds when the system converges to the persistent set ($x_i \to p_i > 0$ for $i \in P$) and other non-persistent species become extinct ($x_i \to p_i = 0$ for $i \notin P$). By rewriting (17) as

$$\boldsymbol{r}\cdot\boldsymbol{x} = -\frac{1}{x_M^2}\frac{\mathrm{d}x_M}{\mathrm{d}t} = \frac{\mathrm{d}}{\mathrm{d}t}\left(\frac{1}{x_M}\right) \tag{21}$$

and inserting this into (20), we obtain

$$\frac{\mathrm{d}L_p(\boldsymbol{x})}{\mathrm{d}t} \geq -\xi_M \frac{\mathrm{d}}{\mathrm{d}t}\left(\frac{1}{x_M}\right). \tag{22}$$

Using this inequality, we demonstrate

$$\begin{aligned} \left\langle \frac{\mathrm{d}L_p(\boldsymbol{x})}{\mathrm{d}t} \right\rangle_T &\equiv \frac{1}{T}\int_0^T \frac{\mathrm{d}L_p(\boldsymbol{x})}{\mathrm{d}t}\mathrm{d}t \\ &\geq -\frac{1}{T}\int_0^T \xi_M \frac{\mathrm{d}}{\mathrm{d}t}\left(\frac{1}{x_M}\right)\mathrm{d}t \\ &= -\frac{1}{T}\left[\frac{\xi_M}{x_M} - \log x_M\right]_0^T \\ &\to 0 \quad (T \to \infty), \end{aligned} \tag{23}$$

which means that $L_p(\boldsymbol{x})$ is an *average Lyapunov function* [12]. Using the trivial inequality

$$L_p(\boldsymbol{x}) = \sum_{i=1}^{M} p_i \log x_i \leq p_i \log x_i \tag{24}$$

for the persistent species $0 \leq x_i, p_i \leq 1$ and (23), the population density x_i of the persistent species ($i \in P$) satisfies

$$\begin{aligned} -\infty &< \frac{L_p(\boldsymbol{x}(0))}{p_i} \leq \lim_{t\to\infty} \frac{L_p(\boldsymbol{x}(t))}{p_i} \\ &\leq \lim_{t\to\infty} \log x_i(t), \end{aligned} \tag{25}$$

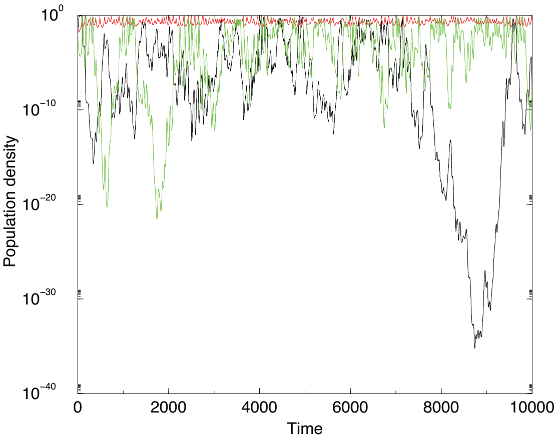

Fig. 1 (Color online only) The population density of the "environmental" species $x_{N+1}(t)$ (red), and the top predator $x_N(t)$ (green) and the basal producer $x_1(t)$ (black) vs. time t of the RE corresponding to the hierarchically ordered random LVE with $N = 63$. The number of persistent species is $S = 28$ for this sample of the random matrix B and random (r_i).

which means the system of the persistent species is strongly persistent. □

Since $\tilde{\alpha}_i(\boldsymbol{p})$ is the *transversal eigenvalue* [12], $\tilde{\alpha}_i(\boldsymbol{p}) = 0$ for the persistent species $i \in P$ denotes that the saturated fixed point $\boldsymbol{p}$ is linearly neutrally stable in terms of the flow on the boundary $x_i = 0$ for $\forall i \notin P$ in the same way as int the RE with antisymmetric interactions [7]. The hyperplane of that boundary is filled with neutrally stable orbits around $\boldsymbol{p}$, and the hyperplane as a whole constitutes a (non- transitive) attracting set for almost all the initial conditions.

Note that Theorem 1 holds without the condition of the hierarchical order (7), and the theorem itself does not give any information on S , the number of persistent species, which actually depends on the value of r_i and b_{ij}. If r_i and b_{ij} of the LVE (1) and (5)-(7) takes a random value chosen from a Gaussian ensemble (with zero mean and a finite variance) independently, mass extinction occurs and only $S \sim O(1)$ species can coexist even if N is large. However, even if r_i and b_{ij} are random, $S \sim O(N/2)$ species can coexist for $N \to \infty$ if lower-ranking species are more productive ($r_i > r_j$ for $i < j$), which is verified by numerical simulations (Fig.1). The dependence of S on the parameters of random r_i and b_{ij} is now in progress and will be reported elsewhere. Note that this is the first example of the chaotic coexistence of an arbitrary number of species in the food web model in the "unstable triangle region" ($\forall i\, a_{ii} = 0$ and the interaction matrix A has symmetric elements) of the phase diagram presented in [8].

5. DISCUSSION

The RE appears in a variety of models of biological and social dynamics. For example, it was originally proposed as a game dynamical equation [16]. In the context of game theory, the present model can be termed a "zero-sum" game with an environmental strategy M. It also describes autocatalytic reaction networks such as *hypercycles* [17, 18], in which x_i denotes concentration of a polynucleotide. In population genetics it is, moreover, a continuous counterpart of the discrete selection equation where x_i denotes the frequency of allele i in a gene pool. In particular, gene conversion has been modeled by the antisymmetric RE [13, 19]. The present study can contribute some information for those systems.

Concerning the antisymmetric interactions of the LVE, Kerner formulated statistical mechanics and derived some thermodynamic functions[20-22]. Combining his theory and the statistical mechanics of the species abundance distribution (SAD) of the random community model [8, 23-25], a SAD of the average population density p_i of the hierarchically ordered random LVE can be obtained, which will be reported elsewhere.

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