

Stability of Multispecies Prey-predator System

By

M. TANSKY*

Department of Biophysics, Kyoto University, Kyoto, Japan

(Received September 10, 1977)

ABSTRACT The stability criteria of the linearized dynamical system for the multispecies community with prey-predator interactions are investigated. Using the method of Lyapunov function, a generalization of the "qualitative stability criteria" given by Quirk and Ruppert, and May is developed. The stability condition for the community system which has more realistic type of the food web structure is discussed comparing with those of the probabilistic approach developed by Gardner and Ashby, and May.

Introduction

In 1958, Elton declared that generally the species population becomes more stable in structurally complex communities. Since then many ecologists have debated the relationship between the stability and complexity of food webs.

Gardner and Ashby (1970) and May (1972) have investigated this problem using the probabilistic approach. They considered a linearized dynamical system of n -species community $\dot{\xi} = A\xi$, where each non-zero element of matrix A , i. e. a_{ij} is chosen from the random distribution with the mean values zero for $i \neq j$ and -1 for $i = j$, and the variance s^2 for all i and j . Using the theory of random matrix and also the computer simulation, it was shown that, as the connectance defined by the ratio of the number of non-zero non-diagonal elements increases, the real parts of the eigenvalues of the random matrix A tend to become larger.

On the other hand, the stability conditions of the community systems have been also examined using the analytical investigations of the linearized dynamical systems. The stability criteria which are useful especially for the biological community systems were proposed by Quirk and Ruppert (1965) and May (1973), but it can

* Tansky is the acronym for a group composed of the individuals Ei Teramoto, Hiroshi Ashida, Hisao Nakajima, Nanako Shigesada, Kohkichi Kawasaki, and Norio Yamamura.

be applied only to the systems with restricted simple structures.

Here we shall present a generalized stability criteria which can be applied for the community systems with prey-predator interactions and it will be shown that the present analysis gives consistent results with those of the probabilistic approaches.

Stability Condition of Food Web System with Branched Chain Structure

Here we consider a multispecies community composed of s species. If we denote the population or the biomass of the i -th species by x_i , the process can be described by a set of equations of the form

$$\dot{x}_i = F_i(x_1, x_2, \dots, x_s), \quad i=1, 2, \dots, s \quad (1)$$

The function F_i represents the growth rate of the i -th species and is generally given by some non-linear function of x_1, x_2, \dots, x_s . We assume that the equations (1) have equilibrium points in the first orthant and let one of these points be

$$x^0 = (x_1^0, x_2^0, \dots, x_s^0).$$

Then, using the variable $\xi_i = x_i - x_i^0$, we have a linearized system

$$\dot{\xi} = A\xi, \quad (2)$$

where ξ represents a vector of s components ξ_i 's, and the elements of matrix A are given by $a_{ij} = (\partial F_i / \partial x_j)_{x^0}$. This equilibrium point is locally stable when the real parts of all eigenvalues of the matrix A are negative.

The matrix element a_{ij} ($i \neq j$) represents the effect of species j on species i and if the species i is the prey of the predator j , then we can expect (Tansky 1976);

$$a_{ij} < 0, \quad a_{ji} > 0 \quad i \neq j \quad (3)$$

Therefore in the community in which the inter-species interactions are only of the prey-predator type, we can assume the relations

$$a_{ij}a_{ji} \leq 0, \quad i \neq j \quad (4)$$

where the equality holds when there is no interaction between the i -th and j -th species. If other inter-species interactions such as competition and symbiosis are taken into account, the relation (4) does not necessarily hold. However, in this paper we consider the system with this relation (4), though the signs of a_{ii} 's are not a priori restricted.

For the linearized dynamical system (2) we can construct a corresponding food web diagram as shown in Figure 1. Each point represents a species in the community and for each non-zero matrix element a_{ij} , the points of species i and j

are connected by a directed line segment from i to j if $a_{ij} < 0$ and vice-versa if $a_{ij} > 0$. This direction actually shows the direction of energy flow in the real system. All of the species in the food web diagram can be classified into two sub-groups referred to as "loop structure group" (LSG) and "branched chain structure group" (BSG) defined as follows.

Definition: A loop structure group is composed of those species which are interconnected by line segments in such a way that, starting from any one of the species in the group, we can return back to that point along the way of connecting line segments (without regard to the direction of line segment) under the condition that each line segment is passed only once. If there exist more than one such round pathways, all species involved in them are included in the same LSG. A branched chain structure group is composed of those species which are mutually connected by line segments in a branched chain form without constructing any loop structure. These definitions are independent of the direction of energy flow and are concerned only with the connections in the food web diagram.

The useful stability conditions for the food web diagram which does not contain any LSG, referred to as the "qualitative stability criteria", have been proposed by Quirk and Ruppert (1965) and May (1973), and then Jeffries (1974) has pointed out that the criteria are incomplete and discussed the correct version of those criteria. However, in the following discussions, we do not need the detail of this criticism.

The criteria may be essentially summarized as follows:

When only the signs (+, -, or 0) of the individual matrix elements a_{ij} are known, the sufficient conditions that the real parts of all eigenvalues of the matrix A are nonpositive ($\text{Re } \lambda_i \leq 0$ for all i) independent of the actual magnitude of the non-zero elements are

- i) $a_{ii} \leq 0$ for all i
- ii) $a_{ij}a_{ji} \leq 0$ for all $i \neq j$
- iii) for any sequence of 3 or more indices i, j, k, \dots, q, r
(all different), the product $a_{ij}a_{jk} \dots a_{qr}a_{ri} = 0$

These conditions are less restrictive than those given in the original criteria, which are presented for the case that the real parts of eigenvalues are all strictly negative, i. e. $\text{Re } \lambda_i < 0$.

Among the conditions (5), ii) is just our conditions (4) assumed as the prey-predator interactions and iii) represents the condition that the food web diagram does not contain any LSG. Therefore, in this case we can see that $\text{Re } \lambda_i \leq 0$ for all i if the diagonal elements a_{ii} of A are non-positive for all i . Furthermore, when the condition i) is released, we have the following theorem.

Theorem: If the matrix A satisfies the conditions ii) and iii) in (5), then

Re $\lambda_i \leq \kappa$ where κ is the maximum value of diagonal elements of A .

Proof: Let us consider a matrix defined by $B = A - \kappa I$ where we put $\kappa = \max_i a_{ii}$ and I is the identity matrix. The eigenvalue equation of A can be written as

$$|A - \lambda I| = |A - \kappa I - (\lambda - \kappa)I| = |B - \lambda' I|$$

where

$$\begin{aligned} \{B\}_{ij} &= b_{ij} = a_{ij} && \text{for } i \neq j \\ &= a_{ii} - \kappa && \text{for } i = j \end{aligned}$$

The eigenvalues of B are given by

$$\lambda'_i = \lambda_i - \kappa.$$

Obviously the matrix B satisfies the conditions (5), therefore Re $\lambda'_i \leq 0$ and we can conclude that Re $\lambda_i \leq \kappa$. Q. E. D.

This theorem yet allows the case that even if some species have intrinsically unstable properties (i. e. $a_{ii} > 0$ for some i), there is the possibility that the system becomes stable under some suitable connections of prey-predator interactions.

Stability Conditions for General Food Web Structure

Now we shall consider a food web diagram which contains LSG's. The species in the food web diagram can be uniquely divided into a number of LSG's and BSG's. There may exist some neighbouring LSG's which are connected by a single line segment as the group L_1 in Fig. 1. If we regard such a cluster of LSG's as a single LSG, then the food web diagram consists of LSG's and BSG's which are alternately connected with each other. We shall label the LSG's as L_1, L_2, \dots, L_N and the BSG's as B_1, B_2, \dots, B_M . Furthermore if we replace each LSG by a single decorated representative point, the food web diagram can be reduced to a form of BSG as shown in Fig. 1.

Let us assume that L_k and B_h consists of n_k and m_h species ($k=1, 2, \dots, N$; $h=1, 2, \dots, M$) respectively and we shall rearrange the variables ξ of equation (2) into $N+M$ groups corresponding the groups L_1, L_2, \dots, L_N and B_1, B_2, \dots, B_M . If we denote the variable of the i -th species in the L_k by η_i^k and that of the j -th species in the B_h by ζ_j^h , then we can rewrite the equation (2) as

$$\begin{aligned} \dot{\eta}_i^k &= \sum_{j=1}^{n_k} a_{ij}^{kh} \eta_j^k + \sum_{h=1}^M \sum_{j=1}^{m_h} b_{ij}^{kh} \zeta_j^h, \\ \dot{\zeta}_j^h &= \sum_{k=1}^N \sum_{i=1}^{n_k} c_{ji}^{kh} \eta_i^k + \sum_{i=1}^{m_h} d_{ji}^{hh} \zeta_i^h, \end{aligned} \quad (6)$$

where c_{ji}^{hk} is the matrix element of A in equation (2) corresponding the coefficient which relate the i -th species in L_k to the j -th species in B_h , and a_{ij}^{hk} , b_{ij}^{hk} and d_{ij}^{hk} are defined in the same way. The matrix of the linear system (6) is given in a form

$$\mathcal{A} = \begin{pmatrix} A^{11} & 0 & \dots & 0 & B^{11} & B^{12} & \dots & B^{1M} \\ 0 & A^{22} & \dots & 0 & B^{21} & B^{22} & \dots & B^{2M} \\ \dots & \dots & \dots & \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & \dots & A^{NN} & B^{N1} & B^{N2} & \dots & B^{NM} \\ C^{11} & C^{12} & \dots & C^{1N} & D^{11} & 0 & \dots & 0 \\ C^{21} & C^{22} & \dots & C^{2N} & 0 & D^{22} & \dots & 0 \\ \dots & \dots & \dots & \dots & \dots & \dots & \dots & \dots \\ \dots & \dots & \dots & \dots & \dots & \dots & \dots & \dots \\ C^{M1} & C^{M2} & \dots & C^{MN} & 0 & 0 & \dots & D^{MM} \end{pmatrix} \quad (7)$$

where matrix elements A^{kk} , B^{kh} , C^{hk} and D^{hh} themselves are matrices whose (ij) elements are a_{ij}^{hk} , b_{ij}^{kh} , c_{ij}^{hk} and d_{ij}^{hh} , respectively.

Now we shall try to find a Lyapunov function for this system which asserts the stability of the dynamical system (LaSalle and Lefshetz, 1961). Let us consider the function

$$H = \frac{1}{2} \sum_{k=1}^N \sum_{i=1}^{n_k} \alpha_i^k \eta_i^k{}^2 + \frac{1}{2} \sum_{h=1}^M \sum_{j=1}^{m_h} \beta_j^h \zeta_j^h{}^2 \quad (8)$$

then we can show the followings:

Lemma 1: If there exist the positive constants α_i^k and β_j^h which satisfy the equations

$$\begin{aligned} \alpha_i^k b_{ij}^{kh} + \beta_j^h c_{ji}^{hk} &= 0, \\ \beta_i^h d_{ij}^{hh} + \beta_j^h d_{ji}^{hh} &= 0, \quad i \neq j \\ \alpha_i^k &= \alpha^k \quad (\text{a constant independent of } i), \end{aligned} \quad (9)$$

the function H defined by (8) becomes Lyapunov function, under the conditions

i) the diagonal elements of D^{hh} are all negative,

$$d_{jj}^{hh} < 0 \text{ for all } j \text{ and } h \quad (10)$$

ii) the quadratic form of A^{kk} are negative definite,

$$\sum_{i,j}^{n_k} \eta_i^k a_{ij}^{kk} \eta_j^k \leq 0 \quad k = 1, 2, \dots, N \quad (11)$$

Proof: Since α_i^k and β_j^h are positive constants for all i, j, k and h , the function

H satisfies the relation $H \geq 0$ and the equality holds only when all variables η_i^h and ζ_j^h 's are zero. Using the equations (6) and (9), the time derivative of H is obtained as

$$\begin{aligned} \dot{H} &= \sum_k^N \sum_{i,j}^{n_k} \alpha_i^k a_{ij}^{hk} \eta_i^k \eta_j^k + \sum_k^M \sum_k^N \sum_j^{m_h} \sum_i^{n_k} (\alpha_i^k b_{ij}^{kh} + \beta_j^h c_{ji}^{hk}) \eta_i^k \zeta_j^h \\ &\quad + \sum_h^M \sum_j^{m_h} \beta_j^h d_{jj}^{hh} \zeta_j^h{}^2 + \sum_h^M \sum_{i>j}^{m_h} (\beta_i^h d_{ij}^{hh} + \beta_j^h d_{ji}^{hh}) \zeta_i^h \zeta_j^h \\ &= \sum_k^N \sum_{i,j}^{n_k} \alpha_i^k a_{ij}^{hk} \eta_i^k \eta_j^k + \sum_h^M \sum_j^{m_h} \beta_j^h d_{jj}^{hh} \zeta_j^h{}^2 \end{aligned} \quad (12)$$

Thus, under the conditions (10) and (11), we have the relation $\dot{H} \leq 0$. Q. E. D.

Lemma 2: If the matrix elements satisfy the condition,

$$\begin{aligned} b_{ij}^{hh} c_{ji}^{hk} &< 0 \\ d_{ij}^{hh} d_{ji}^{hh} &< 0 \quad i \neq j \end{aligned} \quad (13)$$

We can find the positive constants α_i^h and β_j^h which satisfy the equation (9).

Relation (13) always holds when the inter-species interaction is only of the prey-predator type, as previously noted in the discussion of relation (4).

Proof: First, let us choose one of the LSG's, for example L_1 , and put all the values of α_i^1 ($i=1, 2, \dots, n_1$) in L_1 equal to a positive constant denoted by α^1 . We shall consider the case in which the p -th species in L_1 is directly connected with the q -th species in the neighbouring BSG, denoted by B_h . It can be seen that any species in B_h can be reached from the p -th species in L_1 along a uniquely determined linear chain of line segments. The series of species along the pathway from the p -th species in L_1 to the u -th species in B_h can be represented schematically as

$$p(L_1) - q(B_h) - \dots - t(B_h) - u(B_h).$$

Fig. 2 shows a part of diagram in our consideration. In order to determine the constant β_u^h associated to the u -th species in B_h , we can use the relations (9) iteratively and we obtain

$$\beta_u^h = \left(-\frac{d_{tu}^{hh}}{d_{tu}^{hh}} \right) \dots \dots \left(-\frac{b_{pq}^{1h}}{c_{qp}^{h1}} \right) \alpha^1$$

which has apparently positive value due to the condition (13). In the same way, we can uniquely determine all of β_j^h ($j=1, 2, \dots, m_h$) in B_h as positive constants. Furthermore, if a species at another terminal in B_h is connected with a species in a neighbouring LSG, for instance the species $v(L_h)$ in L_h , α_v^h can be also determined as a positive constant by using the first equation of (9). Then we can put all of the remaining values of α_j^h ($j=1, 2, \dots, n_h$) in L_h to be equal to α_v^h which can be

denoted as α^k . Repeating these procedures for neighbouring groups successively, we can determine α_i^k and β_j^h for all i, j, k and h as positive constants. Q. E. D.

Thus combining the results, we have

Theorem: The sufficient conditions for stability of the dynamical system (6) are given by

- i) $b_{ij}^{hh} c_{ji}^{hh} < 0, \quad d_{ij}^{hh} a_{ji}^{hh} < 0 \quad i \neq j$
- ii) $d_{ii}^{hh} < 0$
- iii) $\sum_{i,j}^{n_2} \eta_i^k a_{ij}^{hh} \eta_j^k \leq 0$

Finally, as for the condition of the quadratic form $\sum_{i,j}^n \eta_i a_{ij} \eta_j$ for a LSG, we have the following theorem.

Theorem: When the conditions

$$a_{ii} < 0$$

$$\sqrt{a_{ii} a_{jj}} \geq \sqrt{l_i l_j} \frac{|a_{ij} + a_{ji}|}{2} \quad i, j = 1, 2, \dots, n \quad (14)$$

are satisfied, where l_i is the number of species which are connected directly with i -th species by line segments, then

$$\sum_{i,j} \eta_i a_{ij} \eta_j \leq 0$$

Proof: Instead of taking the summation about all species in a LSG, we shall take the summation about pairs of species in the following manner. If we regard a term $a_{ii} \eta_i^2$ as the product of l_i and $(1/l_i) a_{ii} \eta_i^2$, and take into account that the i -th species is associated with l_i pairs, the quadratic form can be rewritten as

$$\sum_{i,j} \eta_i a_{ij} \eta_j = \sum_{(ij)} \left[\left\{ \frac{a_{ii}}{l_i} \eta_i^2 + \frac{a_{jj}}{l_j} \eta_j^2 \right\} + (a_{ij} + a_{ji}) \eta_i \eta_j \right]$$

where $\sum_{(ij)}$ denotes the summation over all connected pairs. When $a_{ii} \neq 0$ for all i , the equation becomes

$$\sum_{(ij)} \left[\frac{a_{ii}}{l_i} \left\{ \eta_i + \frac{l_i(a_{ij} + a_{ji})}{2a_{ii}} \eta_j \right\}^2 + \frac{\eta_j^2}{a_{ii}} \left\{ \frac{a_{ii} a_{jj}}{l_j} - \frac{1}{4} l_i (a_{ij} + a_{ji})^2 \right\} \right].$$

Therefore, it is clear that the relations (14) become the sufficient conditions.

Q. E. D.

Hence, the system will be stable if the geometric average of any pair a_{ii} and a_{jj} , which indicate a measure of selfstabilization, is larger than the product of $\sqrt{l_i l_j}$ and the absolute value of arithmetic average of the pair of nondiagonal elements a_{ij} and a_{ji} , which indicate a measure of the prey-predator interactions. The value

$\sum_i l_i/2$ is the total number of line segments in a LSG. Thus it can be seen that the selfstabilization of each species gives again the stabilizing effect to the system containing LSG's and also the increase of the connection in LSG's generally makes the system unstable. This result is consistent with the conclusion of the probabilistic approach given by Gardner and Ashby, and May. Furthermore, in the special case $a_{ii} < 0$ and $|a_{ij} + a_{ji}| = 0$, the stability conditions (14) are always satisfied. This corresponds to the linearized Volterra system with negative diagonal elements, and its stability has been already proved by Goel, Maitra and Montroll (1971).

References

- Gardner, M. R., and Ashby, W. R.: Connectance of large dynamical (cybernetic) systems: critical values for stability. *Nature*, 228, 784 (1970).
- Goel, N. S, Maitra, S. C., and Montroll, E. W.: On the Volterra and other nonlinear models of interacting populations. *Rev. Mod. Phys.* 43, 231-276 (1971).
- Jeffries, C.: Qualitative stability and digraphs in model Ecosystems. *Ecology* 55, 1415-1419 (1974).
- La Salle, J. and Lefschetz, S.: *Stability by Lyapunov's Direct Method with Applications*. Academic Press 1961.
- May, R. M.: *Stability and Complexity in Model Ecosystems*. Princeton Univ. Press, Princeton, New Jersey 1973.
- Quirk, J P., and Ruppert, R.: Qualitative economics and the stability of equilibrium. *Rev. Econ. Studies* 32, 311-326 (1965).
- Tansky, M.: Structure, stability, and efficiency of ecosystem p. 205 (*Progress in Theoretical Biology*, Vol. 4.) Academic Press, 1976.