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QUALITATIVE STABILITY AND DIGRAPHS IN MODEL ECOSYSTEMS[1]

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Abstract. Roughly speaking, an ecosystem is called "qualitatively stable" when one may conclude solely on the basis of the qualitative effects of member species on each other, that the system is stable. The conditions for qualitative stability are rather severe, particularly for ecosystems with great species diversity. Nonetheless, qualitative stability conditions may be met in nature by very simple ecosystems. In a recent paper, R. M. May (1973) presented necessary but insufficient conditions for qualitative stability. In this report, sufficient conditions are expressed in terms of the food web design viewed as a "signed digraph."

Key words: Community matrix; food chain; food web; interaction matrix; model ecosystem; qualitative stability; signed digraph; stability; trophic web.

INTRODUCTION

Suppose a community of n species exists in equilibrium. Suppose one member species is then subjected to a small but sudden population increase or decrease. Other species populations may show immediate changes away from equilibrium. The manipulated species itself, if initially increased, may begin to decline because of self-regulation. Conversely, if a self-regulating manipulated species is first reduced, it will then initially increase toward equilibrium. These immediate, direct changes may be referred to as first-order effects and generally may be more prone to qualitative than quantitative description.

Such first-order effects may be described by the equation

$$dx_i/dt = \sum_{j=1}^{n} a_{ij}x_j \qquad (1)$$

where $\{a_{ij}\}$ is the "interaction matrix" or "community matrix" and where $(0, 0, \ldots, 0)$ represents the equilibrium state of the population levels $\{x_i\}$. The variables $\{x_i\}$ represent the difference between population levels and the given population levels at equilibrium. May (1971, 1973) gives additional interpretations of the role of (1) in ecology.

Of primary importance in discussing equilibrium is the nature of the stability of equilibrium. Suppose the system, following a perturbation, approaches with time a limit, namely the equilibrium point. If such limiting behavior will follow any slight perturbation, then the system is called "asymptotically stable." It may be shown that (1) is asymptotically stable if and only if the real part of each eigenvalue of $\{a_{ij}\}$ is negative.[3]

Suppose the system (1) based on some given matrix is asymptotically stable. Suppose the magnitudes (but not the signs!) of the non-zero entries in the matrix are randomly changed. If every new system so obtained is always asymptotically stable, then the original matrix is called "qualitatively stable." Thus qualitative stability actually depends only on the qualitative nature, that is, the sign of the non-zero entries of a matrix.

May (1973), following Quirk and Ruppert (1965), proposed the following conditions for the qualitative stability of (1):

i) $a_{ii} \leq 0$ for all i;
ii) $a_{ii} < 0$ for at least one i;
iii) $a_{ij}a_{ji} \leq 0$ for all $i \neq j$;
iv) $a_{ij}a_{jk} \ldots a_{qr}a_{ri} = 0$ for any sequence of three or more distinct indices $i, j, k, \ldots, q, r$; and
v) determinant $\{a_{ij}\} \neq 0$.

These criteria imply certain constraints on the signs of entries in $\{a_{ij}\}$, but no absolute values for non-zero entries are implied.

These conditions, however, are insufficient as the following matrix shows:

$$\begin{pmatrix} -a & b & c \\ 0 & 0 & -d \\ 0 & e & 0 \end{pmatrix}.$$

The numbers a, d, e are assumed positive. This matrix could be associated with a system of three species in which the first is self-regulating and the second is preyed upon by the third. Although this

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[3] Moreover, if the real part of each eigenvalue of $\{a_{ij}\}$ is nonpositive and if no eigenvalue with zero real part is repeated in the minimal polynomial of $\{a_{ij}\}$, then (1) is neutrally stable. In the remaining cases, (1) is unstable.

matrix satisfies the conditions, its eigenvalues are $-a$ and $\pm\sqrt{-de}$. Thus the system (1) associated with this matrix would be neutrally stable but not asymptotically stable.

A second model may be based on the matrix

$$\begin{pmatrix} 0 & -1 & 0 & 0 & 0 \\ 1 & 0 & -1 & 0 & 0 \\ 0 & 1 & -1 & -1 & 0 \\ 0 & 0 & 1 & 0 & -1 \\ 0 & 0 & 0 & 1 & 0 \end{pmatrix}.$$

This matrix could be associated with a five-species ecosystem model in which one species is preyed upon by a second; the second by a third; the third by a fourth; and the fourth by a fifth. The third species is self-regulating. Although the matrix satisfies the criteria, its eigenvalues are $\pm\sqrt{-1}$, -0.36 (approximately), and $-0.32 \pm 0.16\sqrt{-1}$ (approximately). Thus the model associated with this matrix would also be neutrally stable but not asymptotically stable.

A rather different model involving five species would be associated with the matrix

$$\begin{pmatrix} -a & * & * & * & * \\ 0 & 0 & -b & *' & *' \\ 0 & c & 0 & *' & *' \\ 0 & 0 & 0 & 0 & -d \\ 0 & 0 & 0 & e & 0 \end{pmatrix},$$

where each $*$, $*'$ denotes an arbitrary real number; a, b, c, d, e are all positive; and $bc = de$. This matrix satisfies the criteria, and its eigenvalues are $-a$, $\pm\sqrt{-bc}$, $\pm\sqrt{-bc}$. Nonetheless, a dynamic system based upon this matrix is actually unstable provided at least one of the $*'$ entries is non-zero.

Conditions (i) through (v) are therefore insufficient to guarantee asymptotic stability. Condition (ii) (at least one species self-regulating) is unnecessary for neutral stability, as referring to the classical Lotka-Volterra predator–prey model shows. The purpose of this report is to formulate a replacement for condition (ii). As will be shown, qualitative stability depends very much on which species are self-regulating.

THEORY

I feel that an easily accessible way to approach qualitative stability and a way that should have direct significance in ecological theory entails the use of digraphs. A digraph (short for "directed graph") consists of n points (here representing species populations) together with from zero to n^2 connecting directed lines (representing interactions). The digraph in Fig. 1 indicates that the level of x_1 affects the rates of change of x_1 and x_2; that is, $a_{11} \neq 0$ and $a_{21} \neq 0$ in (1). A "+" or a "−" may be written near a line to denote the qualitative nature of the effect. The signs correspond to the signs of the matrix entries, and a digraph so described is called "signed."

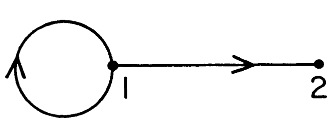

FIG. 1. A simple digraph.

Now a "p-cycle" in a digraph is a set of p distinct points with the property that a circuit may be traced among the p points by following p directed lines. Each p-cycle must involve precisely p lines; "figure eights" and so on are not considered cycles. The following are cycles:

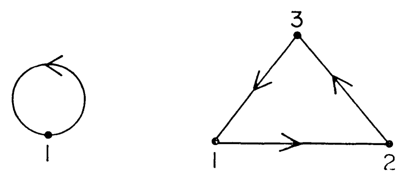

FIG. 2. A 1-cycle and a 3-cycle.

However, the following is *not* a 3-cycle:

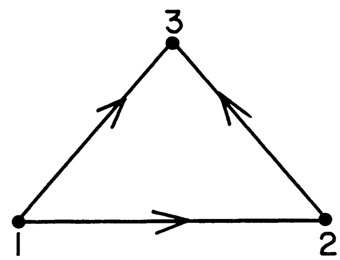

FIG. 3. A digraph which is not a 3-cycle.

Cycles may occur within complex digraphs. There are a 1-cycle, a 2-cycle, and a 3-cycle in the digraph in Fig. 4.

Obviously a signed digraph with n points may be associated with any $n \times n$ matrix, using the signs of the non-zero entries in the matrix. Thus condition (iv) is equivalent to the absence of p-cycles with $p \geqslant 3$. For more fun with digraphs, see Roberts (1971).

Next a "predation community" is defined. If two species are involved in a 2-cycle, and if the 2-cycle involves one "+" line and one "−" line, then the species may be regarded as predator and prey, or parasite and host. The species are said to be related by a "predation link." Associate with a fixed species all the other species, if any, to which it is related by predation links. Then associate with those species all additional species related by predation links, and so on. The maximal set of all such species so related to the first species is called the

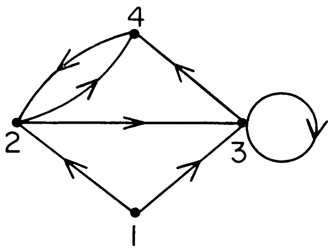

FIG. 4. A digraph with a 1-cycle, a 2-cycle, and a 3-cycle.

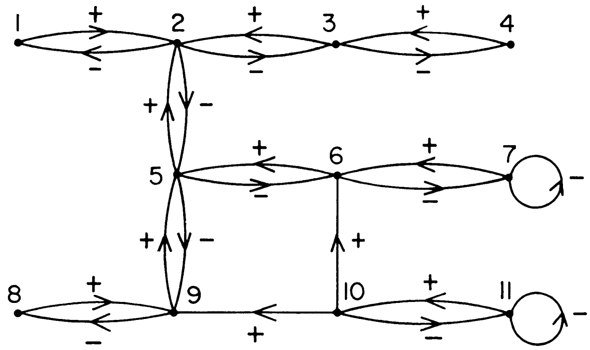

FIG. 6. A digraph with two predation communities, the larger of which passes the color test.

"predation community" containing the first species. For the sake of completeness, a species not connected by a predation link to any other species is also called a predation community, albeit trivially so. Clearly any digraph may be partitioned into predation communities. If no predation links occur in a digraph, then the digraph has n trivial predation communities, each with one species. To illustrate all this, in the signed digraph in Fig. 5 three predation communities occur: $\{x_1\}$, $\{x_2,x_3,x_4,x_5\}$, and $\{x_6,x_7\}$.

Qualitative Stability Conditions

In terms of a matrix $\{a_{ij}\}$ satisfying conditions (i), (iii), (iv), and (v), a matrix $\{\tilde{a}_{ij}\}$ may be defined as follows: replace by zero each entry in $\{a_{ij}\}$ that is associated with a line in the digraph of $\{a_{ij}\}$ which is involved in no cycles. From $\{\tilde{a}_{ij}\}$ a new dynamical system may be defined:

$$dx_i/dt = \sum_{j=1}^{n} \tilde{a}_{ij} x_j. \tag{2}$$

As shown in Appendix I, either (1) is asymptotically stable or (2) is neutrally stable. In this section a necessary condition on the digraph of $\{\tilde{a}_{ij}\}$, which amounts to a condition on the digraph of $\{a_{ij}\}$, is found for the neutral stability of (2). If $\{\tilde{a}_{ij}\}$ fails to meet the condition, then (1) must be asymptotically stable. The graphic analog of obtaining $\{\tilde{a}_{ij}\}$ from $\{a_{ij}\}$ is *simply the erasure of all lines connecting predation communities.*

As shown in Appendix I the neutral stability of (2) implies the existence of a closed, finite trajectory for (2) along which any self-regulating species must remain at equilibirum ($x_i = 0$). Suppose some x_j

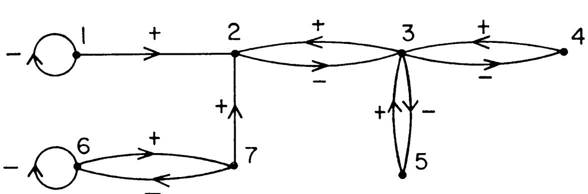

FIG. 5. A digraph with three predation communities.

is connected by a predation link to no second species. It may be shown using condition (v) ($\{a_{ij}\}$ is nonsingular) that such a species must be self-regulating. Thus the species that change along the closed, finite trajectory must be in non-trivial predation communities, those with two or more species.

In a predation community oscillating species and non-oscillating species must be connected as follows. Considering the equation for dx_j/dt, any oscillating species x_j must be connected to at least one other oscillating species. Considering the equation for dx_k/dt, any non-oscillating species x_k (for example, a self-regulating species) which is connected to one oscillating species must be connected to at least one other oscillating species.

This may be summarized by defining the following "color test." A predation community passes the color test provided each point in the associated digraph may be colored black or white with the result that

a) each self-regulating point is black;
b) there is at least one white point;
c) each white point is connected by a predation link to at least one other white point;
d) each black point connected by a predation link to one white point, is connected by a predation link to at least one other white point.

Thus, in terms of this color test, we replace condition (ii) by the following:

ii)′ each predation community in the signed digraph of $\{a_{ij}\}$ fails the color test. Conditions (i), (ii)′, (iii), (iv), and (v) imply asymptotic stability for (1).

To illustrate all this we consider the signed digraph in Fig. 6.

Species 1 through 9 comprise a predation community, as do species 10 and 11. If one attempts to color the latter, species 11 must be black, and so species 10 must be black as well. Thus the predation community consisting of species 10 and 11 fails the color test. However, the scheme whereby species 1, 2, 3, 4, 8, and 9 are colored white and species 5, 6, 7 are colored black shows that the predation community consisting of species 1 through 9 passes the color test. Thus the associated dynamic system (1) is not necessarily asymptotically stable.

To show how asymptotic stability may arise, suppose x_1 were made self-regulating. This would lead to failure of the color test for species 1 through 9 and hence asymptotic stability. The reader may draw the signed digraphs associated with the matrices in the Introduction, show that some predation communities in those systems pass the color test, and derive what modifications would ensure asymptotic stability.

Discussion

The real parts of the eigenvalues of matrices satisfying conditions (i), (ii), (iii), (iv), and (v) are either negative ("almost all" cases) or zero. Some importance attaches to the distinction between the Lotka-Volterra predator–prey models with purely imaginary eigenvalues (without self-regulation) and those with eigenvalues with negative real parts. Accuracy in determining conditions for qualitative stability may be defended along similar lines. In both cases self-regulating interactions are crucial, and in the latter case the location of self-regulating species in the food web of an ecosystem model is critical.

Appendix I

To prove that conditions (i), (iii), and (iv) ensure that the eigenvalues of $\{a_{ij}\}$ are non-positive, I first show that a line involved in no cycle may be disregarded without affecting the eigenvalues. In terms of $\{a_{ij}\}$ define a new matrix $\{A_{ij}\}$ by $A_{ij} = x\delta_{ij} - a_{ij}$, where x is an indeterminate and $\delta_{ij} = 1$ if $i = j$, $\delta_{ij} = 0$ if $i \neq j$. The eigenvalues of $\{a_{ij}\}$ are the roots of the polynomial equation: determinant $\{A_{ij}\} = 0$. Suppose some matrix entry a_{pq}, $p \neq q$, is associated with a line involved in no cycle. This implies the vanishing of each product $a_{pq}a_{qp}$, $a_{ip}a_{pq}a_{qi}$, $a_{ij}a_{jp}a_{pq}a_{qi}$, . . . , where p, q, i, j, . . . are all distinct indices. Thus the products $A_{qp}A_{pq}$, $A_{ip}A_{pq}A_{qi}$, $A_{ij}A_{jp}A_{pq}A_{qi}$, . . . all vanish. By the definition of determinant, this implies the vanishing in the expansion of determinant $\{A_{ij}\}$ of each addend in which A_{pq} is a factor. Thus A_{pq}, or a_{pq}, may as well be zero insofar as eigenvalues are concerned.

Let $\{\tilde{a}_{ij}\}$ denote the matrix obtained from $\{a_{ij}\}$ by replacing by zero all those entries in $\{a_{ij}\}$ associated with lines which are involved in no cycles. The point of the previous paragraph is that $\{a_{ij}\}$ and $\{\tilde{a}_{ij}\}$ have the same eigenvalues.

Now the digraph associated with $\{\tilde{a}_{ij}\}$ has no lines except lines in cycles. The cycles, according to condition (iv), must be 1-cycles or 2-cycles. Thus the digraph associated with a_{ij} actually consists of one or more independent predation communities. It remains only to demonstrate that the eigenvalues of each such predation community have non-positive real parts. Now it may be shown using condition (v) (determinant $\{a_{ij}\} \neq 0$) that any species comprising a trivial predation community is necessarily self-regulating. Therefore in what follows a single non-trivial predation community is considered, and $\{\tilde{a}_{ij}\}$ is allowed to denote the restricted interaction matrix.

Since no p-cycles, $p \geqslant 3$, are allowed, there may be no instances of predation links themselves forming a loop among some species. That is, if one species is preyed upon by a second, and the second by a third, then the first may not be preyed upon by the third; and so on.

Define n positive constants $\lambda_1, \lambda_2, \ldots, \lambda_n$ as follows. Let $\lambda_1 = 1$. For each species x_i that has a predation link with x_1, let λ_i be defined by $\lambda_i = -a_{1i}/a_{i1}$, so $\lambda_i a_{i1} = -\lambda_1 a_{1i}$. The $\{\lambda_i\}$ are positive because in a predation community $a_{ij} > 0$ if and only if $a_{ji} < 0$, for all $i \neq$ j. This process may be expanded throughout the predation community precisely without contradiction because of the absence of loops of predation links. Finally, $\lambda_i a_{ij} = -\lambda_j a_{ji}$ for all $i \neq j$ such that $a_{ij} \neq 0$, and hence, of course, for all $i \neq j$.

Define a function φ by $\varphi = \sum_{i=1}^{n} \lambda_i x_i^2$. Since each $\lambda_i > 0$, $\varphi > 0$ except at $(0, 0, \ldots, 0)$ where $\varphi = 0$. Furthermore,

$$d\varphi/dt = \sum_{i=1}^{n} 2\lambda_i x_i dx_i/dt$$
$$= 2 \sum_{i=1}^{n} \sum_{j=1}^{n} \lambda_i x_i a_{ij} x_j.$$

With the use of $\lambda_i a_{ij} = -\lambda_j a_{ji}$ for $i \neq j$ this reduces to

$$d\varphi/dt = 2 \sum_{i=1}^{n} \lambda_i a_{ii} x_i^2.$$

Since each $a_{ii} \leqslant 0$, it follows that $d\varphi/dt \leqslant 0$ except at $(0, 0, \ldots, 0)$ where $d\varphi/dt = 0$. Together these properties imply that φ is a Lyapunov function which guarantees that the eigenvalues of $\{\tilde{a}_{ij}\}$ are non-positive (Rosen 1970:73–75).

In summary, the eigenvalues of $\{\tilde{a}_{ij}\}$ restricted to each predation community are non-positive, so the eigenvalues of $\{\tilde{a}_{ij}\}$ are non-positive; thus the eigenvalues of $\{a_{ij}\}$ are non-positive. Assume henceforth that determinant $\{a_{ij}\} \neq 0$.

Now the existence of this Lyapunov function guarantees that either the eigenvalues of $\{\tilde{a}_{ij}\}$ are negative—in which case the eigenvalues of $\{a_{ij}\}$ are negative and so (1) is asymptotically stable—or the system

$$dx_i/dt = \sum_{j=1}^{n} \tilde{a}_{ij} x_j \qquad (2)$$

is neutrally stable. If the system (2) is neutrally stable, then there must be a finite, closed trajectory aside from the trivial equilibrium point trajectory. Along this trajectory $d\varphi/dt = 2\sum_{i=1}^{n} \lambda_i a_{ii} x_i^2 = 0$. Thus any self-crowding species (for which $a_{ii} < 0$ so $\lambda_i a_{ii} < 0$) must remain at equilibrium ($x_i = 0$) along the closed trajectory. The central idea of the "color test" condition in the text is to exclude the possibility of neutral stability for (2) and so insure asymptotic stability for (1).

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ADDED IN PROOF

As well as being sufficient, conditions (i), (ii)′, (iii), (iv), and (v) are necessary for qualitative stability of (1). Also, the quantitative condition (v) may be replaced by a qualitative condition (v)′: there is at least one way to erase all but n lines in the signed digraph of $\{a_{ij}\}$ leaving each node in a cycle.