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QUALITATIVE STABILITY IN MODEL ECOSYSTEMS¹

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Abstract. We discuss deductions that can be made as to the stability of multispecies communities, knowing only the structure of the food web, i.e., knowing only the signs of the elements in the interaction matrix. Systems which are stable in these circumstances are called qualitatively stable and have been treated in economic and other contexts. The discussion touches upon general aspects of the relation between complexity and stability in multispecies systems, and in particular suggests that on stability grounds predator-prey bonds should be more common than mutualistic ones. This result is not intuitively obvious, but is a feature of many real-world ecosystems.

A wide variety of mathematical models have recently been studied, with a view to elucidating general features of the relation between complexity and stability in multispecies communities. Roughly speaking, complexity may be measured by the number and nature of the individual links in the trophic web, and stability by the tendency for relatively small population perturbations to damp out, returning the system to its equilibrium configuration (other usages of the terms are, of course, possible). Thus Gardner and Ashby (1970) and May (1972) have studied the stability character of large, complex ecosystem models in which the trophic web links are assembled (connected) at random; the stability is an interesting function of the number of species and the level of connectance. Drawing upon Kauffman's (1970*a, b*) and others' analytic and computer work, Levins (1970) argues that "the dynamics of a broad class of complex systems will result in simplification through instability." May (1971*a*) has reviewed work on the dynamical stability of multispecies generalizations of the familiar Lotka-Volterra predator-prey models, and many people have made numerical systems-analysis studies of the stability properties of specific multispecies systems (e.g., reviews by Watt 1968, May 1971*b*).

In one form or another, all this work makes assumptions about the *magnitudes* of the interactions between species in the community. The present note sets out some things that can be said, knowing only the topological structure of the trophic web, i.e., knowing only the *signs* (+, −, or 0) of the interactions between the various species.

More specifically, consider a community with n populations, $N_i(t)$, labelled by the index $i = 1, 2, \dots, n$. The dynamics of the community may in general be described by some nonlinear set of first-order differential equations. The possible equilibrium or time-independent populations, N_i^* , in such a system are found by setting all the growth rates zero,

and solving the consequent algebraic equations. To study the stability of the equilibrium community, one writes

$$N_i(t) = N_i^* + x_i(t), \quad (1)$$

where the quantities $x_i(t)$ measure the initially relatively small perturbations to the equilibrium configuration. Then, expanding the n nonlinear population equations about the equilibrium point, the dynamics of small disturbances are described by a set of n linear first-order differential equations, whose structure is summarized by an $n \times n$ matrix of interaction coefficients:

$$dx_i(t)/dt = \sum_{j=1}^n a_{ij} x_j(t). \quad (2)$$

Alternatively, in matrix notation,

$$d\mathbf{x}(t)/dt = \mathbf{A} \mathbf{x}(t). \quad (3)$$

Here \mathbf{x} is the $n \times 1$ column matrix of the x_i , and \mathbf{A} is the $n \times n$ "interaction matrix" or "community matrix" (Levins 1968), whose elements a_{ij} describe the effect of species j upon species i near equilibrium. The necessary and sufficient condition for the equilibrium point to be stable, in the above sense, is that all the eigenvalues of the interaction matrix (which can be found by turning the handle of some well-defined mathematical machinery) have negative real parts. For a fuller account, see Maynard Smith (1968) or Rosen (1970). To follow the theme of the present note, such detail is not necessary.

This matrix \mathbf{A} is clearly a quantity of direct biological significance. A diagram of the trophic web immediately shows which elements a_{ij} are zero (no web link); the type of interaction sets the sign of the non-zero elements; and the details of the interactions determine the magnitude of these elements. The sign structure of this $n \times n$ matrix is directly tied to Odum's (1953) scheme which classifies interactions between species in terms of the signs of the effects produced. He characterizes the effect of species j upon species i as positive, neutral, or negative (that is, $a_{ij} +, 0$, or $-$) depending on whether the

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population of species i is increased, is unaffected, or is decreased by the presence of species j . Thus for the pair of matrix elements a_{ij} and a_{ji} we can construct a table of all possible interaction types:

		Effect of species j on i (i.e., sign of a_{ij})		
		+	0	-
Effect of species i on j (i.e., sign of a_{ji})	+	++	+0	+-
	0	0+	00	0-
	-	-+	-0	--

Apart from complete independence, there are five distinguishably different categories of interaction between any given pair of species, namely commensalism (+0), amensalism (-0) mutualism or symbiosis (++), competition (--), and general predator-prey (+-) including plant-herbivore, parasite-host, and so on. For a more thorough exposition, see Williamson (1972, Ch. 9).

In short, on the one hand, this matrix summarizes the biology of the situation and encapsulates the character of the species' interactions, and, on the other hand, it gives the system's stability properties.

What can be said, knowing only the sign of the individual matrix elements (+, -, or 0) and nothing else?

In general, if a matrix can be shown to be necessarily stable (i.e., all eigenvalues having negative real parts), altogether independent of the actual magnitude of the non-zero elements, the matrix is called "qualitatively stable." This is an important subject in mathematical economics, where often no quantitative information is available (Quirk and Ruppert 1965, Maybee and Quirk 1969).

The situation in ecology is similar. The sign of the interaction matrix elements can often be found by inspecting the food web diagram, even in the total absence of any quantitative data.

The necessary and sufficient conditions for a matrix to be qualitatively stable are set out in the next section. If the signs (+, -, or 0) of the various matrix elements satisfy these detailed criteria, then the system is stable. If the criteria are not obeyed, nothing can be said: the matrix may be stable or unstable, depending on the actual magnitudes of the matrix elements. Usually this set of mathematically rigorous qualitative stability criteria will not apply exactly to complicated real-world situations, but even so they are useful in suggesting general tendencies.

Some particular examples and consequences are discussed below. Of the conditions the web (or its matrix) must satisfy to be qualitatively stable, one worth remarking is that reciprocal pairs of elements a_{ij} and a_{ji} must either be of opposite sign, or at least one be zero. That is to say, the interspecific relationships prey-predator, commensalism, amensalism are

all compatible with qualitative stability, but competition and mutualism or symbiosis are not. This is a mathematically rigorous statement, and it may be plausibly extended into the broader, if rougher, statement that competition or mutualism between two species is less conducive to overall web stability than is a predator-prey relationship.

This is an interesting result, for it suggests that on stability grounds we would expect strong predator-prey bonds to be more common than mutualistic ones. It is a result which is not intuitively obvious, yet is a feature of many real-world ecosystems.

QUALITATIVE STABILITY CONDITIONS

In mathematical terms, the necessary and sufficient conditions for an $n \times n$ matrix \mathbf{A} , with elements a_{ij} , to be qualitatively stable are (Quirk and Ruppert 1965):

$$(i) \ a_{ii} \leq 0, \text{ all } i. \quad (4)$$

$$(ii) \ a_{ii} \neq 0, \text{ for at least one } i. \quad (5)$$

$$(iii) \ \text{The product } a_{ij} a_{ji} \leq 0, \text{ all } i \neq j. \quad (6)$$

$$(iv) \ \text{For any sequence of three or more indices } i, j, k, \dots, q, r \text{ (with } i \neq j \neq k \neq \dots \neq q \neq r), \text{ the product}$$

$$a_{ij} a_{jk} \dots a_{qr} a_{ri} = 0. \quad (7)$$

$$(v) \ \text{The determinant of the matrix, } \det \mathbf{A} \neq 0. \quad (8)$$

Remember that if conditions (i) through (v) are not all fulfilled, it does not necessarily mean the matrix is unstable, but rather that a detailed knowledge of the actual magnitudes of the matrix elements (instead of merely their signs) is needed.

It is to be emphasized that this relates to stability with respect to relatively small amplitude perturbations. A full nonlinear analysis, covering large amplitude disturbances, is beyond our scope.

AN ILLUSTRATIVE EXAMPLE

For an application of these ideas, consider the two trophic webs shown in Fig. 1. Figure 1(a) depicts

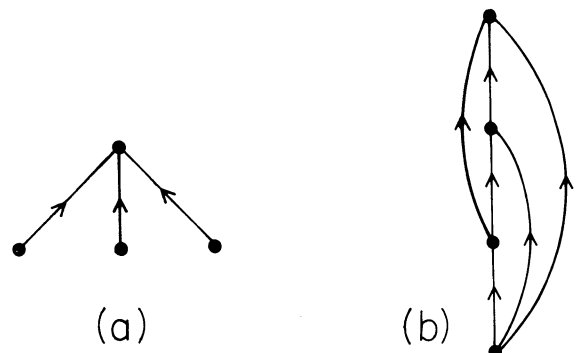


FIG. 1. Two possible food web structures for a four-species community.

one of the simplest four-species communities, with the minimum number of interspecific links (this system may be visualized as a herbivore species feeding upon three plant species). Conversely, Fig. 1(b) represents the four-species community with the maximum number of links in the web (and may be conceptualized as one plant species and a three-tiered hierarchy of omnivores).

If there are no intraspecific density-dependent effects whatsoever, then an equilibrium community containing all four species can be possible in case (b), but not usually in case (a). Thus in order to have a nontrivial example to begin with, we assume all four populations in both webs have density-dependent intraspecific interactions, of the usual stabilizing, negative feedback kind. With this assumption, there can in general be an equilibrium solution containing all four species, and we can take the next step of investigating the *stability* of this possible equilibrium configuration.

Such a stability analysis hinges on the interaction matrix discussed above. The diagonal matrix elements, a_{ii} , will all have negative sign in both cases (a) and (b), corresponding to the kind of intraspecific interactions assumed in the preceding paragraph. The sign of the remaining, off-diagonal, matrix element follows from the web structures of Fig. 1(a) and 1(b), as discussed in the introductory section. Accordingly, the stability character of the food web 1(a) is set by a matrix with the sign pattern

$$\mathbf{A}_a = \begin{pmatrix} - & + & + & + \\ - & - & 0 & 0 \\ - & 0 & - & 0 \\ - & 0 & 0 & - \end{pmatrix}, \quad (9)$$

and that of the web 1(b) by

$$\mathbf{A}_b = \begin{pmatrix} - & + & + & + \\ - & - & + & + \\ - & - & - & + \\ - & - & - & - \end{pmatrix}. \quad (10)$$

It is clear that the matrix \mathbf{A}_a satisfies the conditions (i)–(v), and therefore is qualitatively stable. The matrix \mathbf{A}_b fails to satisfy condition (iv), and thus is not qualitatively stable: \mathbf{A}_b may or may not correspond to a stable equilibrium, depending on the detailed numerical magnitudes of the various matrix elements.

This conclusion is somewhat at variance with the conventional wisdom, which dictates that the more complex web of Fig. 1(b) is in general the more stable one, and the comparatively simple web of 1(a) the less stable. Indeed, one undergraduate text poses Fig. 1 as an exercise on the “diversity-stability rule,” the answer being that “according to theory” 1(b) is the most stable four-species community, and 1(a) the least stable. The example drives home the

forceful argument of Southwood and Way (1970), and others, that one must be cautious in making generalizations about the relation between population stability and the number of links in the food web structure.

This rather artificial illustration was admittedly chosen for the theory of qualitative stability to be applicable, and one should not read too much into it. Most natural webs will be too complicated to satisfy the constraints (i)–(v). However, the qualitative stability conditions can bypass much cumbersome algebra in those circumstances where they do pertain (so that one may simplify the work, for example, of Bulgakova 1968a, b); such circumstances are most likely to arise where the web has a relatively small number of species, or of links.

In brief, for the food web described by Fig. 1(a), the equilibrium four-species community (if it exists) is necessarily stable to small perturbations, regardless of the detailed magnitudes of the interaction coefficients. For the community represented by Fig. 1(b), we cannot tell from the structure of the web alone whether the equilibrium configuration (if it exists) is stable or not.

DISCUSSION

It is worth restating the qualitative stability criteria (i)–(v) in biological terms.

The first two conditions pertain to intraspecific effects. Condition (i) requires that no population exhibit a destabilizing positive feedback in its intraspecific interactions, and condition (ii) further demands that at least one population in the community actually exhibit a self-stabilizing effect. Condition (iii) has the consequences mentioned in the introduction, and is discussed again below; that symbiotic relations (++) have the same qualitative stability character as competitive ones (--) may not be intuitively obvious. Condition (iv) forbids closed loops of three or more members, in the sense that the effects of i on r , r on q , ..., k on j , and finally j back on i are all non-zero. Without the trivial overriding condition (v), requiring \mathbf{A} to be non-singular, the system would be underdetermined; there would in effect be more populations than there were equations, and one or more populations could be assigned arbitrary values.

One can construct quite complicated model webs which, upon application of these criteria, are immediately seen to be necessarily stable. However, most large natural webs will obviously violate both (iii) and (iv), so that an analysis of their stability properties require the interaction magnitudes to be taken into account. Even so, the general tendencies revealed by qualitative stability theory are useful.

As noted in the introductory section, the condition (iii) says that commensal, amensal, and predator-

prey interactions are consistent with qualitative stability, whereas symbiotic and competitive interactions are not. This rigorous conclusion admits the plausible generalization that competitive and symbiotic relations are less compatible with overall community stability than are commensal, amensal, and predator-prey relations. It is tempting to speculate that such community stability considerations may play a role in explaining why mutualism "is a fascinating biological topic, but its importance in populations in general is small" (Williamson 1972: 95). Indeed, Williamson's subsequent argument that many conventional examples of predator-prey (+-) are in fact closer to commensalism (+0) or amensalism (0-) may be pursued to suggest that not a few conventional examples of mutualism (++) are in fact closer to commensalism (+0). (For example, in Aruego's (1970) delightful children's book *Symbiosis*, at least four of the nine pairs may be held to be commensals.)

All in all, rich trophic complexity and a diversity of different kinds of interaction between species is not conducive to qualitative stability. Insofar as the theory of qualitative stability relates to the muddled complexity-stability question, it is to re-echo the theme (Levins 1970, May 1971a, b, 1972) that, in general mathematical models, increased complexity tends to beget diminished stability.

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