

EFFECTS OF DIFFUSION ON THE STABILITY OF THE EQUILIBRIUM IN MULTI-SPECIES ECOLOGICAL SYSTEMS

■ GERALD ROSEN,
Department of Physics,
Drexel University,
Philadelphia, PA 19104, U.S.A.

Continuous population distributions that undergo self-diffusion, migrational cross-diffusion and interaction in a region of (1-, 2- or 3-dimensional) space are described dynamically by a governing system of nonlinear reaction-diffusion equations. It is shown that the constants associated with migrational cross-diffusion are ordinarily nonnegative or nonpositive, contingent on the type of species interaction. A simple sign relationship obtains between the latter diffusivity constants and the rate constants for species interaction in the neighborhood of a spatially uniform equilibrium state, and this relationship of signs serves to simplify the general stability theory for the growth or decay of arbitrary perturbations on a spatially uniform equilibrium state. The stability of the equilibrium state is analyzed and discussed in detail for the case of a generic two-species model, where the self-diffusion and migrational cross-diffusion of species act to either stabilize or destabilize the equilibrium, depending essentially on the character of the species interaction and also on the magnitude of the Helmholtz eigenvalues associated with the region and boundary conditions. In particular, for a prey-predator or host-parasite model, self-diffusion usually helps to stabilize the equilibrium state and migrational cross-diffusion can only act as an additional stabilizing influence, as evidenced generally by the experiments on such two-species systems. Sufficient conditions are derived for stability of the equilibrium state in the general case for an arbitrarily large number of interacting species. It is shown that the equilibrium state is always stable if all species undergo significant self-diffusion and the Helmholtz eigenvalues are suitably large.

I. Introduction. Spatial variations in the density of biological populations are evident throughout nature and have been the subject of several important experimental investigations (Nicholson, 1933; Nicholson and Bailey, 1935; Gause, 1934, 1935, 1936; Huffaker, 1958; Huffaker, Shea and Herman, 1963; Pimentel, Nagle and Madden, 1963; Luckinbill, 1973). Such experiments suggest that self-diffusion and/or migrational cross-diffusion can act to stabilize

and permit coexistence of species in an ecology that would otherwise be unstable. It is possible to study the effects of self-diffusion and migrational cross-diffusion in a much simpler context which admits analytical treatment, namely, a generic n -species ecological model that features a spatially homogeneous equilibrium state. Clearly, the analysis of diffusive effects on the stability of spatially homogeneous equilibrium states is a logical preliminary to the study of the diffusive stabilization of specialized population distributions with spatially inhomogeneous equilibria in nature, and indeed the general method developed here provides a basis for such specialized extensions. The purpose of the present communication is to report necessary and sufficient conditions for the stability of a spatially uniform equilibrium state in an n -species ecological model with continuous population distributions that undergo self-diffusion, migrational cross-diffusion, and interaction in a region of (1-, 2- or 3-dimensional) space. The results obtained here show that the latter effects can act to either stabilize or destabilize the spatially uniform equilibrium state, depending essentially on the character of the species interaction and also on the size and boundary of the spatial region (more precisely, on the magnitude of the Helmholtz eigenvalues associated with the region and boundary conditions). It should be noted that the analysis in this paper breaks new ground by studying the most general phenomenological theory for continuous population distributions that undergo (Fick-type) self-diffusion, migrational cross-diffusion and interaction in an arbitrary spatial region (compare, for example, with Levin, 1975; Maynard Smith, 1974 and works cited therein).

II. Governing system of reaction-diffusion equations. Let $c_i = c_i(\mathbf{x}, t)$ denote the concentration (3-dimensional space) or density (2- and 1-dimensional space) of the i th participating biological species in the ecological model. It is assumed that c_i is a nonnegative continuously differentiable function for all \mathbf{x} and all $t \geq 0$. The time rate of change of c_i at a fixed spatial point is given by

$$\partial c_i / \partial t = -\nabla \cdot \mathbf{f}_i + Q_i(\mathbf{c}), \quad (1)$$

in which \mathbf{f}_i is the total diffusional flux for the i th species and $Q_i(\mathbf{c})$, an algebraic function of the n -tuple $\mathbf{c} = (c_1, \dots, c_n)$, expresses the local rate of production of the i th species due to biological interactions. By evoking a generalized Fick-law representation, the total diffusional flux is given by

$$\mathbf{f}_i = -c_i \sum_{j=1}^n D_{ij} \nabla (\ln c_j), \quad (2)$$

where D_{ij} is the diffusivity constant which relates the influence of the gradient of the j th species on the flux of the i th species. For self-diffusion of the i th

species we have $D_{ii} \geq 0$, while the signs of the D_{ij} for migrational cross-diffusion with $i \neq j$ depend on the character of the interaction between the i th and j th species, as shown for the main types of species interaction in Table I. For example, if j is a predator and i its prey, then the ij migrational cross-diffusion term in \mathbf{f}_i is generally opposite in direction to $\nabla(\ln c_j)$, implying $D_{ij} > 0$, while the ji migrational cross-diffusion term in \mathbf{f}_j is generally parallel to $\nabla(\ln c_i)$, implying $D_{ji} < 0$, provided that both prey and predator are motile and respond appropriately to spatial variations in the distribution of the other species; of course, either D_{ij} may vanish (for a nonmotile or nonresponsive

TABLE I
Main Types of Species Interaction and Signs of Associated Diffusivity and Rate Constants

Symbol for interaction	Type of interaction	Signs of associated diffusivity and rate constants
N	i, j noninteracting	$D_{ij} = 0 = D_{ji}, \quad Q'_{ij} = 0 = Q'_{ji}$
P	i prey of j predator or i host of j parasite	$D_{ij} \geq 0 \geq D_{ji}, \quad Q'_{ij} < 0 < Q'_{ji}$
C	i, j competitor species	$D_{ij} \geq 0 \leq D_{ji}, \quad Q'_{ij} < 0 > Q'_{ji}$
S	i, j symbiotic species	$D_{ij} \leq 0 \leq D_{ji}, \quad Q'_{ij} > 0 < Q'_{ji}$
NP (or NS)	j saprophytic on waste products of i	$D_{ij} = 0 \geq D_{ji}, \quad Q'_{ij} = 0 < Q'_{ji}$
NC	j inhibited or destroyed by waste products of i	$D_{ij} = 0 \leq D_{ji}, \quad Q'_{ij} = 0 > Q'_{ji}$

prey or predator) and thus we have the general condition $D_{ij} \geq 0 \geq D_{ji}$ stated for a P (prey–predator) type of interaction in Table I. The same assumptions regarding the signs for the migrational cross-diffusion flux coefficients are implicit in the work of other authors (e.g., Maynard Smith, 1974, p. 71).

Substituting (2) into (1) and introducing the more convenient dependent variables $\xi_i \equiv \ln(c_i/\bar{c}_i) = \xi_i(\mathbf{x}, t)$ with the \bar{c}_i 's disposable positive reference constants, we obtain the system of governing reaction–diffusion equations

$$\partial \xi_i / \partial t = \sum_{j=1}^n D_{ij} (\nabla^2 \xi_j + \nabla \xi_i \cdot \nabla \xi_j) + R_i(\xi), \tag{3}$$

in which the rate functions $R_i(\xi) \equiv \bar{c}_i^{-1} Q_i(\mathbf{c})$ are assumed to be expressed in terms of the n -tuple $\xi = (\xi_1, \dots, \xi_n)$. Let us suppose that the rate expressions admit the spatially uniform equilibrium state $\mathbf{c} \equiv \bar{\mathbf{c}} = (\bar{c}_1, \dots, \bar{c}_n)$ satisfying

the algebraic equations $Q_i(\bar{\mathbf{c}}) = 0$ or equivalently $R_i(\mathbf{0}) = 0$. In the neighborhood of the equilibrium state the components of ξ are small in absolute magnitude compared to unity, and by dropping terms quadratic and of higher order in ξ , (3) takes the approximate linearized form

$$\partial \xi_i / \partial t = \sum_{j=1}^n (D_{ij} \nabla^2 \xi_j + Q'_{ij} \xi_j), \quad (4)$$

where an array of rate constants appears as $Q'_{ij} \equiv (\partial R_i / \partial \xi_j)_{\xi=0} = (\bar{c}_j / \bar{c}_i) (\partial Q_i / \partial c_j)_{c=\bar{c}}$. Reflecting the nature of the self-interaction of the i th species in the neighborhood of the equilibrium, the rate constant Q'_{ii} may be positive (i th species freely reproductive), equal to zero (e.g., as in the n -species Volterra model with $\partial R_i / \partial \xi_i \equiv 0$), or negative (e.g., as in the n -species Verhulst-Volterra model with $\partial R_i / \partial \xi_i < 0$); with the singular exception of a human population, the latter case with $Q'_{ii} < 0$ for $i = 1, \dots, n$ will ordinarily be manifest for interdependent animal populations in a realistic many-species ecological model (Tanner, 1966). The signs of the Q'_{ij} for $i \neq j$ are generally fixed by the character of the interaction between the i th and j th species, as shown for the main types of species interaction in Table I. For every type of interaction we have $D_{ij} Q_{ij} \leq 0$ for all values of $i \neq j$, or equivalently

$$D_{ij} = -\gamma_{ij} Q'_{ij}, \quad \gamma_{ij} \geq 0, i \neq j \quad (5)$$

for a certain array of nonnegative γ_{ij} . The relationship between the signs of off-diagonal elements in the diffusivity and rate constant arrays, as shown in Table I and expressed by (5), plays a key role in the general stability theory for the equilibrium state of an ecological model with diffusion based on the governing equations (4).

III. General perturbative solution in the neighborhood of the equilibrium state.

Let us first consider an unbounded spatial region and an arbitrary continuous initial distribution for each ξ_i with the property that

$$\lim_{|\mathbf{x}| \rightarrow \infty} \xi_i(\mathbf{x}, 0) = 0.$$

For such a localized perturbation on the equilibrium state we have a Fourier integral representation

$$\xi_j(\mathbf{x}, 0) = \int [f_j^{(+)}(\mathbf{k}, 0)(\cos \mathbf{k} \cdot \mathbf{x}) + f_j^{(-)}(\mathbf{k}, 0)(\sin \mathbf{k} \cdot \mathbf{x})] d\mathbf{k}, \quad (6)$$

in which $f_j^{(\pm)}(\mathbf{k}, 0)$ are Fourier amplitude functions dependent on the real

wave-vector \mathbf{k} . The associated solution to (4) subject to (6) is given by

$$\xi_j(\mathbf{x}, t) = \int [f_j^{(+)}(\mathbf{k}, t)(\cos \mathbf{k} \cdot \mathbf{x}) + f_j^{(-)}(\mathbf{k}, t)(\sin \mathbf{k} \cdot \mathbf{x})] d\mathbf{k}, \tag{7}$$

where the time-dependent amplitude functions satisfy the system of ordinary differential equations

$$df_i^{(\pm)}(\mathbf{k}, t)/dt = \sum_{j=1}^n \hat{Q}_{ij} f_j^{(\pm)}(\mathbf{k}, t) \tag{8}$$

with the constant coefficients

$$\hat{Q}_{ij} = -D_{ij} |\mathbf{k}|^2 + Q'_{ij} = \begin{cases} -D_{ii} |\mathbf{k}|^2 + Q'_{ii} & \text{for } i = j \\ (1 + \gamma_{ij} |\mathbf{k}|^2) Q'_{ij} & \text{for } i \neq j \end{cases} \tag{9}$$

in view of (4) and (5). Notice that (8) is identical to the system of equations that would obtain in the stability theory without diffusion except for the appearance of \hat{Q}_{ij} in place of Q'_{ij} ; according to the final member in (9), \hat{Q}_{ij} has the same sign as Q'_{ij} , with $|\hat{Q}_{ij}| \geq |Q'_{ij}|$, for all $i \neq j$.

The integrals over all continuous wave-numbers in (6) and (7) are to be replaced by infinite sums over Helmholtz eigenfunctions in \mathbf{x} (associated with the spatial region and linear homogeneous boundary conditions on ξ) for an arbitrary finite bounded spatial region (Aris, 1975; Rosen, 1974; Rosen and Fizell, 1975), the discrete positive eigenvalues of the negative Laplacian operator $-\nabla^2$ replacing the continuous nonnegative values of $|\mathbf{k}|^2$ for the unbounded spatial domain. Following other authors (e.g., Keller, 1970), it is assumed here that the (Robin) boundary conditions on ξ preclude the spatially homogeneous perturbative mode with $\mathbf{k} = 0$. All subsequent equations in this paper hold good for an arbitrary finite bounded spatial region if $|\mathbf{k}|^2 (\geq k_{min}^2$ with k_{min}^{-1} usually of the order of the length extension of the region) is interpreted as a Helmholtz eigenvalue for the region and boundary conditions of interest.

It is well-known that every solution to (8) for fixed \mathbf{k} approaches zero for large t ,

$$\lim_{t \rightarrow \infty} f_i^{(\pm)}(\mathbf{k}, t) = 0,$$

if and only if all (complex) eigenvalues of the matrix $\hat{Q} = (\hat{Q}_{ij})$ have negative real parts, i.e. if \hat{Q} is a so-called *stability matrix* (Bellman, 1970). Moreover, it is a simple matter to prove that (7) gives $\xi_j(\mathbf{x}, \infty) = 0$ for all \mathbf{x} if and only if $f_j^{(\pm)}(\mathbf{k}, \infty) = 0$ for all $\mathbf{k} \neq 0$, the spatially uniform perturbative mode with $\mathbf{k} = 0$ being excluded by the localization condition

$$\lim_{|\mathbf{x}| \rightarrow \infty} \xi_i(\mathbf{x}, 0) = 0$$

which implies that $f_i^{(\pm)}(0, 0) = 0$ and hence $f_i^{(\pm)}(0, t) \equiv 0$ by virtue of (8). Thus, the spatially homogeneous equilibrium is stable if and only if (9) is a stability matrix for all values of $|\mathbf{k}|^2 > 0$ with the standard conjecture of "linear stability" commonly made in the literature (and probably amenable to rigorous proof in the present case), i.e. that the stability of the $\xi \equiv 0$ solution to the nonlinear (3) is concomitant with the stability of the $\xi \equiv 0$ solution to the associated linear equations (4). Before considering conditions under which (9) is a stability matrix in the case of general n , let us derive and discuss the necessary and sufficient conditions for the case $n = 2$.

IV. Stability of the equilibrium state in a two-species model. For an ecological model with $n = 2$, \hat{Q} is a stability matrix if and only if

$$\text{tr } \hat{Q} \equiv \hat{Q}_{11} + \hat{Q}_{22} < 0, \quad \det \hat{Q} \equiv \hat{Q}_{11}\hat{Q}_{22} - \hat{Q}_{12}\hat{Q}_{21} > 0 \quad (10)$$

and hence from (9) we obtain the necessary and sufficient conditions for the equilibrium to be stable against perturbations in the \mathbf{k} eigenmode:

$$(D_{11} + D_{22}) |\mathbf{k}|^2 > (Q'_{11} + Q'_{22}), \quad (11)$$

$$(D_{11} |\mathbf{k}|^2 - Q'_{11})(D_{22} |\mathbf{k}|^2 - Q'_{22}) > Q'_{12}Q'_{21}(1 + \gamma_{12} |\mathbf{k}|^2)(1 + \gamma_{21} |\mathbf{k}|^2). \quad (12)$$

The condition (11) is satisfied automatically for all \mathbf{k} if $(Q'_{11} + Q'_{22}) < 0$ or for all \mathbf{k} with sufficiently large $|\mathbf{k}|$ if at least one of the species undergoes self-diffusion, the presence of the self-diffusion terms making (11) a less stringent condition on $(Q'_{11} + Q'_{22})$ for stability. The full content of (12) is revealed by considering the types of species interaction in Table I.

Cases N, NP and NC. $Q'_{12}Q'_{21} = 0$ and (12) becomes

$$(D_{11} |\mathbf{k}|^2 - Q'_{11})(D_{22} |\mathbf{k}|^2 - Q'_{22}) > 0, \quad (13)$$

which in combination with (11) yields the necessary and sufficient conditions for stability

$$Q'_{11} < D_{11} |\mathbf{k}|^2, \quad Q'_{22} < D_{22} |\mathbf{k}|^2. \quad (14)$$

The latter conditions are satisfied for all \mathbf{k} with sufficiently large $|\mathbf{k}|$ if D_{11} and D_{22} are both nonzero, or for all \mathbf{k} if Q'_{11} and Q'_{22} are both negative. Thus, the self-diffusion of either or both species always helps to stabilize the equilibrium state for these types of species interaction, while the migrational cross-diffusion (say with $D_{12} \neq 0$) does not influence the stability at all.

Cases C and S. $Q'_{12}Q'_{21} > 0$ and the right side of (12) is a positive quantity.

Hence, in view of (11) we have (14) holding *a fortiori* as necessary conditions for stability. From the standpoint of requirements on the rate constants Q'_{ij} , condition (12) is usually made less stringent by the presence of the self-diffusion terms, which increase the value of the left side of (12) with increasing $|\mathbf{k}|$ if (14) is satisfied. The contrary to this usual effect of self-diffusion occurs if $D_{11}, D_{22}, (D_{11}^{-1}Q'_{11} + D_{22}^{-1}Q'_{22})$ are all positive and $|\mathbf{k}|^2 < \frac{1}{2}(D_{11}^{-1}Q'_{11} + D_{22}^{-1}Q'_{22})$ or if $D_{ii} = 0 < Q'_{ii}$ for $i = 1$ or 2 with $(D_{11} + D_{22}) > 0$, for then the left side of (12) decreases as $|\mathbf{k}|$ increases from zero. Without exception condition (12) is made more stringent by the presence of the migrational cross-diffusion terms, which always increase the value of the right side of (12) with increasing $|\mathbf{k}|$. Thus, the necessary and sufficient conditions (11) and (12) show that the self-diffusion of either or both species usually helps to stabilize the equilibrium state (special cases excepted), while the migrational cross-diffusion always acts as a destabilizing influence. In the limit of short wave-lengths with $|\mathbf{k}|$ very large in relative magnitude, the equilibrium state is stable against perturbations if and only if $D_{11}D_{22} > D_{12}D_{21}$.

Case P. $Q'_{12}Q'_{21} < 0$ and (12) becomes

$$(D_{11}|\mathbf{k}|^2 - Q'_{11})(D_{22}|\mathbf{k}|^2 - Q'_{22}) > -|Q'_{12}Q'_{21}|(1 + \gamma_{12}|\mathbf{k}|^2)(1 + \gamma_{21}|\mathbf{k}|^2), \tag{15}$$

which in combination with (11) implies that the conditions (14) are sufficient but not necessary for stability; in fact, if both factors in parentheses on the left side of (15) are positive, then the magnitude of the (negative) term on the right side is of no consequence for stability. From (11) and (15) it follows that

$$(Q'_{ii} - D_{ii}|\mathbf{k}|^2) < [|Q'_{12}Q'_{21}|(1 + \gamma_{12}|\mathbf{k}|^2)(1 + \gamma_{21}|\mathbf{k}|^2)]^\dagger \tag{16}$$

for $i = 1, 2$ are necessary (but not sufficient) conditions for stability. Condition (15) is usually made less stringent by the presence of both the self-diffusion and migrational cross-diffusion terms, the exception to the usual behavior of the left side occurring for the special parameter values cited above under Cases C and S. Thus, self-diffusion usually helps to stabilize the equilibrium state, and migrational cross-diffusion can only act as an additional stabilizing influence. Moreover, the equilibrium is always stable against perturbations of short wavelength with $|\mathbf{k}|$ very large in relative magnitude if both species undergo self-diffusion ($D_{11}D_{22} > 0$).

Experiments on the prey-predator ciliates *Paramecium* and *Didinium* support these stability conditions qualitatively for the special case with self-diffusion of the prey species negligible ($D_{11} = 0 < D_{22}, Q'_{11} > 0 > Q'_{22}$). It has been observed that coexistence of *Paramecium-Didinium* populations can be effected by artificially induced migrational cross-diffusion (Gause, 1934,

1935, 1936), i.e. increasing the effective value of the right side of (16), in accord with the direction of the latter inequality for enhanced stability. Reducing the food supply of the *Paramecium*, i.e. decreasing the value of Q'_{11} , and rendering the medium viscous, i.e. decreasing the value of D_{22} , also has been shown to effect experimental coexistence (Luckinbill, 1973), in accord with (15) for $D_{11} = 0$. In these experiments a "stable equilibrium" actually features oscillations in the populations about mean-values because of time-delay effects (Maynard Smith, 1974).

Experiments on the prey-predator mites *Eotetranychus* and *Typhlodromus* (Huffaker, 1958; Huffaker, Shea and Herman, 1963) also provide qualitative support for the stability conditions derived here. Increasing the spatial complexity and thus heterogeneity of such a system, and hence the role played by self-diffusion and migrational cross-diffusion of the species, helps to stabilize the populations of the mites and to forestall their extinction.

The same type of qualitative evidence for the role played by self-diffusion and migrational cross-diffusion in a *P* type of interaction is also provided by host-parasite experiments (Nicholson, 1933; Nicholson and Bailey, 1935; Pimentel, Nagel and Madden, 1963). In general such systems persist longer if they feature greater spatial complexity and population distributions that vary significantly with \mathbf{x} because of the stabilizing influence of diffusion of the species, in agreement with the theoretical conditions (11) and (15).

V. Sufficient conditions for stability of the equilibrium state with n arbitrarily large. In all cases discussed in the preceding section for $n = 2$, stability of the equilibrium state obtains if the stabilizing effect of self-diffusion is dominant over (possibly destabilizing influences of) the interaction and migrational cross-diffusion. Quantitatively, the equilibrium is always stable for sufficiently large values of $D_{min} |\mathbf{k}|^2$ where $D_{min} \equiv \min_i \{D_{ii}\}$. That the latter statement is true for any multi-species system with arbitrary n is shown by the sufficient conditions for stability derived in the following paragraphs.

First, let us assume that $\bar{Q}_{ii} = -D_{ii} |\mathbf{k}|^2 + Q'_{ii}$ is negative for $i = 1, \dots, n$ and put $\alpha \equiv \min_i \{-\bar{Q}_{ii}\} = \min_i \{|\bar{Q}_{ii}|\} (> 0)$. Then from (8) it follows that

$$\frac{1}{2} df^2(t)/dt \leq (-\alpha + \beta)f^2(t) \tag{17}$$

with

$$f^2(t) \equiv \sum_{i=1}^n [f_i^{(\pm)}(\mathbf{k}, t)]^2 \tag{18}$$

and β defined as the maximum eigenvalue of the real symmetric matrix B where $B_{ii} \equiv 0, B_{ij} \equiv \frac{1}{2}(Q_{ij} + Q_{ji})$ for $i \neq j$. The differential inequality (17) can be integrated to yield

$$f^2(t) \leq f^2(0) \exp(-2(\alpha - \beta)t) \tag{19}$$

and thus for $\alpha > \beta$ we have $f^2(\infty) = 0$ for any initial value. The sum of the squares of the n real eigenvalues of B is given by

$$\sum_{i,j=1}^n (B_{ij})^2,$$

while the sum of the eigenvalues vanishes because

$$\text{tr } B \equiv \sum_{i=1}^n B_{ii} = 0.$$

Therefore we have

$$\beta^2 \leq (1 - n^{-1}) \sum_{i,j} (B_{ij})^2 = \frac{1}{2}(1 - n^{-1}) \sum_{i \neq j} (\hat{Q}_{ij}\hat{Q}_{ij} + \hat{Q}_{ij}\hat{Q}_{ji}) \tag{20}$$

where the double summations run over $i, j = 1, \dots, n$ with $i = j$ terms omitted in the final member of (20). Hence, we have established that \hat{Q} is a stability matrix and every solution to (8) approaches zero for large t if

$$-\hat{Q}_{ii} > [\frac{1}{2}(1 - n^{-1}) \sum_{j \neq k} (\hat{Q}_{jk}\hat{Q}_{jk} + \hat{Q}_{jk}\hat{Q}_{kj})]^\dagger \equiv \Lambda \tag{21}$$

for all $i = 1, \dots, n$. In view of (9) this sufficient condition for stability of the equilibrium becomes

$$D_{ii} | \mathbf{k} |^2 - Q'_{ii} > \Lambda, \tag{22}$$

where Λ defined by (21) is independent of the self-diffusion or self-interaction rate constants. Thus, for sufficiently large values of $D_{min} | \mathbf{k} |^2$ with $D_{min} \equiv \min_i \{D_{ii}\}$ the equilibrium state is always stable. Notice that it is possible to have $\hat{Q}_{ij} = -\hat{Q}_{ji}$ for $i \neq j$ and $\Lambda = 0$ if and only if all interactions are either of type N or P .

An alternative sufficient condition for stability, resembling (21) in form but homogenously linear in $|\hat{Q}_{jk}|$ for $j \neq k$, can be stated by evoking a well-known theorem on matrices that is used in economics theory. An $n \times n$ real matrix \hat{Q} is said to be *quasidominant negative-diagonal* if there exist n positive constants p_1, \dots, p_n such that

$$-p_i \hat{Q}_{ii} > \sum_{j(i \neq j)=1}^n p_j |\hat{Q}_{ij}| \tag{23}$$

for all values of $i = 1, \dots, n$. A quasidominant negative-diagonal \hat{Q} is a stability matrix, according to the theorem (McKenzie, 1966), which is also

valid if $|\hat{Q}_{ij}|$ is replaced by $|\hat{Q}_{ji}|$ in the defining conditions (23) since the n eigenvalues of the transpose of \hat{Q} are the same as the n eigenvalues of \hat{Q} . Clearly, \hat{Q} given by (9) is quasidominant negative-diagonal for sufficiently large values of $D_{ii} |k|^2$ for all i , since (23) with $p_1 = \dots = p_n \equiv 1$ yields

$$D_{ii} |k|^2 - Q'_{ii} > \sum_{j(\neq i)=1}^n |\hat{Q}_{ij}| \equiv \Lambda_i. \tag{24}$$

The right side of (24) depends on the enumerator index i , in contrast to the right side of (22), and thus (23) or (24) is a less demanding sufficient condition for stability in certain cases. Moreover, we have the important quantitative result: *If*

$$D_{ii} > (\theta_i + k_{cr}^{-2}) \left(\sum_{j(\neq i)=1}^n |Q'_{ij}| \right) + \frac{1}{2} k_{cr}^{-2} (Q'_{ii} + |Q'_{ii}|) \tag{25}$$

for all i with $\theta_i \equiv \max_j (\gamma_{ji})$ and k_{cr}^2 a certain positive constant, then the equilibrium is stable for all $|k|^2 \geq k_{cr}^2$. For the proof, put $p_i \equiv (1 + |k|^2 \theta_i)^{-1}$ and note that (9) implies

$$-p_i \hat{Q}_{ii} \equiv (1 + |k|^2 \theta_i)^{-1} (D_{ii} |k|^2 - Q'_{ii}) > \sum_{j(\neq i)=1}^n |Q'_{ij}| \tag{26}$$

for $|k|^2 \geq k_{cr}^2$ if (25) is satisfied. But from (9) we have

$$\sum_{j(\neq i)=1}^n p_j |\hat{Q}_{ij}| \equiv \sum_{j(\neq i)=1}^n (1 + |k|^2 \theta_j)^{-1} (1 + \gamma_{ij} |k|^2) |Q'_{ij}| \leq \sum_{j(\neq i)=1}^n |Q'_{ij}| \tag{27}$$

for all values of $|k|^2$. In view of the inequalities (26) and (27), it follows that (23) is satisfied by \hat{Q} for the prescribed set of positive p_i , and therefore \hat{Q} is a stability matrix. Condition (25) can also be stated in the substitutive form with $|Q'_{ij}|$ replaced by $|\hat{Q}_{ji}|$ and θ_i defined as $\max_j (\gamma_{ij})$, since (23) yields an alternative sufficient condition for \hat{Q} to be a stability matrix if $|\hat{Q}_{ij}|$ is replaced by $|\hat{Q}_{ji}|$.

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LITERATURE

Aris, R. 1975. *The Mathematical Theory of Diffusion and Reaction in Permeable Catalysts*, Vol. 2, pp. 120–126, London: Oxford University Press.
 Bellman, R. 1970. *Methods of Nonlinear Analysis*, pp. 104–126. London: Academic Press.
 Gause, G. F. 1934. "Experimental Analysis of Vito Volterra's Mathematical Theory of the Struggle for Existence." *Science* **79**, 16–17.
 ———. 1935. "Experimental Demonstration of Volterra's Periodic Oscillations in Numbers of Animals." *J. Exp. Biol.* **12**, 44–48.

- . 1936. "Further Studies of Interaction Between Predator and Prey." *J. Anim. Ecol.* **5**, 1-18.
- Huffaker, C. B. 1958. "Experimental Studies on Predation: Dispersion Factors and Predator-Prey Oscillations." *Hilgardia* **27**, 305-329.
- Huffaker, C. B., K. P. Shea and S. G. Herman. 1963. "Experimental Studies on Predation: Complex Dispersion and Levels of Food in an Acarine Predator-Prey Interaction." *Hilgardia* **37**, 305-309.
- Keller, E. F. and L. A. Segel. 1970. "Initiation of Slime Mold Aggregation Viewed as an Instability." *J. Theor. Biol.* **26**, 399-415.
- Levin, S. A. 1975. *Ecosystem Analysis and Prediction*. Philadelphia SIAM Publications.
- Luckinbill, L. S. 1973. "Coexistence in Laboratory Populations of *Paramecium aurelia* and its Predator *Didinium nasutum*." *Ecology* **54**, 1320-1327.
- Maynard Smith, J. 1974. *Models in Ecology*, pp. 33-35. Cambridge: Cambridge University Press.
- McKenzie, L. 1966. "Matrices with Dominant Diagonals and Economic Theory." *Proc. Symp. Math. Methods Soc. Sci.*, pp. 47-62. Stanford: Stanford University Press.
- Nicholson, A. J. 1933. "The Balance of Animal Populations." *J. Anim. Ecol.* **2**, 132-178.
- Nicholson, A. J. and V. A. Bailey. 1935. "The Balance of Animal Populations." *Proc. Zool. Soc., Lond.* **3**, 551-598.
- Pimentel, D., W. P. Nagel and J. L. Madden. 1963. "Space-time Structure of the Environment and the Survival of Parasite-Host Systems." *Am. Natur.* **97**, 141-167.
- Rosen, G. 1974. "Global Theorems for Species Distributions Governed by Reaction-Diffusion Equations." *J. Chem. Phys.* **61**, 3676-3679.
- Rosen, G. and R. G. Fitzell. 1975. "Bounds on the Total Population for Species Governed by Reaction-Diffusion Equations in Arbitrary Regions." *Bull. Math. Biol.* **37**, 71-78.
- Tanner, J. T. 1966. "Effects of Population Density on Growth Rates of Animal Populations." *Ecology* **47**, 733-745.

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