(iv) Routh-Hurwitz Stability Criterion

If A is a $m \times m$ matrix, the equation (2.17) for the eigenvalues λ comes down to an mth order polynomial equation

$$\lambda^m + a_1\lambda^{m-1} + a_2\lambda^{m-2} + \cdots + a_m = 0. \qquad (A.19)$$

A formal general expression (the Routh-Hurwitz criterion) can now be written down, giving constraints on the coefficients $a_1, a_2, \ldots, a_m$ which are necessary and sufficient to ensure all eigenvalues lie in the left half complex plane.

Rather than explain this abstract expression, which no one in their right mind is going to use on $m > 5$ anyway, we catalogue the explicit Routh-Hurwitz stability conditions for $m = 2, 3, 4$, and 5.

$$m = 2 \qquad a_1 > 0;\ a_2 > 0. \qquad (A.20)$$

$$m = 3 \qquad a_1 > 0;\ a_3 > 0;\ a_1a_2 > a_3. \qquad (A.21)$$

$$m = 4 \qquad a_1 > 0;\ a_3 > 0;\ a_4 \geqslant 0;$$

$$a_1a_2a_3 > a_3^2 + a_1^2a_4. \qquad (A.22)$$

$$m = 5 \qquad a_i > 0[i = 1, 2, 3, 4, 5];$$

$$a_1a_2a_3 > a_3^2 + a_1^2a_4;$$

$$(a_1a_4 - a_5)(a_1a_2a_3 - a_3^2 - a_1^2a_4) > a_5(a_1a_2 - a_3)^2 + a_1a_5^2. \qquad (A.23)$$

(v) Eigenvalues of Some Special Matrices

Case I. The $m \times m$ matrix with diagonal elements 1, and all other elements α,

$$A = \begin{pmatrix} 1 & \alpha & \alpha & \cdot & \alpha \\ \alpha & 1 & \alpha & \cdot & \cdot \\ \alpha & \alpha & 1 & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ \alpha & \cdot & \cdot & \cdot & 1 \end{pmatrix} \qquad (A.24)$$

is well known to have eigenvalues (e.g. Levins, 1968a, Ch. 3)

$$\begin{aligned} \lambda &= 1 - \alpha \text{ [with multiplicity } (m-1)] \\ \lambda &= 1 + (m-1)\alpha \text{ [once].} \end{aligned} \qquad (A.25)$$

Case II. The $m \times m$ matrix with diagonal elements 1, superdiagonal and subdiagonal elements α, and all other elements zero,

$$A = \begin{pmatrix} 1 & \alpha & 0 & 0 & \cdot & 0 \\ \alpha & 1 & \alpha & 0 & \cdot & \cdot \\ 0 & \alpha & 1 & \alpha & \cdot & \cdot \\ 0 & 0 & \alpha & 1 & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ 0 & \cdot & \cdot & \cdot & \cdot & 1 \end{pmatrix} \qquad (A.26)$$

was studied by Laplace. Defining the mth order determinant $D(m) = \det\ |A(m) - \lambda I|$, the eigenvalues can be found from the recursion relation

$$D(m) = (1 - \lambda)D(m-1) - \alpha^2 D(m-2).$$

The solution of this difference equation can be written

$$D(m) = \alpha^m \frac{\sin\,(m+1)\theta}{\sin\theta}, \qquad (A.27)$$

with the definition $\cos\theta = (1 - \lambda)/(2\alpha)$. It follows that the eigenvalues λ_k $[k = 1, 2, \ldots, m]$ are

$$\lambda_k = 1 - 2\alpha\cos\left(\frac{\pi k}{m+1}\right). \qquad (A.28)$$

Case III. Particularly interesting is the general class of $m \times m$ matrices whose rows are cyclic permutations of the first one

$$A = \begin{pmatrix} c_0 & c_1 & c_2 & c_3 & \cdot & c_{m-1} \\ c_{m-1} & c_0 & c_1 & c_2 & \cdot & \cdot \\ c_{m-2} & c_{m-1} & c_0 & c_1 & \cdot & \cdot \\ c_{m-3} & c_{m-2} & c_{m-1} & c_0 & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ c_1 & \cdot & \cdot & \cdot & \cdot & c_0 \end{pmatrix} \qquad \text{(A.29)}$$

The eigenvalues λ_k $[k = 0, 1, \ldots, m-1]$ are given by the expressions

$$\lambda_k = \sum_{\ell=0}^{m-1} c_\ell \exp\left[\frac{2\pi i}{m} k\ell\right]. \qquad \text{(A.30)}$$

Proof (Berlin and Kac, 1952): Let Δ be the matrix

$$\Delta = \begin{pmatrix} 1 & 1 & 1 & \cdot & 1 \\ r_0 & r_1 & r_2 & \cdot & \cdot \\ r_0^2 & r_1^2 & r_2^2 & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ r_0^{m-1} & \cdot & \cdot & \cdot & r_{m-1}^{m-1} \end{pmatrix}$$

where the m quantities $r_k = \exp\,[(2\pi i/m)k]$ are the mth roots of unity. By using the cyclic properties of the matrix A, and the relation $r^m = 1$, the elements of the matrix $A\Delta$ can be seen to be

$$(A\Delta)_{ij} = \left[\sum_{\ell=0}^{m-1} c_\ell r_{j-1}^\ell\right] r_{j-1}^{i-1}.$$

That is, with the above definition (A.30) for λ,

$$(A\Delta)_{ij} = \lambda_{j-1}(\Delta)_{ij}.$$

And, since the matrix Δ is nonsingular, these λ are manifestly the eigenvalues of A. Berlin and Kac also construct the eigenvectors, but we will not pursue this.

If the matrix A is symmetric, so that $c_i = c_{m-i}$ $(i = 1, 2, \ldots)$, it is easily seen from (A.30) that the eigenvalues occur in pairs $\lambda_k = \lambda_{m-k}$, with the exception of λ_0 (and of $\lambda_{m/2}$ if m is even). The expression (A.30) reduces to

$$\lambda_k = \sum_{\ell=0}^{m-1} c_\ell \cos\left(\frac{2\pi k\ell}{m}\right). \qquad \text{(A.31)}$$

If we put $c_0 = 1$, and all other $c_i = \alpha$, we recover the familiar result (A.25) for the matrix (A.24).

If, further, the matrix elements steadily decrease as one moves away from the diagonal, $c_0 > c_1 > c_2 > c_3 \ldots$, as is the case in many interesting contexts, the minimum eigenvalue can be seen in the limit $m \gg 1$ to be

$$\lambda_{\min} = c_0 - 2c_1 + 2c_2 - 2c_3 + \cdots \qquad \text{(A.32)}$$

The maximum eigenvalue is λ_0,

$$\lambda_{\max} = c_0 + 2c_1 + 2c_2 + 2c_3 + \cdots \qquad \text{(A.33)}$$

In this case, two limits are worth noting. If the diagonal elements are much larger than any others, the eigenvalues are all essentially equal, of value c_0; if all the elements are nearly equal, there is one dominant eigenvalue of value approximately mc_0, and the remaining $(m-1)$ eigenvalues cluster around zero, often in an essentially singular manner.

To use these results on our competition matrices, we may for large m pretend the resource spectrum is cyclic (so that the species labeled 0 adjoins that labeled $m-1$), whereupon matrices such as (6.15) are slightly modified to become members of the above class. In this way equation (A.32) leads to the specific result (6.17) for the matrix (6.15), and to the general result (6.22) for the general matrix (6.5) (May, 1972g). For large matrices, $m \gg 1$, the artifice is justified by the fact that "end effects" at the extremes of the resource spectrum are relatively unimportant. That this trick of imposing artificial cyclic boundary conditions does not affect the eigenvalues for $m \gg 1$ is a point made clear in the literature on the physicists' Ising model, where the trick is applied to linear chains or plane lattices in exactly the same sense as here in Chapter 6. For a more thorough discussion of the asymptotic validity of the procedure, see for example Newell and Montroll (1953) or Green and Hurst (1964). Further to substantiate this point, consider the $m \times m$ matrix (A.29) with $c_0 = 1$, $c_1 = c_{m-1} = \alpha$, and all other $c_i = 0$. This is just the matrix (A.26), with the addition of an extra element α in both the upper right-hand corner, and the lower left-hand corner (i.e. with cyclic boundary conditions imposed). From (A.31) the eigenvalues of this matrix are

$$\lambda_k = 1 + 2\alpha \cos(2\pi k/m),$$

with $k = 0, 1, \ldots, m-1$, or equivalently (writing $j = 2k - m$)

$$\lambda_j = 1 - 2\alpha \cos\left(\frac{\pi j}{m}\right), \tag{A.34}$$

where j runs over the even integers up to $2m$ if m is even, and over the odd integers to $2m-1$ if m is odd. Comparing with the eigenvalues (A.28) of the matrix (A.26), we see the eigenvalue distributions of the two matrices are significantly different for small m, but for large m the expressions (A.28) and (A.34) are effectively identical, and the easily obtained result (A.34) serves as a good approximation for the eigenvalues of the matrix (A.26)

APPENDIX III

This appendix proves the assertions made in Chapter 2, and illustrated by Figure 2.3, as to the relation between the

stability criteria for homologous pairs of differential and difference equations. The analysis aims to be of wider usefulness in indicating how the discussion of differential equation models throughout the book may in principle be taken over and applied to difference equation models in biological systems with discrete growth.

For the m-species community described by the general system of difference equations (2.25), the equilibrium populations are given by equation (2.9). To study the stability of this equilibrium point with respect to small disturbances, we as before write the perturbed populations as $N_i(t) = N_i^* + x_i(t)$ (equation (2.10)), and then obtain linearized equations for the initially small perturbations $x_i(t)$ by Taylor-expanding equations (2.25) around the equilibrium point:

$$x_i(t+\tau) - x_i(t) = \tau \sum_{j=1}^{m} a_{ij} x_j(t). \tag{A.35}$$

Here the coefficients a_{ij} are defined by precisely the same recipe (2.13) as for the corresponding differential equations (2.8). Equation (A.35) may alternatively be expressed in matrix form (the analogue of equation (2.12)) as

$$\mathbf{x}(t+\tau) = B\mathbf{x}(t). \tag{A.36}$$

Clearly the elements b_{ij} of the $m \times m$ matrix B are

$$b_{ij} = \tau a_{ij} + \delta_{ij};$$

that is

$$B = \tau A + I. \tag{A.37}$$

In analogy with equation (2.14), for the set of linear difference equations (A.35) the solutions may be written

$$x_i(t) = \sum_{j=1}^{m} C_{ij} (\mu_j)^{t/\tau}. \tag{A.38}$$