Chapter 16
Discrete Epidemic Models

16.1 Single-Species Discrete Population Models

The continuous population models that we have considered in previous chapters model population and epidemic processes that occur continuously in time. In particular, they assume that births and deaths in the population occur continuously. This assumption is true for the human population, but many insect and plant populations have discrete, nonoverlapping generations. Such populations reproduce during specific time intervals of the year. Consequently, population censuses are taken at those specific times. As a result, modeling such populations and the distribution of disease in them should happen at discrete times. In this chapter we introduce discrete single-species population and epidemic models.

16.1.1 Simple Discrete Population Models

We assume that we measure the population at discrete, equally spaced, moments of time: $t_0, t_1, \ldots, t_n, \ldots$, and we find that the population numbers at these moments of time are N_t, where t takes the values of $t_0, t_1, \ldots, t_n, \ldots$. For simplicity, we will set $N_{t_n} = N_n$. Thus, the population size is described by a sequence: $N_1, N_2, \ldots, N_n, \ldots$. A discrete population model can be written in the following general form:

$$N_{n+1} = \mathscr{F}(N_n), \tag{16.1}$$

where $\mathscr{F}$ is a specified function of N_n. That is, if we know the population size at time t_n, the model tells us what the populations size at time t_{n+1} should be. Such a model is equipped with a given initial condition: the population size N_0 at time t_0 is given. Another way to rewrite Eq. (16.1) is

$$N_{n+1} = N_n f(N_n). \tag{16.2}$$

The function $f(N_n)$ is called a *fitness function* or *per capita rate of population growth* or *net reproduction rate*.

Definition 16.1. Equations of the form (16.1) are called *difference equations*.

Such difference equations are of *first order*, because they contain only one time step. They are also *autonomous*, because $\mathscr{F}$ does not depend explicitly on the time t_n. The simplest discrete population model is derived under the assumption that individuals die with constant probability d. Furthermore, we assume that b individuals are born per individual in the population. The model then becomes

$$N_{n+1} = N_n + bN_n - dN_n,$$

that is, the number of individuals at the time step t_{n+1} is the number from the time step t_n plus those who have been born, minus those who have died. Defining $\mathscr{R} = 1 + b - d$, we obtain the following *linear* discrete equation of population growth:

$$N_{n+1} = \mathscr{R}N_n. \tag{16.3}$$

The parameter $\mathscr{R}$ is called the *net reproduction number*. We note that $\mathscr{R} > 0$, since b and d are probabilities and are less than one. Model (16.3) is a discrete analogue of the Malthusian equation. Equation (16.3) is a special case of Eq. (16.2) with $f(N_n) = \mathscr{R}$. Model (16.3) can be solved. Given initial population size N_0, we have

$$
\begin{aligned}
N_1 &= \mathscr{R}N_0, \\
N_2 &= \mathscr{R}N_1 = \mathscr{R}^2 N_0, \\
&\vdots \\
N_n &= \mathscr{R}N_{n-1} = \mathscr{R}^n N_0.
\end{aligned}
\tag{16.4}
$$

If $\mathscr{R} > 1$, then each individual on average leaves more than one descendant, and the population grows geometrically. If $\mathscr{R} < 1$, then each individual leaves fewer than one descendant, and the population declines geometrically. If $\mathscr{R} = 1$, the population remains constant. These model predictions are valid under the assumption that the resources are unlimited.

In practice, populations do not experience unlimited growth, so models that predict asymptotically bounded growth are more realistic. One such model is the discrete analogue of the logistic equation. To derive such an analogue, we approximate the continuous time derivative with $N_{n+1} - N_n$, assuming that the time step is equal to one. Thus the discrete logistic equation takes the form

$$N_{n+1} = N_n + rN_n \left(1 - \frac{N_n}{K}\right). \tag{16.5}$$

First we factor N_n and $r + 1$. Furthermore, we make the following changes in dependent variables and parameters:

$$y_n = \frac{r}{r+1}\frac{N_n}{K} \qquad a = r+1.$$

We obtain a classical form for the discrete logistic equation:

$$y_{n+1} = ay_n(1 - y_n).$$

This method for producing discrete equations is not foolproof, however. The discrete logistic equation above is not well posed, in the sense that its solutions can become negative. This is not hard to see. Suppose we start from $y_0 = 0.5$ and $a = 6$. Then $y_1 = 1.5$. Consequently, $y_2 < 0$. Thus, the logistic equation is not a very good discrete population model.

We can derive a discrete version of the **simplified logistic model**. Suppose the population increases in each time interval by a constant amount Λ, and that $\gamma \leq 1$ is the probability for survival of individuals to the next time period. Then the **simplified logistic model** takes the form

$$N_{n+1} = \Lambda + \gamma N_n. \tag{16.6}$$

This model can also be solved explicitly:

$$
\begin{aligned}
N_1 &= \Lambda + \gamma N_0, \\
N_2 &= \Lambda + \gamma(\Lambda + \gamma N_0) = \gamma^2 N_0 + (1 + \gamma)\Lambda, \\
&\vdots \\
N_n &= \gamma^n N_0 + (1 + \gamma + \cdots + \gamma^{n-1})\Lambda.
\end{aligned}
\tag{16.7}
$$

Hence,

$$
N_n =
\begin{cases}
N_0 + \Lambda n, & \gamma = 1, \\
\gamma^n \left(N_0 - \dfrac{\Lambda}{1 - \gamma} \right) + \dfrac{\Lambda}{1 - \gamma}, & \gamma < 1.
\end{cases}
\tag{16.8}
$$

Other discrete population models have been proposed that guarantee that the population remains positive for all times. One such model, proposed by Bill Ricker [138], is the **Ricker model**:

$$N_{n+1} = N_n e^{r\left(1 - \frac{N_n}{K}\right)}. \tag{16.9}$$

Another model also widely used is the **Beverton–Holt model** [23], also called the Verhulst equation:

$$N_{n+1} = \frac{rN_n}{A + N_n}. \tag{16.10}$$

A generalization of the Beverton–Holt model can be made that is known as the **Hassell equation** [72]:

$$N_{n+1} = \frac{rN_n}{(A + N_n)^b}, \tag{16.11}$$

where $b > 0$ is a positive parameter.

16.1.2 Analysis of Single-Species Discrete Models

Difference equations also have solutions that do not depend on time, called *equilibria*. Since the solution does not depend on time, all members of the sequence have the same value, that is, we have

$$N_n = N^* \qquad \text{for} \quad \text{all} \quad n \geq 0.$$

Consequently, equilibria of the difference equation (16.1) must satisfy $N^* = \mathscr{F}(N^*)$.

Definition 16.2. A value N^* that satisfies

$$N^* = \mathscr{F}(N^*)$$

is called a *fixed point* of the function $\mathscr{F}$.

Example 16.1. Consider the equilibria of the logistic equation

$$N^* = N^* + rN^* \left(1 - \frac{N^*}{K} \right).$$

The solutions of this equation are $N_1^* = 0$ and $N_2^* = K$, that is, the equilibria in the discrete case are exactly the same as in the continuous case. The equilibrium $N_1^* = 0$ is called a *trivial equilibrium*, while the equilibrium $N_2^* = K$ is called a *nontrivial equilibrium*.

To describe the behavior of the solutions near an equilibrium, we use again a process called *linearization*. Let N^* be the equilibrium, and u_n the perturbation of the solution from the equilibrium, that is,

$$N_n = N^* + u_n.$$

Substituting this equation into Eq. (16.1), we have $u_{n+1} + N^* = \mathscr{F}(u_n + N^*)$. Expanding $\mathscr{F}$ in a Taylor series and neglecting all terms containing powers of u_n greater than one, we obtain

$$u_{n+1} + N^* = \mathscr{F}(N^*) + \mathscr{F}'(N^*)u_n.$$

Recall that since N^* is an equilibrium, we have $N^* = \mathscr{F}(N^*)$. Hence, we obtain the following linearized equation:

$$u_{n+1} = \mathscr{F}'(N^*)u_n. \tag{16.12}$$

We note that $\mathscr{F}'(N^*)$ is a fixed number, which may be positive or negative. If we consider

$$u_{n+1} = |\mathscr{F}'(N^*)|u_n, \tag{16.13}$$

then Eq. (16.13) is exactly the discrete Malthus equation. Consequently, we have the following:

1. If $|\mathscr{F}'(N^*)| < 1$, then $u_n \to 0$. Hence, $N_n - N^* \to 0$ and $N_n \to N^*$. This is the case if N_0 is close enough to N^*, that is, this result is local. In this case, we call N^* *locally asymptotically stable.*
2. If $|\mathscr{F}'(N^*)| > 1$, then $u_n \to \infty$. Hence $N_n - N^* \to \infty$, and N_n diverges from N^*. This is the case if N_0 is close enough to N^*. In this case, we call N^* *unstable.*

We note that if $|\mathscr{F}'(N^*)| = 1$, we cannot draw conclusions from the local analysis. We summarize the above discussion in the following theorem:

Theorem 16.1. *The equilibrium N^* of the discrete equation (16.1) is locally asymptotically stable if and only if $|\mathscr{F}'(N^*)| < 1$. The equilibrium N^* of the discrete equation (16.1) is unstable if and only if $|\mathscr{F}'(N^*)| > 1$.*

To illustrate the use of the theorem above, we consider the local stability of the equilibria of the logistic equation.

Example 16.2. In the case of the logistic equation (16.5), the function $\mathscr{F}$ is given by

$$\mathscr{F}(N) = N + rN\left(1 - \frac{N}{K}\right).$$

The derivative is given by

$$\mathscr{F}'(N) = 1 + r\left(1 - \frac{N}{K}\right) - \frac{r}{K}N.$$

In the case of the trivial equilibrium $N^* = 0$, we have

$$\mathscr{F}'(0) = 1 + r > 1.$$

Consequently, the trivial equilibrium is always unstable. Now we consider the nontrivial equilibrium $N^* = K$. We have

$$\mathscr{F}'(K) = 1 - r.$$

So if $|1 - r| < 1$, or equivalently, if $0 < r < 2$, then the nontrivial equilibrium is locally asymptotically stable.

When $r > 2$, simulations suggests that the logistic equation can experience very complex behavior. To investigate this behavior through simulations, we will study the nondimensionalized version of the logistic equation:

$$y_{n+1} = \rho y_n(1 - y_n). \tag{16.14}$$

Recall that $\rho = 1 + r$, so we can expect complex behavior for $\rho > 3$. We notice that the corresponding equilibria of the nondimensional logistic model are $y^* = 0$ and $y^* = 1$. The first complexity that appears is a 2-cycle.
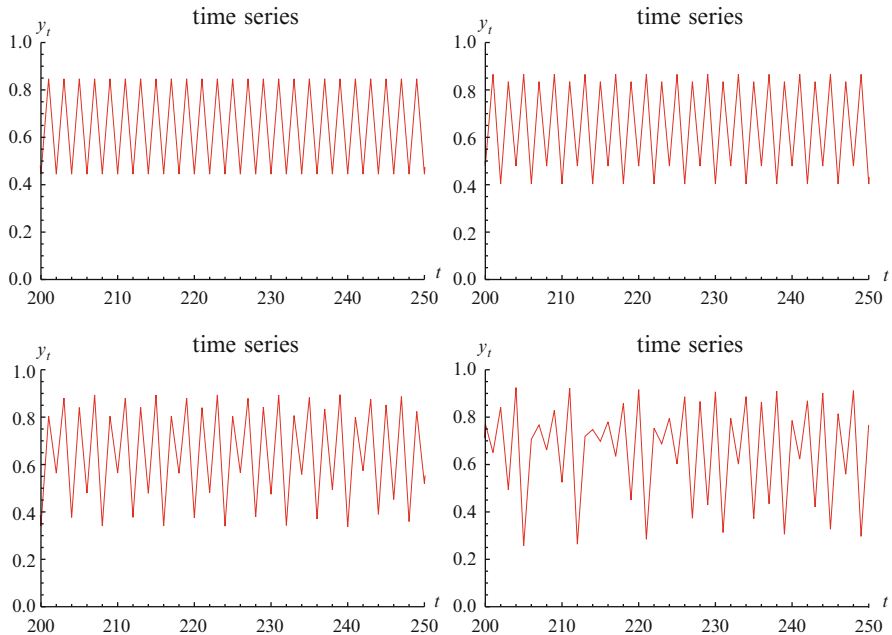
Fig. 16.1 The figure shows time series of the model $y_{n+1} = \rho y_n(1 - y_n)$ for different values of ρ. The first figure shows a two-cycle with $\rho = 3.43$. The second figure on the *top line* shows a 4-cycle with $\rho = 3.47$. The *left* figure on the *bottom row* shows an 8-cycle with $\rho = 3.58$. The *right* figure on the *bottom row* shows chaos with $\rho = 3.7$

Definition 16.3. A *2-cycle* of model (16.1) is a system of two solutions y_1 and y_2 such that

$$y_1 = \mathscr{F}(y_2),$$
$$y_2 = \mathscr{F}(y_1). \tag{16.15}$$

In model (16.14), $\mathscr{F}(y) = \rho y(1 - y)$. As ρ increases, the system experiences a process, called *period-doubling*, to a 4-cycle. Similarly, a *4-cycle* of model (16.14) is a system of four solutions y_1, y_2, y_2, y_4 such that

$$y_1 = \mathscr{F}(y_4),$$
$$y_2 = \mathscr{F}(y_1),$$
$$y_3 = \mathscr{F}(y_2), \tag{16.16}$$
$$y_4 = \mathscr{F}(y_3).$$

Further period-doubling occurs to an 8-cycle. The period-doubling continues until the system begins to exhibit chaos. We illustrate period-doubling and chaos in Fig. 16.1.

We need single-species discrete population models to capture the demographic processes in epidemic models. Many books focus on single-species discrete models and provide an excellent introduction to these models (for instance, see [27, 90]).

16.2 Discrete Epidemic Models

Just like single-species population models, discrete epidemic models can also be obtained from a discretization of the continuous epidemic models. However, this approach results in models that have issues like those of the discrete logistic equation. To avoid these problems, a modeling approach specific to discrete models should be taken. We follow here the approach of Castillo-Chavez and Yakubu [39].

16.2.1 A Discrete SIS Epidemic Model

We begin with a general population model

$$N_{n+1} = f(N_n) + \gamma N_n, \tag{16.17}$$

where $\gamma < 1$ is the probability of survival to the next time period, and $f(N_n)$ is a recruitment function. We assume that the disease does not affect the population dynamics, that is, we assume that the disease is nonfatal and does not affect the birth process. We will build an SIS epidemic process on top of the demographic process. We denote by S_n and I_n the susceptible and infected individuals at time t_n. Individuals survive with probability $\gamma < 1$ (die with probability $1 - \gamma$) in each generation. Infected individuals recover with probability $1 - \sigma$ (do not recover with probability $\sigma < 1$) in each generation. In each generation, susceptible individuals become infected with probability $1 - G$ (remain susceptible with probability G). The function G is a function of the prevalence I_n/N_n, which is weighted with coefficient α. The model assumes a sequential process: at each generation, γS_n susceptibles survive, and the surviving susceptibles become infected with probability $1 - G$. Similarly, γI_n infected individuals survive, and the surviving ones recover with probability $(1 - \sigma)$:

$$S_{n+1} = f(N_n) + \gamma S_n G\left(\frac{\alpha I_n}{N_n}\right) + \gamma(1 - \sigma)I_n,$$

$$I_{n+1} = \gamma S_n \left(1 - G\left(\frac{\alpha I_n}{N_n}\right)\right) + \gamma \sigma I_n. \tag{16.18}$$

The function G must satisfy the following conditions:

1. $G : [0, \infty) \to [0, 1]$.
2. $G(0) = 1$.
3. G is a monotone decreasing function with $G'(x) < 0$ and $G''(x) \geq 0$.

An example of such a function that we will use is $G(x) = e^{-x}$. Another example is $G(x) = A/(x + A)$. Adding the two equations in system (16.18) gives Eq. (16.17).

16.2.2 Analysis of Multidimensional Discrete Models

In this subsection, we introduce the techniques that help us analyze systems of discrete equations. Suppose that we are given the following system:

$$\mathbf{x}_{n+1} = \mathscr{F}(\mathbf{x}_n), \tag{16.19}$$

where $\mathbf{x}$ is an M-dimensional vector of variables. As before, an *equilibrium* of system (16.19) is the solution of the problem

$$\mathbf{x}^* = \mathscr{F}(\mathbf{x}^*).$$

To find the behavior of the solutions near an equilibrium, we use linearization. We set $\mathbf{x}_n = \mathbf{u}_n + \mathbf{x}^*$. We obtain the following linear system:

$$\mathbf{u}_{n+1} = \mathbf{J}(\mathbf{x}^*)\mathbf{u}_n, \tag{16.20}$$

where $\mathbf{J}$ is the Jacobian of the system, that is,

$$\mathbf{J}(\mathbf{x}^*) = \begin{pmatrix} \dfrac{\partial \mathscr{F}_1}{\partial x_1} & \cdots & \dfrac{\partial \mathscr{F}_1}{\partial x_M} \\ & & \vdots \\ \dfrac{\partial \mathscr{F}_M}{\partial x_1} & \cdots & \dfrac{\partial \mathscr{F}_M}{\partial x_M} \end{pmatrix} |_{\mathbf{x}=\mathbf{x}^*}. \tag{16.21}$$

Definition 16.4. An equilibrium point $\mathbf{x}^*$ is said to be *locally asymptotically stable* if there exists a neighborhood U of x^* such that for each starting value $\mathbf{x}_0 \in U$, we get

$$\lim_{n \to \infty} \mathbf{x}_n = \mathbf{x}^*. \tag{16.22}$$

The equilibrium point $\mathbf{x}^*$ is called *unstable* if x^* is not (locally asymptotically) stable.

The limit (16.22) holds if for system (16.20), we have $\lim_{n \to \infty} \mathbf{u}_n = 0$. The following theorem gives the conditions for convergence of solutions of the linear system (16.20) to zero:

Theorem 16.2. *Let $\mathbf{J}$ be an $M \times M$ matrix with $\rho(\mathbf{J}) < 1$, where*

$$\rho(\mathbf{J}) = \max\{|\lambda| : \lambda \text{ is an eigenvalue of } \mathbf{J}\}.$$

Then every solution of (16.20) satisfies

$$\lim_{n \to \infty} \mathbf{u}_n = 0.$$

If $\rho(\mathbf{J}) > 1$, then there are solutions that go to infinity.

This implies the following criterion for stability of an equilibrium $\mathbf{x}^*$ of system (16.19).

Theorem 16.3. *Consider the nonlinear autonomous system (16.19). Suppose $\mathscr{F}$: $\mathscr{D} \to \mathscr{D}$, where $\mathscr{D} \subset \mathbf{R}^M$ and $\mathscr{D}$ is an open set. Suppose $\mathscr{F}$ is twice continuously differentiable in some neighborhood of a fixed point $\mathbf{x}^* \in \mathscr{D}$. Let $\mathbf{J}(\mathbf{x}^*)$ be the Jacobian matrix of $\mathscr{F}$ evaluated at $\mathbf{x}^*$. Then the following hold:*

1. *$\mathbf{x}^*$ is locally asymptotically stable if all eigenvalues of $\mathbf{J}(\mathbf{x}^*)$ have magnitude less than one.*
2. *$\mathbf{x}^*$ is unstable if at least one eigenvalue of $\mathbf{J}(\mathbf{x}^*)$ has magnitude greater than one.*

The Routh–Hurwitz criterion will not be helpful here in determining which matrices are stable, since Routh–Hurwitz identifies matrices whose eigenvalues lie in the left half of the complex plane. However, there is an analogous criterion that can help determine whether the spectral radius of a matrix is smaller than one. This criterion is called the **Jury conditions**. Let

$$p(\lambda) = |\mathbf{J} - \lambda I| = a_M \lambda^M + \cdots + a_1 \lambda + a_0,$$

where $a_M = 1$. To introduce the Jury conditions, we first have to introduce the **Jury array**. The Jury array is composed as follows: First we write out a row of the coefficients, and then we write out another row with the same coefficients in reverse order. The first two rows of the Jury array are composed of the coefficients of the polynomial $p(\lambda)$ above. Once we have the first two rows of the **a** coefficients, the next two rows are of the **b** coefficients, and so on. We obtain the array of Table 16.1, where the **b** coefficients, **c** coefficients, etc., are composed as follows:

Table 16.1 Jury array

Number	Coeff.	Coeff.	Coeff.	Coeff.	Coeff.
(1)	a_0	a_1	$\ldots$	a_{M-1}	a_M
(2)	a_M	a_{M-1}	$\ldots$	a_1	a_0
(3)	b_0	b_1	$\ldots$	b_{M-1}	
(4)	b_{M-1}	b_{M-2}	$\ldots$	b_0	
$\vdots$	$\vdots$	$\vdots$	$\vdots$		
(2M-3)	v_0	v_1	v_2		

$$b_k = \begin{vmatrix} a_0 & a_{M-k} \\ a_M & a_k \end{vmatrix} \qquad c_k = \begin{vmatrix} b_0 & b_{M-1-k} \\ b_{M-1} & b_k \end{vmatrix} \qquad d_k = \begin{vmatrix} c_0 & c_{M-2-k} \\ c_{M-2} & c_k \end{vmatrix}.$$

Jury Conditions
The Jury conditions require *all* of the following conditions to be met. If
all the conditions are satisfied, then the spectral radius of the matrix is
less than one, and the matrix is stable:

1. $p(1) > 0$.
2. $(-1)^M p(-1) > 0$.
3. $|a_0| < a_M$.
4. Once the Jury array has been composed, the Jury conditions also require

$$
\begin{aligned}
|b_0| &> |b_{M-1}|, \\
|c_0| &> |c_{M-2}|, \\
|d_0| &> |d_{M-3}|. \\
&\vdots
\end{aligned}
\tag{16.23}
$$

In the case $M = 1$, the Jury conditions do not apply, but in this case, the eigenvalue is known explicitly, and its magnitude can be compared with one. In the cases $M = 2, 3, 4$, we write the Jury conditions in Table 16.2.

Table 16.2 Jury Conditions

Degree	Condition	Condition	Condition	Condition	Condition
$M = 2$	$p(1) > 0$	$p(-1) > 0$	$|a_0| < 1$		
$M = 3$	$p(1) > 0$	$p(-1) < 0$	$|a_0| < 1$	$|a_0^2 - 1| > |a_0 a_2 - a_1|$	
$M = 4$	$p(1) > 0$	$p(-1) > 0$	$|a_0| < 1$	$|a_0^2 - 1| > |a_0 a_3 - a_1|$	$|b_0^2 - b_3^2| > |b_0 b_2 - b_3 b_1|$

16.2.3 Analysis of the SIS Epidemic Model

In this section, we analyze model (16.18) with a specific fertility function. In particular, we choose the discrete simplified logistic model, where we know that the population tends to a constant size as $n \to \infty$. We will study the following epidemic model with a general force of infection G:

$$
\begin{aligned}
S_{n+1} &= \Lambda + \gamma S_n G\left(\frac{\alpha I_n}{N_n}\right) + \gamma(1 - \sigma)I_n, \\
I_{n+1} &= \gamma S_n \left(1 - G\left(\frac{\alpha I_n}{N_n}\right)\right) + \gamma \sigma I_n.
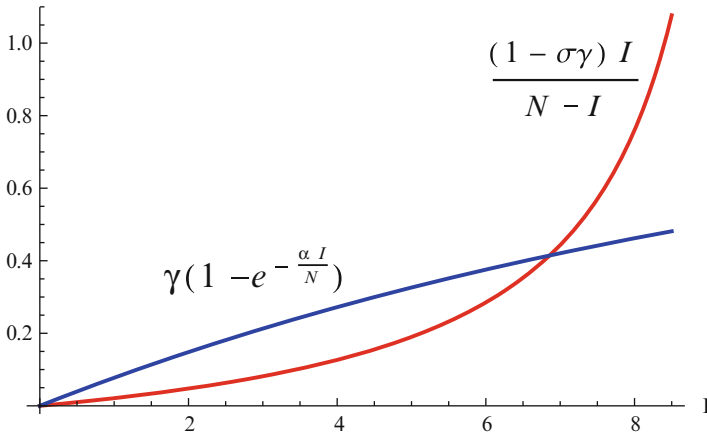\end{aligned}
\tag{16.24}
$$

Fig. 16.2 The figure shows the two functions on the two sides of Eq. (16.27). Here $\alpha = 0.9$, $\sigma = 0.9$, $\gamma = 0.9$, and $N = 10$

The equilibria of the system above satisfy

$$S = \Lambda + \gamma S G\left(\frac{\alpha I}{N}\right) + \gamma(1 - \sigma)I,$$

$$I = \gamma S\left(1 - G\left(\frac{\alpha I}{N}\right)\right) + \gamma\sigma I. \tag{16.25}$$

Adding the equations, we have $N = \Lambda + \gamma N$. Hence $N = \Lambda/(1 - \gamma)$. The system clearly has the disease-free equilibrium $\mathscr{E}_0 = (N, 0)$. To find the endemic equilibria, we write $S = N - I$ and substitute in the equation for I:

$$(1 - \sigma\gamma)I = \gamma(N - I)\left(1 - G\left(\frac{\alpha I}{N}\right)\right). \tag{16.26}$$

This is a nonlinear equation for I. It has $I = 0$ as a solution. We need to find a condition under which this equation has a nonzero solution. The equation can be rewritten also as

$$(1 - \sigma\gamma)\frac{I}{N - I} = \gamma\left(1 - G\left(\frac{\alpha I}{N}\right)\right). \tag{16.27}$$

The function on the right is increasing and concave down. The function on the left is increasing and concave up, tending to infinity as $I \to N$. Besides the common point at zero, these functions have another unique common point if and only if the slope at zero of the function on the left is smaller than the slope at zero of the function on the right (see Fig. 16.2), that is, if

$$(1 - \sigma\gamma) < -\alpha\gamma G'(0).$$

This condition gives the reproduction number. We define

$$\mathcal{R}_0 = \frac{-\alpha\gamma G'(0)}{(1-\sigma\gamma)}. \tag{16.28}$$

We note that the reproduction number is positive, since $G'(0) < 0$. We summarize these results in the following proposition:

Proposition 16.1. *Assume $\mathcal{R}_0 < 1$. Then model (16.24) has only the disease-free equilibrium $\mathcal{E}_0 = (N,0)$. If $\mathcal{R}_0 > 1$, then model (16.24) has the disease-free equilibrium and a unique endemic equilibrium $\mathcal{E}^* = (S^*,I^*)$, where $I^* > 0$ is the unique positive solution of Eq. (16.27) and $S^* = N - I^*$.*

We use the theoretical results in the previous subsection to establish the local stability of equilibria. The following theorem summarizes the results:

Theorem 16.4. *The disease-free equilibrium is locally asymptotically stable if $\mathcal{R}_0 < 1$ and unstable if $\mathcal{R}_0 > 1$. The endemic equilibrium is locally asymptotically stable if $\mathcal{R}_0 > 1$.*

Proof. We begin by computing the generic form of the Jacobian:

$$J = \begin{pmatrix} \gamma G\left(\frac{\alpha I}{N}\right) - \gamma\alpha\frac{SI}{N^2}G'\left(\frac{\alpha I}{N}\right) & \gamma\alpha\left[\frac{S}{N} - \frac{SI}{N^2}\right]G'\left(\frac{\alpha I}{N}\right) + \gamma(1-\sigma) \\ \gamma\left(1 - G\left(\frac{\alpha I}{N}\right)\right) + \gamma\alpha\frac{SI}{N^2}G'\left(\frac{\alpha I}{N}\right) & -\gamma\alpha\left[\frac{S}{N} - \frac{SI}{N^2}\right]G'\left(\frac{\alpha I}{N}\right) + \gamma\sigma \end{pmatrix}, \tag{16.29}$$

where we recall that $N = S + I$. To find the stability of the disease-free equilibrium, we evaluate the Jacobian at the disease-free equilibrium:

$$J(\mathcal{E}_0) = \begin{pmatrix} \gamma G(0) & \gamma\alpha G'(0) + \gamma(1-\sigma) \\ \gamma(1 - G(0)) & -\gamma\alpha G'(0) + \gamma\sigma \end{pmatrix}. \tag{16.30}$$

The characteristic equation now becomes $|J(\mathcal{E}_0) - \lambda I| = 0$. Recall that $G(0) = 1$, so the characteristic determinant is upper triangular, and the eigenvalues are $\lambda_1 = \gamma$ and $\lambda_2 = -\gamma\alpha G'(0) + \gamma\sigma$. Both eigenvalues are positive, and λ_1 is by assumption less than one, while λ_2 is less than one if and only if $\mathcal{R}_0 < 1$.

To determine the stability of the endemic equilibrium, we first observe that from equality (16.26), we have the following inequality:

$$(1 - \gamma\sigma) > -\gamma(1 - G(\frac{\alpha I^*}{N^*})) - \alpha\gamma\frac{S^*}{N^*}G'(\frac{\alpha I^*}{N^*}). \tag{16.31}$$

This inequality simply says that at the point where the two curves intersect, the slope of the left one is larger than the slope of the right one. This is easy to see from their graphs. The characteristic polynomial is given by

$$|J - \lambda I| = \begin{vmatrix} \gamma G\left(\frac{\alpha I}{N}\right) - \gamma\alpha\frac{SI}{N^2}G'\left(\frac{\alpha I}{N}\right) - \lambda & \gamma\alpha\left[\frac{S}{N} - \frac{SI}{N^2}\right]G'\left(\frac{\alpha I}{N}\right) + \gamma(1-\sigma) \\ \gamma\left(1 - G\left(\frac{\alpha I}{N}\right)\right) + \gamma\alpha\frac{SI}{N^2}G'\left(\frac{\alpha I}{N}\right) & -\gamma\alpha\left[\frac{S}{N} - \frac{SI}{N^2}\right]G'\left(\frac{\alpha I}{N}\right) + \gamma\sigma - \lambda \end{vmatrix}.$$

$$(16.32)$$

We can manipulate the determinant to simplify the characteristic polynomial. In particular, adding the first line to the second, we have

$$|J - \lambda I| = \begin{vmatrix} \gamma G\left(\frac{\alpha I^*}{N^*}\right) - \gamma\alpha\frac{SI}{N^2}G'\left(\frac{\alpha I^*}{N^*}\right) - \lambda & \gamma\alpha\left[\frac{S^*}{N^*} - \frac{S^*I^*}{N^{*2}}\right]G'\left(\frac{\alpha I^*}{N^*}\right) + \gamma(1-\sigma) \\ \gamma - \lambda & \gamma - \lambda \end{vmatrix} = 0.$$

$$(16.33)$$

Factoring out $\gamma - \lambda$, we see that one of the eigenvalues is $\lambda_1 = \gamma$. This eigenvalue is positive and less than one. The second eigenvalue is obtained from the remaining determinant

$$\begin{vmatrix} \gamma G\left(\frac{\alpha I^*}{N^*}\right) - \gamma\alpha\frac{SI}{N^2}G'\left(\frac{\alpha I^*}{N^*}\right) - \lambda & \gamma\alpha\left[\frac{S^*}{N^*} - \frac{S^*I^*}{N^{*2}}\right]G'\left(\frac{\alpha I^*}{N^*}\right) + \gamma(1-\sigma) \\ 1 & 1 \end{vmatrix} = 0.$$

$$(16.34)$$

This gives, after some simplification,

$$\lambda_2 = -\gamma\left(1 - G\left(\frac{\alpha I^*}{N^*}\right)\right) - \alpha\gamma\frac{S^*}{N^*}G'\left(\frac{\alpha I^*}{N^*}\right) + \gamma\sigma.$$

Inequality (16.31) implies that $\lambda_2 < 1$. Furthermore, $\lambda_2 > -\gamma\left(1 - G\left(\frac{\alpha I^*}{N^*}\right)\right) > -1$. Hence $|\lambda_2| < 1$, and the endemic equilibrium is locally asymptotically stable. $\square$

In this SIS example, we did not necessarily need the Jury conditions, because the two-equation model can be reduced to a single equation if we take into account the fact that the total population size is asymptotically constant.

16.3 Discrete SEIS Model

One can formulate discrete variants of all classical continuous epidemic models. In this section, we formulate a discrete version of an SEIS model that consists of three equations: one for the susceptible S_n, one for the exposed E_n, and one for the

infectious I_n individuals. We will use again an asymptotically constant population size and a general function for the force of infection. The model takes the form

$$S_{n+1} = \Lambda + \gamma S_n G\left(\frac{\alpha I_n}{N_n}\right) + \gamma(1-\delta)I_n,$$

$$E_{n+1} = \gamma S_n\left(1 - G\left(\frac{\alpha I_n}{N_n}\right)\right) + \gamma\sigma E_n,$$

$$I_{n+1} = \gamma(1-\sigma)E_n + \gamma\delta I_n, \tag{16.35}$$

where γ is the probability of survival to the next time period, $1-\sigma$ is the probability of progression to infectiousness, and $1-\delta$ is the probability of recovery. Again, the function G must satisfy the following conditions:

1. $G : [0,\infty) \to [0,1]$.
2. $G(0) = 1$.
3. G is a monotone decreasing function with $G'(x) < 0$ and $G''(x) \geq 0$.

Equilibria are solutions of the following system:

$$S = \Lambda + \gamma SG\left(\frac{\alpha I}{N}\right) + \gamma(1-\delta)I,$$

$$E = \gamma S\left(1 - G\left(\frac{\alpha I}{N}\right)\right) + \gamma\sigma E,$$

$$I = \gamma(1-\sigma)E + \gamma\delta I. \tag{16.36}$$

Adding the three equations, we have $N = \Lambda + \gamma N$. This gives the equilibrium total population size $N = \Lambda/(1-\gamma)$. The system has the disease-free equilibrium $\mathcal{E}_0 = (\frac{\Lambda}{1-\gamma},0,0)$. Problem 16.4 asks you to compute the reproduction number, which is given by the following expression:

$$\mathcal{R}_0 = \frac{-\alpha\gamma^2(1-\sigma)G'(0)}{(1-\sigma\gamma)(1-\delta\gamma)}. \tag{16.37}$$

Problem 16.4 asks you to establish the following proposition:

Proposition 16.2. *If $\mathcal{R}_0 < 1$, then the disease-free equilibrium is locally asymptotically stable. If $\mathcal{R}_0 > 1$, the disease-free equilibrium is unstable, and there is a unique endemic equilibrium.*

To obtain the equation for the endemic equilibrium, we express E in terms of I from the last equation in system (16.36): $E = QI$, where

$$Q = \frac{1-\gamma\delta}{\gamma(1-\sigma)}.$$

We can express S in terms of I: $S = N - QI - I$. We replace these values in the second equation to obtain an equation for I:

$$(1 - \gamma\sigma)QI = \gamma(N - (Q+1)I)\left(1 - G\left(\frac{\alpha I}{N}\right)\right). \tag{16.38}$$

Every value of I that solves Eq. (16.38) gives an equilibrium $\mathscr{E} = (S^*, E^*, I^*)$. As before, it can be seen that the equation above has a unique nontrivial equilibrium $I^* > 0$. At the unique endemic equilibrium, the slopes of the two curves are related as follows:

$$(1 - \gamma\sigma)Q > -\gamma(Q+1)\left(1 - G\left(\frac{\alpha I^*}{N}\right)\right) - \alpha\gamma\frac{S^*}{N}G'\left(\frac{\alpha I^*}{N}\right). \tag{16.39}$$

Replacing the value of Q and taking a common denominator leads to the inequality

$$(1 - \gamma\sigma)(1 - \gamma\delta) > -\gamma(1 - \gamma\delta + \gamma(1 - \sigma))\left(1 - G\left(\frac{\alpha I^*}{N}\right)\right)$$

$$- \alpha\gamma^2(1 - \sigma)\frac{S^*}{N}G'\left(\frac{\alpha I^*}{N}\right). \tag{16.40}$$

Now we are ready to establish a partial result on the stability of the endemic equilibrium:

Proposition 16.3. *Assume $\mathscr{R}_0 > 1$. If*

$$\sigma + \delta + G\left(\frac{\alpha I^*}{N}\right) - 1 > 0,$$

then the unique endemic equilibrium $\mathscr{E} = (S^*, E^*, I^*)$ is locally asymptotically stable.

Proof. The Jacobian at the endemic equilibrium is given by

$$J = \begin{pmatrix} \gamma G\left(\frac{\alpha I}{N}\right) - A & -A & \gamma\alpha\frac{S}{N}G'\left(\frac{\alpha I}{N}\right) - A + \gamma(1 - \delta) \\ \gamma\left(1 - G\left(\frac{\alpha I}{N}\right)\right) + A & \gamma\sigma + A & -\gamma\alpha\frac{S}{N}G'\left(\frac{\alpha I}{N}\right) + A \\ 0 & \gamma(1 - \sigma) & \gamma\delta \end{pmatrix}, \tag{16.41}$$

where $A = \gamma\alpha\frac{SI}{N^2}G'\left(\frac{\alpha I}{N}\right)$. We consider the characteristic equation $|J - \lambda I| = 0$. Adding the first and the third rows in the determinant to the second row, we obtain

$$\begin{vmatrix} \gamma G\left(\frac{\alpha I}{N}\right) - A - \lambda & -A & \gamma\alpha\frac{S}{N}G'\left(\frac{\alpha I}{N}\right) - A + \gamma(1 - \delta) \\ \gamma - \lambda & \gamma - \lambda & \gamma - \lambda \\ 0 & \gamma(1 - \sigma) & \gamma\delta - \lambda \end{vmatrix} = 0. \tag{16.42}$$

Factoring out $\gamma - \lambda$, we see that the first eigenvalue is $\lambda_1 = \gamma$. This eigenvalue is positive and less than one. The remaining eigenvalues are solutions of the characteristic equation

$$\begin{vmatrix} \gamma G\left(\dfrac{\alpha I}{N}\right) - A - \lambda & -A & \gamma\alpha\dfrac{S}{N}G'\left(\dfrac{\alpha I}{N}\right) - A + \gamma(1-\delta) \\ 1 & 1 & 1 \\ 0 & \gamma(1-\sigma) & \gamma\delta - \lambda \end{vmatrix} = 0. \quad (16.43)$$

From here we obtain the quadratic polynomial

$$\begin{aligned} p(\lambda) \;=\;& \lambda^2 - (\gamma\delta + \gamma G - \gamma(1-\sigma))\lambda \\ & + [-\gamma^2(1-\sigma)G + \alpha\gamma^2(1-\sigma)\dfrac{S}{N}G' \\ & + \gamma^2(1-\sigma)(1-\delta) + \gamma^2\delta G] = 0, \quad (16.44) \end{aligned}$$

where G and G' have the usual argument. We can write the polynomial as $p(\lambda) = \lambda^2 + a_1\lambda + a_0$. Rewriting inequality (16.40) as

$$\alpha\gamma^2(1-\sigma)\dfrac{S^*}{N}G'\left(\dfrac{\alpha I^*}{N}\right) > -\;\gamma(1-\gamma\delta + \gamma(1-\sigma))\left(1 - G\left(\dfrac{\alpha I^*}{N}\right)\right)$$
$$-\;(1-\gamma\sigma)(1-\gamma\delta), \quad (16.45)$$

we will use it to bound the polynomial from below. Applying this inequality to the constant term of the polynomial $p(\lambda)$, we have

$$\begin{aligned} p(\lambda) \;>\;& \lambda^2 - (\gamma\delta + \gamma G - \gamma(1-\sigma))\lambda \\ & + [-\gamma^2(1-\sigma-\delta)G - \gamma(1-\gamma\delta + \gamma(1-\sigma))(1-G) \\ & - (1-\gamma\sigma)(1-\gamma\delta) + \gamma^2(1-\sigma)(1-\delta)] \\ =\;& \lambda^2 - (\gamma\delta + \gamma G - \gamma(1-\sigma))\lambda \\ & + [\gamma^2(1-\sigma-\delta)(1-G) - \gamma(1-\gamma\delta + \gamma(1-\sigma))(1-G) \\ & - (1-\gamma\sigma)(1-\gamma\delta) + \gamma^2\sigma\delta]. \end{aligned}$$
$$(16.46)$$

On combining the coefficients of the two terms $(1-G)$, the above right-hand side simplifies to

$$p(\lambda) > \lambda^2 - (\gamma\delta + \gamma G - \gamma(1-\sigma))\lambda - \gamma(1-G) - 1 + \gamma\delta + \gamma\sigma.$$

We need to check the Jury conditions. Clearly, $p(1) > 0$. Furthermore, according to our assumption,

$$p(-1) > 2\gamma(\delta + \sigma + G - 1) > 0.$$

Finally, we need to show that the constant term of the polynomial $p(\lambda)$ satisfies $|a_0| < 1$. We bound the constant term from above and from below:

$$a_0 > -\gamma(1-G) - 1 + \gamma\delta + \gamma\sigma = \gamma(\delta + \sigma + G - 1) - 1 > -1.$$

In addition, if $1 - \delta - \sigma > 0$, then

$$a_0 < \gamma^2(1-\delta)(1-\sigma) - \gamma(1-\delta-\sigma)G < 1.$$

If $1 - \delta - \sigma < 0$, we have

$$a_0 < \gamma^2(1-\delta-\sigma)(1-G) + \gamma^2\sigma\delta < \gamma^2\sigma\delta < 1.$$

We conclude that $|a_0| < 1$. The Jury conditions now imply that the endemic equilibrium is stable. $\square$

In conclusion, discrete models look simpler and perhaps more natural, but their analysis is far more complicated than the analysis of continuous models. Furthermore, even very simple single-species discrete models are capable of exhibiting very complex, even chaotic, dynamics.

16.4 Next-Generation Approach for Discrete Models

As the discrete models become more and more realistic, computation of $\mathscr{R}_0$ becomes harder or impossible to do via the Jacobian approach. In analogy with the continuous case, a version of the next-generation approach for discrete models was developed [9].

16.4.1 Basic Theory

To introduce the next-generation approach for discrete models, let $\mathbf{x} = (x^1,\ldots,x^m)^T$ be the vector of dependent variables, and let

$$\mathbf{x}_{n+1} = \mathbf{F}(\mathbf{x}_n) \qquad n = 0, 1, \ldots$$

be the dynamical system over discrete time intervals with $F : \mathbb{R}_+^m \longrightarrow \mathbb{R}_+^m$ and $F \in C^1(\mathbb{R}_+^m)$. As in the continuous case, we order the variables so that the first $k < m$, denoted by $\mathbf{y} = (y^1,\ldots,y^k)^T$, are the infected states such as exposed, infectious, isolated, and the remaining $m - k$ states $\mathbf{z} = (z^{k+1},\ldots,z^m)^T$ are the uninfected states, such as susceptible, recovered, vaccinated. In this case, the system can be written as

$$\begin{pmatrix} \mathbf{y}_{n+1} \\ \mathbf{z}_{n+1} \end{pmatrix} = \begin{pmatrix} \mathbf{F}_0(\mathbf{x}_n) \\ \mathbf{F}_1(\mathbf{x}_n) \end{pmatrix}. \tag{16.47}$$

We assume that there exists a unique disease-free equilibrium where $\mathbf{y} = 0$, and therefore the disease-free equilibrium is given by $(0, \mathbf{z}^*)^T$. Furthermore, linearizing the discrete system around the disease-free equilibrium gives

$$\xi_{n+1} = J\xi_n,$$

where ξ_n is the vector of perturbations, and J is the Jacobian evaluated at the disease-free equilibrium. The $m \times m$ Jacobian has the following form:

$$J = \begin{pmatrix} F + T & 0 \\ A & C \end{pmatrix}, \tag{16.48}$$

where $k \times k$ submatrices F and T are nonnegative, 0 is the zeroth matrix. Furthermore, we assume that $F + T$ is irreducible. Matrix F is a result of differentiation and evaluation at the disease-free equilibrium of the new infections, and matrix T is the result of differentiation and evaluation at the disease-free equilibrium of the transition states (recovery, death). The submatrix F is known as the fertility matrix, and T as the transition matrix. We assume that the disease-free equilibrium is locally asymptotically stable, that is $\rho(C) < 1$, where $\rho(C)$ is the spectral radius of C. In addition, we require $\rho(T) < 1$. Since J is block-triangular, the stability of the disease-free equilibrium depends on the eigenvalues of $F + T$. The next-generation matrix is

$$Q = F(I - T)^{-1},$$

where I is the $k \times k$ identity matrix. The basic reproduction number is defined as the spectral radius of the matrix Q, that is,

$$\mathcal{R}_0 = \rho(F(I - T)^{-1}).$$

16.4.2 Examples

In this subsection, we introduce several more complex discrete epidemic models and use the next-generation approach to compute the reproduction number.

16.4.2.1 SEIS Model

As a first example, we illustrate the theory on example (16.35). For this model, the infected vector is $\mathbf{y} = (E, I)^T$, and the uninfected vector is $\mathbf{z} = (S)$. Arranging the system so that the first equations are for the infected variables, we have

$$E_{n+1} = \gamma S_n \left(1 - G\left(\frac{\alpha I_n}{N_n}\right)\right) + \gamma \sigma E_n,$$

$$I_{n+1} = \gamma(1-\sigma)E_n + \gamma \delta I_n,$$

$$S_{n+1} = \Lambda + \gamma S_n G\left(\frac{\alpha I_n}{N_n}\right) + \gamma(1-\delta)I_n.$$

$$(16.49)$$

The disease-free equilibrium is given by $(0, 0, \frac{\Lambda}{1-\gamma})$. The Jacobian is given by

$$J = \begin{pmatrix} \gamma\sigma & -\gamma\alpha G'(0) & 0 \\ \gamma(1-\sigma) & \gamma\delta & 0 \\ 0 & \gamma\alpha G'(0) + \gamma(1-\delta) & \gamma \end{pmatrix}. \qquad (16.50)$$

First, $C = (\gamma)$ and $\rho(C) = \gamma < 1$. The Jacobian is block-triangular. The important step is to identify the matrices F and T. The new infections term is associated with the function G. Hence the matrix F is given by

$$F = \begin{pmatrix} 0 & -\gamma\alpha G'(0) \\ 0 & 0 \end{pmatrix}. \qquad (16.51)$$

We notice that the entries in F are nonnegative, since $G'(0) < 0$. The transition matrix T is given by

$$T = \begin{pmatrix} \gamma\sigma & 0 \\ \gamma(1-\sigma) & \gamma\delta \end{pmatrix}. \qquad (16.52)$$

Using Mathematica, we can invert $I - T$ to obtain

$$(I-T)^{-1} = \begin{pmatrix} \dfrac{1}{1-\gamma\sigma} & 0 \\ \dfrac{\gamma(1-\sigma)}{(1-\gamma\delta)(1-\gamma\sigma)} & \dfrac{1}{1-\gamma\delta} \end{pmatrix}. \qquad (16.53)$$

Hence,

$$F(I-T)^{-1} = \begin{pmatrix} \dfrac{-\gamma^2\alpha G'(0)(1-\sigma)}{(1-\gamma\delta)(1-\gamma\sigma)} & \dfrac{-\gamma\alpha G'(0)}{1-\gamma\delta} \\ 0 & 0 \end{pmatrix}. \qquad (16.54)$$

The spectral radius of the above matrix gives the reproduction number

$$\mathscr{R}_0 = \frac{-\gamma^2\alpha G'(0)(1-\sigma)}{(1-\gamma\delta)(1-\gamma\sigma)}.$$

16.4.2.2 A Two-Patch SIS Model

In this subsection we introduce a two-patch SIS model based on the one-patch SIS model (16.18). We assume that the movement occurs after the infection and recovery

process. Individuals move from patch one to patch two with probability d_1 and vice versa with probability d_2. We furthermore assume that the probability of survival of individuals in both patches is the same. This assumption can be easily relaxed.

The SIS model with movement takes the form

$$S^1_{n+1} = (1-d_1)[\Lambda_1 + \gamma S^1_n G_1\left(\frac{\alpha_1 I^1_n}{N^1_n}\right) + \gamma(1-\sigma_1)I^1_n]$$

$$+d_2[\Lambda_2 + \gamma S^2_n G_2\left(\frac{\alpha_2 I^2_n}{N^2_n}\right) + \gamma(1-\sigma_2)I^2_n],$$

$$I^1_{n+1} = (1-d_1)[\gamma S^1_n\left(1 - G_1\left(\frac{\alpha_1 I^1_n}{N^1_n}\right)\right) + \gamma\sigma_1 I^1_n]$$

$$+d_2[\gamma S^2_n\left(1 - G_2\left(\frac{\alpha_2 I^2_n}{N^2_n}\right)\right) + \gamma\sigma_2 I^2_n],$$

$$S^2_{n+1} = +d_1[\Lambda_1 + \gamma S^1_n G_1\left(\frac{\alpha_1 I^1_n}{N^1_n}\right) + \gamma(1-\sigma_1)I^1_n]$$

$$+(1-d_2)[\Lambda_2 + \gamma S^2_n G_2\left(\frac{\alpha_2 I^2_n}{N^2_n}\right) + \gamma(1-\sigma_2)I^2_n],$$

$$I^2_{n+1} = d_1[\gamma S^1_n\left(1 - G_1\left(\frac{\alpha_1 I^1_n}{N^1_n}\right)\right) + \gamma\sigma_1 I^1_n]$$

$$+(1-d_2)[\gamma S^2_n\left(1 - G_2\left(\frac{\alpha_2 I^2_n}{N^2_n}\right)\right) + \gamma\sigma_2 I^2_n]. \qquad (16.55)$$

We begin by determining the disease-free equilibrium. It is given by $\mathscr{E}_0 = (S^1, 0, S^2, 0)$, where S^1 and S^2 are solutions of the following system:

$$\begin{aligned} S^1 &= (1-d_1)[\Lambda_1 + \gamma S^1] + d_2[\Lambda_2 + \gamma S^2], \\ S^2 &= d_1[\Lambda_1 + \gamma S^1] + (1-d_2)[\Lambda_2 + \gamma S^2]. \end{aligned} \qquad (16.56)$$

First, we see that

$$N = S^1 + S^2 = \frac{\Lambda_1 + \Lambda_2}{1 - \gamma}.$$

Solving system (16.56), we obtain

$$S^1 = \frac{(1-(1-d_2)\gamma)[(1-d_1)\Lambda_1 + d_2\Lambda_2] + d_2\gamma[d_1\Lambda_1 + (1-d_2)\Lambda_2]}{\Delta},$$
$$S^2 = \frac{d_1\gamma[(1-d_1)\Lambda_1 + d_2\Lambda_2] + (1-(1-d_1)\gamma)[d_1\Lambda_1 + (1-d_2)\Lambda_2]}{\Delta}, \qquad (16.57)$$

where $\Delta = (1-(1-d_1)\gamma)(1-(1-d_2)\gamma) - d_1 d_2\gamma^2$. The matrix C is given by

$$C = \begin{pmatrix} (1-d_1)\gamma & d_2\gamma \\ d_1\gamma & (1-d_2)\gamma \end{pmatrix}. \qquad (16.58)$$

It is not hard to show that $\rho(C) = \gamma < 1$. Next, we construct the matrix $F + T$:

$$F + T = \begin{pmatrix} (1 - d_1)[-\gamma\alpha_1 G'_1(0) + \gamma\sigma_1] & d_2[-\gamma\alpha_2 G'_2(0) + \gamma\sigma_2] \\ d_1[-\gamma\alpha_1 G'_1(0) + \gamma\sigma_1] & (1 - d_2)[-\gamma\alpha_2 G'_2(0) + \gamma\sigma_2] \end{pmatrix}. \quad (16.59)$$

The matrix F consists of all terms that involve G'; the matrix T consists of all remaining terms. Therefore,

$$F = \begin{pmatrix} -(1 - d_1)\gamma\alpha_1 G'_1(0) & -d_2\gamma\alpha_2 G'_2(0) \\ -d_1\gamma\alpha_1 G'_1(0) & -(1 - d_2)\gamma\alpha_2 G'_2(0) \end{pmatrix}, \quad (16.60)$$

and the matrix $I - T$ is given by

$$I - T = \begin{pmatrix} 1 - (1 - d_1)\gamma\sigma_1 & -d_2\gamma\sigma_2 \\ -d_1\gamma\sigma_1 & 1 - (1 - d_2)\gamma\sigma_2 \end{pmatrix}. \quad (16.61)$$

To invert $I - T$, we compute the determinant $\Delta = (1 - (1 - d_1)\gamma\sigma_1)(1 - (1 - d_2)\gamma\sigma_2) - d_1 d_2\gamma^2\sigma_1\sigma_2$. Hence,

$$(I - T)^{-1} = \frac{1}{\Delta}\begin{pmatrix} 1 - (1 - d_2)\gamma\sigma_2 & d_2\gamma\sigma_2 \\ d_1\gamma\sigma_1 & 1 - (1 - d_1)\gamma\sigma_1 \end{pmatrix}. \quad (16.62)$$

The next-generation matrix takes the form

$$F(I - T)^{-1} = \frac{1}{\Delta}\begin{pmatrix} A & B \\ C & D \end{pmatrix}, \quad (16.63)$$

where

$$\begin{aligned} A &= -(1 - d_1)\gamma\alpha_1 G'_1(0)[1 - (1 - d_2)\gamma\sigma_2] - d_1 d_2\gamma^2\sigma_1\alpha_2 G'_2(0), \\ B &= -(1 - d_1)d_2\gamma^2\sigma_2\alpha_1 G'_1(0) - d_2\gamma\alpha_2 G'_2(0)[1 - (1 - d_1)\gamma\sigma_1], \\ C &= -d_1\gamma\alpha_1 G'_1(0)[1 - (1 - d_2)\gamma\sigma_2] - d_1(1 - d_2)\gamma^2\sigma_1\alpha_2 G'_2(0), \\ D &= -d_1 d_2\gamma^2\sigma_2\alpha_1 G'_1(0) - (1 - d_2)\gamma\alpha_2 G'_2(0)[1 - (1 - d_1)\gamma\sigma_1]. \end{aligned} \quad (16.64)$$

The reproduction number is given by

$$\mathscr{R}_0 = \rho(F(I - T)^{-1}) = \frac{A + D + \sqrt{(A - D)^2 + 4BC}}{2\Delta}.$$

We note that in this example, it would have been impossible to compute $\mathscr{R}_0$ with the Jacobian approach.

16.4.2.3 A Discrete SARS Model

In this section, we consider a discrete SARS model with quarantine and isolation. Let S_n denote the susceptibles, E_n the exposed, I_n the individuals showing symptoms, Q_n the quarantined, J_n the isolated, and R_n the recovered individuals. In SARS,

the exposed individuals are infectious with reduced infectivity. The coefficient of reduction is q. The model takes the form

$$S_{n+1} = \Lambda + \gamma\alpha_1 S_n G\left(\frac{I_n + qE_n}{N_n - Q_n - J_n}\right) + \gamma\rho(1-\alpha_1)S_n + \gamma\alpha_4(1-\eta_1)Q_n,$$

$$E_{n+1} = \gamma\alpha_1 S_n \left(1 - G\left(\frac{I_n + qE_n}{N_n - Q_n - J_n}\right)\right) + \gamma E_n(\alpha_2\sigma + (1-\alpha_2)\rho),$$

$$I_{n+1} = \alpha_2\gamma(1-\sigma)E_n + \gamma I_n(\alpha_3\sigma + (1-\alpha_3)r_2),$$

$$Q_{n+1} = \gamma(1-\rho)((1-\alpha_1)S_n + (1-\alpha_2)E_n) + \gamma Q_n(\alpha_4\eta_1 + (1-\alpha_4)\eta_2),$$

$$J_{n+1} = \alpha_3\gamma(1-\sigma)I_n + (1-\alpha_4)\gamma(1-\eta_2)Q_n + \gamma r_1 J_n,$$

$$R_{n+1} = \gamma(1-r_1)J_n + \gamma(1-\alpha_3)(1-r_2)I_n + \gamma R_n, \tag{16.65}$$

where the parameters are given in Table 16.3.

Table 16.3 Parameter meanings

Parameter	Meaning	Parameter	Meaning
Λ	Recruitment	γ	Probability of survival
q	Reduction in infectivity for exposed	$1-\rho$	Probability of quarantine
$1-\sigma$	Probability of isolation	α_i	Convex combination coefficients
$1-r_1$	Probability of recovery of isolated	$1-r_2$	Probability of recovery of infected
$1-\eta_1$	Probability of ending quarantine to susceptible class	$1-\eta_2$	Probability of ending the quarantine to isolated class

We apply the next-generation approach to compute the reproduction number. The disease-free equilibrium is given by $\mathscr{E}_0 = (S^*, 0, 0, 0, 0, 0)$, where

$$S^* = \frac{\Lambda}{1-\gamma}.$$

The vector of infected classes is (E, I, Q, J). Hence, the matrix $F + T$ is given by

$$F + T = \begin{pmatrix} -\gamma\alpha_1 qG'(0) + \alpha_2\gamma\sigma + (1-\alpha_2)\gamma\rho & -\gamma\alpha_1 G'(0) & 0 & 0 \\ \alpha_2\gamma(1-\sigma) & \gamma(\alpha_3\sigma + (1-\alpha_3)r_2) & 0 & 0 \\ \gamma(1-\rho)(1-\alpha_2) & 0 & \gamma(\alpha_4\eta_1 + (1-\alpha_4)\eta_2) & 0 \\ 0 & \alpha_3\gamma(1-\sigma) & \gamma(1-\alpha_4)(1-\eta_2) & \gamma r_1 \end{pmatrix}.$$

$$\tag{16.66}$$

The matrix F is written as $F = (f_{ij})$, where $f_{11} = -\gamma q\alpha_1 G'(0)$ and $f_{12} = -\gamma\alpha_1 G'(0)$, while the remaining entries are zero. The matrix $I - T$ is given by

$$
I - T = \begin{pmatrix}
1 - \alpha_2 \gamma \sigma - (1 - \alpha_2) \gamma \rho & 0 & 0 & 0 \\
- \alpha_2 \gamma (1 - \sigma) & 1 - \gamma(\alpha_3 \sigma + (1 - \alpha_3) r_2) & 0 & 0 \\
- \gamma (1 - \rho)(1 - \alpha_2) & 0 & 1 - \gamma(\alpha_4 \eta_1 + (1 - \alpha_4) \eta_2) & 0 \\
0 & - \alpha_3 \gamma (1 - \sigma) & - \gamma(1 - \alpha_4)(1 - \eta_2) & 1 - \gamma r_1
\end{pmatrix}.
$$

$$(16.67)$$

Because of the structure of F, only the first 2×2 block of $(I - T)^{-1}$ is important for the reproduction number. Because of the block-triangular form of $I - T$, that first 2×2 block of $(I - T)^{-1}$ is obtained from inverting the first 2×2 block of $(I - T)$. Thus we have

$$
(I - T)^{-1} = \begin{pmatrix}
\dfrac{1}{1 - \alpha_2 \gamma \sigma - (1 - \alpha_2) \gamma \rho} & 0 & 0 \ 0 \\
\dfrac{\alpha_2 \gamma (1 - \sigma)}{\Delta} & \dfrac{1}{1 - \gamma(\alpha_3 \sigma + (1 - \alpha_3) r_2)} & 0 \ 0 \\
* & * & * \ * \\
* & * & * \ *
\end{pmatrix}, \quad (16.68)
$$

where $\Delta = (1 - \alpha_2 \gamma \sigma - (1 - \alpha_2) \gamma \rho)(1 - \gamma(\alpha_3 \sigma + (1 - \alpha_3) r_2))$. The matrix $F(I - T)^{-1}$ has a very simple form, whose principal eigenvalue is not hard to determine. Hence, the reproduction number is given by

$$
\mathcal{R}_0 = \rho(F(I - T)^{-1}) = \frac{-\gamma \alpha_1 q G'(0)}{1 - \alpha_2 \gamma \sigma - (1 - \alpha_2) \gamma \rho} + \frac{-\alpha_1 \gamma G'(0) \alpha_2 \gamma (1 - \sigma)}{\Delta}.
$$

The first term of the reproduction number gives the number of secondary infections produced by an exposed individual; the second term gives the number of secondary infections produced by an infectious individual.

Problems

16.1. Ricker Model
Consider the Ricker model (16.9).

(a) Find the equilibria of the Ricker model.
(b) Determine the stability of the equilibria of the Ricker model.
(c) Does the Ricker model have 2-cycles?
(d) Does the Ricker model exhibit chaos?

16.2. Beverton–Holt Model
Consider the Beverton-Holt model (16.10).

(a) Find the equilibria of the Beverton–Holt model.
(b) Determine the stability of the equilibria of the Beverton–Holt model.
(c) Does the Beverton–Holt model have 2-cycles?
(d) Does the Beverton–Holt model exhibit chaos?

16.3. Hassell Model
Consider the Hassell model (16.11).

(a) Find the equilibria of the Hassell model.
(b) Determine the stability of the equilibria of the Hassell model.
(c) Does the Hassell model have 2-cycles?
(d) Does the Hassell model exhibit chaos?

16.4. SEIS Epidemic Model
Consider the discrete SEIS model (16.35).

(a) Derive the reproduction number $\mathscr{R}_0$.
(b) Use the Jury conditions to show that if $\mathscr{R}_0 < 1$, then the disease-free equilibrium is locally asymptotically stable. If $\mathscr{R}_0 > 1$, then the disease-free equilibrium is unstable.
(c) Show that if $\mathscr{R}_0 > 1$, there is a unique endemic equilibrium.

16.5. SI Epidemic Model
Consider the following SI epidemic model:

$$S_{n+1} = \Lambda + \gamma S_n G\left(\frac{\alpha I_n}{N_n}\right),$$

$$I_{n+1} = \gamma S_n \left(1 - G\left(\frac{\alpha I_n}{N_n}\right)\right) + \gamma \sigma I_n,$$

$$\text{(16.69)}$$

where G has the same properties as in the text and $\sigma < 1$.

(a) Derive the reproduction number $\mathscr{R}_0$.
(b) Use the Jury conditions to show that if $\mathscr{R}_0 < 1$, then the disease-free equilibrium is locally asymptotically stable. If $\mathscr{R}_0 > 1$, then the disease-free equilibrium is unstable.
(c) Show that if $\mathscr{R}_0 > 1$, there is a unique endemic equilibrium.
(d) Consider the stability of the endemic equilibrium. When is it stable?

16.6. SIRS Epidemic Model
Consider the following SIRS epidemic model:

$$S_{n+1} = \Lambda + \gamma S_n G\left(\frac{\alpha I_n}{N_n}\right) + \gamma(1 - \delta)R_n,$$

$$I_{n+1} = \gamma S_n \left(1 - G\left(\frac{\alpha I_n}{N_n}\right)\right) + \gamma \sigma I_n,$$

$$R_{n+1} = \gamma(1 - \sigma)I_n + \gamma \delta R_n, \qquad\qquad\qquad\qquad \text{(16.70)}$$

where G has the same properties as in the text.

(a) Derive the reproduction number $\mathscr{R}_0$.
(b) Use the Jury conditions to show that if $\mathscr{R}_0 < 1$, then the disease-free equilibrium is locally asymptotically stable. If $\mathscr{R}_0 > 1$, then the disease-free equilibrium is unstable.
(c) Show that if $\mathscr{R}_0 > 1$, then there is a unique endemic equilibrium.
(d) Consider the stability of the endemic equilibrium. When is it stable?

16.7. SIS Epidemic Model with Environmental Transmission

Consider the following SIS epidemic model with environmental transmission:

$$S_{n+1} = \Lambda + \gamma S_n e^{-\frac{\alpha I_n}{N_n} - \beta P_n} + \gamma(1-\sigma)I_n,$$
$$I_{n+1} = \gamma S_n \left(1 - e^{-\frac{\alpha I_n}{N_n} - \beta P_n}\right) + \gamma \sigma I_n,$$
$$P_{n+1} = \rho I_n + \delta P_n, \tag{16.71}$$

where P_n is the amount of the pathogen in the environment.

(a) Derive the reproduction number $\mathscr{R}_0$.
(b) Use the Jury conditions to show that if $\mathscr{R}_0 < 1$, then the disease-free equilibrium is locally asymptotically stable. If $\mathscr{R}_0 > 1$, then the disease-free equilibrium is unstable.
(c) Show that if $\mathscr{R}_0 > 1$, then there is a unique endemic equilibrium.
(d) Consider the stability of the endemic equilibrium. When is it stable?

16.8. SIRS Epidemic Model with Vaccination

Consider the following SIRS epidemic model:

$$S_{n+1} = \Lambda + \rho \gamma S_n G\left(\frac{\alpha I_n}{N_n}\right) + \gamma(1-\delta)R_n + (1-\rho)\gamma \psi S_n,$$
$$I_{n+1} = \rho \gamma S_n \left(1 - G\left(\frac{\alpha I_n}{N_n}\right)\right) + \gamma \sigma I_n,$$
$$R_{n+1} = \gamma(1-\sigma)I_n + (1-\rho)\gamma(1-\psi)S_n + \gamma \delta R_n, \tag{16.72}$$

where G has the same properties as in the text.

(a) Derive the reproduction number $\mathscr{R}_0$.
(b) Use the Jury conditions to show that if $\mathscr{R}_0 < 1$, then the disease-free equilibrium is locally asymptotically stable. If $\mathscr{R}_0 > 1$, then the disease-free equilibrium is unstable.
(c) Show that if $\mathscr{R}_0 > 1$, there is a unique endemic equilibrium.
(d) Consider the stability of the endemic equilibrium. When is it stable?

16.9. SIS Epidemic Model with Two Strains

Consider the following SIS epidemic model with two strains:

$$S_{n+1} = \Lambda + \gamma S_n e^{-(\alpha_1 I_n + \alpha_2 J_n)} + \gamma(1 - \sigma_1)I_n + \gamma(1 - \sigma_2)J_n,$$

$$I_{n+1} = \gamma \frac{\alpha_1 S_n I_n}{\alpha_1 I_n + \alpha_2 J_n}\left(1 - e^{-(\alpha_1 I_n + \alpha_2 J_n)}\right) + \gamma \sigma_1 I_n,$$

$$J_{n+1} = \gamma \frac{\alpha_2 S_n J_n}{\alpha_1 I_n + \alpha_2 J_n}\left(1 - e^{-(\alpha_1 I_n + \alpha_2 J_n)}\right) + \gamma \sigma_2 J_n,$$

$$\tag{16.73}$$

where I_n denotes infection with strain one, and J_n denotes infection with strain two.

(a) Derive the reproduction numbers of strain one and strain two $\mathscr{R}_1$ and $\mathscr{R}_2$. Set $\mathscr{R}_0 = \max\{\mathscr{R}_1, \mathscr{R}_2\}$.

(b) Use the Jury conditions to show that if $\mathscr{R}_0 < 1$, then the disease-free equilibrium is locally asymptotically stable. If $\mathscr{R}_0 > 1$, then the disease-free equilibrium is unstable.

(c) Show that if $\mathscr{R}_1 > 1$, there is a unique endemic equilibrium corresponding to strain one. Show that if $\mathscr{R}_2 > 1$, there is a unique endemic equilibrium corresponding to strain two.

(d) Consider the stability of the endemic equilibrium corresponding to strain one. When is it stable?

16.10. SIS Epidemic Model with Two Strains and Mutation

Consider the following SIS epidemic model with two strains:

$$S_{n+1} = \Lambda + \gamma S_n e^{-(\alpha_1 I_n + \alpha_2 J_n)} + \rho\gamma(1 - \sigma_1)I_n + \gamma(1 - \sigma_2)J_n,$$

$$I_{n+1} = \gamma \frac{\alpha_1 S_n I_n}{\alpha_1 I_n + \alpha_2 J_n}\left(1 - e^{-(\alpha_1 I_n + \alpha_2 J_n)}\right) + \rho\gamma\sigma_1 I_n + (1 - \rho)\mu\gamma I_n,$$

$$J_{n+1} = \gamma \frac{\alpha_2 S_n J_n}{\alpha_1 I_n + \alpha_2 J_n}\left(1 - e^{-(\alpha_1 I_n + \alpha_2 J_n)}\right) + \gamma\sigma_2 J_n + (1 - \rho)(1 - \mu)\gamma I_n,$$

$$\tag{16.74}$$

where I_n denotes infection with strain one, and J_n denotes infection with strain two.

(a) Derive the reproduction numbers of strain one and strain two $\mathscr{R}_1$ and $\mathscr{R}_2$. Set $\mathscr{R}_0 = \max\{\mathscr{R}_1, \mathscr{R}_2\}$.

(b) Use the Jury conditions to show that if $\mathscr{R}_0 < 1$, then the disease-free equilibrium is locally asymptotically stable. If $\mathscr{R}_0 > 1$, then the disease-free equilibrium is unstable.

(c) Show that if $\mathscr{R}_1 > 1$, there is a unique endemic equilibrium corresponding to strain one. Show that there is a unique coexistence equilibrium.

(d) Consider the stability of the endemic equilibrium corresponding to strain one. When is it stable?