

Chapter 3

The SIR Model with Demography: General Properties of Planar Systems

3.1 Modeling Changing Populations

Models that do not explicitly include births and deaths occurring in the population are called *epidemic models without explicit demography*. They are useful for epidemic modeling on a short time scale, particularly for modeling epidemic outbreaks such as influenza. Omitting population change requires that the disease develop on a much shorter time scale than the period in which significant change in the population size can occur (such as births and deaths). This is valid for *fast* diseases like the childhood diseases and influenza. On the other hand, there are *slow* diseases, such as HIV, tuberculosis, and hepatitis C, that develop for a long period of time even on an individual level. In this case, the total population does not remain constant for long periods of time, and the demography of the population cannot be ignored.

To incorporate the population change in epidemic models, we need population models of the growth of the human population. There are several classical population models that are typically considered in the literature.

Population growth is the rate of change in a population over time, and it can be approximated as the change in the number of individuals of any species in a population per unit time. The study of growth and change of human populations is called *demography*. Modeling and projecting the growth of human populations is in general not a simple matter, but for the purposes of epidemic modeling, we will use several simple population models.

3.1.1 The Malthusian Model

The **Malthusian model**, sometimes called the exponential model, is essentially an exponential growth model based on the assumption that the rate of change of a population is proportional to the total population size. The model is named after the Reverend Thomas Malthus (1766–1834), who authored *An Essay on*

the Principle of Population, one of the earliest and most influential books on populations. The Malthusian model is based on the following assumptions: (1) All individuals are identical, that is, they are not classified by age, sex, or other characteristics. (2) The environment is constant in space and time, in particular, resources are unlimited. With these assumptions, if $N(t)$ is the total population size, and b is the per capita birth rate, while μ is the per capita death rate, then the Malthusian model becomes

$$N'(t) = bN(t) - \mu N(t) = rN(t), \quad (3.1)$$

where $r = b - \mu$ is the population growth rate. The solution to this equation is an exponential $N(t) = N(0)e^{rt}$. The population is growing exponentially if $r > 0$, decreasing exponentially if $r < 0$, and constant if $r = 0$.

We compare the performance of population models with world population data. Table 3.1 gives the world's human population since 1950.

Table 3.1 World population size 1950–2010^a

Year	Population	Year	Population
1950	2,556,505,579	1980	4,452,686,744
1952	2,635,724,824	1982	4,615,366,900
1954	2,729,267,486	1984	4,776,577,665
1956	2,834,435,383	1986	4,941,825,082
1958	2,947,380,005	1988	5,114,949,044
1960	3,042,389,609	1990	5,288,828,246
1962	3,139,645,212	1992	5,456,405,468
1964	3,280,890,090	1994	5,619,031,095
1966	3,420,438,740	1996	5,779,990,768
1968	3,562,227,755	1998	5,935,741,324
1970	3,712,813,618	2000	6,088,683,554
1972	3,867,163,052	2002	6,241,717,680
1974	4,017,615,739	2004	6,393,120,940
1976	4,161,423,905	2006	6,545,884,439
1978	4,305,496,751	2008	6,700,765,879
–	–	2010	6,853,019,414

^a Data taken from <http://www.census.gov/ipc/www/idb/worldpop.php>

With the simple population models in this section, many methods for estimating the parameters can work. One of the most powerful methods, however, is **calibration** or **curve fitting**. Curve fitting is the process of identifying the parameters of a curve, or mathematical function, that has the best fit to a series of data points. We discuss more thoroughly fitting epidemic models to data in Chap. 6. Here we only compare the population models with the available data.

Calibration is greatly expedited through the use of software such as Mathematica, Matlab, or R to fit the model to the data. For the Malthusian model, we have an explicit solution, and we can fit the solution function to the data. Since the initial condition for the data is not at zero, the solution to the Malthus model becomes $N(t) = Ae^{r(t-1950)}$. We fit both A and r . Fitting in Mathematica can be done with the

command `NonlinearModelFit`. The result of the fit of the world population data to the Malthusian model is given in Fig. 3.1, where the population is taken in millions.

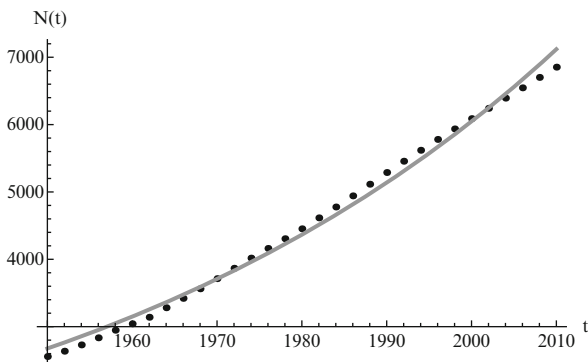


Fig. 3.1 World population data alongside Malthusian model predictions. The estimated values of the parameters are $A = 2676.29$ and $r = 0.0163$. The least-squares error of the fit is $E = 402,533$

3.1.2 The Logistic Model as a Model of Population Growth

The Malthus model assumes that the population's per capita growth rate is constant and that the population has unlimited resources by which to grow. In most cases, however, populations live in an environment that has a finite capacity to support only a certain population size. When the population size approaches this capacity, the per capita growth rate declines or becomes negative. This property of the environment to limit population growth is captured by the logistic model. The logistic model was developed by the Belgian mathematician Pierre Verhulst (1838), who suggested that the per capita growth rate of the population may be a decreasing function of population density:

$$\frac{1}{N(t)}N'(t) = r \left(1 - \frac{N}{K} \right),$$

which gives the classical logistic model that we studied in Chap. 2. At low densities $N(t) \approx 0$, the population growth rate is maximal and equals r . The parameter r can be interpreted as the population growth rate in the absence of intraspecific competition. The population growth rate declines with population number N and reaches 0 when $N = K$. The parameter K is the upper limit of population growth, and it is called the **carrying capacity** of the environment. It is usually interpreted as the quantity of resources expressed in the number of organisms that can be supported by those resources. If population number exceeds K , then population growth rate becomes negative, and population declines. The logistic model has been used unsuccessfully for the projection of human populations. The main difficulty appears to be determining the carrying capacity of a human population. It is believed that human populations do not have a carrying capacity, and even if they do, that the

carrying capacity is not constant. For those reasons, the logistic model is rarely used to model human populations. However, when compared to population data, the logistic equation usually performs admirably in modeling the data for short periods of time. We use the logistic model to model the world population data. The results are given in Fig. 3.2.

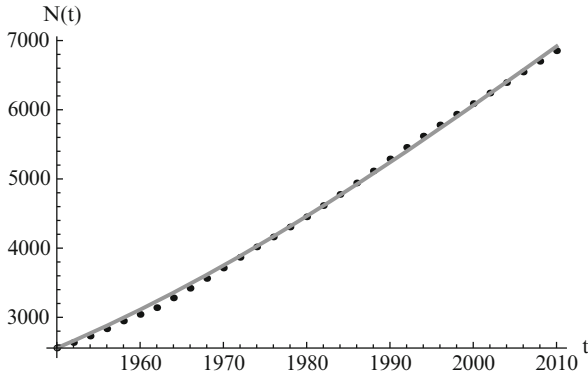


Fig. 3.2 World population data alongside logistic model predictions. The estimated values of the parameters are $K = 13,863.9$ and $r = 0.0247$. The least-squares error of the fit is $E = 56,659.3$

3.1.3 A Simplified Logistic Model

The third model of population growth is a simplified version of the logistic model. It assumes constant birth rate, independent of population size. It also assumes constant per capita death rate. The model becomes

$$N'(t) = \Lambda - \mu N.$$

Here Λ is the total birth rate, and μ is the per capita natural death rate. Then μN is the total death rate. This model can be solved. The solution is

$$N(t) = N_0 e^{-\mu t} + \frac{\Lambda}{\mu} (1 - e^{-\mu t}).$$

It is not hard to see that if $t \rightarrow \infty$, then $N(t) \rightarrow \frac{\Lambda}{\mu}$. This limit quantity is called the limit population size. The simplified logistic model is the one most often used to model population dynamics in epidemic models. However, its performance with data is modest. We illustrate how the simplified logistic model fits the world population data in Fig. 3.3. We saw in Chap. 2 that if T is the time spent in a class (or a compartment), then the per capita rate at which the individuals leave that class (compartment) is given by $\frac{1}{T}$. So if the per capita recovery rate was α , then

$$\alpha = \frac{1}{T},$$

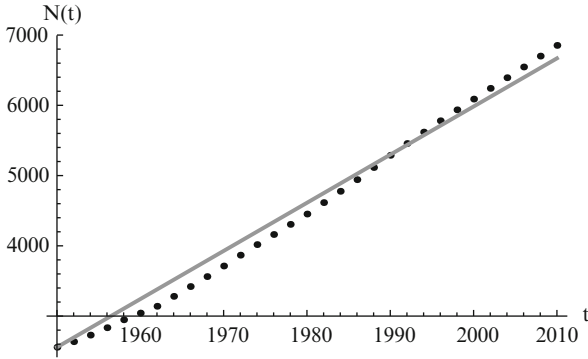


Fig. 3.3 World population data alongside the simplified logistic model predictions. The estimated values of the parameters are $\mu = 5.54 \times 10^{-12}$ and $\Lambda = 68.5$, and we have preset $N(1950) = 2556.5$. The least-squares error of the fit is $E = 703,482$

or equivalently, $\frac{1}{\alpha}$ is the time spent in the infectious compartment. Similar reasoning can be applied to the compartment “life.” If μ is the natural death rate, then $1/\mu$ should be the average lifespan of an individual human being. From fitting the simplified logistic model to world data, we estimated $\mu = 5.54 \times 10^{-12}$, which gives a lifespan of 1.8×10^{11} years—quite unrealistic. If the lifespan is limited to biologically realistic values, such as a lifespan of 65 years, then the fit becomes worse.

3.2 The SIR Model with Demography

To incorporate the demographics into the SIR epidemic model, we assume that all individuals are born susceptible. Individuals from each class die at a per capita death rate μ , so the total death rate in the susceptible class is μS , while in the infective class, it is μI , and in the removed class, it is μR . The epidemic model with demography becomes

$$\begin{aligned} S'(t) &= \Lambda - \beta IS - \mu S, \\ I'(t) &= \beta IS - \alpha I - \mu I, \\ R'(t) &= \alpha I - \mu R. \end{aligned} \tag{3.2}$$

We add the three equations to obtain the total population. The model of the total population is $N'(t) = \Lambda - \mu N$, where $N = S + I + R$. The population size is not constant, but it is asymptotically constant, since $N(t) \rightarrow \frac{\Lambda}{\mu}$ as $t \rightarrow \infty$.

When the population is nonconstant and the incidence is proportional to the product of I and S , we say that the incidence is given by the **law of mass action**, analogously to terms from chemical kinetic models, whereby chemicals react by bumping randomly into each other. For this reason, this incidence is called the **mass action incidence**:

$$\text{mass action incidence} = \beta SI.$$

Another type of incidence that is very commonly used in epidemic models is the **standard incidence**. It is similar to the mass action incidence, but it is normalized by the total population size. In particular,

$$\text{standard incidence} = \frac{\beta SI}{N}.$$

The mass action incidence and the standard incidence agree when the total population size is a constant, but they differ if the total population size is variable. Mass action incidence is used in diseases for which disease-relevant contact increases with an increase in the population size. For instance, in influenza and SARS, contacts increase as the population size (and density) increase. Standard incidence is used for diseases for which the contact rate cannot increase indefinitely and is limited even if the population size increases. This is the case in sexually transmitted diseases, where the number of contacts cannot increase indefinitely.

We notice as before that the first two equations in (3.2) are independent of the third, and we consider the two-dimensional system

$$\begin{aligned} S'(t) &= \Lambda - \beta IS - \mu S, \\ I'(t) &= \beta IS - \alpha I - \mu I, \end{aligned} \quad (3.3)$$

where $R = N - S - I$. Mathematically, the SIR system can be written in the general form

$$\begin{aligned} S'(t) &= f(S, I), \\ I'(t) &= g(S, I). \end{aligned} \quad (3.4)$$

This is a system of differential equations with two equations and the two unknowns S and I . The incidence term makes both f and g nonlinear functions. So system (3.4) is a nonlinear system of differential equations. System (3.4) is also **autonomous**, since f and g do not depend explicitly on the time variable; that is, the coefficients of system (3.3) are constants and not functions of time.

What are the units of the quantities in this model? Since S is measured in number of people, it follows that S' is measured in number of people per unit of time. The total birth rate Λ is measured in number of people born per unit of time. The per capita death rate μ is measured in $[\text{unit of time}]^{-1}$. Thus, μS is measured again in number of people per unit of time. The most difficult term is βIS . Since the force of infection βI is a per capita rate, it has units $[\text{time}]^{-1}$. Consequently, the transmission coefficient β must have units of $[\text{number of people} \times \text{time}]^{-1}$.

A customary transformation of the system (3.3) that simplifies the system and reduces the number of parameters is often performed. There is a simplification that consists in a change of variables that transforms both the independent variable and the dependent variables into nondimensional quantities. Hence, we say that we have transformed the system into a **nondimensional form**.

Two parameters have units [unit of time]⁻¹: α and μ . Since t is in [unit of time], we have to multiply t by one of the rates to obtain a unitless quantity. It is best to define $\tau = (\alpha + \mu)t$. Observe that τ is a dimensionless quantity. Because of the nature of the change, this change will remove the parameter multiplying I . Let $N(t) = N(\frac{\tau}{\alpha + \mu}) = \hat{N}(\tau)$. Similarly, $I(t) = \hat{I}(\tau)$. By the chain rule, we have

$$\begin{aligned}\frac{d\hat{S}}{d\tau} &= \frac{1}{\alpha + \mu} \frac{dS}{dt}, \\ \frac{d\hat{I}}{d\tau} &= \frac{1}{\alpha + \mu} \frac{dI}{dt}.\end{aligned}\tag{3.5}$$

We rescale the \hat{S} and \hat{I} variables with the total limiting population size. Hence $x(t) = \frac{\mu\hat{S}}{\Lambda}$ and $y(t) = \frac{\mu\hat{I}}{\Lambda}$. The new dependent variables $x(\tau)$ and $y(\tau)$ are also dimensionless quantities. The system for them becomes

$$\begin{aligned}x' &= \rho(1 - x) - \mathcal{R}_0xy, \\ y' &= (\mathcal{R}_0x - 1)y,\end{aligned}\tag{3.6}$$

where

$$\rho = \mu/(\alpha + \mu) \qquad \mathcal{R}_0 = \frac{\Lambda\beta}{\mu(\alpha + \mu)}$$

are both dimensionless parameters. The notation \mathcal{R}_0 is not random. As we will see later, this dimensionless quantity is indeed the reproduction number. Notice that we have reduced the number of parameters from five to two. The dimensionless form of the SIR model with demography is equivalent to the original one, since the solutions of both systems have the same long-term behavior.

3.3 Analysis of Two-Dimensional Systems

We cannot solve the SIR model with demography analytically, but we can obtain some information about the behavior of the solutions. The long-term behavior of the solutions is particularly important from an epidemiological perspective, since we would like to know what will happen to the disease in the long run: will it die out, or will it establish itself in the population and become *endemic*?

3.3.1 Phase-Plane Analysis

We write the system (3.6) in general form

$$\begin{aligned}x' &= f(x, y), \\y' &= g(x, y),\end{aligned}\tag{3.7}$$

where $f(x, y) = \rho(1 - x) - \mathcal{R}_0xy$ and $g(x, y) = (\mathcal{R}_0x - 1)y$. To answer the question above, we have to investigate the long-term behavior of the solutions. Instead of considering $x(\tau)$ and $y(\tau)$ as functions of τ , or equivalently, $S(t)$ and $I(t)$ as functions of t , we treat τ as a parameter and consider the curves in the (x, y) -plane, obtained from the points $(x(\tau), y(\tau))$ as τ varies as a parameter. By considering the solution curves in the (x, y) -plane, we say that we are considering the **phase plane**.

Definition 3.1. Curves in the phase plane representing the functional relation between x and y , with τ as a parameter, are called *orbits* or *trajectories*.

The long-term behavior of the trajectories depends largely on the **equilibrium points**, that is, on time-independent solutions of the system. Equilibrium points are solutions for which $x' = 0$ and $y' = 0$.

Definition 3.2. All points (x^*, y^*) , where x^* and y^* are constants that satisfy the system

$$\begin{aligned}f(x^*, y^*) &= 0, \\g(x^*, y^*) &= 0,\end{aligned}\tag{3.8}$$

are called *equilibria* or *singular points*.

For the dimensionless SIR model with demography, we have

$$\begin{aligned}\rho(1 - x) - \mathcal{R}_0xy &= 0, \\(\mathcal{R}_0x - 1)y &= 0.\end{aligned}\tag{3.9}$$

We have that if $y = 0$, that is, there are no infectives, then $x = 1$; that is, everyone is susceptible. This gives the first equilibrium in the (x, y) -plane, $(1, 0)$. This is the disease-free equilibrium. The disease-free equilibrium is also a **boundary equilibrium**, since it lies on the boundary of the feasible region $x \geq 0$, $y \geq 0$. If $y \neq 0$, then from the second equation, we have $x = 1/\mathcal{R}_0$. From the first equation, we have $y = \rho(1 - 1/\mathcal{R}_0)$. Thus the second equilibrium is the point

$$\mathcal{E} = \left(\frac{1}{\mathcal{R}_0}, \rho \left(1 - \frac{1}{\mathcal{R}_0} \right) \right).$$

This is the endemic equilibrium. The endemic equilibrium exists only in the case $\mathcal{R}_0 > 1$. This equilibrium is also called an **interior equilibrium**.

System (3.6) allows us to compute the slope at each point of a trajectory in the (x, y) -plane. The parameter τ can be eliminated by dividing the equations in system (3.6):

$$\frac{dy}{dx} = \frac{g(x, y)}{f(x, y)}.$$

This quotient is defined for all points in the (x, y) -plane except the equilibria. For any nonequilibrium point (x_0, y_0) in the phase plane, we can compute the expression

$$\left. \frac{dy}{dx} \right|_{(x_0, y_0)} = \frac{g(x, y)}{f(x, y)}$$

which gives the slope of the trajectory in the (x, y) -plane, with tangent vector

$$(f(x_0, y_0), g(x_0, y_0))^T.$$

This vector also gives the direction of the trajectory. The tangent vector is not defined at the equilibria, since the flow stops at those points and they are fixed points.

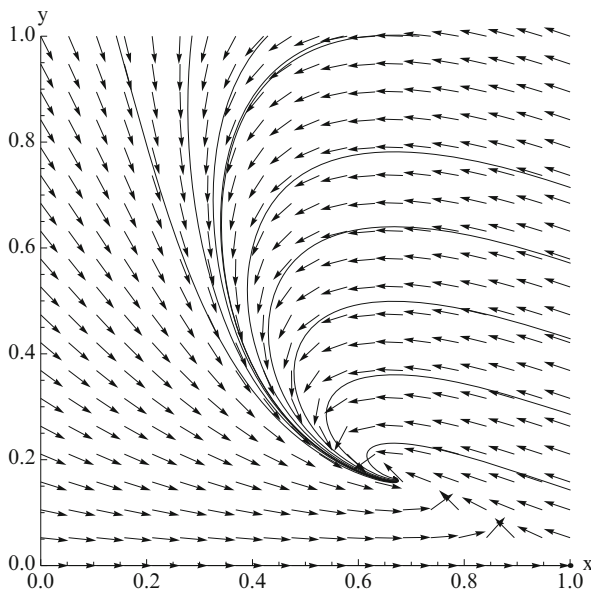


Fig. 3.4 The vector field of the dimensionless SIR model alongside solutions of the model for several initial conditions

The collection of tangent vectors defines a **direction field**. The direction field can be used as a visual aid in sketching a family of solutions called a **phase-plane portrait** or a **phase-plane diagram**. A phase-plane portrait of the dimensionless SIR model is given in Fig 3.4. The creation of the whole phase portrait is a tedious

job and is done only by computer. An easier method to obtain information about the direction of the flow is to analyze the direction of the flow along the x -zero and y -zero isoclines, or nullclines.

Definition 3.3. The x -zero isocline or x -nullcline for the system (3.7) is the set of all points in the (x, y) -plane satisfying

$$f(x, y) = 0.$$

The y -zero isocline or y -nullcline for the system (3.7) is the set of all points in the (x, y) -plane satisfying

$$g(x, y) = 0.$$

We can determine the nullclines for the dimensionless SIR model. Setting $\rho(1-x) - \mathcal{R}_0xy = 0$ gives the x -nullcline

$$y = \frac{\rho}{\mathcal{R}_0} \frac{1-x}{x}.$$

Setting $(\mathcal{R}_0x - 1)y = 0$ gives two y -nullclines: $y = 0$, which is the x -axis, and the vertical line $x = \frac{1}{\mathcal{R}_0}$. The points where an x -nullcline intersects a y -nullcline give the equilibrium points of the system. There are two scenarios for the SIR dimensionless system.

$\mathcal{R}_0 < 1$ In this case, there is only one intersection of an x -nullcline and a y -nullcline. The x -nullcline intersects the y -nullcline $y = 0$ at the point $(1, 0)$, the disease-free equilibrium. Since $1/\mathcal{R}_0 > 1$, the y -nullcline $x = 1/\mathcal{R}_0$ does not intersect the x -nullcline in the positive quadrant.

$\mathcal{R}_0 > 1$ In this case, there are two intersections of an x -nullcline and a y -nullcline. In the first intersection, the x -nullcline intersects the y -nullcline $y = 0$ at the point $(1, 0)$, which represents the disease-free equilibrium. In the second intersection, since $1/\mathcal{R}_0 < 1$, the y -nullcline $x = 1/\mathcal{R}_0$ intersects the x -nullcline $1/\mathcal{R}_0 < 1$ at the point \mathcal{E} , which gives the endemic equilibrium.

To determine the direction of the vector field along the nullclines, we can use the following general rules:

1. On the x -nullclines, the tangent vector is

$$(0, g(x_0, y_0))^T$$

and is parallel to the y -axis. The direction of the tangent is given by the sign of $g(x_0, y_0)$. If $g(x_0, y_0) > 0$, the direction vector points upward. If $g(x_0, y_0) < 0$, the directional vector points downward.

2. On the y -nullclines, the tangent vector is

$$(f(x_0, y_0), 0)^T$$

and is parallel to the x -axis. The direction of the tangent vector is determined by the sign of $f(x_0, y_0)$. If $f(x_0, y_0) > 0$, the direction vector points to the right. If $f(x_0, y_0) < 0$, the direction vector points to the left.

We determine the direction field along nullclines for the dimensionless SIR model. We consider the case $\mathcal{R}_0 > 1$. The case $\mathcal{R}_0 < 1$ is similar. The results are illustrated in Fig. 3.5.

1. On the x -nullcline, the tangent vector is $(0, g(x_0, y_0))^T$, where (x_0, y_0) is a point on the nullcline. The tangent vector is parallel to the y -axis. Since $g(x_0, y_0) = (\mathcal{R}_0 x_0 - 1)y_0$ and $y_0 > 0$, the sign of $g(x_0, y_0)$ is determined by the first term in the product. Thus, if $x_0 < 1/\mathcal{R}_0$, then $g(x_0, y_0) < 0$, and the vector points downward. If $x_0 > 1/\mathcal{R}_0$, then $g(x_0, y_0) > 0$, and the vector points upward.
2. On the y -nullclines, the tangent vector is $(f(x_0, y_0), 0)^T$, where (x_0, y_0) is a point on a y -nullcline. The tangent vector is parallel to the x -axis. Since there are two y -nullclines, we consider two cases:

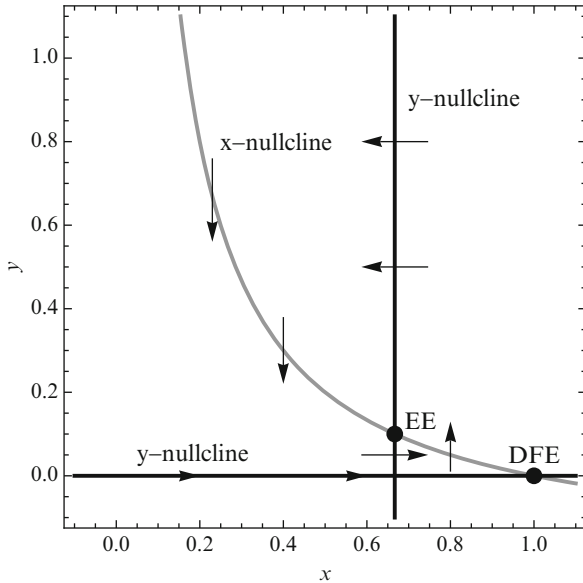


Fig. 3.5 Phase-plane analysis of the dimensionless SIR model. Nullclines and the direction of the vector field along them

$y = 0$ On the nullcline $y = 0$, $f(x_0, y_0) = \rho(1 - x_0)$. We have $f(x_0, y_0) > 0$ if $x_0 < 1$, and the tangent vector points to the right. Furthermore, we have $f(x_0, y_0) < 0$ if $x_0 > 1$, and the tangent vector points to the left.

$x = \frac{1}{\mathcal{R}_0}$ On the y -nullcline $x = \frac{1}{\mathcal{R}_0}$, we have $f(x_0, y_0) = \rho \left(1 - \frac{1}{\mathcal{R}_0}\right) - y_0$. We have that $y_0 > \rho \left(1 - \frac{1}{\mathcal{R}_0}\right)$ if the point (x_0, y_0) is on the y -nullcline

above the intersection of the y -nullcline with the x -nullcline. Hence, $f(x_0, y_0) < 0$, and the tangent vector points to the left. Furthermore, we have that $y_0 < \rho \left(1 - \frac{1}{\mathcal{R}_0}\right)$ if the point (x_0, y_0) is on the y -nullcline below the intersection of the y -nullcline with the x -nullcline. Hence, $f(x_0, y_0) > 0$, and the tangent vector points to the right.

3.3.2 Linearization

Just as with first-order nonlinear equations, we can obtain information about the behavior of the solutions near an equilibrium through *linearization*. If (x^*, y^*) is an equilibrium, we consider the perturbation of a solution starting from an initial condition close to the equilibrium:

$$u(\tau) = x(\tau) - x^* \quad v(\tau) = y(\tau) - y^*.$$

We note again that $u(\tau)$ and $v(\tau)$ are functions of τ but are not necessarily nonnegative. Writing $x(\tau) = u(\tau) + x^*$, $y(\tau) = v(\tau) + y^*$, and substituting in the original system, we obtain

$$\begin{aligned} u' &= f(u + x^*, v + y^*), \\ v' &= g(u + x^*, v + y^*). \end{aligned} \tag{3.10}$$

Assuming that f and g have at least second-order continuous partial derivatives, we expand in a Taylor series using the theorem for functions of two variables. We show that expansion for f ; the process for g is the same.

$$\begin{aligned} f(u + x^*, v + y^*) &= f(x^*, y^*) + f_x(x^*, y^*)u(\tau) + f_y(x^*, y^*)v(\tau) \\ &\quad + f_{xx}(x^*, y^*)u^2(\tau)/2 + f_{xy}(x^*, y^*)u(\tau)v(\tau) \\ &\quad + f_{yy}(x^*, y^*)v^2(\tau)/2 + \dots \end{aligned} \tag{3.11}$$

The terms with the second partial derivatives are multiplied by u^2 , uv , and v^2 , all second-order terms in the perturbations. If the perturbations are small, $u \approx 0$ and $v \approx 0$, then the second-order terms are even smaller, so we may ignore them. Thus,

$$\begin{aligned} u' &\approx f(x^*, y^*) + f_x(x^*, y^*)u(\tau) + f_y(x^*, y^*)v(\tau), \\ v' &\approx g(x^*, y^*) + g_x(x^*, y^*)u(\tau) + g_y(x^*, y^*)v(\tau). \end{aligned} \tag{3.12}$$

Since (x^*, y^*) is an equilibrium, $f(x^*, y^*) = 0$ and $g(x^*, y^*) = 0$. We obtain the **linearized system**

$$\begin{aligned} u' &= f_x(x^*, y^*)u(\tau) + f_y(x^*, y^*)v(\tau), \\ v' &= g_x(x^*, y^*)u(\tau) + g_y(x^*, y^*)v(\tau). \end{aligned} \tag{3.13}$$

The matrix of the partial derivatives of the functions $f(x, y)$ and $g(x, y)$ is called the Jacobian matrix. The matrix of the system above is the Jacobian matrix evaluated at an equilibrium (x^*, y^*) . All entries of this matrix are given constants:

$$J = \begin{pmatrix} f_x(x, y) & f_y(x, y) \\ g_x(x, y) & g_y(x, y) \end{pmatrix} \Big|_{x=x^*, y=y^*} \quad (3.14)$$

An important result, called the **Hartman–Grobman theorem** justifies drawing conclusions about a nonlinear system from studying the linearized system. The Hartman–Grobman theorem says roughly that the solutions of an $n \times n$ autonomous system of ordinary differential equations in a neighborhood of a steady state look “qualitatively” just like the solutions of the linearized system (3.13) near the point $(0, 0)$. This result holds only when the equilibrium is a **hyperbolic equilibrium**, that is, when none of the eigenvalues of J have zero real part.

3.3.3 Two-Dimensional Linear Systems

The linearized system (3.13) can be written in the form

$$\begin{aligned} u' &= au(\tau) + bv(\tau), \\ v' &= cu(\tau) + dv(\tau), \end{aligned} \quad (3.15)$$

where a, b, c, d are given constants. The system (3.15) is a two-dimensional linear homogeneous system. The behavior of solutions of such systems has been completely studied. In this subsection, we review what is known about two-dimensional linear systems. The equilibria of linear two-dimensional systems are solutions to the linear system of equations

$$\begin{aligned} au(\tau) + bv(\tau) &= 0, \\ cu(\tau) + dv(\tau) &= 0. \end{aligned} \quad (3.16)$$

Such systems always have $(0, 0)$ as a solution. The equilibrium $(0, 0)$ is the only equilibrium if the matrix

$$A = \begin{pmatrix} a & b \\ c & d \end{pmatrix} \quad (3.17)$$

of the system is invertible, that is, $\text{Det}A \neq 0$. We will assume that this condition holds, because if it doesn't, there is a continuum of equilibria. Thus, we assume that $ad - bc \neq 0$. If the matrix A is obtained from the linearization and is the Jacobian evaluated at an equilibrium (x^*, y^*) , the condition $\text{Det}J \neq 0$ means that the equilibrium is **isolated**; that is, there is a disk around it that does not contain other equilibria. Looking for exponential solutions of the linearized system (3.15), we set

$$u(\tau) = \bar{u}e^{\lambda\tau} \quad v(\tau) = \bar{v}e^{\lambda\tau},$$

where \bar{u} and \bar{v} are nonzero constants. Substituting in the system and canceling $e^{\lambda\tau}$, we obtain the following system for \bar{u} and \bar{v} :

$$\begin{aligned} a\bar{u} + b\bar{v} &= \lambda\bar{u}, \\ c\bar{u} + d\bar{v} &= \lambda\bar{v}. \end{aligned} \quad (3.18)$$

This is a linear homogeneous system for \bar{u} and \bar{v} . We want this system to have a nonzero solution, since our perturbations should be nonzero. This can happen only if the determinant of the system is zero, so we have

$$\begin{vmatrix} a - \lambda & b \\ c & d - \lambda \end{vmatrix} = 0. \quad (3.19)$$

By expanding the determinant $(a - \lambda)(d - \lambda) - bc = 0$, we obtain the **characteristic equation** of the linearized system:

$$\lambda^2 - p\lambda + q = 0, \quad (3.20)$$

where $p = a + d = \text{Tr}J$, and $q = ad - bc = \text{Det}J$. Thus p is the trace and q is the determinant of the Jacobian matrix. The solutions of the characteristic equation are called the **eigenvalues** of the Jacobian matrix. The main question that we address is when the perturbations u and v approach zero, in which case the equilibrium (x^*, y^*) will be locally asymptotically stable. Given the eigenvalues, we have three cases for the solution of the system of perturbations (3.15).

Case 1 The eigenvalues of the Jacobian are real and distinct, say λ_1 and λ_2 . In this case, the solution of the system (3.15) is given by

$$\begin{aligned} u(\tau) &= C_1 e^{\lambda_1 \tau} + C_2 e^{\lambda_2 \tau}, \\ v(\tau) &= C_3 e^{\lambda_1 \tau} + C_4 e^{\lambda_2 \tau}, \end{aligned} \quad (3.21)$$

where C_1, \dots, C_4 are arbitrary constants. Clearly, in this case, $u \rightarrow 0$ and $v \rightarrow 0$ if and only if $\lambda_1 < 0$ and $\lambda_2 < 0$.

Case 2 The eigenvalues of the Jacobian are real and equal, say λ . In this case, the solution of the system (3.15) is given by

$$\begin{aligned} u(\tau) &= C_1 e^{\lambda \tau} + C_2 \tau e^{\lambda \tau}, \\ v(\tau) &= C_3 e^{\lambda \tau} + C_4 \tau e^{\lambda \tau}, \end{aligned} \quad (3.22)$$

where C_1, \dots, C_4 are arbitrary constants. Clearly, in this case, $u \rightarrow 0$ and $v \rightarrow 0$ if and only if $\lambda < 0$.

Case 3 The eigenvalues of the Jacobian are complex conjugates, say $\lambda_1 = \xi + \eta i$ and $\lambda_2 = \xi - \eta i$. In this case, the real solution of the system (3.15) is given by

$$\begin{aligned} u(\tau) &= C_1 e^{\xi \tau} \sin \eta \tau + C_2 e^{\xi \tau} \cos \eta \tau, \\ v(\tau) &= C_3 e^{\xi \tau} \sin \eta \tau + C_4 e^{\xi \tau} \cos \eta \tau, \end{aligned} \quad (3.23)$$

where C_1, \dots, C_4 are arbitrary constants. Clearly, in this case, $u \rightarrow 0$ and $v \rightarrow 0$ if and only if $\xi < 0$; that is, the eigenvalues have negative real part.

We summarize this result in the following widely used theorem.

Theorem 3.1. *A necessary and sufficient condition for an equilibrium to be locally asymptotically stable is that all eigenvalues of the Jacobian have negative real part.*

For two-dimensional systems, there is a simple necessary and sufficient condition that all eigenvalues of a matrix have negative real part.

Theorem 3.2. *Assume that J is a 2×2 matrix with constant entries and $\text{Det}J \neq 0$. Assume that J has been obtained as a linearization around the equilibrium (x^*, y^*) . Then the equilibrium (x^*, y^*) is locally asymptotically stable if and only if*

$$\text{Tr}J < 0 \quad \text{and} \quad \text{Det}J > 0.$$

The equilibrium (x^, y^*) is unstable if and only if*

$$\text{Tr}J > 0 \quad \text{or} \quad \text{Det}J < 0.$$

Remark 3.1. The asymptotic stability of the equilibrium (x^*, y^*) of the nonlinear system is equivalent to the asymptotic stability of the $(0, 0)$ equilibrium of the linear system obtained from the linearization around the equilibrium (x^*, y^*) . The only exception occurs when $\text{Tr}J = 0$ and $\text{Det}J > 0$. In this case, the characteristic equation has eigenvalues with zero real part. Consequently, the $(0, 0)$ equilibrium of the linear system may be stable, but there are no implications for the stability of the (x^*, y^*) equilibrium of the nonlinear system.

The origin of a two-dimensional linear system can be classified as one of four types: **node**, **spiral**, **saddle**, or **center**. In addition, the origin can be classified as stable or unstable. This classification depends on whether the eigenvalues are real or complex, positive or negative when real, or with positive or negative real part when complex. We have the following cases:

- Node** The origin is said to be a *node* if the eigenvalues are real and of the same sign. If the two eigenvalues are negative, the node is a **stable node**. If both eigenvalues are positive, the node is an **unstable node**. If the eigenvalues are real and equal, the node that corresponds to them is called **degenerate**. If two eigenvectors correspond to the double eigenvalue, the degenerate node is called **proper**. If only one eigenvector corresponds to the double eigenvalue, the degenerate node is called **improper**.
- Saddle** The origin is a saddle if the eigenvalues are real and of opposite sign. A saddle is always unstable.
- Spiral** The origin is a spiral (or focus) if the eigenvalues are complex with nonzero real part. If the real part is negative, the focus is a **stable focus**; if the real part is positive, the focus is an **unstable focus**.

Center The origin is a center if the eigenvalues are complex with zero real part (purely imaginary). In this case, every orbit is periodic. The center is stable but not asymptotically.

The type of the equilibrium can be inferred from the coefficients of the characteristic equation (3.20). See Table 3.2.

Table 3.2 Relations between the coefficients of the characteristic equation and the type of the equilibrium

Coefficients	Trace and determinant	Type
$q < 0$	$\text{Det}J < 0$	Saddle (unstable)
$q > 0, p < 0, \Delta = p^2 - 4q \geq 0$	$\text{Det}J > 0, \text{Tr} J < 0$	Stable node
$q > 0, p < 0, \Delta = p^2 - 4q < 0$	$\text{Det}J > 0, \text{Tr} J < 0$	Stable focus
$q > 0, p > 0, \Delta = p^2 - 4q \geq 0$	$\text{Det}J > 0, \text{Tr} J > 0$	Unstable node
$q > 0, p > 0, \Delta = p^2 - 4q < 0$	$\text{Det}J > 0, \text{Tr} J > 0$	Unstable focus
$q > 0, p = 0$	$\text{Det}J > 0, \text{Tr} J = 0$	Center

3.4 Analysis of the Dimensionless SIR Model

We saw that the dimensionless SIR model (3.6) has two equilibria. The disease-free equilibrium $(1, 0)$ always exists, while the endemic equilibrium \mathcal{E} exists only if $\mathcal{R}_0 > 1$.

3.4.1 Local Stability of the Equilibria of the SIR Model

The local stability of equilibria is determined by the eigenvalues of the Jacobian computed at that equilibrium. The Jacobian of the dimensionless SIR model at an equilibrium (x^*, y^*) is

$$J = \begin{pmatrix} -\rho - \mathcal{R}_0 y^* & -\mathcal{R}_0 x^* \\ \mathcal{R}_0 y^* & \mathcal{R}_0 x^* - 1 \end{pmatrix}. \quad (3.24)$$

To obtain the stability of the disease-free equilibrium, we evaluate J at $(1, 0)$:

$$J = \begin{pmatrix} -\rho & -\mathcal{R}_0 \\ 0 & \mathcal{R}_0 - 1 \end{pmatrix}. \quad (3.25)$$

The two eigenvalues are $\lambda_1 = -\rho$ and $\lambda_2 = \mathcal{R}_0 - 1$. Since the matrix is upper triangular, the eigenvalues are the diagonal entries of the matrix. The first eigenvalue is clearly negative. The second eigenvalue is negative if $\mathcal{R}_0 < 1$. In this case, the disease-free equilibrium is a stable node. The second eigenvalue λ_2 is positive if $\mathcal{R}_0 > 1$. In this case, the disease-free equilibrium is unstable. It is a saddle.

The next step is to investigate the local stability of the endemic equilibrium. We consider the Jacobian at the endemic equilibrium:

$$J = \begin{pmatrix} -\rho - \mathcal{R}_0 y^* & -\mathcal{R}_0 x^* \\ \mathcal{R}_0 y^* & \mathcal{R}_0 x^* - 1 \end{pmatrix}. \quad (3.26)$$

We notice that from the equilibrium equations we have $\mathcal{R}_0 x^* - 1 = 0$. The Jacobian becomes

$$J = \begin{pmatrix} -\rho - \mathcal{R}_0 y^* & -\mathcal{R}_0 x^* \\ \mathcal{R}_0 y^* & 0 \end{pmatrix}. \quad (3.27)$$

By inspection, the trace of this matrix is negative, $\text{Tr } J = -\rho - \mathcal{R}_0 y^* < 0$. The determinant is given by $\text{Det } J = \mathcal{R}_0^2 x^* y^* > 0$. By Theorem 3.2, the endemic equilibrium is locally asymptotically stable.

To determine the type of the endemic equilibrium, we consider the characteristic equation

$$\begin{vmatrix} -\rho - \mathcal{R}_0 y^* - \lambda & -\mathcal{R}_0 x^* \\ \mathcal{R}_0 y^* & -\lambda \end{vmatrix} = 0. \quad (3.28)$$

Expanding the determinant, we obtain the characteristic equation of the endemic equilibrium:

$$\lambda^2 + (\rho + \mathcal{R}_0 y^*)\lambda + \mathcal{R}_0^2 x^* y^* = 0.$$

Since the endemic equilibrium is explicitly known, we can express the coefficients of the characteristic equation in terms of the parameters of the system:

$$\begin{aligned} \rho + \mathcal{R}_0 y^* &= \rho + \mathcal{R}_0 \rho \left(1 - \frac{1}{\mathcal{R}_0}\right) = \rho \mathcal{R}_0, \\ \mathcal{R}_0^2 x^* y^* &= \mathcal{R}_0^2 \frac{1}{\mathcal{R}_0} \rho \left(1 - \frac{1}{\mathcal{R}_0}\right) = \rho(\mathcal{R}_0 - 1). \end{aligned} \quad (3.29)$$

The characteristic equation becomes

$$\lambda^2 + \rho \mathcal{R}_0 \lambda + \rho(\mathcal{R}_0 - 1) = 0.$$

Hence the roots of the characteristic equation are $\lambda_{1,2} = (-\rho \mathcal{R}_0 \pm \sqrt{\Delta})/2$, where $\Delta = (\rho \mathcal{R}_0)^2 - 4\rho(\mathcal{R}_0 - 1)$. Hence if $\Delta > 0$, the characteristic equation has two negative real roots, and the endemic equilibrium is a stable node. If $\Delta < 0$, then the characteristic equation has two complex conjugate roots with negative real part. The endemic equilibrium in this case is a stable focus. The dependent variables $x(\tau)$ and $y(\tau)$ tend to the endemic equilibrium through damped oscillations (see Fig. 3.6). We can compute an approximate period of the oscillation by noting that the mean infectious period $\frac{1}{\alpha}$ is much shorter than the mean lifespan $\frac{1}{\mu}$. That implies that $\alpha \gg \mu$ and $\rho \approx 0$. Hence ρ^2 is very small and can be neglected. Neglecting the quadratic roots for ρ from the expression for the roots of the characteristic equation, we obtain $\lambda_{1,2} = -\rho \mathcal{R}_0/2 \pm i\sqrt{\rho(\mathcal{R}_0 - 1)} = \xi \pm \eta i$. Then the solutions of the linearized problem are of the form $Ce^{\xi\tau} \cos \eta\tau$, that is, functions that oscillate with

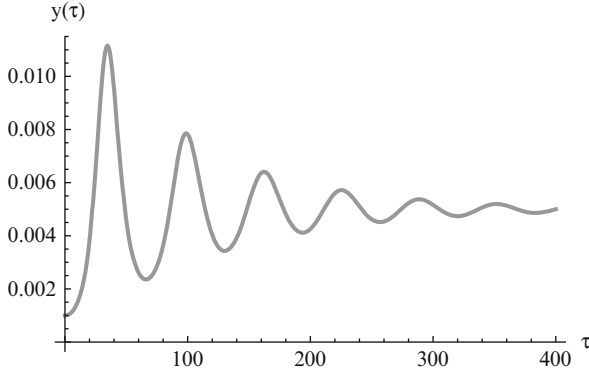


Fig. 3.6 Damped oscillations in the proportion of infectives $x(\tau)$ of the dimensionless SIR model; $\rho = 0.01$, $\mathcal{R}_0 = 2$

decreasing amplitude and approximate period equal to $2\pi/\eta$. Thus, the solution exhibits damped oscillations with period T given by

$$T = \frac{2\pi}{\sqrt{\rho(\mathcal{R}_0 - 1)}}.$$

The following theorem summarizes the results on existence and stability of equilibria of the SIR model with demography.

Theorem 3.3. *Assume $\mathcal{R}_0 < 1$. Then there exists a unique equilibrium, the disease-free equilibrium $(1, 0)$, which is locally stable. If $\mathcal{R}_0 > 1$, there are two equilibria: the disease-free equilibrium $(1, 0)$, which is unstable, and the endemic equilibrium \mathcal{E} , which is locally asymptotically stable.*

3.4.2 The Reproduction Number of the Disease \mathcal{R}_0

The expression for \mathcal{R}_0 in terms of the original parameters of the system is

$$\mathcal{R}_0 = \frac{\beta\Lambda}{\mu(\alpha + \mu)}.$$

The parameter \mathcal{R}_0 is the *reproduction number of the disease*.

Epidemiologically, the reproductive number of the disease tells us how many secondary cases one infected individual will produce in an entirely susceptible population during its period as an infective. Can we see this in the expression that gives \mathcal{R}_0 ?

1. Notice that a population that consists of only susceptible individuals has $\frac{\Lambda}{\mu}$ individuals in the long run.
2. Notice that $\alpha + \mu$ is the rate at which individuals leave the infective class. This means that the average time spent as an infective individual is $\frac{1}{\alpha + \mu}$ time units.

3. The number of transmissions per unit of time is given by the incidence rate βIS . If there is only one infective, $I = 1$, and everybody else is susceptible, $S = \frac{\Lambda}{\mu}$, then the number of transmissions by one infective per unit of time is $\frac{\beta\Lambda}{\mu}$.
4. Thus, the number of transmissions that one infective individual can make during the entire time he/she remains infective if everybody else is susceptible is

$$\frac{\beta\Lambda}{\mu(\alpha + \mu)}.$$

And this is exactly \mathcal{R}_0 .

The reproduction number of the disease has the following threshold role:

1. If $\mathcal{R}_0 < 1$, then there exists only the disease-free equilibrium. It can be shown that it is attractive, so that every solution of the ODE system approaches this equilibrium, and the disease disappears from the population.
2. If $\mathcal{R}_0 > 1$, then there are two equilibria: the disease-free equilibrium and the endemic equilibrium. The disease-free equilibrium is not attractive in the sense that solutions of the ODE system that start very close to it tend to move away. The endemic equilibrium is attractive, so that solutions of the ODE system approach it as time goes to infinity. Thus, in this case, the disease remains endemic in the population.

3.4.3 Forward Bifurcation

The expression for the endemic equilibrium \mathcal{E} shows that the dimensionless quantity corresponding to infective individuals y^* is a function of the disease reproduction number \mathcal{R}_0 . It is customary to plot the infective individuals (or y^*) as a function of \mathcal{R}_0 in the positive (x, y) -plane, where the x -axis is the reproduction number \mathcal{R}_0 , and the y -axis is the equilibrium level of the infective individuals y^* . This produces a bifurcation diagram called a **forward bifurcation diagram**, since the endemic equilibrium bifurcates “forward” and exists only for values of the reproduction number greater than one. We have

$$y^* = \begin{cases} 0 & \text{for all } \mathcal{R}_0 < 1 \\ \rho \left(1 - \frac{1}{\mathcal{R}_0}\right) & \mathcal{R}_0 > 1. \end{cases} \quad (3.30)$$

The plot is given in Fig. 3.7.

We plot the locally stable equilibria with solid lines and the unstable equilibria with dashed lines. Hence, since the disease-free equilibrium $y^* = 0$ is locally asymptotically stable for $\mathcal{R}_0 < 1$, it is plotted with a solid line. The endemic equilibrium is also locally asymptotically stable for $\mathcal{R}_0 > 1$ and is also plotted with a solid line. The disease-free equilibrium is unstable for $\mathcal{R}_0 > 1$, and it is plotted with a dashed line.

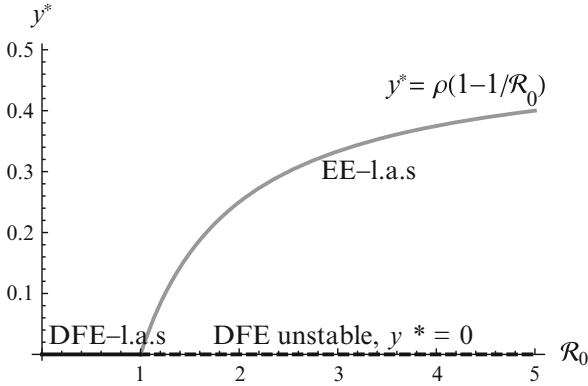


Fig. 3.7 Forward bifurcation diagram with respect to the reproduction number. *Continuous lines* denote stable equilibria. *Dashed lines* denote unstable equilibria

3.5 Global Stability

An equilibrium is called *globally stable* if it is stable for almost all initial conditions, not just those that are close to it. Global stability of an equilibrium cannot always be proved. An equilibrium that is locally stable may be globally stable if there are no other locally stable equilibria coexisting with it. For the SIR model, we have two cases. In the case $\mathcal{R}_0 < 1$, the disease-free equilibrium is the only equilibrium, and it is locally asymptotically stable. It may be expected that it is also globally stable. We establish that in the next subsection. In the case $\mathcal{R}_0 > 1$, the endemic equilibrium is the only locally stable equilibrium, so we may expect that it is also globally stable. We establish that later.

3.5.1 Global Stability of the Disease-Free Equilibrium

Global stability of the disease-free equilibrium can be established for many models, particularly for models for which the disease-free equilibrium is the only equilibrium when $\mathcal{R}_0 < 1$. We note that global stability of the disease-free equilibrium cannot be established for all models. Establishing global stability for the SIR model is perhaps possible through many different techniques. We present one that works well for many models, including partial differential equation models.

Theorem 3.4. *Assume $\mathcal{R}_0 < 1$. Then the disease-free equilibrium is globally stable.*

Proof. Working again with the dimensionless SIR model (3.6), we first notice that if $x(0) > 1$, then $x'(\tau) < 0$, so $x(\tau)$ is a decreasing function if $x > 1$. Assume $\tau_0 > 0$ exists such that $x(\tau_0) = 1$; then $x'(\tau_0) < 1$ and $x(\tau) \leq 1$ for all $\tau \geq \tau_0$. If $x(0) \leq 1$, we may take $\tau_0 = 0$. We consider the equation for $y(\tau)$:

$$y'(\tau) = (\mathcal{R}_0 x - 1)y(\tau). \quad (3.31)$$

For $\tau \geq \tau_0$, we have

$$y'(\tau) \leq (\mathcal{R}_0 - 1)y(\tau).$$

Integrating, we have $y(\tau) = y(\tau_0)e^{(\mathcal{R}_0-1)(\tau-\tau_0)}$. Hence if $\mathcal{R}_0 < 1$, then $\lim_{\tau \rightarrow \infty} y(\tau) = 0$. It is somewhat more cumbersome to see that $x \rightarrow 1$. First, we notice that $\limsup_{\tau \rightarrow \infty} x \leq 1$. We need \limsup , since we do not know that the limit actually exists. From the equation for x , we have

$$x' \leq \rho(1-x),$$

which can be solved in the same way as the corresponding equality would be solved. We have

$$x(\tau) \leq e^{-\rho\tau}x(0) + \rho \int_0^\tau e^{-\rho(\tau-s)} ds.$$

Hence $\limsup_{\tau \rightarrow \infty} x \leq 1$. On the other hand, since $\lim_{\tau \rightarrow \infty} y = 0$, this implies that for every ε , there exists $\tau_0 > 0$ such that $y \leq \varepsilon$ for $\tau > \tau_0$. For these values of τ , we have

$$x' \geq \rho(1-x) - \varepsilon\mathcal{R}_0x.$$

Integrating the inequality, we obtain

$$x(\tau) \geq e^{-(\rho+\varepsilon\mathcal{R}_0)\tau}x(0) + \rho \int_0^\tau e^{-(\rho+\varepsilon\mathcal{R}_0)(\tau-s)} ds.$$

This inequality implies that

$$\liminf_{\tau \rightarrow \infty} x \geq \frac{\rho}{\rho + \varepsilon\mathcal{R}_0}.$$

Since the inequality holds for every ε , this means that $\liminf_{\tau \rightarrow \infty} x \geq 1$. Furthermore, the \liminf and the \limsup are the same, the limit as $\tau \rightarrow \infty$ of x exists, and

$$\lim_{\tau \rightarrow \infty} x = 1.$$

This completes the proof of the global stability of the disease-free equilibrium. \square

3.5.2 Global Stability of the Endemic Equilibrium

We consider again the dimensionless SIR model

$$\begin{aligned} x' &= \rho(1-x) - \mathcal{R}_0xy, \\ y' &= (\mathcal{R}_0x - 1)y. \end{aligned} \tag{3.32}$$

This is a planar system. There is theory developed specifically for planar systems that can facilitate understanding of the solution behavior and the proof of global stability. To introduce the main results of that theory, consider a general planar system

$$\begin{aligned} x' &= f(x, y) & x(0) &= u_1^0, \\ y' &= g(x, y) & y(0) &= u_2^0. \end{aligned} \quad (3.33)$$

Let $u(t) = (x(t), y(t))$ be a solution curve with initial condition $u^0 = (u_1^0, u_2^0)$.

Definition 3.4. The omega limit set of the point u^0 , denoted by $\omega(u^0)$, consists of all points $a \in R^2$ for which there is a sequence t_j , $j = 1, 2, \dots$, such that

$$u(t_j) \rightarrow a \quad t_j \rightarrow \infty.$$

Definition 3.5. A *homoclinic orbit* is a trajectory of a flow of a dynamical system that joins a saddle equilibrium point to itself. A *heteroclinic orbit* (sometimes called a heteroclinic connection) is a path in phase space that joins two different equilibrium points.

A *manifold* is a mathematical space that on a small scale resembles Euclidean space of a specific dimension. For instance, a line and a circle are one-dimensional manifolds, while a plane and a sphere are two-dimensional manifolds.

Definition 3.6. A *separatrix* is a phase curve that meets a hyperbolic equilibrium point or connects the stable and unstable manifolds of a pair of equilibrium points. A separatrix marks a boundary between sectors with phase curves with different properties.

Definition 3.7. A *separatrix cycle* consists of the union of a finite number of equilibria p_j for $j = 1, \dots, m$ and separatrices Γ_j such that the flow on Γ_j is from p_j to p_{j+1} and $p_{m+1} = p_1$.

Definition 3.8. A *compound separatrix cycle* or a *graphic* is the union of a finite number of compatibly oriented separatrix cycles.

The types of omega limit sets for an arbitrary orbit of a planar system is given by the following theorem.

Theorem 3.5 (Poincaré–Bendixson Trichotomy). Assume that $X \subseteq R^2$, where X is an open set, contains only finitely many equilibria. Let $u(t)$ be a solution in X that is defined and bounded on $[0, \infty)$ with $\omega(u^0) \subseteq X$. Then one of the following holds:

1. $\omega(u^0)$ consists of an equilibrium.
2. $\omega(u^0)$ is a periodic orbit.
3. $\omega(u^0)$ a graphic.

Assume that X is the open first quadrant. If $\mathcal{R}_0 > 1$, then the dimensionless SIR model has a unique equilibrium in X , the endemic equilibrium. Hence, the omega limit set of every initial point in X is the endemic equilibrium, a potential periodic orbit, or a graphic. To rule out possible periodic orbits and graphics inside X , one can use the Dulac–Bendixson criterion, which applies to planar systems only.

Theorem 3.6 (Dulac–Bendixson Criterion). *Let $Z \subseteq X$ be open and simply connected. Assume the following:*

1. *The functions f and g are continuously differentiable on Z .*
2. *There exists a function $D : Z \rightarrow \mathbb{R}$, continuously differentiable on Z , such that*

$$\frac{\partial(Df)}{\partial x} + \frac{\partial(Dg)}{\partial y}$$

is either strictly positive almost everywhere on Z or strictly negative almost everywhere on Z .

Then Z contains no periodic orbits or graphics.

Definition 3.9. The function D is called the *Dulac function*.

If $D \equiv 1$, then the Dulac criterion is referred to as the Bendixson criterion.

Theorem 3.7. *Assume $\mathcal{R}_0 > 1$. The system (3.6) has no periodic orbits or graphics in \mathbb{R}_+^2 .*

Proof. We will apply the Dulac–Bendixson criterion. Let $Z = X$ be the open first quadrant. Let $f(x, y) = \rho(1 - x) - \mathcal{R}_0xy$ and $g(x, y) = (\mathcal{R}_0x - 1)y$. Applying the Dulac–Bendixson criterion directly with $D = 1$ gives

$$\frac{\partial f}{\partial x} + \frac{\partial g}{\partial y} = -\rho - \mathcal{R}_0y + \mathcal{R}_0x - 1.$$

This expression has unspecified sign, which potentially may change. The term that disrupts the definiteness of the sign is \mathcal{R}_0x . Thus, we have to “eliminate” this term. This suggests that we use $D(x, y) = 1/y$. We take Z to be the open first quadrant. Then D is continuously differentiable in Z . Furthermore, we have

$$\frac{\partial Df}{\partial x} + \frac{\partial Dg}{\partial y} = -\frac{\rho}{y} - \mathcal{R}_0 < 0.$$

Thus, the system has no periodic orbits or graphics in the open first quadrant. This implies that choices two and three of the Poincaré–Bendixson theorem are ruled out as an option. \square

The next theorem shows the global stability of the endemic equilibrium for system (3.6).

Theorem 3.8. *Assume $\mathcal{R}_0 > 1$. The endemic equilibrium (x^*, y^*) of system (3.6) is globally stable whenever $I(0) > 0$.*

Proof. We apply Poincaré–Bendixson theorem. First, we have to show that all solutions of system (3.6) are bounded. To see this, we add the two equations in (3.6). Set $\hat{\rho} = \min\{\rho, 1\}$. Then

$$x' + y' \leq \rho - \hat{\rho}(x + y).$$

Hence,

$$x + y \leq \kappa e^{-\hat{\rho}t} + \frac{\rho}{\hat{\rho}}(1 - e^{-\hat{\rho}t}),$$

where κ is the value of the initial condition. We obtain that

$$\limsup_t (x + y) \leq \frac{\rho}{\hat{\rho}},$$

that is, solutions remain bounded. We conclude that the first quadrant is positively invariant with respect to the solutions of (3.6) and contains the omega limit set of every initial condition. Therefore, we can apply Poincaré–Bendixson theorem. When $\mathcal{R}_0 > 1$, if $y(0) = 0$, then the solutions will stay on the x -axis and converge to the disease-free equilibrium. If $y(0) > 0$, that is, $u^0 = (x(0), y(0)) \in X$, then we claim that the disease-free equilibrium does not belong to the omega limit set of u^0 . Suppose the disease-free equilibrium belongs to $\omega(u^0)$. Then, since the disease-free equilibrium is an unstable saddle, it has a stable manifold that is given by the x -axis. That is the case, because each solution that starts from $y(0) = 0$, that is, that starts on the x -axis, stays on the x -axis and converges to the disease-free equilibrium. Hence, the stable manifold of the disease-free equilibrium is not in X . Hence, $\omega(u^0)$ would have to contain another equilibrium, namely the endemic equilibrium. But since the endemic equilibrium is locally asymptotically stable, every solution that gets close to it, stays close to it. Therefore, the disease-free equilibrium does not belong to $\omega(u^0)$. Hence, the omega limit set of u^0 consists of the endemic equilibrium only. All solutions with $I(0) > 0$ converge to the endemic equilibrium. \square

3.6 Oscillations in Epidemic Models

In the previous sections, we saw that the most basic SIR epidemic model has a unique endemic equilibrium, which is globally stable if $\mathcal{R}_0 > 1$. This means that every solution converges to a stationary state. On the other hand, many times, the incidence or the prevalence data of various diseases exhibit periodicity. This is particularly true of childhood diseases. For instance, data on measles in New York City for the period 1928–1963 suggests that the disease persisted in the form of periodic outbreaks. That can be clearly seen from the monthly case data on measles for New York City, illustrated in Fig. 3.8.

Can simple epidemic models capture the oscillations exhibited in data? That would be the case if the epidemic model had a stable periodic solution. System (3.7) has a periodic solution (or a cycle) if there is an orbit $(x(t), y(t))$ such that $x(t + T) = x(t)$ and $y(t + T) = y(t)$ for some appropriate value T , called the *period*. The cycle is stable if solutions that start from close initial conditions converge to the cycle. It is well known that ODE models that reduce to a one-dimensional dynamical system do not have cycles, and cannot capture oscillations in data. However, planar ODE systems, including planar epidemic models, can exhibit periodicity.

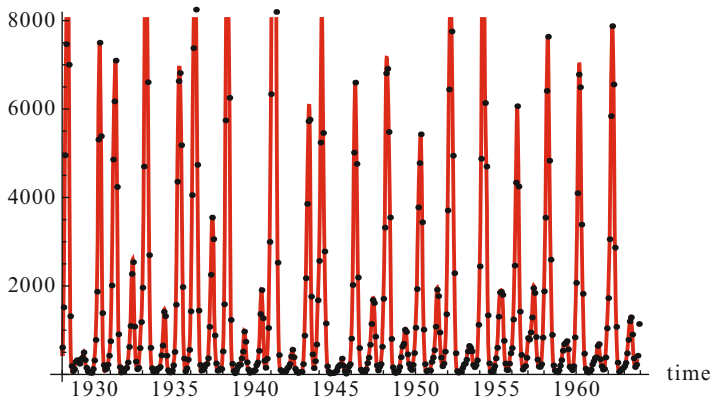


Fig. 3.8 Monthly case data for measles for New York City in the period 1928–1963. The data are given as data points. The *continuous curve* is an interpolation. The figure clearly shows recurrent outbreaks

The periodic solutions typically arise from a single endemic equilibrium that loses stability through a bifurcation called a **Hopf bifurcation**. Hopf bifurcations occur when a pair of complex conjugate eigenvalues of the linearization around a nontrivial fixed point cross the imaginary axis of the complex plane with nonzero speed. In that case, a stable limit cycle may bifurcate from the fixed point, which at the same time loses stability. Hopf bifurcations occur in planar ODE systems as well as in higher-dimensional systems.

The existence of a periodic solution can be deduced from the Hopf bifurcation theorem, which we state below for planar systems. To introduce the theorem, we need to restate the problem (3.7) to include a parameter. We write the system (3.7) in the form

$$\begin{aligned} x' &= f(x, y; \mu), \\ y' &= g(x, y; \mu), \end{aligned} \quad (3.34)$$

where we explicitly acknowledge that f and g depend on the parameter μ . Furthermore, let $(x^*(\mu), y^*(\mu))$ be an equilibrium of the system (3.34) that also depends on the parameter. We linearize the system (3.34) around the equilibrium $(x^*(\mu), y^*(\mu))$. The Jacobian of the linearization is given by

$$J(x^*(\mu), y^*(\mu)) = \begin{pmatrix} f_x(x^*, y^*; \mu) & f_y(x^*, y^*; \mu) \\ g_x(x^*, y^*; \mu) & g_y(x^*, y^*; \mu) \end{pmatrix}. \quad (3.35)$$

Assume that the Jacobian has eigenvalues $\lambda_{\pm} = \alpha(\mu) \pm i\beta(\mu)$, where $i = \sqrt{-1}$. In terms of the trace of the Jacobian, $\text{Tr}J$, and determinant of the Jacobian, $\text{Det}J$, the eigenvalues are given by

$$\lambda_{\pm} = \frac{\text{Tr}J \pm \sqrt{(\text{Tr}J)^2 - 4\text{Det}J}}{2}. \quad (3.36)$$

For a Hopf bifurcation to occur, we must have, for some parameter value $\mu = \mu_0$, that the following conditions hold:

$$\begin{aligned} \text{Tr}J(x^*(\mu_0), y^*(\mu_0)) &= 0, \\ \text{Det}J(x^*(\mu_0), y^*(\mu_0)) &> 0. \end{aligned} \quad (3.37)$$

When these conditions are satisfied, the eigenvalues of the Jacobian are purely imaginary. If in addition to the above conditions, the *transversality condition* is satisfied,

$$\frac{d}{d\mu}\alpha(\mu)|_{\mu=\mu_0} = d \neq 0, \quad (3.38)$$

then a Hopf bifurcation occurs at the bifurcation point $(x^*(\mu_0), y^*(\mu_0); \mu_0)$. At such a Hopf bifurcation for some μ near μ_0 , small-amplitude oscillations (limit cycles) bifurcate from the equilibrium solution. The amplitude of these oscillations approaches zero as μ approaches μ_0 . Hopf theory guarantees the existence of such periodic orbits for $\mu \approx \mu_0$ only; it does not guarantee the existence of the oscillations for μ farther away from μ_0 .

To state the Hopf bifurcation theorem, we rewrite system (3.34) in the form

$$\begin{aligned} x' &= j_{11}(\mu)x + j_{12}(\mu)y + f_1(x, y; \mu), \\ y' &= j_{21}(\mu)x + j_{22}(\mu)y + g_1(x, y; \mu), \end{aligned} \quad (3.39)$$

where $j_{11}(\mu) = f_x(x^*, y^*; \mu)$, $j_{12}(\mu) = f_y(x^*, y^*; \mu)$, $j_{21}(\mu) = g_x(x^*, y^*; \mu)$, $j_{22}(\mu) = g_y(x^*, y^*; \mu)$. The complete Hopf bifurcation theorem, which is given below, gives also a third condition that is rarely checked.

Theorem 3.9 (Hopf Bifurcation Theorem). *Let f and g in (3.34) have continuous third-order derivatives in x and y . Assume that $(0, 0)$ is an equilibrium of (3.39) and that the Jacobian matrix J defined by (3.35) is valid for all values of $\mu \approx \mu_0$. In addition, assume that the eigenvalues of J are $\alpha(\mu) \pm i\beta(\mu)$. Suppose in addition that for $\mu = \mu_0$, the following conditions hold:*

1. *Nonhyperbolicity condition: $\alpha(\mu_0) = 0$ and $\beta(\mu_0) = \omega \neq 0$.*
2. *Transversality condition: the eigenvalues cross the imaginary axis with nonzero speed*

$$\frac{d}{d\mu}\alpha(\mu)|_{\mu=\mu_0} = d \neq 0. \quad (3.40)$$

3. *Genericity condition: $a \neq 0$, where*

$$\begin{aligned} a &= \frac{1}{16} (f_{xxx} + f_{xyy} + g_{xxy} + g_{yyy}) \\ &\quad + \frac{1}{16\omega} (f_{xy}(f_{xx} + f_{yy}) - g_{xy}(g_{xx} + g_{yy}) - f_{xx}g_{xx} + f_{yy}g_{yy}), \end{aligned} \quad (3.41)$$

where $f_{xy} = \frac{\partial^2 f}{\partial x \partial y}|_{\mu=\mu_0}(x^*, y^*)$, etc.

Then system (3.34) has a periodic solution for $\mu > \mu_0$ if $ad < 0$ and for $\mu < \mu_0$ if $ad > 0$. In the case $ad < 0$, the bifurcation is called *supercritical*, and the bifurcating

periodic solution is stable. In the case $ad > 0$, the bifurcation is called subcritical, and the bifurcating periodic solution is unstable. An approximate period of the periodic solution is given by

$$T = \frac{2\pi}{\omega}.$$

Before we continue with an example of Hopf bifurcation, we summarize the options for the stability of an equilibrium in a planar system based on the use of the trace and the determinant of the Jacobian. This theorem gives a quick and very efficient way to deduce the stability of an equilibrium.

Theorem 3.10. *Consider the planar system*

$$\begin{aligned} x' &= f(x, y), \\ y' &= g(x, y), \end{aligned} \tag{3.42}$$

and let (x^*, y^*) be an equilibrium of that system. Then the Jacobian of system (3.42) evaluated at that equilibrium is given by

$$J(x^*, y^*) = \begin{pmatrix} f_x(x^*, y^*) & f_y(x^*, y^*) \\ g_x(x^*, y^*) & g_y(x^*, y^*) \end{pmatrix}. \tag{3.43}$$

The following results give the stability of the equilibrium (x^*, y^*) :

1. Equilibrium (x^*, y^*) is locally asymptotically stable if and only if $\text{Tr}J < 0$ and $\text{Det}J > 0$.
2. Equilibrium (x^*, y^*) is a saddle if and only if $\text{Det}J < 0$.
3. Equilibrium (x^*, y^*) loses stability and undergoes Hopf bifurcation if and only if for some value of the parameter μ , called μ_0 , the following hold:

$$\begin{aligned} \text{Tr}J(x^*(\mu_0), y^*(\mu_0)) &= 0, \\ \text{Det}J(x^*(\mu_0), y^*(\mu_0)) &> 0. \end{aligned} \tag{3.44}$$

In addition, we must also have

$$\left. \frac{d\text{Tr}J}{d\mu} \right|_{\mu=\mu_0} \neq 0.$$

To illustrate the application of the Hopf bifurcation theorem, we consider a simple modification of the SIR model (3.3). Assume that the transmission coefficient of infection β is not constant but linear in the number of infecteds: $\beta(1 + \nu I)$, where $\nu > 0$ is a parameter. This means that either the contact rate increases with the number of infectious individuals or the probability of transmission does so. Thus, new infections occur at a much faster pace compared to the standard mass action incidence. The model becomes [6]

$$\begin{aligned} S'(t) &= \Lambda - \beta(1 + \nu I)IS - \mu S, \\ I'(t) &= \beta(1 + \nu I)IS - (\alpha + \mu)I, \end{aligned} \tag{3.45}$$

where we have omitted the equation for recovered individuals R . We will investigate this model without nondimensionalizing it. The total population size $N = S + I + R$ satisfies $N' = \Lambda - \mu N$. We assume that the initial total population size is given by $N_0 = S_0 + I_0 + R_0$. The disease-free equilibrium $\mathcal{E}_0 = \left(\frac{\Lambda}{\mu}, 0\right)$ of model (3.45) always exists. The reproduction number of the model (3.45) is given by

$$\mathcal{R}_0 = \frac{\Lambda\beta}{\mu(\mu + \alpha)}. \quad (3.46)$$

It can be shown (see Problem 3.3) that the disease-free equilibrium is locally stable if $\mathcal{R}_0 < 1$ and unstable if $\mathcal{R}_0 > 1$.

The endemic equilibria of the system are solutions to the following system:

$$\begin{aligned} \Lambda - \beta(1 + \nu I)S - \mu S &= 0, \\ \beta(1 + \nu I)S - (\alpha + \mu) &= 0. \end{aligned} \quad (3.47)$$

From the second equation, we see that $\beta(1 + \nu I)S = (\alpha + \mu)$. Substituting this expression into the first equation, we can express S in terms of I :

$$S = \frac{\Lambda}{\mu} - \frac{\mu + \alpha}{\mu} I. \quad (3.48)$$

Hence, substituting in $\beta(1 + \nu I)S = (\alpha + \mu)$, we obtain the following quadratic equation for I :

$$(1 + \nu I) \left[\frac{\Lambda}{\mu} - \frac{\mu + \alpha}{\mu} I \right] = \frac{\mu + \alpha}{\beta}. \quad (3.49)$$

If we denote by $f(I)$ the parabola on the left-hand side of (3.49), then the endemic equilibria of model (3.45) are given by the intersections of the parabola with the horizontal line $y = (\mu + \alpha)/\beta$ (see Fig. 3.9). If $f(0) > (\mu + \alpha)/\beta$, or equivalently, if $\mathcal{R}_0 > 1$, then there is always a unique (positive) equilibrium $\mathcal{E}^* = (S^*, I^*)$. That is the scenario that is shown in Fig. 3.9. If $f(0) < (\mu + \alpha)/\beta$, or equivalently, if $\mathcal{R}_0 < 1$, then there may be two equilibria if the maximum of the parabola occurs to the right of the y -axis and the horizontal line lies below the maximum of the parabola. Since the maximum of the parabola is achieved at

$$I_m = \frac{1}{2\nu} \left[\frac{\Lambda\nu}{\mu + \alpha} - 1 \right],$$

the maximum of the parabola is to the right of the y -axis if and only if $I_m > 0$. Hence, there will be two endemic equilibria if the maximum of the parabola is above the horizontal line, that is, if

$$(1 + \nu I_m) \left[\frac{\Lambda}{\mu} - \frac{\mu + \alpha}{\mu} I_m \right] > \frac{\mu + \alpha}{\beta}. \quad (3.50)$$

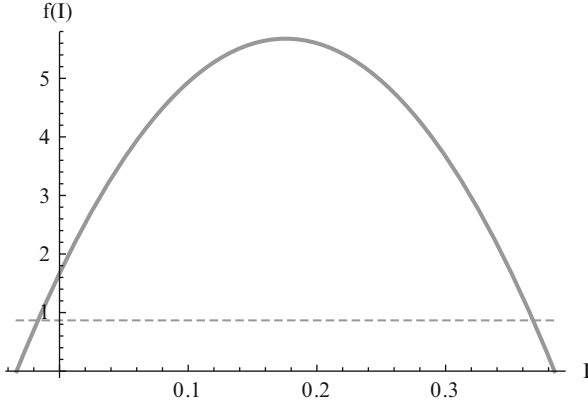


Fig. 3.9 The graph shows intersections of the function $f(I)$ with the horizontal line $y = (\mu + \alpha)/\beta$ in Eq. (3.49). Each intersection gives one nontrivial equilibrium of the model (3.45). The figure shows the case $\mathcal{R}_0 > 1$, and there is a unique (positive) equilibrium I^*

If two endemic equilibria exist, we denote them by $\mathcal{E}_1 = (S_1^*, I_1^*)$ and $\mathcal{E}_2 = (S_2^*, I_2^*)$, where $I_1^* < I_2^*$ and the corresponding value of S is computed from (3.48). The stability of the equilibria is given by the Jacobian

$$J = \begin{pmatrix} -\beta(1 + \nu I)I - \mu & -\beta \nu IS - (\mu + \alpha) \\ \beta(1 + \nu I)I & \beta \nu IS \end{pmatrix}, \quad (3.51)$$

where we have used the equality $\beta(1 + \nu I)S = (\alpha + \mu)$ to simplify the Jacobian. The characteristic equation of the Jacobian $|J - \lambda I| = 0$ is a quadratic polynomial in λ given by

$$\lambda^2 + B\lambda + C = 0, \quad (3.52)$$

where B and C are given by

$$\begin{aligned} B &= \mu + \beta(1 + \nu I)I - \beta \nu IS \\ C &= \beta(1 + \nu I)I(\mu + \alpha) - \mu \beta \nu IS, \end{aligned} \quad (3.53)$$

and I is any equilibrium. We note that the endemic equilibria differ in the slope of the tangent line to the curve of $f(I)$ at each equilibrium. In particular, if $\mathcal{R}_0 > 1$, the slope of the tangent at the equilibrium satisfies $f'(I^*) < 0$. When there are two equilibria, we have $f'(I_1^*) > 0$ while $f'(I_2^*) < 0$. The slope of $f(I)$ is given by

$$f'(I) = \frac{\mu + \alpha}{\mu} \left[\frac{\Lambda \nu}{\mu + \alpha} - 1 - 2\nu I \right].$$

On the other hand, C can be rewritten in the form (where S has been replaced with (3.48))

$$C = (\mu + \alpha)\beta I \left[1 + 2vI - \frac{\Lambda v}{\mu + \alpha} \right].$$

It is evident from the above two expressions that the sign of C is opposite the sign of $f'(I)$. Hence, if $\mathcal{R}_0 > 1$, the unique endemic equilibrium I^* gives $C > 0$. When $\mathcal{R}_0 < 1$ and there are two equilibria, we have for the lower one $C < 0$ and for the upper one $C > 0$. Hence, when two equilibria are present, the lower one \mathcal{E}_1 is unstable, since $C < 0$ means that the characteristic equation (3.52) has one positive and one negative root. The local stability of \mathcal{E}^* and \mathcal{E}_2 depends on the sign of B . If $B > 0$, then each of these equilibria is stable. However, for some value of the parameter $v = v_0$, we may have

$$\mu + \beta(1 + v_0I)I - \beta v_0IS = 0,$$

and then a Hopf bifurcation may occur. To see that this condition may hold, we exhibit a specific numerical example. To decide on parameter values, we first decide on a time unit. We will measure time in years. Since $1/\mu$ gives an average lifespan of individuals, if we take $\mu = 0.2$, that will give a lifespan of 5 years. For the human population, that lifespan will be adequate for some childhood diseases. The lifespan can describe well many animal populations. Furthermore, $1/\alpha$ corresponds to a duration of infectiousness. Hence, if we take $\alpha = 26$, that will correspond to duration of infectiousness of about 2 weeks. The remaining parameters are taken as $\beta = 0.005$ and $\Lambda = 1250$. We think of $B(v) = \mu + \beta(1 + vI)I - \beta vIS$ as a function of the parameter v . Since these parameters give $\mathcal{R}_0 = 1.19275$, we focus on the stability of the endemic equilibrium \mathcal{E}^* . We note that I^* and S^* are also functions of v . We plot $B(v)$ against v in Fig. 3.10.

We check the transversality condition for \mathcal{E}^* also numerically. We notice that the real part of the eigenvalues of (3.52) is given by

$$\Re(\lambda) = \frac{-(\mu + \beta(1 + vI)I - \beta vIS)}{2}.$$

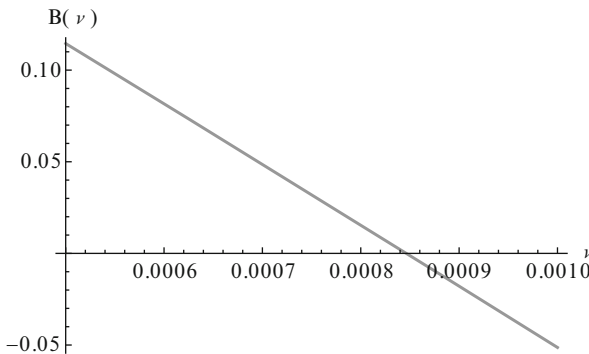


Fig. 3.10 The graph of $B(v)$ shows clearly that B changes sign as the parameter v passes through the critical value $v_0 = 0.000846293$

To differentiate $\Re(\lambda)$ with respect to ν , we have to differentiate $B(\nu)$ with respect to ν and evaluate the results at $\nu = \nu_0$. Figure 3.10 suggests that

$$\frac{dB(\nu)}{d\nu}\Big|_{\nu=\nu_0} < 0.$$

Differentiating the real part of the roots of the characteristic equation (3.52), we have

$$\frac{\partial \Re(\lambda)}{\partial \nu} = -\frac{1}{2} \frac{dB(\nu)}{d\nu}\Big|_{\nu=\nu_0} > 0.$$

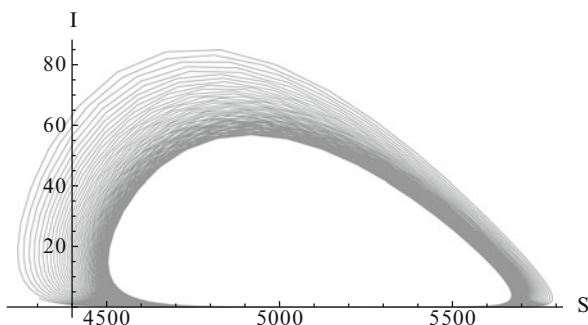


Fig. 3.11 The graph shows oscillations in the (S, I) -plane that converge to a periodic orbit. Initial conditions are $S(0) = 40,000$, $I(0) = 15$. The plot is made for $t \geq 200$

Hence, the transversality condition is satisfied. Assuming $a \neq 0$, we may conclude from the Hopf bifurcation theorem that a periodic solution bifurcates from the stable endemic equilibrium \mathcal{E}^* . We cannot conclude that the bifurcation is supercritical or subcritical without computing a . Therefore, we do not know whether the bifurcating solution is stable. We checked the stability of the bifurcating oscillatory solution numerically. We chose $\nu = 0.00117$. The equilibrium is given by $\mathcal{E}^* = (5191, 8)$. The real part of the roots of the characteristic equation is $\Re(\lambda) = 0.054228$. From the simulations we performed, it appears that the bifurcating oscillatory solution in this case is stable (see Fig. 3.11), and the number of susceptible and infected individuals tend to a periodic orbit.

Problems

3.1. Census data for the population of the United States (in millions) are given in Table 3.3. Fit each of the three population models, Malthus model, logistic model, and constrained logistic model, to the data and determine the least-squares error. Which model fits the data best?

Table 3.3 Population of the US (in millions)

Year	Population (million)	Year	Population (million)
1790	3.9	1910	92.0
1800	5.3	1920	105.7
1810	7.2	1930	122.8
1820	9.6	1940	131.7
1830	12.9	1950	150.7
1840	17.1	1960	179.0
1850	23.1	1970	205.0
1860	31.4	1980	226.5
1870	38.6	1990	248.7
1880	50.2	2000	281.4
1890	62.9	2010	310.0
1900	76.0	–	–

3.2. Consider the following SIS epidemic model with disease-induced mortality γ :

$$\begin{aligned} S' &= \Lambda - \beta IS + \alpha I - \mu S, \\ I' &= \beta IS - (\alpha + \gamma + \mu)I, \end{aligned} \quad (3.54)$$

where S is the number of susceptibles, I is the number of infected, β is the transmission rate, α is the recovery rate, Λ is the birth rate, μ is the natural death rate.

- Sketch the nullclines of the system and the direction of the vector field along them. Confirm your results by plotting the vector field with solutions.
- Determine the reproduction number and equilibria of the system.
- Calculate the Jacobian of each equilibrium and determine the stability.
- Use the Dulac criterion to rule out periodic solutions.
- Use the Poincaré–Bendixson theorem to show convergence to equilibrium.

3.3. Consider model (3.45):

$$\begin{aligned} S'(t) &= \Lambda - \beta(1 + \nu I)IS - \mu S, \\ I'(t) &= \beta(1 + \nu I)IS - (\alpha + \mu)I, \end{aligned} \quad (3.55)$$

where S is the number of susceptibles, I is the number of infected, β is the transmission rate, α is the recovery rate, Λ is the birth rate, μ is the natural death rate, and ν is a proportionality constant.

- Derive the reproduction number \mathcal{R}_0 for that model.
- Show that the disease-free equilibrium $\left(\frac{\Lambda}{\mu}, 0\right)$ is locally stable if $\mathcal{R}_0 < 1$ and unstable if $\mathcal{R}_0 > 1$.
- Argue that if $\mathcal{R}_0 > 1$, there is always a unique endemic equilibrium.

3.4. Non-dimensionalization

Consider the SIS model with saturating incidence in the size of the susceptibles.

$$\begin{aligned} S'(t) &= \Lambda - \frac{\beta IS}{1 + \sigma S} + \alpha I - \mu S, \\ I'(t) &= \frac{\beta IS}{1 + \sigma S} - (\alpha + \mu)I. \end{aligned} \quad (3.56)$$

- What are the units of the parameters?
- Rescale the system above into a nondimensional system both in the time variable and in the dependent variables.
- Determine conditions for the existence of an endemic equilibrium.

3.5. Multiple Equilibria

Consider the following SIS epidemic model with disease-induced mortality γ :

$$\begin{aligned} S' &= \Lambda - \frac{\beta IS}{A + I^2} + \alpha I - \mu S, \\ I' &= \frac{\beta IS}{A + I^2} - (\alpha + \gamma + \mu)I, \end{aligned} \quad (3.57)$$

where S is the number of susceptibles, I is the number of infected, β is the transmission rate, α is the recovery rate, Λ is the birth rate, μ is the natural death rate.

- Determine the reproduction number and equilibria of the system.
- Sketch the nullclines of the system and the direction of the vector field along them. Confirm your results by plotting the vector field with solutions.
- Calculate the Jacobian of each equilibrium and determine the stability.
- Use the Dulac criterion to rule out periodic solutions.

3.6. Fox Rabies

The following model has been proposed to model fox rabies [26]:

$$\begin{aligned} S' &= rSe^{-aS} - \beta IS - \mu S, \\ I' &= \beta IS - (\alpha + \mu)I, \end{aligned} \quad (3.58)$$

where S is the number of susceptibles, I is the number of infected, β is the transmission rate, α is the disease-induced death rate, r and a are constants associated with declining with population size per capita birth rate re^{-aS} , and μ is the natural death rate.

- Determine the reproduction number and equilibria of the system.
- Sketch the nullclines of the system and the direction of the vector field along them. Confirm your results by plotting the vector field with solutions.
- Calculate the Jacobian of each equilibrium and determine the stability.
- Use the Dulac criterion to rule out periodic solutions.

3.7. Hopf Bifurcation

The following model has been proposed to model the saturating contact rate:

$$\begin{aligned}S' &= rS \left(1 - \frac{S}{K}\right) - \frac{\beta IS}{1 + \alpha S} - \mu S, \\I' &= \frac{\beta IS}{1 + \alpha S} - (\gamma + \mu)I,\end{aligned}\tag{3.59}$$

where S is the number of susceptibles, I is the number of infected, β is the transmission rate, α is a parameter that measures the inhibitory effect, γ is the recovery rate, r and K are constants associated with the logistic population growth, and μ is the natural death rate.

- (a) Determine the reproduction number and equilibria of the system.
- (b) Calculate the Jacobian of each equilibrium and determine the stability.
- (c) Use the Hopf bifurcation theorem to show the presence of periodic solutions.
Use a computer algebra system to graph the periodic solution in the phase plane together with the vector field.