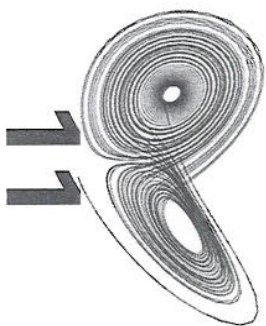


12. Let  $X' = F(X)$  be a planar system with no equilibrium points. Suppose the flow  $\phi_t$  generated by  $F$  preserves area (that is, if  $U$  is any open set, the area of  $\phi_t(U)$  is independent of  $t$ ). Show that every solution curve is a closed set.
13. Let  $\gamma$  be a closed orbit of a planar system. Let  $\lambda$  be the period of  $\gamma$ . Let  $\{\gamma_n\}$  be a sequence of closed orbits. Suppose the period of  $\gamma_n$  is  $\lambda_n$ . If there are points  $X_n \in \gamma_n$  such that  $X_n \rightarrow X \in \gamma$ , prove that  $\lambda_n \rightarrow \lambda$ . (This result can be false for higher dimensional systems. It is true, however, that if  $\lambda_n \rightarrow \mu$ , then  $\mu$  is an integer multiple of  $\lambda$ .)
14. Consider a system in  $\mathbb{R}^2$  having only a finite number of equilibria.
- Show that every limit set is either a closed orbit or the union of equilibrium points and solutions  $\phi_t(X)$  such that  $\lim_{t \rightarrow \infty} \phi_t(X)$  and  $\lim_{t \rightarrow -\infty} \phi_t(X)$  are these equilibria.
  - Show by example (draw a picture) that the number of distinct solution curves in  $\omega(X)$  may be infinite.
15. Let  $X$  be a recurrent point of a planar system, that is, there is a sequence  $t_n \rightarrow \pm\infty$  such that
- $$\phi_{t_n}(X) \rightarrow X.$$
- Prove that either  $X$  is an equilibrium or  $X$  lies on a closed orbit.
  - Show by example that there can be a recurrent point for a nonplanar system that is not an equilibrium and does not lie on a closed orbit.
16. Let  $X' = F(X)$  and  $X' = G(X)$  be planar systems. Suppose that
- $$F(X) \cdot G(X) = 0$$
- for all  $X \in \mathbb{R}^2$ . If  $F$  has a closed orbit, prove that  $G$  has an equilibrium point.
17. Let  $\gamma$  be a closed orbit for a planar system, and let  $\mathcal{U}$  be the bounded, open region inside  $\gamma$ . Show that  $\gamma$  is not simultaneously the omega and alpha limit set of points of  $\mathcal{U}$ . Use this fact and the Poincaré-Bendixson theorem to prove that  $\mathcal{U}$  contains an equilibrium that is not a saddle. (*Hint*: Consider the limit sets of points on the stable and unstable curves of saddles.)



## Applications in Biology

In this chapter we make use of the techniques developed in the previous few chapters to examine some nonlinear systems that have been used as mathematical models for a variety of biological systems. In Section 11.1 we utilize the preceding results involving nullclines and linearization to describe several biological models involving the spread of communicable diseases. In Section 11.2 we investigate the simplest types of equations that model a predator/prey ecology. A more sophisticated approach is used in Section 11.3 to study the populations of a pair of competing species. Instead of developing explicit formulas for these differential equations, we instead make only qualitative assumptions about the form of the equations. We then derive geometric information about the behavior of solutions of such systems based on these assumptions.

### 11.1 Infectious Diseases

The spread of infectious diseases such as measles or malaria may be modeled as a nonlinear system of differential equations. The simplest model of this type is the SIR model. Here we divide a given population into three disjoint groups. The population of susceptible individuals is denoted by  $S$ , the infected population by  $I$ , and the recovered population by  $R$ . As usual, each of these is a function of time. We assume for simplicity that the total population is constant, so that  $(S + I + R)' = 0$ .

In the most basic case we make the assumption that, once an individual has been infected and subsequently has recovered, that individual cannot be reinfected. This is the situation that occurs for such diseases as measles, mumps, and smallpox, among many others. We also assume that the rate of transmission of the disease is proportional to the number of encounters between susceptible and infected individuals. The easiest way to characterize this assumption mathematically is to put  $S' = -\beta SI$  for some constant  $\beta > 0$ . We finally assume that the rate at which infected individuals recover is proportional to the number of infected. The SIR model is then

$$\begin{aligned} S' &= -\beta SI \\ I' &= \beta SI - \nu I \\ R' &= \nu I \end{aligned}$$

where  $\beta$  and  $\nu$  are positive parameters.

As stipulated, we have  $(S + I + R)' = 0$ , so that  $S + I + R$  is a constant. This simplifies the system, for if we determine  $S(t)$  and  $I(t)$ , we then derive  $R(t)$  for free. Hence it suffices to consider the two-dimensional system

$$\begin{aligned} S' &= -\beta SI \\ I' &= \beta SI - \nu I. \end{aligned}$$

The equilibria for this system are given by the  $S$ -axis ( $I = 0$ ). Linearization at  $(S, 0)$  yields the matrix

$$\begin{pmatrix} 0 & -\beta S \\ 0 & \beta S - \nu \end{pmatrix},$$

so the eigenvalues are 0 and  $\beta S - \nu$ . This second eigenvalue is negative if  $0 < S < \nu/\beta$  and positive if  $S > \nu/\beta$ .

The  $S$ -nullclines are given by the  $S$  and  $I$  axes. On the  $I$ -axis, we have  $I' = -\nu I$ , so solutions simply tend to the origin along this line. The  $I$ -nullclines are  $I = 0$  and the vertical line  $S = \nu/\beta$ . Hence we have the nullcline diagram depicted in Figure 11.1. From this it appears that, given any initial population  $(S_0, I_0)$  with  $S_0 > \nu/\beta$  and  $I_0 > 0$ , the susceptible population decreases monotonically, while the infected population at first rises, but eventually reaches a maximum and then declines to 0.

We can actually prove this analytically, because we can explicitly compute a function that is constant along solution curves. Note that the slope of the vector field is a function of  $S$  alone:

$$\frac{I'}{S'} = \frac{\beta SI - \nu I}{-\beta SI} = -1 + \frac{\nu}{\beta S}.$$

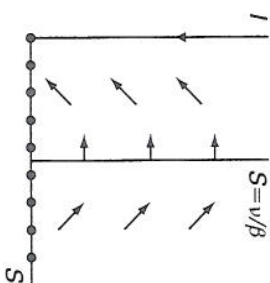


Figure 11.1 The nullclines and direction field for the SIR model.

Hence we have

$$\frac{dI}{dS} = \frac{dI/dt}{dS/dt} = -1 + \frac{\nu}{\beta S},$$

which we can immediately integrate to find

$$I = I(S) = -S + \frac{\nu}{\beta} \log S + \text{constant}.$$

Hence the function  $I + S - (\nu/\beta) \log S$  is constant along solution curves. It then follows that there is a unique solution curve connecting each equilibrium point in the interval  $\nu/\beta < S < \infty$  to one in the interval  $0 < S < \nu/\beta$  as shown in Figure 11.2.

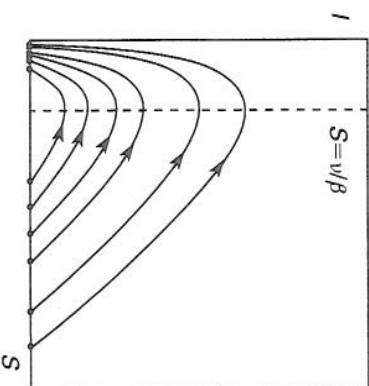


Figure 11.2 The phase portrait for the SIR system.

A slightly more complicated model for infectious diseases arises when we assume that recovered individuals may lose their immunity and become reinfected with the disease. Examples of this type of disease include malaria and tuberculosis. We assume that the return of recovered individuals to the class  $S$  occurs at a rate proportional to the population of recovered individuals. This leads to the SIRS model (where the extra  $S$  indicates that recovered individuals may reenter the susceptible group). The system becomes

$$\begin{aligned} S' &= -\beta SI + \mu R \\ I' &= \beta SI - \nu I \\ R' &= \nu I - \mu R. \end{aligned}$$

Again we see that the total population  $S + I + R$  is a constant, which we denote by  $\tau$ . We may eliminate  $R$  from this system by setting  $R = \tau - S - I$ :

$$\begin{aligned} S' &= -\beta SI + \mu(\tau - S - I) \\ I' &= \beta SI - \nu I. \end{aligned}$$

Here  $\beta$ ,  $\mu$ ,  $\nu$ , and  $\tau$  are all positive parameters.

Unlike the SIR model, we now have at most two equilibria, one at  $(\tau, 0)$  and the other at

$$(S^*, I^*) = \left( \frac{\nu}{\beta}, \frac{\mu(\tau - \frac{\nu}{\beta})}{\nu + \mu} \right).$$

The first equilibrium point corresponds to no disease whatsoever in the population. The second equilibrium point only exists when  $\tau \geq \nu/\beta$ . When  $\tau = \nu/\beta$ , we have a bifurcation as the two equilibria coalesce at  $(\tau, 0)$ . The quantity  $\nu/\beta$  is called the *threshold level* for the disease.

The linearized system is given by

$$Y' = \begin{pmatrix} -\beta I - \mu & -\beta S - \mu \\ \beta I & \beta S - \nu \end{pmatrix} Y.$$

At the equilibrium point  $(\tau, 0)$ , the eigenvalues are  $-\mu$  and  $\beta\tau - \nu$ , so this equilibrium point is a saddle provided that the total population exceeds the threshold level. At the second equilibrium point, a straightforward computation shows that the trace of the matrix is negative, while the determinant is positive. It then follows from the results in Chapter 4 that both eigenvalues have negative real parts, and so this equilibrium point is asymptotically stable.

Biologically, this means that the disease may become established in the community only when the total population exceeds the threshold level. We will only consider this case in what follows.

Note that the SIRS system is only of interest in the region given by  $I, S \geq 0$  and  $S + I \leq \tau$ . Denote this triangular region by  $\Delta$  (of course!). Note that the  $I$ -axis is no longer invariant, while on the  $S$ -axis, solutions increase up to the equilibrium at  $(\tau, 0)$ .

**Proposition.** *The region  $\Delta$  is positively invariant.*

*Proof.* We check the direction of the vector field along the boundary of  $\Delta$ . The field is tangent to the boundary along the lower edge  $I = 0$  as well as at  $(0, \tau)$ . Along  $S = 0$  we have  $S' = \mu(\tau - I) > 0$ , so the vector field points inward for  $0 < I < \tau$ . Along the hypotenuse, if  $0 < S \leq \nu/\beta$ , we have  $S' = -\beta SI < 0$  and  $I' = I(\beta S - \nu) \leq 0$  so the vector field points inward. When  $\nu/\beta < S < \tau$  we have

$$-1 < \frac{I'}{S'} = -1 + \frac{\nu}{\beta S} \leq 0$$

so again the vector field points inward. This completes the proof. ■

The  $I$ -nullclines are given as in the SIR model by  $I = 0$  and  $S = \nu/\beta$ . The  $S$ -nullcline is given by the graph of the function

$$I = I(S) = \frac{\mu(\tau - S)}{\beta S + \mu}.$$

A calculus student will compute that  $I'(S) < 0$  and  $I''(S) > 0$  when  $0 \leq S < \tau$ . So this nullcline is the graph of a decreasing and concave up function that passes through both  $(\tau, 0)$  and  $(0, \tau)$ , as displayed in Figure 11.3. Note that in this phase portrait, all solutions appear to tend to the equilibrium point  $(S^*, I^*)$ ; the proportion of infected to susceptible individuals tends to a “steady state.” To prove this, however, one would need to eliminate the possibility of closed orbits encircling the equilibrium point for a given set of parameters  $\beta, \mu, \nu$ , and  $\tau$ .

## 11.2 Predator/Prey Systems

We next consider a pair of species, one of which consists of predators whose population is denoted by  $y$  and the other its prey with population  $x$ . We assume that the prey population is the total food supply for the predators. We also

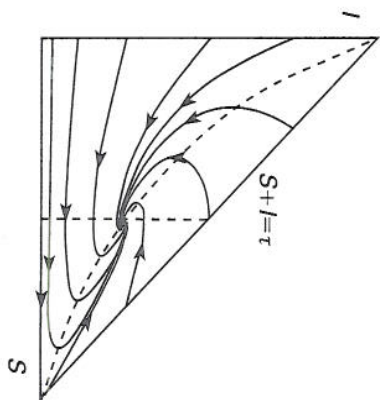


Figure 11.3 The nullclines and phase portrait in  $\Delta$  for the SIRS system. Here  $\beta = \nu = \mu = 1$  and  $\tau = 2$ .

assume that, in the absence of predators, the prey population grows at a rate proportional to the current population. That is, as in Chapter 1, when  $y = 0$  we have  $x' = ax$  where  $a > 0$ . So in this case  $x(t) = x_0 \exp(at)$ . When predators are present, we assume that the prey population decreases at a rate proportional to the number of predator/prey encounters. As in the previous section, one simple model for this is  $bxy$  where  $b > 0$ . So the differential equation for the prey population is  $x' = ax - bxy$ .

For the predator population, we make more or less the opposite assumptions. In the absence of prey, the predator population declines at a rate proportional to the current population. So when  $x = 0$  we have  $y' = -cy$  with  $c > 0$ , and thus  $y(t) = y_0 \exp(-ct)$ . The predator species becomes extinct in this case. When there are prey in the environment, we assume that the predator population increases at a rate proportional to the predator/prey meetings, or  $axy$ . We do not at this stage assume anything about overcrowding. Thus our simplified predator/prey system (also called the Volterra-Lotka system) is

$$\begin{aligned}x' &= ax - bxy = x(a - by) \\y' &= -cy + dxy = y(-c + dx)\end{aligned}$$

where the parameters  $a$ ,  $b$ ,  $c$ , and  $d$  are all assumed to be positive. Since we are dealing with populations, we only consider  $x, y \geq 0$ .

As usual, our first job is to locate the equilibrium points. These occur at the origin and at  $(x, y) = (c/d, a/b)$ . The linearized system is

$$X' = \begin{pmatrix} a - by & -bx \\ -c + dx & X \end{pmatrix},$$

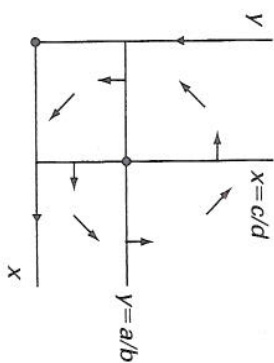


Figure 11.4 The nullclines and direction field for the predator/prey system.

so when  $x = y = 0$  we have a saddle with eigenvalues  $a$  and  $-c$ . We know the stable and unstable curves: They are the  $y$ - and  $x$ -axes, respectively.

At the other equilibrium point  $(c/d, a/b)$ , the eigenvalues are pure imaginary  $\pm i\sqrt{ac}$ , and so we cannot conclude anything at this stage about stability of this equilibrium point.

We next sketch the nullclines for this system. The  $x$ -nullclines are given by the straight lines  $x = 0$  and  $y = a/b$ , whereas the  $y$ -nullclines are  $y = 0$  and  $x = c/d$ . The nonzero nullcline lines separate the region  $x, y > 0$  into four basic regions in which the vector field points as indicated in Figure 11.4. Hence the solutions wind in the counterclockwise direction about the equilibrium point.

From this, we cannot determine the precise behavior of solutions: They could possibly spiral in toward the equilibrium point, spiral toward a limit cycle, spiral out toward “infinity” and the coordinate axes, or else lie on closed orbits. To make this determination, we search for a Liapunov function  $L$ . Employing the trick of *separation of variables*, we look for a function of the form

$$L(x, y) = F(x) + G(y).$$

Recall that  $\dot{L}$  denotes the time derivative of  $L$  along solutions. We compute

$$\begin{aligned}\dot{L}(x, y) &= \frac{d}{dt} L(x(t), y(t)) \\ &= \frac{dF}{dx} x' + \frac{dG}{dy} y' .\end{aligned}$$

Hence

$$\dot{L}(x, y) = x \frac{dF}{dx} (a - by) + y \frac{dG}{dy} (-c + dx).$$

We obtain  $L \equiv 0$  provided

$$\frac{x \frac{dF/dx}{dx - c} \equiv \frac{y \frac{dG/dy}{by - a}}$$

Since  $x$  and  $y$  are independent variables, this is possible if and only if

$$\frac{x \frac{dF/dx}{dx - c} = \frac{y \frac{dG/dy}{by - a}} = \text{constant}.$$

Setting the constant equal to 1, we obtain

$$\begin{aligned} \frac{dF}{dx} &= d - \frac{c}{x}, \\ \frac{dG}{dy} &= b - \frac{a}{y}. \end{aligned}$$

Integrating, we find

$$\begin{aligned} F(x) &= dx - c \log x, \\ G(y) &= by - a \log y. \end{aligned}$$

Thus the function

$$L(x, y) = dx - c \log x + by - a \log y$$

is constant on solution curves of the system when  $x, y > 0$ .

By considering the signs of  $\partial L/\partial x$  and  $\partial L/\partial y$  it is easy to see that the equilibrium point  $Z = (c/d, a/b)$  is an absolute minimum for  $L$ . It follows that  $L$  [or, more precisely,  $L - L(Z)$ ] is a Liapunov function for the system. Therefore  $Z$  is a stable equilibrium.

We note next that there are no limit cycles; this follows from Corollary 6 in Section 10.6 because  $L$  is not constant on any open set. We now prove the following theorem.

**Theorem.** *Every solution of the predator/prey system is a closed orbit (except the equilibrium point  $Z$  and the coordinate axes).*

**Proof.** Consider the solution through  $W \neq Z$ , where  $W$  does not lie on the  $x$ - or  $y$ -axis. This solution spirals around  $Z$ , crossing each nullcline infinitely often. Thus there is a doubly infinite sequence  $\dots < t_{-1} < t_0 < t_1 < \dots$  such that  $\phi_{t_n}(W)$  is on the line  $x = c/d$ , and  $t_n \rightarrow \pm\infty$  as  $n \rightarrow \pm\infty$ . If  $W$  is not on a closed orbit, the points  $\phi_{t_n}(W)$  are monotone along the line

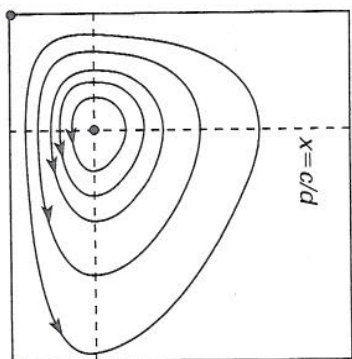


Figure 11.5 The nullclines and phase portrait for the predator/prey system.

$x = c/d$ , as discussed in the previous chapter. Since there are no limit cycles, either  $\phi_{t_n}(W) \rightarrow Z$  as  $n \rightarrow \infty$  or  $\phi_{t_n}(W) \rightarrow Z$  as  $n \rightarrow -\infty$ . Since  $L$  is constant along the solution through  $W$ , this implies that  $L(W) = L(Z)$ . But this contradicts minimality of  $L(Z)$ . This completes the proof. ■

The phase portrait for this predator/prey system is displayed in Figure 11.5. We conclude that, for any given initial populations  $(x(0), y(0))$  with  $x(0) \neq 0$  and  $y(0) \neq 0$ , other than  $Z$ , the populations of predator and prey oscillate cyclically. No matter what the populations of prey and predator are, neither species will die out, nor will its population grow indefinitely.

Now let us introduce overcrowding into the prey equation. As in the logistic model in Chapter 1, the equations for prey, in the absence of predators, may be written in the form

$$x' = ax - \lambda x^2.$$

We also assume that the predator population obeys a similar equation

$$y' = -cy - \mu y^2$$

when  $x = 0$ . Incorporating the assumptions above yields the predator/prey equations for species with limited growth:

$$\begin{aligned} x' &= x(a - by - \lambda x) \\ y' &= y(-c + dx - \mu y). \end{aligned}$$

As before, the parameters  $a, b, c, d$  as well as  $\lambda$  and  $\mu$  are all positive. When  $y = 0$ , we have the logistic equation  $x' = x(a - \lambda x)$ , which yields equilibria at the origin and at  $(a/\lambda, 0)$ . As we saw in Chapter 1, all nonzero solutions on the  $x$ -axis tend to  $a/\lambda$ .

When  $x = 0$ , the equation for  $y$  is  $y' = -cy - \mu y^2$ . Since  $y' < 0$  when  $y > 0$ , it follows that all solutions on this axis tend to the origin. Thus we confine attention to the upper-right quadrant  $\mathcal{Q}$  where  $x, y > 0$ .

The nullclines are given by the  $x$ - and  $y$ -axes, together with the lines

$$L: a - by - \lambda x = 0$$

$$M: -c + dx - \mu y = 0.$$

Along the lines  $L$  and  $M$ , we have  $x' = 0$  and  $y' = 0$ , respectively. There are two possibilities, according to whether these lines intersect in  $\mathcal{Q}$  or not.

We first consider the case where the two lines do not meet in  $\mathcal{Q}$ . In this case we have the nullcline configuration depicted in Figure 11.6. All solutions to the right of  $M$  head upward and to the left until they meet  $M$ ; between the lines  $L$  and  $M$  solutions now head downward and to the left. Thus they either meet  $L$  or tend directly to the equilibrium point at  $(a/\lambda, 0)$ . If solutions cross  $L$ , they then head right and downward, but they cannot cross  $L$  again. Thus they too tend to  $(a/\lambda, 0)$ . Thus all solutions in  $\mathcal{Q}$  tend to this equilibrium point. We conclude that, in this case, the predator population becomes extinct and the prey population approaches its limiting value of  $a/\lambda$ .

We may interpret the behavior of solutions near the nullclines as follows. Since both  $x'$  and  $y'$  are never both positive, it is impossible for both prey

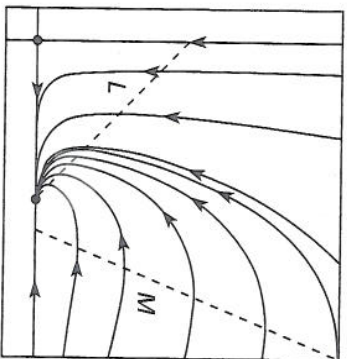


Figure 11.6 The nullclines and phase portrait for a predator/prey system with limited growth when the nullclines do not meet in  $\mathcal{Q}$ .

and predators to increase at the same time. If the prey population is above its limiting value, it must decrease. After a while the lack of prey causes the predator population to begin to decrease (when the solution crosses  $M$ ). After that point the prey population can never increase past  $a/\lambda$ , and so the predator population continues to decrease. If the solution crosses  $L$ , the prey population increases again (but not past  $a/\lambda$ ), while the predators continue to die off. In the limit the predators disappear and the prey population stabilizes at  $a/\lambda$ .

Suppose now that  $L$  and  $M$  cross at a point  $Z = (x_0, y_0)$  in the quadrant  $\mathcal{Q}$ ; of course,  $Z$  is an equilibrium. The linearization of the vector field at  $Z$  is

$$X' = \begin{pmatrix} -\lambda x_0 & -bx_0 \\ dy_0 & -\mu y_0 \end{pmatrix} X.$$

The characteristic polynomial has trace given by  $-\lambda x_0 - \mu y_0 < 0$  and determinant  $(bd + \lambda\mu)x_0 y_0 > 0$ . From the trace-determinant plane of Chapter 4, we see that  $Z$  has eigenvalues that are either both negative or both complex with negative real parts. Hence  $Z$  is asymptotically stable.

Note that, in addition to the equilibria at  $Z$  and  $(0, 0)$ , there is still an equilibrium at  $(a/\lambda, 0)$ . Linearization shows that this equilibrium is a saddle; its stable curve lies on the  $x$ -axis. See Figure 11.7.

It is not easy to determine the basin of  $Z$ , nor do we know whether there are any limit cycles. Nevertheless we can obtain some information. The line  $L$  meets the  $x$ -axis at  $(a/\lambda, 0)$  and the  $y$ -axis at  $(0, a/b)$ . Let  $\Gamma$  be a rectangle whose corners are  $(0, 0)$ ,  $(p, 0)$ ,  $(0, q)$ , and  $(p, q)$  with  $p > a/\lambda$ ,  $q > a/b$ , and the point  $(p, q)$  lying in  $M$ . Every solution at a boundary point of  $\Gamma$  either

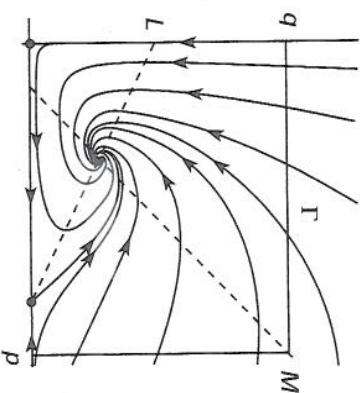


Figure 11.7 The nullclines and phase portrait for a predator/prey system with limited growth when the nullclines do meet in  $\mathcal{Q}$ .

enters  $\Gamma$  or is part of the boundary. Therefore  $\Gamma$  is positively invariant. Every point in  $Q$  is contained in such a rectangle.

By the Poincaré-Bendixson theorem, the  $\omega$ -limit set of any point  $(x, y)$  in  $\Gamma$ , with  $x, y > 0$ , must be a limit cycle or contain one of the three equilibria  $(0, 0)$ ,  $Z$ , or  $(a/\lambda, 0)$ . We rule out  $(0, 0)$  and  $(a/\lambda, 0)$  by noting that these equilibria are saddles whose stable curves lie on the  $x$ - or  $y$ -axes. Therefore  $\omega(x, y)$  is either  $Z$  or a limit cycle in  $\Gamma$ . By Corollary 4 of the Poincaré-Bendixson theorem any limit cycle must surround  $Z$ .

We observe further that any such rectangle  $\Gamma$  contains *all* limit cycles, because a limit cycle (like any solution) must enter  $\Gamma$ , and  $\Gamma$  is positively invariant. Fixing  $(p, q)$  as above, it follows that for any initial values  $(x(0), y(0))$ , there exists  $t_0 > 0$  such that  $x(t) < p, y(t) < q$  if  $t \geq t_0$ . We conclude that in the long run, a solution either approaches  $Z$  or else spirals down to a limit cycle.

From a practical standpoint a solution that tends toward  $Z$  is indistinguishable from  $Z$  after a certain time. Likewise, a solution that approaches a limit cycle  $\gamma$  can be identified with  $\gamma$  after it is sufficiently close. We conclude that any population of predators and prey that obeys these equations eventually settles down to either a constant or periodic population. Furthermore, there are absolute upper bounds that no population can exceed in the long run, no matter what the initial populations are.

### 11.3 Competitive Species

We consider now two species that compete for a common food supply. Instead of analyzing specific equations, we follow a different procedure: We consider a large class of equations about which we assume only a few qualitative features. In this way considerable generality is gained, and little is lost because specific equations can be very difficult to analyze.

Let  $x$  and  $y$  denote the populations of the two species. The equations of growth of the two populations may be written in the form

$$\begin{aligned} x' &= M(x, y)x \\ y' &= N(x, y)y \end{aligned}$$

where the growth rates  $M$  and  $N$  are functions of both variables. As usual, we assume that  $x$  and  $y$  are nonnegative. So the  $x$ -nullclines are given by  $x = 0$  and  $M(x, y) = 0$  and the  $y$ -nullclines are  $y = 0$  and  $N(x, y) = 0$ . We make the following assumptions on  $M$  and  $N$ :

1. Because the species compete for the same resources, if the population of either species increases, then the growth rate of the other goes down.

Hence

$$\frac{\partial M}{\partial y} < 0 \quad \text{and} \quad \frac{\partial N}{\partial x} < 0.$$

2. If either population is very large, both populations decrease. Hence there exists  $K > 0$  such that

$$M(x, y) < 0 \quad \text{and} \quad N(x, y) < 0 \quad \text{if } x \geq K \text{ or } y \geq K.$$

3. In the absence of either species, the other has a positive growth rate up to a certain population and a negative growth rate beyond it. Therefore there are constants  $a, b > 0$  such that

$$\begin{aligned} M(x, 0) &> 0 \text{ for } x < a \quad \text{and} \quad M(x, 0) < 0 \text{ for } x > a, \\ N(0, y) &> 0 \text{ for } y < b \quad \text{and} \quad N(0, y) < 0 \text{ for } y > b. \end{aligned}$$

By conditions (1) and (3) each vertical line  $\{x\} \times \mathbb{R}$  meets the set  $\mu = M^{-1}(0)$  exactly once if  $0 \leq x \leq a$  and not at all if  $x > a$ . By condition (1) and the implicit function theorem,  $\mu$  is the graph of a nonnegative function  $f: [0, a] \rightarrow \mathbb{R}$  such that  $f^{-1}(0) = a$ . Below the curve  $\mu$ ,  $M$  is positive and above it,  $M$  is negative. In the same way the set  $\nu = N^{-1}(0)$  is a smooth curve of the form

$$\{(x, y) \mid x = g(y)\},$$

where  $g: [0, b] \rightarrow \mathbb{R}$  is a nonnegative function with  $g^{-1}(0) = b$ . The function  $N$  is positive to the left of  $\nu$  and negative to the right.

Suppose first that  $\mu$  and  $\nu$  do not intersect and that  $\mu$  is below  $\nu$ . Then the phase portrait can be determined immediately from the nullclines. The equilibria are  $(0, 0)$ ,  $(a, 0)$ , and  $(0, b)$ . The origin is a source, while  $(a, 0)$  is a saddle (assuming that  $(\partial M/\partial x)(a, 0) < 0$ ). The equilibrium at  $(0, b)$  is a sink [again assuming that  $(\partial N/\partial y)(0, b) < 0$ ]. All solutions with  $y_0 > 0$  tend to the asymptotically stable equilibrium  $(0, b)$  with the exception of solutions on the  $x$ -axis. See Figure 11.8. In the case where  $\mu$  lies above  $\nu$ , the situation is reversed, and all solutions with  $x_0 > 0$  tend to the sink that now appears at  $(a, 0)$ .

Suppose now that  $\mu$  and  $\nu$  intersect. We make the assumption that  $\mu \cap \nu$  is a finite set, and at each intersection point,  $\mu$  and  $\nu$  cross *transversely*, that is, they have distinct tangent lines at the intersection points. This assumption may be eliminated; we make it only to simplify the process of determining the flow.

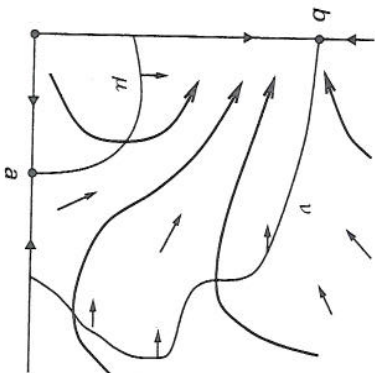


Figure 11.8 The phase portrait when  $\mu$  and  $\nu$  do not meet.

The nullclines  $\mu$  and  $\nu$  and the coordinate axes bound a finite number of connected open sets in the upper-right quadrant: These are the basic regions where  $x' \neq 0$  and  $y' \neq 0$ . They are of four types:

- A:  $x' > 0, y' > 0$       B:  $x' < 0, y' > 0$ ;
- C:  $x' < 0, y' < 0$       D:  $x' > 0, y' < 0$ .

Equivalently, these are the regions where the vector field points northeast, northwest, southwest, or southeast, respectively. Some of these regions are indicated in Figure 11.9. The boundary  $\partial\mathcal{R}$  of a basic region  $\mathcal{R}$  is made up of points of the following types: points of  $\mu \cap \nu$ , called *vertices*; points on  $\mu$  or  $\nu$  but not on both nor on the coordinate axes, called *ordinary boundary points*; and points on the axes.

A vertex is an equilibrium; the other equilibria lie on the axes at  $(0, 0)$ ,  $(a, 0)$ , and  $(0, b)$ . At an ordinary boundary point  $Z \in \partial\mathcal{R}$ , the vector field is either vertical (if  $Z \in \mu$ ) or horizontal (if  $Z \in \nu$ ). This vector points either into or out of  $\mathcal{R}$  since  $\mu$  has no vertical tangents and  $\nu$  has no horizontal tangents. We call  $Z$  an *inward* or *outward* point of  $\partial\mathcal{R}$ , accordingly. Note that, in Figure 11.9, the vector field either points inward at all ordinary points on the boundary of a basic region, or else it points outward at all such points. This is no accident, for we have:

**Proposition.** *Let  $\mathcal{R}$  be a basic region for the competitive species model. Then the ordinary boundary points of  $\mathcal{R}$  are either all inward or all outward.*

**Proof.** There are only two ways in which the curves  $\mu$  and  $\nu$  can intersect at a vertex  $P$ . As  $y$  increases along  $\nu$ , the curve  $\nu$  may either pass from below  $\mu$

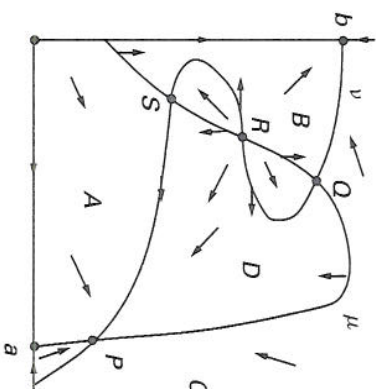


Figure 11.9 The basic regions when the nullclines  $\mu$  and  $\nu$  intersect.

to above  $\mu$ , or from above to below  $\mu$ . These two scenarios are illustrated in Figures 11.10a and b. There are no other possibilities since we have assumed that these curves cross transversely.

Since  $x' > 0$  below  $\mu$  and  $x' < 0$  above  $\mu$ , and since  $y' > 0$  to the left of  $\nu$  and  $y' < 0$  to the right, we therefore have the following configurations for the vector field in these two cases. See Figure 11.11.

In each case we see that the vector field points inward in two opposite basic regions abutting  $P$ , and outward in the other two basic regions.

If we now move along  $\mu$  or  $\nu$  to the next vertex along this curve, we see that adjacent basic regions must maintain their inward or outward configuration. Therefore, at all ordinary boundary points on each basic region, the vector field either points outward or points inward, as required. ■

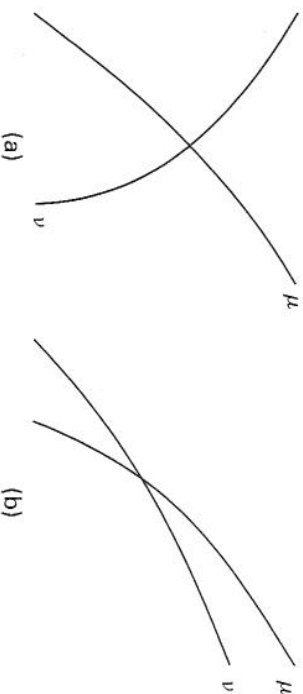


Figure 11.10 In (a),  $\nu$  passes from below  $\mu$  to above  $\mu$  as  $y$  increases. The situation is reversed in (b).



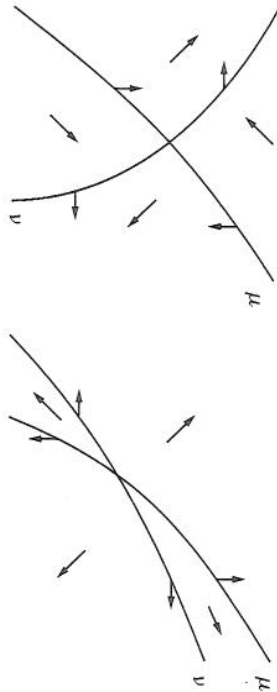


Figure 11.11 Configurations of the vector field near vertices.

As a consequence of the proposition, it follows that each basic region and its closure is either positively or negatively invariant. What are the possible  $\omega$ -limit points of this system? There are no closed orbits. A closed orbit must be contained in a basic region, but this is impossible since  $x(t)$  and  $y(t)$  are monotone along any solution curve in a basic region. Therefore all  $\omega$ -limit points are equilibria.

We note also that each solution is defined for all  $t \geq 0$ , because any point lies in a large rectangle  $\Gamma$  with corners at  $(0, 0)$ ,  $(x_0, 0)$ ,  $(0, y_0)$ , and  $(x_0, y_0)$  with  $x_0 > a$  and  $y_0 > b$ ; such a rectangle is positively invariant. See Figure 11.12. Thus we have shown:

**Theorem.** *The flow  $\phi_t$  of the competitive species system has the following property: For all points  $(x, y)$ , with  $x \geq 0, y \geq 0$ , the limit*

$$\lim_{t \rightarrow \infty} \phi_t(x, y)$$

*exists and is one of a finite number of equilibria.*

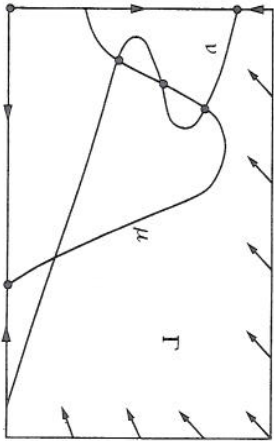


Figure 11.12 All solutions must enter and then remain in  $\Gamma$ .

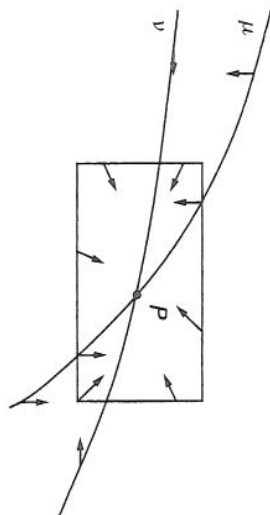


Figure 11.13 This configuration of  $\mu$  and  $\nu$  leads to an asymptotically stable equilibrium point.

We conclude that the populations of two competing species always tend to one of a finite number of limiting populations.

Examining the equilibria for stability, one finds the following results. A vertex where  $\mu$  and  $\nu$  each have negative slope, but  $\mu$  is steeper, is asymptotically stable. See Figure 11.13. One sees this by drawing a small rectangle with sides parallel to the axes around the equilibrium, putting one corner in each of the four adjacent basic regions. Such a rectangle is positively invariant; since it can be arbitrarily small, the equilibrium is asymptotically stable.

This may also be seen as follows. We have

$$\text{slope of } \mu = -\frac{M_x}{M_y} < \text{slope of } \nu = -\frac{N_x}{N_y} < 0,$$

where  $M_x = \partial M/\partial x$ ,  $M_y = \partial M/\partial y$ , and so on, at the equilibrium. Now recall that  $M_y < 0$  and  $N_x < 0$ . Therefore, at the equilibrium point, we also have  $M_x < 0$  and  $N_y < 0$ . Linearization at the equilibrium point yields the matrix

$$\begin{pmatrix} xM_x & xM_y \\ yN_x & yN_y \end{pmatrix}.$$

The trace of this matrix is  $xM_x + yN_y < 0$  while the determinant is  $xy(M_x N_y - M_y N_x) > 0$ . Thus the eigenvalues have negative real parts, and so we have a sink.

A case-by-case study of the different ways  $\mu$  and  $\nu$  can cross shows that the only other asymptotically stable equilibrium in this model is  $(0, b)$  when  $(0, b)$  is above  $\mu$ , or  $(a, 0)$  when  $(a, 0)$  is to the right of  $\nu$ . All other equilibria are unstable. There must be at least one asymptotically stable equilibrium. If  $(0, b)$  is not one, then it lies under  $\mu$ ; and if  $(a, 0)$  is not one, it lies over  $\mu$ . In that case  $\mu$  and  $\nu$  cross, and the first crossing to the left of  $(a, 0)$  is asymptotically stable.

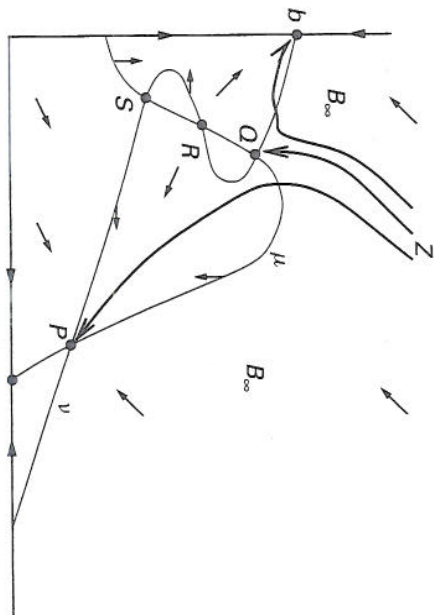


Figure 11.14 Note that solutions on either side of the point  $Z$  in the stable curve of  $Q$  have very different fates.

For example, this analysis tells us that, in Figure 11.14, only  $P$  and  $(0, b)$  are asymptotically stable; all other equilibria are unstable. In particular, assuming that the equilibrium  $Q$  in Figure 11.14 is hyperbolic, then it must be a saddle because certain nearby solutions tend toward it, while others tend away. The point  $Z$  lies on one branch of the stable curve through  $Q$ . All points in the region denoted  $B_\infty$  to the left of  $Z$  tend to the equilibrium at  $(0, b)$ , while points to the right go to  $P$ . Thus as we move across the branch of the stable curve containing  $Z$ , the limiting behavior of solutions changes radically. Since solutions just to the right of  $Z$  tend to the equilibrium point  $P$ , it follows that the populations in this case tend to stabilize. On the other hand, just to the left of  $Z$ , solutions tend to an equilibrium point where  $x = 0$ . Thus in this case, one of the species becomes extinct. A small change in initial conditions has led to a dramatic change in the fate of populations. Ecologically, this small change could have been caused by the introduction of a new pesticide, the importation of additional members of one of the species, a forest fire, or the like. Mathematically, this event is a jump from the basin of  $P$  to that of  $(0, b)$ .

## 11.4 Exploration: Competition and Harvesting

In this exploration we will investigate the competitive species model where we allow either harvesting (emigration) or immigration of one of the species. We

consider the system

$$\begin{aligned}x' &= x(1 - ax - y) \\y' &= y(b - x - y) + h.\end{aligned}$$

Here  $a$ ,  $b$ , and  $h$  are parameters. We assume that  $a$ ,  $b > 0$ . If  $h < 0$ , then we are harvesting species  $y$  at a constant rate, whereas if  $h > 0$ , we add to the population  $y$  at a constant rate. The goal is to understand this system completely for all possible values of these parameters. As usual, we only consider the regime where  $x, y \geq 0$ . If  $y(t) < 0$  for any  $t > 0$ , then we consider this species to have become extinct.

1. First assume that  $h = 0$ . Give a complete synopsis of the behavior of this system by plotting the different behaviors you find in the  $a, b$  parameter plane.
2. Identify the points or curves in the  $ab$ -plane where bifurcations occur when  $h = 0$  and describe them.
3. Now let  $h < 0$ . Describe the  $ab$ -parameter plane for various (fixed)  $h$ -values.
4. Repeat the previous exploration for  $h > 0$ .
5. Describe the full three-dimensional parameter space using pictures, flip books, 3D models, movies, or whatever you find most appropriate.

### EXERCISES

1. For the SIRS model, prove that all solutions in the triangular region  $\Delta$  tend to the equilibrium point  $(\tau, 0)$  when the total population does not exceed the threshold level for the disease.
2. Sketch the phase plane for the following variant of the predator/prey system:

$$\begin{aligned}x' &= x(1 - x) - xy \\y' &= y\left(1 - \frac{y}{x}\right).\end{aligned}$$

3. A modification of the predator/prey equations is given by

$$\begin{aligned}x' &= x(1 - x) - \frac{axy}{x + 1} \\y' &= y(1 - y)\end{aligned}$$

where  $a > 0$  is a parameter.

- (a) Find all equilibrium points and classify them.  
 (b) Sketch the nullclines and the phase portraits for different values of  $a$ .  
 (c) Describe any bifurcations that occur as  $a$  varies.

4. Another modification of the predator/prey equations is given by

$$\begin{aligned}x' &= x(1-x) - \frac{xy}{x+b} \\y' &= y(1-y)\end{aligned}$$

where  $b > 0$  is a parameter.

- (a) Find all equilibrium points and classify them.  
 (b) Sketch the nullclines and the phase portraits for different values of  $b$ .  
 (c) Describe any bifurcations that occur as  $b$  varies.

5. The equations

$$\begin{aligned}x' &= x(2-x-y), \\y' &= y(3-2x-y)\end{aligned}$$

satisfy conditions (1) through (3) in Section 11.3 for competing species. Determine the phase portrait for this system. Explain why these equations make it mathematically possible, but extremely unlikely, for both species to survive.

6. Consider the competing species model

$$\begin{aligned}x' &= x(a-x-ay) \\y' &= y(b-bx-y)\end{aligned}$$

where the parameters  $a$  and  $b$  are positive.

- (a) Find all equilibrium points for this system and determine their stability type. These types will, of course, depend on  $a$  and  $b$ .  
 (b) Use the nullclines to determine the various phase portraits that arise for different choices of  $a$  and  $b$ .  
 (c) Determine the values of  $a$  and  $b$  for which there is a bifurcation in this system and describe the bifurcation that occurs.  
 (d) Record your findings by drawing a picture of the  $ab$ -plane and indicating in each open region of this plane the qualitative structure of the corresponding phase portraits.

7. Two species  $x, y$  are in *symbiosis* if an increase of either population leads to an increase in the growth rate of the other. Thus we assume

$$\begin{aligned}x' &= M(x, y)x \\y' &= N(x, y)y\end{aligned}$$

with

$$\frac{\partial M}{\partial y} > 0 \quad \text{and} \quad \frac{\partial N}{\partial x} > 0$$

and  $x, y \geq 0$ . We also suppose that the total food supply is limited; hence for some  $A > 0, B > 0$  we have

$$\begin{aligned}M(x, y) &< 0 \quad \text{if } x > A, \\N(x, y) &< 0 \quad \text{if } y > B.\end{aligned}$$

If both populations are very small, they both increase; hence

$$M(0, 0) > 0 \quad \text{and} \quad N(0, 0) > 0.$$

Assuming that the intersections of the curves  $M^{-1}(0), N^{-1}(0)$  are finite, and that all are transverse, show the following:

- (a) Every solution tends to an equilibrium in the region  $0 < x < A, 0 < y < B$ .  
 (b) There are no sources.  
 (c) There is at least one sink.  
 (d) If  $\partial M/\partial x < 0$  and  $\partial N/\partial y < 0$ , there is a unique sink  $Z$ , and  $Z$  is the  $\omega$ -limit set for all  $(x, y)$  with  $x > 0, y > 0$ .

8. Give a system of differential equations for a pair of mutually destructive species. Then prove that, under plausible hypotheses, two mutually destructive species cannot coexist in the long run.

9. Let  $y$  and  $x$  denote predator and prey populations. Let

$$\begin{aligned}x' &= M(x, y)x \\y' &= N(x, y)y\end{aligned}$$

where  $M$  and  $N$  satisfy the following conditions.

- (a) If there are not enough prey, the predators decrease. Hence for some  $b > 0$

$$N(x, y) < 0 \quad \text{if } x < b.$$

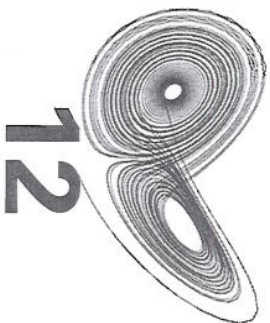
- (b) An increase in the prey improves the predator growth rate; hence  $\partial N/\partial x > 0$ .
- (c) In the absence of predators a small prey population will increase; hence  $M(0, 0) > 0$ .
- (d) Beyond a certain size, the prey population must decrease; hence there exists  $A > 0$  with  $M(x, y) < 0$  if  $x > A$ .
- (e) Any increase in predators decreases the rate of growth of prey; hence  $\partial M/\partial y < 0$ .
- (f) The two curves  $M^{-1}(0)$ ,  $N^{-1}(0)$  intersect transversely and at only a finite number of points.

Show that if there is some  $(u, v)$  with  $M(u, v) > 0$  and  $N(u, v) > 0$  then there is either an asymptotically stable equilibrium or an  $\omega$ -limit cycle. Moreover, show that, if the number of limit cycles is finite and positive, one of them must have orbits spiraling toward it from both sides.

10. Consider the following modification of the predator/prey equations:

$$\begin{aligned}x' &= x(1 - x) - \frac{axy}{x + c} \\y' &= by \left(1 - \frac{y}{x}\right)\end{aligned}$$

where  $a$ ,  $b$ , and  $c$  are positive constants. Determine the region in the parameter space for which this system has a stable equilibrium with both  $x, y \neq 0$ . Prove that, if the equilibrium point is unstable, this system has a stable limit cycle.



## Applications in Circuit Theory

In this chapter we first present a simple but very basic example of an electrical circuit and then derive the differential equations governing this circuit. Certain special cases of these equations are analyzed using the techniques developed in Chapters 8 through 10 in the next two sections; these are the classical equations of Lienard and van der Pol. In particular, the van der Pol equation could perhaps be regarded as one of the fundamental examples of a nonlinear ordinary differential equation. It possesses an oscillation or periodic solution that is a periodic attractor. Every nontrivial solution tends to this periodic solution; no linear system has this property. Whereas asymptotically stable equilibria sometimes imply death in a system, attracting oscillators imply life. We give an example in Section 12.4 of a continuous transition from one such situation to the other.

### 12.1 An RLC Circuit

In this section, we present our first example of an electrical circuit. This circuit is the simple but fundamental series RLC circuit displayed in Figure 12.1. We begin by explaining what this diagram means in mathematical terms. The circuit has three *branches*, one resistor marked by  $R$ , one inductor marked by  $L$ , and one capacitor marked by  $C$ . We think of a branch of this circuit as a