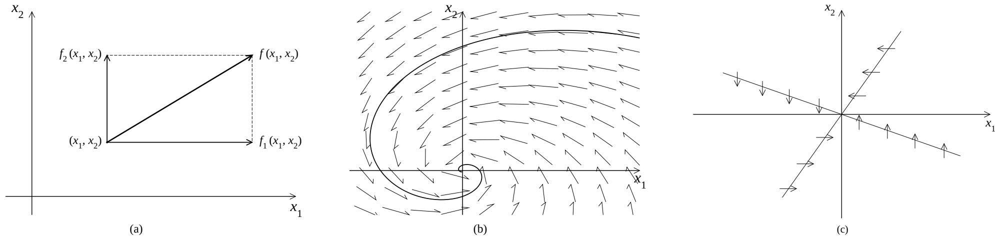

Figure 3.6. *(a) Construction of the vector field for (3.14); (b) The vector field for Example 3.4.2 and one typical trajectory; (c) the nullclines with vector field at the nullclines.*

3.4 Qualitative Analysis of 2×2 Systems

In this section, we develop a qualitative theory for systems of two differential equations, much in the spirit of Section 3.2 where we introduced phase-line and vector-field analyses. Here, we will use *phase-plane* analysis, *vector-field* analysis and the *phase portrait*. With these methods, the qualitative behaviour of a system of equations can be understood without solving the equations explicitly. Explicit solution methods can be found in textbooks on ODEs (such as Boyce and DiPrima [21]).

Consider a system of two differential equations,

$$\begin{aligned} x_1' &= f_1(x_1, x_2), \\ x_2' &= f_2(x_1, x_2). \end{aligned} \tag{3.14}$$

At each $x = (x_1, x_2) \in \mathbb{R}^2$, the *vector field* $f(x) = (f_1(x), f_2(x))$ represents a vector, as shown in Figure 3.6. A solution $x(t) = (x_1(t), x_2(t))$ represents a parametric curve in the (x_1, x_2) plane, called a *trajectory* or an *orbit*, whose tangent vector $x'(t) = (x_1'(t), x_2'(t))$ is specified by the *vector field* $f(x(t)) = (f_1(x_1(t), x_2(t)), f_2(x_1(t), x_2(t)))$. We can obtain a good impression of the overall dynamics if we plot many vectors in the (x_1, x_2) plane. For each chosen point (x_1, x_2), we calculate $(f_1(x_1, x_2),\ f_2(x_1, x_2))$ and sketch this vector. We repeat this procedure at many different points until the whole plane is filled with vectors. In Figure 3.6 (a), we show how to calculate one such vector.

Since solution curves are tangential to the vector field, f, we often can follow trajectories just by following the arrows. In Figure 3.6 (b), a typical solution curve is shown (in this case, we have a stable spiral converging at the origin). The vector field can be used to sketch more than one typical solutions, starting at different initial conditions. The sketch of the (x_1, x_2) plane with a number of typical solutions is called a *phase portrait*. Of course, "typical" is a rather vague notion and you need some experience to be able to decide which solutions represent the qualitative behaviour. We will demonstrate and practice this in what follows.

Many computer packages provide a routine to draw the vector field and the phase portrait of an ODE system. In Chapter 8, we will learn how to do this with Maple.

Another helpful tool for obtaining insight into the phase portrait are *nullclines* (or 0-*isoclines*). The x_1-nullcline, n_1, is the set of points (x_1, x_2) such that $x_1' = f(x_1, x_2) = 0$, that is,

$$n_1 := \{(x_1, x_2) | f_1(x_1, x_2) = 0\}.$$

Similarly, the x_2-nullcline, n_2, is

$$n_2 := \{(x_1, x_2) | f_2(x_1, x_2) = 0\}.$$

On the x_1-nullcline, n_1, all vectors of the vector field are vertical (since $x_1' = 0$). Similarly, on n_2, all vectors are horizontal (since $x_2' = 0$). At intersections of n_1 and n_2, we have $x_1' = 0$ and $x_2' = 0$. Hence a *steady state* or *equilibrium point* exists at any intersection of n_1 and n_2. In Figure 3.6 (c), we show the nullclines corresponding to the vector field of Figure 3.6 (b) and the corresponding steady state at the origin.

In general, *equilibria*, or *steady states* of (3.14) are solutions of

$$f_1(x_1, x_2) = 0, \qquad f_2(x_1, x_2) = 0,$$

which we denote by $(\bar{x}_1, \bar{x}_2)$. The steady states play an important role in the understanding of the model dynamics. In many cases, if the behaviour near each steady state is known, then the global behaviour of solutions can be understood quite well. It turns out that we can classify all possible types of behaviour which can occur near a steady state. We will do so in the following two sections. In Section 3.4.1, we first treat specific linear systems. After that, we generalize to arbitrary linear systems. In Section 3.4.2, we consider nonlinear systems. Phase-plane analysis will then be applied to the population interaction model (in Section 3.4.3) and the epidemic model (in Section 3.4.4).

3.4.1 Phase-Plane Analysis: Linear Systems

Step 1: Specific Linear Systems

1a) Real eigenvalues

Consider the simplest linear system,

$$\begin{aligned} x_1' &= \lambda_1 x_1, \\ x_2' &= \lambda_2 x_2, \end{aligned} \tag{3.15}$$

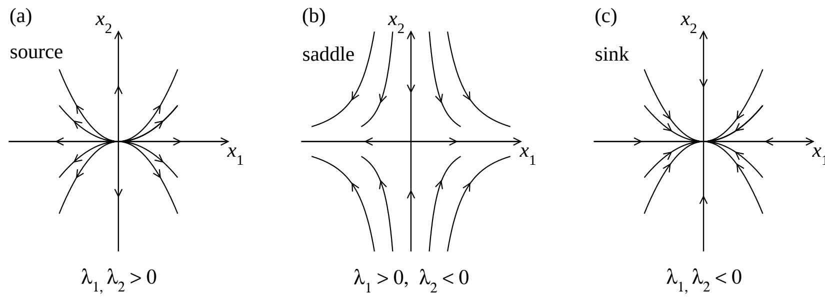

Figure 3.7. *Three qualitatively different phase portraits for system (3.15) depending on the sign pattern of λ_1 and λ_2. (a) $\lambda_1, \lambda_2 > 0$; (b) $\lambda_1 > 0$, $\lambda_2 < 0$; (c) $\lambda_1, \lambda_2 < 0$.*

whose unique steady state is the origin, $(\bar{x}_1, \bar{x}_2) = (0, 0)$. In matrix form, we can write

$$\frac{d}{dt}\begin{pmatrix} x_1 \\ x_2 \end{pmatrix} = \begin{pmatrix} \lambda_1 & 0 \\ 0 & \lambda_2 \end{pmatrix}\begin{pmatrix} x_1 \\ x_2 \end{pmatrix}.$$

Note that λ_1 and λ_2 are the *eigenvalues* of the matrix

$$A = \begin{pmatrix} \lambda_1 & 0 \\ 0 & \lambda_2 \end{pmatrix}.$$

Solutions to (3.15) are

$$x_1(t) = x_1(0)e^{\lambda_1 t}, \qquad x_2(t) = x_2(0)e^{\lambda_2 t}.$$

Plotting the parametric curves $(x_1(t), x_2(t))$ for different initial values $(x_1(0), x_2(0))$, we arrive at three distinct phase portraits, depending on the signs of λ_1 and λ_2, as shown in Figure 3.7.

Case (a): If both eigenvalues λ_1 and λ_2 are positive, then all solutions diverge from the steady state $(0, 0)$. In Figure 3.7 (a), several trajectories are shown for positive, negative, or mixed initial conditions. In this case, the steady state $(0, 0)$ is called a *source* or an *unstable node.*

Case (b): If the eigenvalues have opposite signs, $\lambda_1 > 0$ and $\lambda_2 < 0$, say, then $x_1(t)$ is exponentially increasing, while $x_2(t)$ is decreasing. All solutions approach the x_1-axis, as shown in Figure 3.7 (b). In this case, the steady state $(0, 0)$ is called a *saddle.*

Case (c): If both eigenvalues are negative, then all solutions converge to the steady state $(0, 0)$, as shown in Figure 3.7 (c). The steady state is called a *sink* or *stable node.*

1b) Complex eigenvalues

Consider the linear system

$$\frac{d}{dt}\begin{pmatrix} x_1 \\ x_2 \end{pmatrix} = \begin{pmatrix} \alpha & \beta \\ -\beta & \alpha \end{pmatrix}\begin{pmatrix} x_1 \\ x_2 \end{pmatrix}. \tag{3.16}$$

For $\beta \neq 0$, the system has the origin, $(0,0)$, as its only steady state. The coefficient matrix $A = \begin{pmatrix} \alpha & \beta \\ -\beta & \alpha \end{pmatrix}$ has two complex conjugate eigenvalues

$$\lambda_1 = \alpha + \beta i \qquad \text{and} \qquad \lambda_2 = \alpha - \beta i.$$

We can verify (see Exercise 3.9.8) that (3.16) has two special solutions, namely

$$x^{(1)}(t) = e^{\alpha t}\begin{pmatrix} \cos\beta t \\ -\sin\beta t \end{pmatrix}, \qquad x^{(2)}(t) = e^{\alpha t}\begin{pmatrix} \sin\beta t \\ \cos\beta t \end{pmatrix}.$$

The superposition principle of linear systems implies that all solutions to (3.16) are of the form

$$x(t) = c_1 x^{(1)}(t) + c_2 x^{(2)}(t) = a e^{\alpha t}\begin{pmatrix} \cos(\beta t + \phi) \\ -\sin(\beta t + \phi) \end{pmatrix}$$

or

$$\begin{aligned} x_1(t) &= a e^{\alpha t}\cos(\beta t + \phi), \\ x_2(t) &= -a e^{\alpha t}\sin(\beta t + \phi), \end{aligned} \tag{3.17}$$

where a and ϕ are determined by the initial conditions, $(x_1(0), x_2(0))$.

Using (3.17), we can classify three distinct cases, shown in Figure 3.8.

Case (a): $\alpha = 0$, so that both eigenvalues are purely imaginary. All solutions are periodic, and all trajectories are closed orbits surrounding the steady state $(0,0)$, as shown in Figure 3.8 (a). The steady state is called a *center*.

Case (b): $\alpha > 0$, so that both eigenvalues have positive real parts. The exponential function $e^{\alpha t}$ grows for $t > 0$. All trajectories spiral away from the steady state $(0,0)$, as shown in Figure 3.8 (b). The steady state is called an *unstable spiral* or a *spiral source*.

Case (c): $\alpha < 0$, so that both eigenvalues have negative real parts. The exponential function $e^{\alpha t}$ decays for $t > 0$. All trajectories spiral towards the steady state $(0,0)$, as shown in Figure 3.8 (c). The steady state is called a *stable spiral* or a *spiral sink*.

Corresponding solutions $x_1(t)$ for each case are shown in Figure 3.8 as well.

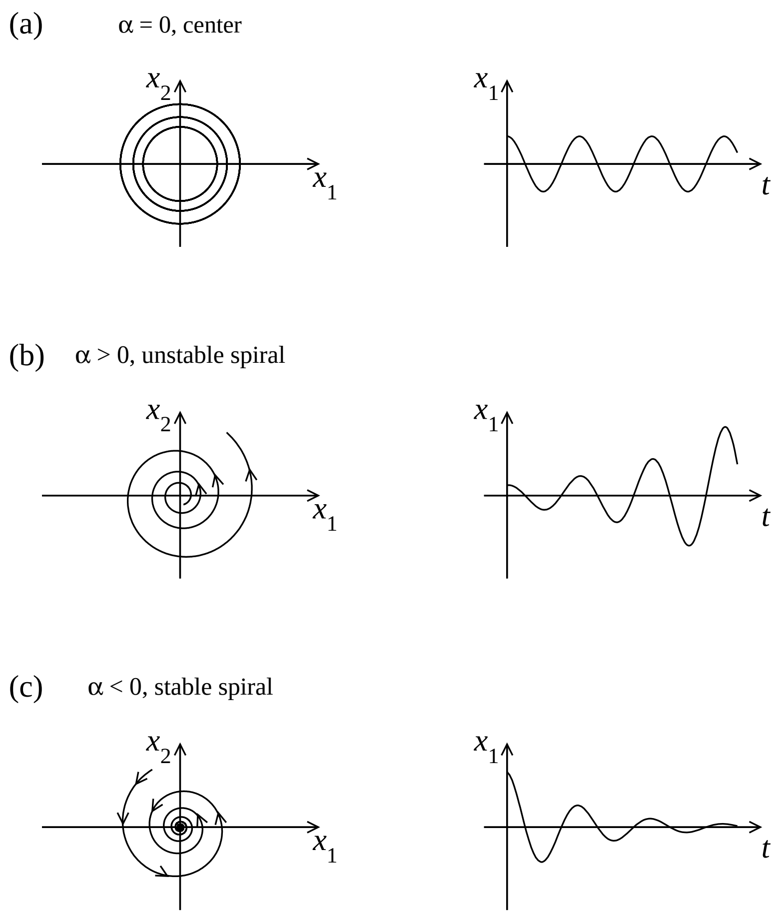

Figure 3.8. *Three qualitatively different cases for system (3.16), depending on the value of the parameter α. (a) $\alpha = 0$; (b) $\alpha > 0$; (c) $\alpha < 0$. Graphs in the left column show phase portraits. Graphs in the right column show a typical solution for $x_1(t)$.*

Step 2: General Linear Systems

We now consider a general linear system,

$$\frac{d}{dt}\begin{pmatrix} x_1 \\ x_2 \end{pmatrix} = \begin{pmatrix} a & b \\ c & d \end{pmatrix}\begin{pmatrix} x_1 \\ x_2 \end{pmatrix}, \qquad A = \begin{pmatrix} a & b \\ c & d \end{pmatrix}. \tag{3.18}$$

If we make the transformation

$$\begin{pmatrix} y_1 \\ y_2 \end{pmatrix} = P^{-1}\begin{pmatrix} x_1 \\ x_2 \end{pmatrix},$$

where P is a 2×2 invertible matrix, then $y = (y_1, y_2)$ satisfies the system

$$\frac{d}{dt}\begin{pmatrix} y_1 \\ y_2 \end{pmatrix} = B\begin{pmatrix} y_1 \\ y_2 \end{pmatrix}, \tag{3.19}$$

where $B = P^{-1}AP$. Systems (3.18) and (3.19) have the same phase portraits.

It is known from linear algebra (see [97]) that if A has two distinct real eigenvalues λ_1 and λ_2 such that $\lambda_1 \neq \lambda_2$, then we can choose P such that

$$B = \begin{pmatrix} \lambda_1 & 0 \\ 0 & \lambda_2 \end{pmatrix}.$$

If A has two complex conjugate eigenvalues $\lambda_1 = \bar{\lambda}_2 = \alpha + \beta i$, then we can choose P such that

$$B = \begin{pmatrix} \alpha & \beta \\ -\beta & \alpha \end{pmatrix}.$$

Thus, we conclude that the phase portraits of (3.18) will be the same as those of systems (3.15) or (3.16), studied earlier. Before presenting a theorem about the stability of the origin, we work out the details of computing the matrix B for two specific examples.

Example 3.4.1: Consider the linear system

$$\begin{aligned} \dot{x} &= 2x - 2y, \\ \dot{y} &= 2x - 3y. \end{aligned} \tag{3.20}$$

In vector matrix notation, we have

$$\frac{d}{dt}\begin{pmatrix} x \\ y \end{pmatrix} = \begin{pmatrix} 2 & -2 \\ 2 & -3 \end{pmatrix}\begin{pmatrix} x \\ y \end{pmatrix}, \quad A = \begin{pmatrix} 2 & -2 \\ 2 & -3 \end{pmatrix}\begin{pmatrix} x \\ y \end{pmatrix}.$$

It is straightforward to verify that the eigenvalues and corresponding eigenvectors of A are $\lambda_1 = 1$, $\zeta_1 = \binom{2}{1}$ and $\lambda_2 = -2$, $\zeta_2 = \binom{1}{2}$.

The eigenvalues of A are real and distinct. If we use the eigenvalues ζ_1 and ζ_2 as columns of a matrix P, we obtain the transformation

$$P = \begin{pmatrix} 2 & 1 \\ 1 & 2 \end{pmatrix}, \quad P^{-1} = \frac{1}{3}\begin{pmatrix} 2 & -1 \\ -1 & 2 \end{pmatrix},$$

then

$$B = P^{-1}AP = \begin{pmatrix} 1 & 0 \\ 0 & -2 \end{pmatrix}.$$

From the solution of the related linear system

$$\frac{d}{dt}\begin{pmatrix} u \\ v \end{pmatrix} = \begin{pmatrix} 1 & 0 \\ 0 & -2 \end{pmatrix}\begin{pmatrix} u \\ v \end{pmatrix}, \tag{3.21}$$

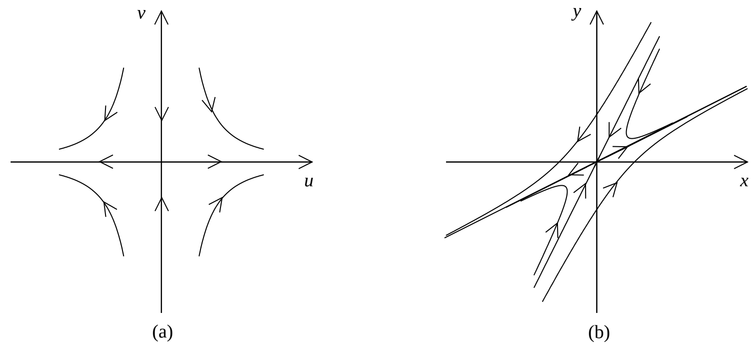

Figure 3.9. *The phase portraits of (3.21) (a) and (3.20) (b).*

we can recover the solution of (3.20) via

$$\begin{pmatrix} x \\ y \end{pmatrix} = P \begin{pmatrix} u \\ v \end{pmatrix}.$$

The phase portrait of (3.21) is shown in Figure 3.9 (a), and the corresponding phase portrait of (3.20) is shown in Figure 3.9 (b). The transformation P maps the unstable direction $\binom{1}{0}$ of (3.21) onto the unstable direction $\binom{2}{1}$ of (3.20). Similarly, the stable direction $\binom{0}{1}$ of (3.21) is mapped onto the stable direction $\binom{1}{2}$ of (3.20). Note that the phase portrait shown in Figure 3.9 (b) is a compressed and rotated version of the phase portrait shown in Figure 3.9 (a).

Example 3.4.2: We consider the system

$$\frac{d}{dt}\begin{pmatrix} x \\ y \end{pmatrix} = \begin{pmatrix} -1 & -2 \\ 2 & -1 \end{pmatrix}\begin{pmatrix} x \\ y \end{pmatrix}.$$

The eigenvalues of the corresponding matrix are $\lambda_1 = -1+2i$ and $\lambda_2 = \bar{\lambda}_1 = -1-2i$. The corresponding (complex) eigenvectors are $\zeta_1 = \binom{i}{1}$ and $\zeta_2 = \binom{-i}{1}$. The solution can be written in the general form

$$\begin{pmatrix} x \\ y \end{pmatrix}(t) = e^{-t}\left(c_1\begin{pmatrix} -\sin(2t) \\ \cos(2t) \end{pmatrix} + c_2\begin{pmatrix} \cos(2t) \\ \sin(2t) \end{pmatrix}\right)$$

(for a reminder on the details, see Boyce and DiPrima [21] or Hirsch and Smale [78]), which describes a rotation that converges to 0 (because of e^{-t}). The steady state $(0,0)$ is a stable spiral. The vector field and one solution curve were shown in Figure 3.6 (b).

In all the cases discussed above, solutions only converge to the steady state at $(0,0)$ when both eigenvalues $\lambda_1, \lambda_2 < 0$ (the origin is a stable node), or when the real part of the eigenvalues satisfies $\alpha < 0$ (the origin is a stable spiral). In these two cases we call the steady state at $(0,0)$ *asymptotically stable*.

We have seen that we can classify the equilibria of a linear system according to the eigenvalues of the corresponding coefficient matrix,

$$A = \begin{pmatrix} a & b \\ c & d \end{pmatrix}.$$

Sometimes it is more convenient to use two other characteristic values of A, namely the *trace*, $\text{tr } A = a + d$, and the *determinant*, $\det A = ad - bc$. It is known that the trace is always the sum of the eigenvalues, $\text{tr } A = \lambda_1 + \lambda_2$, and the determinant is the product, $\det A = \lambda_1\lambda_2$. Moreover, one can use the trace and determinant to calculate the eigenvalues. In Exercise 3.9.9, the reader is asked to show that

$$\lambda_{1,2} = \frac{\text{tr } A}{2} \pm \frac{1}{2}\sqrt{(\text{tr } A)^2 - 4 \det A}. \tag{3.22}$$

Note that the formula in (3.22) holds only for 2×2 matrices. For higher-order matrices, there is no formula of this form.

From (3.22), we see that it is necessary to have $\text{tr } A < 0$ in order to have a steady state that is asymptotically stable (otherwise at least one eigenvalue would have a positive real part). If $\text{tr } A < 0$, then the discriminant, $(\text{tr } A)^2 - 4 \det A$, is either negative or smaller than $(\text{tr } A)^2$. Hence the real part of the eigenvalues is always negative, and $(0, 0)$ is asymptotically stable. We can summarize our conclusions in the following theorem.

Theorem 3.3. *For a linear system, (3.18), the following are equivalent:*

- *the equilibrium* $(0, 0)$ *is asymptotically stable;*
- *all eigenvalues of A have negative real parts;*
- $\det A = ad - bc > 0$ *and* $\text{tr } A = a + d < 0$.

We can treat all different combinations for the sign of trace and determinant, and obtain a complete picture of possible behaviour near an equilibrium point. Figure 3.10 shows the "zoo" of all possible types of behaviour for steady states of two-dimensional systems.

We can summarize the possible types of behaviour as follows:

1. Case $\det A < 0$. Then $(\text{tr } A)^2 - 4 \det A > (\text{tr } A)^2$. From formula (3.22), it follows that there is one positive and one negative eigenvalue, $\lambda_1 > 0$ and $\lambda_2 < 0$, say. Hence, (0,0) is a saddle point. Moreover, solutions grow as $e^{\lambda_1 t}$ in the direction of the eigenvector φ_1 corresponding to λ_1, and solutions decay as $e^{\lambda_2 t}$ in the direction of the eigenvector φ_2 corresponding to λ_2. In Figure 3.10, the *stable* and *unstable* eigenvectors are shown.

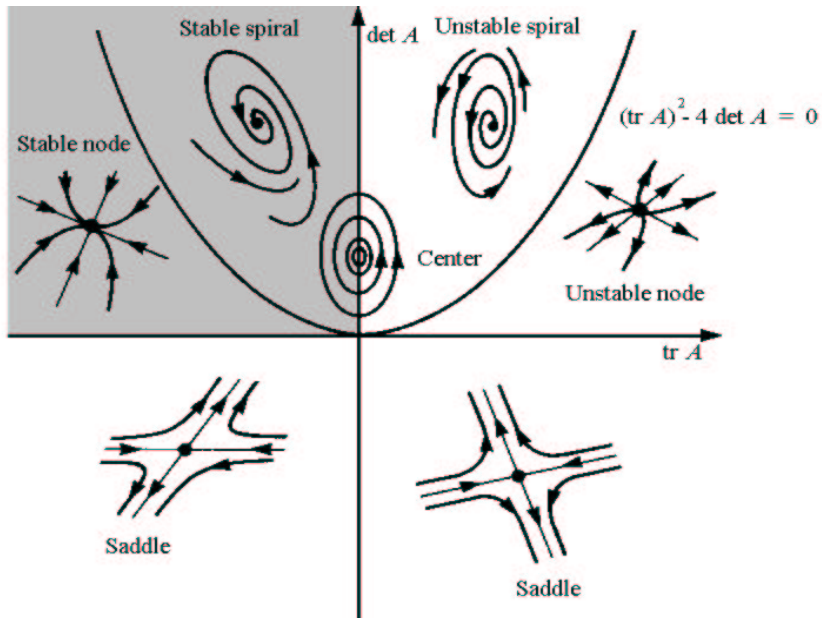

Figure 3.10. *The zoo for the general linear system, (3.18). This is a modified version of Figure 5.14 in Edelstein-Keshet [44] used with permission.*

2. Case $\det A > 0$, $\operatorname{tr} A < 0$. If $(\operatorname{tr} A)^2 < 4 \det A$ (above the parabola in Figure 3.10), then λ_1, λ_2 are complex conjugate eigenvalues with real part $\frac{\operatorname{tr} A}{2} < 0$, and $(0,0)$ is a stable spiral. If $(\operatorname{tr} A)^2 > 4 \det A$ (below the parabola), then λ_1, λ_2 are real, but they have the same sign, and $(0,0)$ is a stable node.

3. Case $\det A > 0$, $\operatorname{tr} A > 0$. Depending on the sign of $(\operatorname{tr} A)^2 - 4 \det A$, we have either an unstable spiral or an unstable node.

4. Case $\det A > 0$, $\operatorname{tr} A = 0$. In this case we have a center.

5. The remaining cases ($\det A = 0$ and $(\operatorname{tr} A)^2 - 4 \det A = 0$) will not be discussed. We refer to Hirsch and Smale [78] for these cases.

3.4.2 Nonlinear Systems and Linearization

Consider a nonlinear system in $\mathbb{R}^2$,

$$\begin{aligned} x_1' &= f_1(x_1, x_2), \\ x_2' &= f_2(x_1, x_2), \end{aligned} \tag{3.23}$$

where f_1 and f_2 are continuously differentiable functions.

In general, each pair $(\bar{x}_1, \bar{x}_2)$ satisfying $f_1(\bar{x}_1, \bar{x}_2) = f_2(\bar{x}_1, \bar{x}_2) = 0$ is called an equilibrium or a steady state for (3.23). We would like to understand the behaviour of the solutions near equilibria.

For linear systems, we observed that solutions converge to $(0, 0)$, they diverge away from $(0, 0)$, or, in the center case, they stay close by. Before we can generalize these observations to nonlinear systems, we need some definitions from dynamical systems theory (see Perko [124]).

Definition 3.4.

a) *A steady state* $(\bar{x}_1, \bar{x}_2)$ *is called* stable *if a solution which starts nearby stays nearby.*

   More formally: $(\bar{x}_1, \bar{x}_2)$ is stable if for all $\varepsilon > 0$, there exists a $\delta > 0$ such that solutions to initial data (x_1^0, x_2^0) with $||(x_1^0, x_2^0) - (\bar{x}_1, \bar{x}_2)|| < \delta$, satisfy $||(x_1(t), x_2(t)) - (\bar{x}_1, \bar{x}_2)|| < \varepsilon$ for all time $t > 0$. Here, $||.||$ denotes the Euclidean vector norm.

b) *A steady state* $(\bar{x}_1, \bar{x}_2)$ *which is not stable is called* unstable *(there is at least one solution which diverges from* $(\bar{x}_1, \bar{x}_2)$*).*

c) *A steady state* $(\bar{x}_1, \bar{x}_2)$ *is called* asymptotically stable *if all solutions near* $(\bar{x}_1, \bar{x}_2)$ *converge to* $(\bar{x}_1, \bar{x}_2)$*.*

   More formally: $(\bar{x}_1, \bar{x}_2)$ *is asymptotically stable if* $(\bar{x}_1, \bar{x}_2)$ *is stable, and there exists a* $\delta > 0$ *such that all solutions with initial data* (x_1^0, x_2^0)*, with* $||(x_1^0, x_2^0) - (\bar{x}_1, \bar{x}_2)|| < \delta$*, satisfy* $\lim_{t\to\infty} ||(x_1(t), x_2(t)) - (\bar{x}_1, \bar{x}_2)|| = 0$.

We can determine the stability of a steady state $(\bar{x}_1, \bar{x}_2)$ by linearizing (3.23). The process is similar to the linearization of discrete-time systems, treated in Section 2.3.2.

Let

$$x_1(t) = \bar{x}_1 + z_1(t),$$
$$x_2(t) = \bar{x}_2 + z_2(t),$$

where $z_1(t)$ and $z_2(t)$ are assumed to be small, so that they can be thought of as perturbations to the steady state. We denote $\bar{x} = (\bar{x}_1, \bar{x}_2)$ and $z = (z_1, z_2)$, and write the Taylor expansion of $f = (f_1, f_2)$ about $(\bar{x}_1, \bar{x}_2)$:

$$f(\bar{x} + z) = f(\bar{x}) + Df(\bar{x}) \cdot z + \text{higher-order terms},$$

where

$$Df(\bar{x}_1, \bar{x}_2) := \begin{pmatrix} a & b \\ c & d \end{pmatrix} = \begin{pmatrix} \frac{\partial f_1}{\partial x_1} & \frac{\partial f_1}{\partial x_2} \\ \frac{\partial f_2}{\partial x_1} & \frac{\partial f_2}{\partial x_2} \end{pmatrix}\Bigg|_{(x_1,x_2)=(\bar{x}_1,\bar{x}_2)}$$

contains the partial derivatives of f evaluated at $(\bar{x}_1, \bar{x}_2)$ (for a reminder on partial derivatives, see Section 4.1). The matrix $Df(\bar{x}_1, \bar{x}_2)$ is called the *Jacobian matrix* of f at $(\bar{x}_1, \bar{x}_2)$.

We substitute the Taylor expansion into (3.23) and we drop the higher-order terms. Since $x_1' = \frac{d}{dt}(\bar{x}_1 + z_1(t)) = z_1'$ and $x_2' = z_2'$, and since $f(\bar{x}) = 0$, we obtain a linear system governing the dynamics of the perturbation (z_1, z_2):

$$\frac{d}{dt}\begin{pmatrix} z_1 \\ z_2 \end{pmatrix} = \begin{pmatrix} a & b \\ c & d \end{pmatrix} \begin{pmatrix} z_1 \\ z_2 \end{pmatrix}. \tag{3.24}$$

We know already from the previous section how to treat linear systems. For most (but not all) steady states, conclusions obtained for the linearized system indeed carry over to the original nonlinear system.

Definition 3.5. $(\bar{x}_1, \bar{x}_2)$ *is called* hyperbolic *if all eigenvalues of the Jacobian* $Df(\bar{x}_1, \bar{x}_2)$ *have nonzero real part.*

Theorem 3.6. *(Hartman-Grobman) Assume that* $(\bar{x}_1, \bar{x}_2)$ *is a hyperbolic equilibrium. Then, in a small neighbourhood of* $(\bar{x}_1, \bar{x}_2)$*, the phase portrait of the nonlinear system, (3.23), is the same as that of the linearized system, (3.24).*

Remark 3.4.1.

1) By Theorems 3.3 and 3.6, at a hyperbolic equilibrium $\bar{x}$, stability properties are determined by the eigenvalues of the Jacobian matrix, $Df(\bar{x}_1, \bar{x}_2)$. This method of linearization may fail for nonhyperbolic equilibria.

2) The phrase "the same as" in the above Theorem refers to *topological equivalence* of vector fields. This means that in a neighbourhood of $(\bar{x}_1, \bar{x}_2)$, there is a homeomorphism (a continuous one-to-one map between open sets) which maps the vector field of the nonlinear system to the vector field of its linearization. In that case, the phase portrait near the stationary point is one of those shown in Figure 3.10. The theory behind the Hartman-Grobman Theorem is beyond the scope of this book, and we refer to Perko [124] for more details.

   For example the two phase portraits in Figure 3.9 are topologically equivalent, and the homeomorphism is given by the matrix P from Example 3.4.1.

3.4.3 Qualitative Analysis of the General Population Interaction Model

In this section, we use the qualitative theory developed above to re-examine the general 2-species model, (3.8). From the 10 different cases summarized in Table 3.1, we select one example for predator-prey, one example for mutualism, and one example for competition, and treat these in detail. The other cases are left as exercises. Before we consider specific cases, we determine the steady states and their linearizations.

We begin by writing (3.8) in vector notation:

$$\frac{d}{dt}\begin{pmatrix} x \\ y \end{pmatrix} = \begin{pmatrix} f_1(x,y) \\ f_2(x,y) \end{pmatrix}, \tag{3.25}$$

with $f_1(x,y) = \alpha x + \beta xy$ and $f_2(x,y) = \gamma y + \delta xy$. To find the x-nullcline, n_x, we set $f_1 = 0$. Hence,

$$n_x = \{(x,y)|x = 0, \text{ or } y = -\frac{\alpha}{\beta}\}.$$

Similarly, the y-nullcline is

$$n_y = \{(x,y)|y = 0, \text{ or } x = -\frac{\gamma}{\delta}\}.$$

The steady states $(\bar{x},\bar{y})$ are intersection points of the nullclines, and they satisfy $f_1(\bar{x},\bar{y}) = 0$ and $f_2(\bar{x},\bar{y}) = 0$. We find two steady states, namely

$$P_1 = (0,0) \quad \text{and} \quad P_2 = \left(-\frac{\gamma}{\delta}, -\frac{\alpha}{\beta}\right).$$

The linearization of (3.25) is given by

$$\frac{d}{dt}\begin{pmatrix} z_1 \\ z_2 \end{pmatrix} = Df(\bar{x},\bar{y})\begin{pmatrix} z_1 \\ z_2 \end{pmatrix},$$

and

$$Df = \begin{pmatrix} \frac{\partial f_1}{\partial x} & \frac{\partial f_1}{\partial y} \\ \frac{\partial f_2}{\partial x} & \frac{\partial f_2}{\partial y} \end{pmatrix} = \begin{pmatrix} \alpha + \beta y & \beta x \\ \delta y & \gamma + \delta x \end{pmatrix}.$$

We evaluate this matrix at the two steady states, P_1 and P_2. For P_1, we find

$$Df(0,0) = \begin{pmatrix} \alpha & 0 \\ 0 & \gamma \end{pmatrix}, \tag{3.26}$$

which has the two eigenvalues $\lambda_1 = \alpha$ and $\lambda_2 = \gamma$. Similarly for P_2, we find

$$Df\left(-\frac{\gamma}{\delta}, -\frac{\alpha}{\beta}\right) = \begin{pmatrix} 0 & -\frac{\beta\gamma}{\delta} \\ -\frac{\alpha\delta}{\beta} & 0 \end{pmatrix} = A.$$

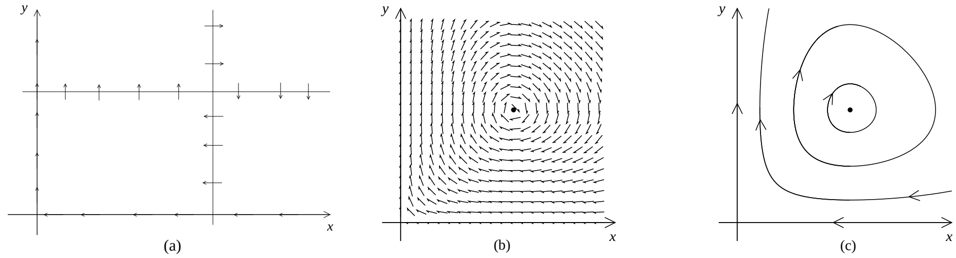

Figure 3.11. *(a) Nullclines; (b) Vector field; and (c) phase portrait for the 2-species model, (3.8), with sign pattern* $(- + + -)$ *(predator-prey).*

Since tr $A = 0$ and det $A = -\alpha\gamma$, formula (3.22) gives that the eigenvalues are given by

$$\lambda_{1/2} = \pm\sqrt{\alpha\gamma}. \tag{3.27}$$

To identify the type of steady states, we need to have more information. In particular, we need to know the signs of the parameters α, β, γ, and δ. Analysis of three specific cases follows.

Case $(- + + -)$: a predator-prey model

We assume that $\alpha < 0$, $\beta > 0$, $\gamma > 0$, and $\delta < 0$. From (3.26), we see that one eigenvalue is negative ($\lambda_1 = \alpha < 0$), and the other eigenvalue is positive ($\lambda_2 = \gamma > 0$). Hence, $P_1 = (0, 0)$ is a saddle.

Before we study $P_2 = \left(-\frac{\gamma}{\delta}, -\frac{\alpha}{\beta}\right)$, we have to ensure that it is *biologically relevant*, i.e., $-\frac{\gamma}{\delta} > 0$ and $-\frac{\alpha}{\beta} > 0$. Since γ, δ and α, β have opposite signs, this is indeed true.

In (3.27), the product $\alpha\gamma < 0$, so that the eigenvalues are purely imaginary, namely

$$\lambda_{1/2} = \pm i\sqrt{|\alpha\gamma|}.$$

Hence $\left(-\frac{\gamma}{\delta}, -\frac{\alpha}{\beta}\right)$ is a center.

Thus, P_2 is not hyperbolic, and the Hartman-Grobman theorem does not apply. We cannot decide the type of steady state: P_2 may be a center, a stable spiral, or an unstable spiral. The theory of Lyapunov functions would help to distinguish between these three possibilities. However, the study of Lyapunov functions is beyond the scope of this text, and we refer to Perko [124]. Accept for now that P_2 is a nonlinear center. The vector field and the phase portrait for the case $(- + + -)$ are shown in Figure 3.11. We observe predator-prey oscillations between periods of high and low population sizes.

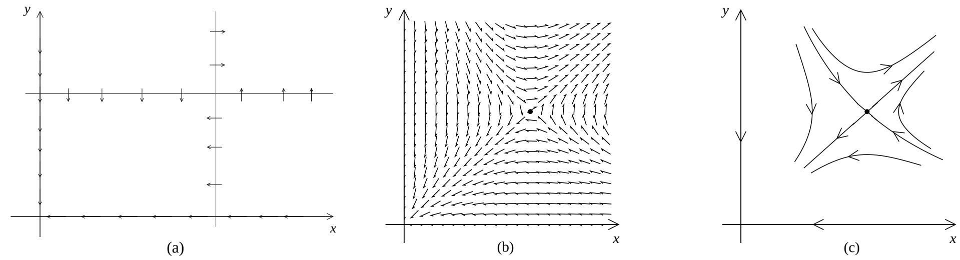

Figure 3.12. *(a) Nullclines; (b) Vector field; and (c) phase portrait for the 2-species model, (3.8), with sign pattern* $(- + -+)$ *(mutualism).*

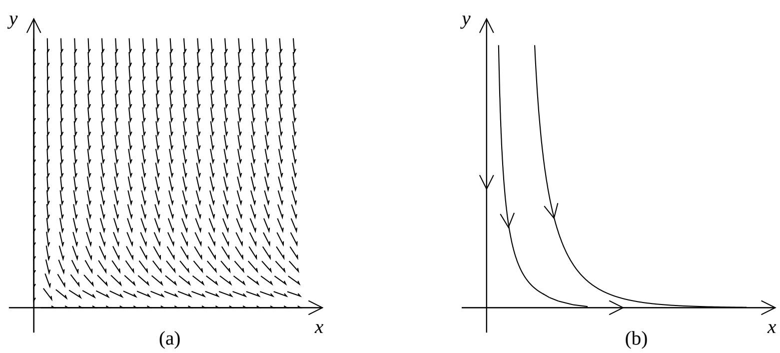

Figure 3.13. *(a) Vector field and (b) phase portrait for the 2-species model, (3.8), with sign pattern* $(+ - --)$ *(competition).*

Case $(- + -+)$**: mutualism of two species which cannot survive alone (**$\alpha < 0$ **and** $\gamma < 0$**)**

The eigenvalues of $Df(0,0)$ are $\alpha < 0$ and $\gamma < 0$ hence $(0,0)$ is a stable node. Also, $-\frac{\alpha}{\beta} > 0$ and $-\frac{\gamma}{\delta} > 0$, hence P_2 is biologically relevant. The product $\alpha\gamma > 0$, hence P_2 is a saddle. The vector field and phase portrait are given in Figure 3.12.

From the phase portrait we see that if the initial populations for x and y are big enough, then both populations can benefit and grow. If one of them is too small initially, then both species go extinct (converge to zero).

Case $(+ - --)$**: a competition model**

In this case $(0,0)$ is a saddle and P_2 is not biologically relevant $(-\frac{\gamma}{\delta} < 0)$. The vector field and phase portrait are given in Figure 3.13. Population y goes extinct while population x can grow without competition.

See Exercise 3.9.11 for the remaining cases.