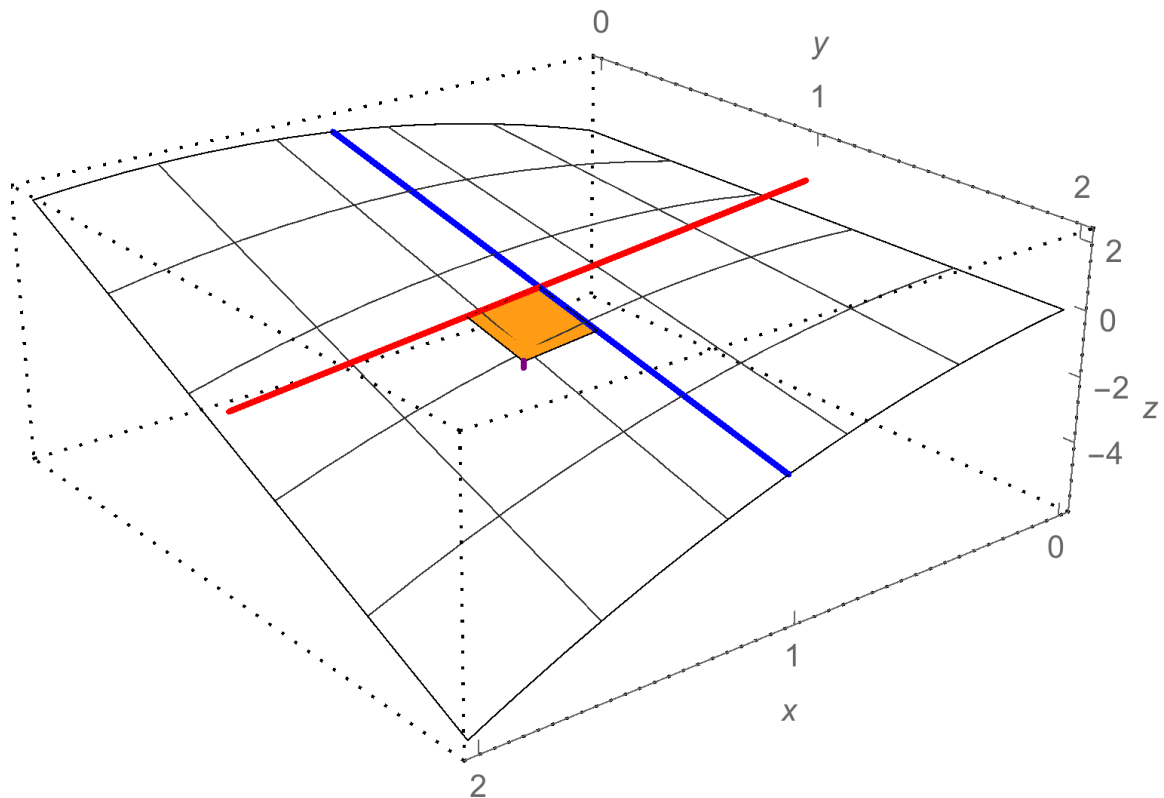


Matrices, Linearization, and the Jacobi matrix



$$\begin{cases} dx/dt = f(x, y) \\ dy/dt = g(x, y) \end{cases} \quad J = \begin{pmatrix} \partial_x f & \partial_y f \\ \partial_x g & \partial_y g \end{pmatrix} \quad \lambda_{1,2} = \frac{\text{tr} \pm \sqrt{\text{tr}^2 - 4 \det}}{2}$$

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Ebook publically available at: <http://tbb.bio.uu.nl/rdb/books/math.pdf>

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Chapter 1

Preface

This reader provides an introduction for the analysis of systems of non-linear differential equations. It starts with introducing the concept of a matrix and its eigenvalues and eigenvectors. Next we show that a linear system of differential equations can be written in a matrix notation, and that its solution can be written as a linear combination of the eigenvalues and eigenvectors of that matrix. Subsequently, we show systems of non-linear ordinary differential equations (ODEs) can be linearized around steady states by taking partial derivatives. Writing these in the form of a matrix the eigenvalues can be used to determine the stability of these equilibrium points.

Finally, we explain an approach to determine these partial derivatives graphically from the vector field in the phase portrait, and provide an introduction to complex numbers (as we regularly encounter complex eigenvalues in systems of ODEs).

This reader was largely compiled from an earlier and more extensive reader called **Mathematics for Biologists** that was written by Alexander Panfilov at the time he was teaching mathematical biology to biology students at Utrecht University. That reader was later adapted by Kirsten ten Tusscher and by Levien van Zon. I shortened and simplified the text in places, made the notation consistent with the reader **Modeling population dynamics**, added Chapter 6, and the examples of the Horn succession model, the Mandelbrot set, and the full linearization of the stable spiral point of the Lotka Volterra model.

August 19, 2016

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Chapter 2

Vectors and Matrices

2.1 Scalars, Vectors and Matrices

Variables that have only one property can be described by a single number, also called a **scalar**. Examples are the number of individuals in a population, N , or the concentration level of a chemical compound in a vessel c . If a variable has several properties, we use a **vector** to describe it (Fig. 2.1). Vectors can be used to describe the forces acting on an object, or the speed and direction with which an object moves, or the number of predators and prey in some area. Mathematically, vectors are written as a row or a column of numbers between brackets, and are thus referred to as either a row or column vector. For example, in a two-dimensional plane in which the force acting on an object has an x -component $V_x = 2$ and an y -component

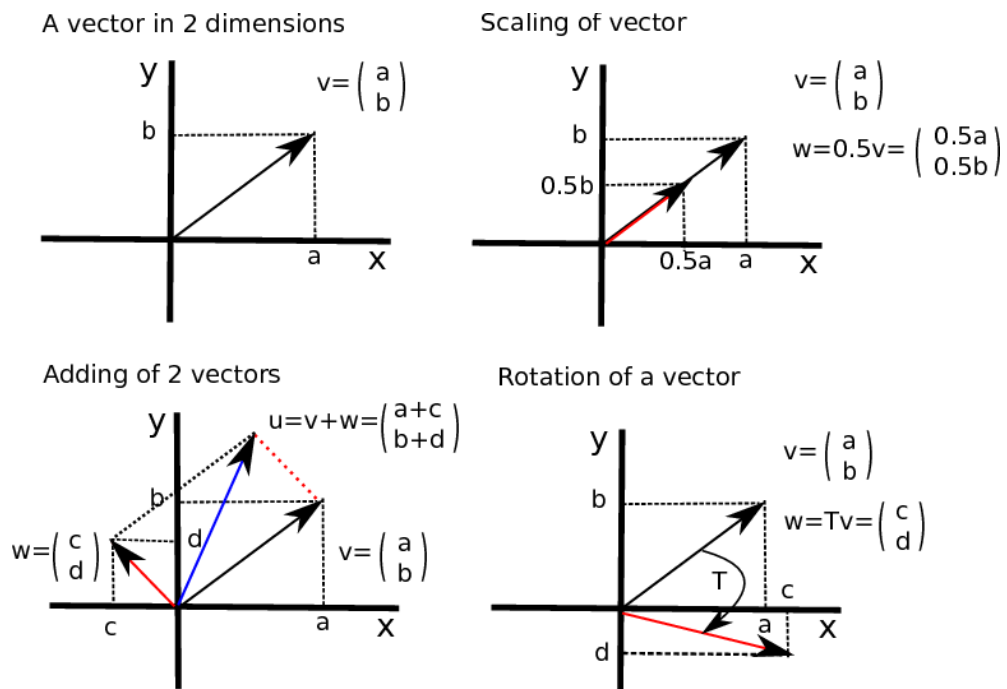


Figure 2.1: Vectors in a 2 dimensional plane: the scaling of a 2D vector, the addition of two 2D vectors, and finally the rotation of a 2D vector by multiplying it with a transformation matrix T .

$V_y = 1$, this force can be represented as:

$$\vec{V} = \begin{pmatrix} 2 \\ 1 \end{pmatrix} \quad \text{or} \quad \vec{V} = (2 \ 1) .$$

The length of the force vector is given by $|\vec{V}| = \sqrt{2^2 + 1^2}$, whereas the direction of the force vector is 2 steps (in a certain unit) in the positive x -direction (to the right) and 1 step in the positive y -direction (upward). The simplest operation that can be performed on a vector is multiplication by a scalar. As the word scalar implies, this simply results in the scaling of the size of the vector, without changing its direction (Fig. 2.1):

$$0.5\vec{V} = 0.5 \begin{pmatrix} 2 \\ 1 \end{pmatrix} = \begin{pmatrix} 0.5 \times 2 \\ 0.5 \times 1 \end{pmatrix} = \begin{pmatrix} 1 \\ 0.5 \end{pmatrix} .$$

An example would be a car that keeps driving in the same direction, but halves its speed.

Another important operation is adding two or more vectors, for example to determine the net resultant force from the sum of all forces acting on an object. Vector addition is achieved by simply adding up the corresponding elements of the different vectors (Fig. 2.1). Addition can only be performed on vectors that are of the same size (same number of elements):

$$\vec{V} + \vec{W} = \begin{pmatrix} 2 \\ 1 \end{pmatrix} + \begin{pmatrix} 1 \\ 3 \end{pmatrix} = \begin{pmatrix} 2+1 \\ 1+3 \end{pmatrix} = \begin{pmatrix} 3 \\ 4 \end{pmatrix} .$$

A more complex operation is the rotation of a vector. Such a rotation can be obtained by multiplying the vector by a so called matrix: $A\vec{V} = \vec{W}$, where \vec{V} is the original vector, \vec{W} is the new resulting vector, and A is the matrix performing the rotation (Fig. 2.1).

Before explaining this in more detail, let us first introduce the concept of a **matrix**. Mathematically speaking, matrices are written as a block of n rows and m columns of numbers, all between brackets:

$$A = \begin{pmatrix} 1 & 4 & 5 \\ 2 & 6 & 10 \end{pmatrix} .$$

This particular matrix A has two rows and three columns, so we say it has a size of 2×3 . Matrices can be used to store and represent data sets. An example would be an experiment in which the expression of a large set of genes is measured over a range of different conditions. By using the rows to represent the different genes and the columns to represent the different conditions, each matrix element would reflect the expression level of a single gene under a particular condition.

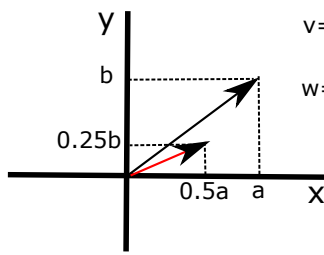
As for vectors, the simplest operation that can be performed on a matrix is the multiplication by a scalar. This is done by multiplying each individual element of the matrix with the scalar. For a general 2×2 matrix this can be written as:

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

A simple example would be the rescaling of experimentally measured fluorescence, in order to find the levels of gene expression for all conditions and genes. A matrix with fluorescence values should then be multiplied by a factor that translates all fluorescence levels into gene expression levels. Like vectors, two matrices A and B can be added up into a new matrix C only if they are of the same size. Both the number of rows and the number of columns should be equal. Matrix addition can then be performed by adding up the corresponding elements of the two matrices:

$$\begin{pmatrix} 1 & 4 & 5 \\ 2 & 6 & 10 \end{pmatrix} + \begin{pmatrix} 2 & 1 & 4 \\ 1 & 3 & 5 \end{pmatrix} = \begin{pmatrix} 1+2 & 4+1 & 5+4 \\ 2+1 & 6+3 & 10+5 \end{pmatrix} = \begin{pmatrix} 3 & 5 & 9 \\ 3 & 9 & 15 \end{pmatrix} .$$

Complex scaling of vector



Shearing of vector parallel to x-axis

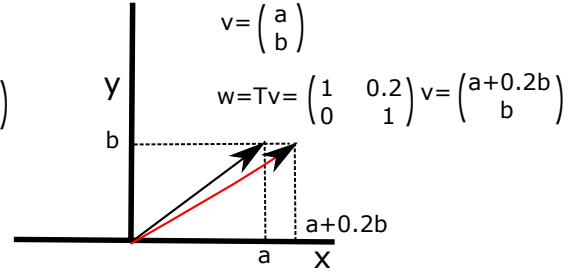


Figure 2.2: Scaling and shearing by matrix transformations of vectors.

For two general 2×2 matrices, this can be written as:

$$\begin{pmatrix} a & b \\ c & d \end{pmatrix} + \begin{pmatrix} x & y \\ z & w \end{pmatrix} = \begin{pmatrix} a+x & b+y \\ c+z & d+w \end{pmatrix}.$$

For the elements in a matrix $C = A + B$, this can be written as:

$$C_{ij} = A_{ij} + B_{ij}.$$

In this notation, C_{ij} means the value in matrix C at row i and column j . A simple example would be a matrix that represents what a shop has in storage, with in the rows different items and in the columns different sizes. In that case the sum of two such matrices would be what two shops have in storage.

Finally, one can multiply a matrix A with a matrix B to obtain a new matrix C (if the number of columns in the first matrix is equal to the number of rows in the second matrix). Matrix multiplication is defined as the products of the rows of the first matrix with the columns of the second matrix. Thus, to find the element in row i and column j of the final matrix we need to multiply the i th row of the first matrix by the j th column of the second matrix¹:

$$C_{ij} = \sum_{k=1}^n A_{ik} B_{kj}.$$

For a product of two 2×2 matrices this gives:

$$\begin{pmatrix} a & b \\ c & d \end{pmatrix} \begin{pmatrix} x & y \\ z & w \end{pmatrix} = \begin{pmatrix} ax + bz & ay + bw \\ cx + dz & cy + dw \end{pmatrix}, \quad (2.1)$$

and from this it follows that multiplication of a matrix by a column vector (simply a matrix with only one column) is given by:

$$\begin{pmatrix} a & b \\ c & d \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix} = \begin{pmatrix} ax + by \\ cx + dy \end{pmatrix}. \quad (2.2)$$

Note that in Eq. (2.1), multiplication with the first matrix A produces a transformation of the second matrix it is multiplied with. In other words, the first matrix is the **transformation**

¹The notation in Eq. (2.1) may require some explanation. The sum-sign \sum basically says: add up a number of expressions, whereby k will be 1 in the first expression, 2 in the second, etcetera, up to $k = n$. In this case, n is the number of columns in the first matrix, and rows in the second. To obtain the value in matrix C , row i , column j , we multiply what is in matrix A , row i , column 1 with the value in matrix B , row 1, column j . We then add to that the product of what is in matrix A , row i , column 2 with the value in matrix B , row 2, column j , and so forth, until we have added the values for all columns and rows.

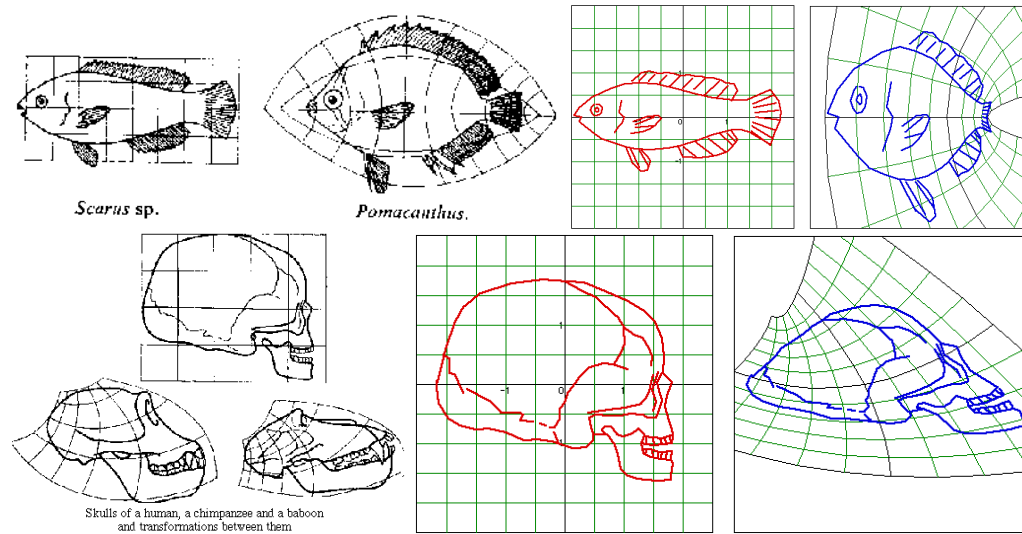


Figure 2.3: On the left the original pictures from “On Growth and Form” by D’Arcy Wentworth Thompson (1942) (which was first published in 1917). On the right pictures from a computer program of the School of Mathematics and Statistics of the University of St. Andrews in Scotland, performing similar shape transformations (<http://www-history.mcs.st-andrews.ac.uk/history/Miscellaneous/darcy.html>). The transformation matrices used apply rotation, scaling and shearing transformations.

matrix, and the second matrix or vector is the one being transformed. Matrix multiplications are not commutative, i.e. $A \times B \neq B \times A$. This means that if the same transformations are applied in a different order, a different outcome will be produced.

A vector can be rotated and/or scaled by a matrix. If we want to scale a vector by a different amount in the x and y directions, this can also be performed by a transformation matrix (see Fig. 2.2):

$$\begin{pmatrix} w_x \\ w_y \end{pmatrix} = \begin{pmatrix} s_x & 0 \\ 0 & s_y \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix}.$$

Similarly, a matrix can be used to apply shearing to a vector. A shear force could stretch a vector is stretched in one direction, e.g., parallel to the x -axis (see Fig. 2.2),

$$\begin{pmatrix} w_x \\ w_y \end{pmatrix} = \begin{pmatrix} 1 & k \\ 0 & 1 \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix}.$$

which results in $w_x = x + ky$ and $w_y = y$.

Note that as matrices can be multiplied with one another to obtain a new matrix, multiplication of rotation, scaling and shearing matrices can result in a single matrix performing a complex transformation. Also note that any point (x, y) on an object can be considered as a vector $\vec{v} = (x \ y)$. Adding these two things up, we can apply complex transformation matrices to objects (basically a collection of points), in order to change them into objects with different orientations, shapes and sizes. This can for example be applied to simulate or deduce the changes in shape and size that occur during development, evolution or growth in animals and plants. Indeed, the famous mathematician and biologist D’Arcy Wentworth Thompson used transformation matrices to show how you could go from the shape of one fish species to that of another fish species, or from the shape of a human skull to the shape of a chimpanzee skull. He called this the theory of transformation, which he described in his 1917 book “On Growth and Form” (see Fig. 2.3 and the re-edited version of the book (Thompson, 1942)).

2.2 Matrices and systems of equations

In this course we will use matrices to write down systems of linear equations. For instance, consider

$$\begin{cases} x - 2y = -5 \\ 2x + y = 10 \end{cases}, \quad (2.3)$$

and write the coefficients in front of x and y in the left hand side as a square matrix:

$$A = \begin{pmatrix} 1 & -2 \\ 2 & 1 \end{pmatrix}.$$

We also have two numbers in the right hand side which we can write as a vector, i.e., $\vec{V} = (-5 \ 10)$. Now if we write x and y as a vector $\vec{X} = (x \ y)$, we can represent the system of Eq. (2.3), using the definition matrix multiplication in Eq. (2.2), as

$$A\vec{X} = \vec{V} \quad \text{or} \quad \begin{pmatrix} 1 & -2 \\ 2 & 1 \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix} = \begin{pmatrix} -5 \\ 10 \end{pmatrix}.$$

What is the solution of this system? From $x - 2y = -5$ we obtain $x = 2y - 5$. Filling this in in $2x + y = 10$ gives us $2(2y - 5) + y = 10$, $4y - 10 + y = 10$, $5y = 20$ so $y = 4$. Filling this back in in $x = 2y - 5$ gives $x = 2 \times 4 - 5 = 8 - 5 = 3$. So the solution is $(x \ y) = (3 \ 4)$.

Let us define the **trace** and **determinant** as two important properties of square matrices. For the 2×2 matrices that we consider in this course these are defined as:

$$\det[A] = \begin{vmatrix} a & b \\ c & d \end{vmatrix} = ad - bc \quad \text{and} \quad \text{tr}[A] = a + d. \quad (2.4)$$

Determinants were invented to study whether a system of linear equations can be solved. It can be shown solutions are only possible when $\det[A] \neq 0$. To see why this is the case consider the following general linear system

$$\begin{cases} ax + by = p \\ cx + dy = q \end{cases}.$$

Start by solving the first equation: $ax + by = p$, i.e., $x = p/a - by/a$. Use this solution to solve the second equation, giving $cp/a - cby/a + dy = q$, and hence $(d - \frac{cb}{a})y = q - \frac{cp}{a}$ or

$$\frac{da - cb}{a}y = \frac{qa - cp}{a} \quad \text{or} \quad y = \frac{qa - cp}{da - cb},$$

which only has a finite solution only if $da - cb$ is not equal to zero. This indeed corresponds to the determinant $ad - cb$ of the matrix defining this linear system, i.e., if the determinant equals zero, there is no solution. Note that we can also determine the determinant of larger square matrices, but their treatment lies outside the scope of this course.

2.3 Forest succession

A famous example of a matrix model in ecology is the model developed by Henry Horn whom studied ecological succession in forests in the USA (Horn, 1975). He recorded the different species of saplings that were present under each species of tree, and assumed that each tree would be replaced by another tree proportional to these sapling densities. Taking time steps of 50 years he also estimated the specific rate of survival of each tree species. This resulted in the following table:

	Gray Birch	Blackgum	Red Maple	Beech
Gray Birch	0.05	0.01	0	0
Blackgum	0.36	0.57	0.14	0.01
Red Maple	0.5	0.25	0.55	0.03
Beech	0.09	0.17	0.31	0.96

with columns summing up to one. Each diagonal element gives the probability that after 50 years a tree is replaced by a tree of the same species (which is the sum of its survival rate (still standing), and the rate of replacement by itself). Each off-diagonal element in this table gives the probability that a particular species is replaced by another species. For example, the fraction of Red Maple trees after 50 years would be 0.5 times the fraction of Gray Birch trees, plus 0.25 times the fraction of Blackgum trees, plus 0.55 times the fraction of Red Maples, plus 0.03 times the fraction of Beech trees. He actually measured several more species, but we give the major four species here for simplicity.

This data can obviously be written as a square matrix:

$$A = \begin{pmatrix} 0.05 & 0.01 & 0 & 0 \\ 0.36 & 0.57 & 0.14 & 0.01 \\ 0.5 & 0.25 & 0.55 & 0.03 \\ 0.09 & 0.17 & 0.31 & 0.96 \end{pmatrix},$$

and the current state of the forest as a column vector, e.g., $\vec{V}_0 = (1 \ 0 \ 0 \ 0)$, which would be a monoculture of just Gray Birch trees. After 50 years the next state of the forest is defined by the multiplication of the initial vector by the matrix:

$$\vec{V}_{50} = A\vec{V}_0 = (0.05 \ 0.36 \ 0.5 \ 0.09) , \quad (2.5)$$

which is a forest with 5% Gray Birch, 36% Blackgum, 50% Red Maple, and 9% Beech trees. Check for yourself that we indeed obey the normal rule of matrix multiplication, and that we obtain the first column of the matrix A because we start with a forest that is just composed of Birch trees. The next state of the forest is

$$\vec{V}_{100} = A\vec{V}_{50} = (0.0061 \ 0.2941 \ 0.3927 \ 0.3071) , \quad (2.6)$$

and so on. This model describes the succession of these types of forest quite realistically (Horn, 1975).

What would we now predict for the ultimate state (climax state) of this forest, and would that depend on the initial vector? Actually, we can already see from the last two equations that after 5000 years, i.e., 100 intervals of 50 years, the state of the forest is given by $\vec{V}_{5000} = A^{100}\vec{V}_0$, where

$$A^{100} = \begin{pmatrix} 0.005 & 0.005 & 0.005 & 0.005 \\ 0.048 & 0.048 & 0.048 & 0.048 \\ 0.085 & 0.085 & 0.085 & 0.085 \\ 0.866 & 0.866 & 0.866 & 0.866 \end{pmatrix}.$$

Now consider an arbitrary vector $\vec{V} = (x \ y \ z \ w)$, where $w = 1 - x - y - z$, and notice that

$$A^{100} \begin{pmatrix} x \\ y \\ z \\ w \end{pmatrix} = \begin{pmatrix} 0.005(x+y+z+w) \\ 0.045(x+y+z+w) \\ 0.085(x+y+z+w) \\ 0.866(x+y+z+w) \end{pmatrix} = \begin{pmatrix} 0.005 \\ 0.045 \\ 0.085 \\ 0.866 \end{pmatrix},$$

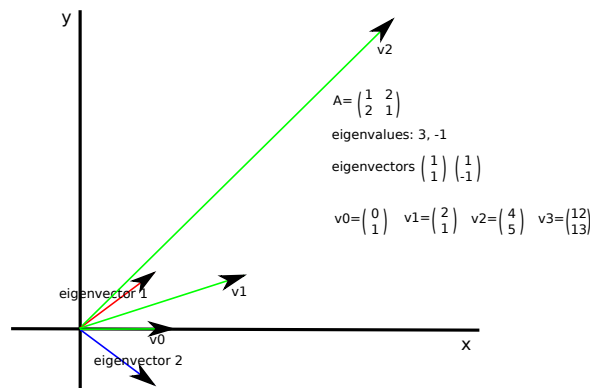


Figure 2.4: Repeated transformation of a vector v_0 by a matrix A produces a vector with a direction closer and closer to the eigenvector of matrix A with the largest eigenvalue.

meaning that the succession converges into climax state. Since all columns of this matrix are identical, we obtain that the state of the forest after 5000 years is independent of the initial vector (because the fractions of the species no longer vary). Next we will show that this climax vector is an eigenvector of the matrix A (i.e., the eigenvector associated with the dominant eigenvalue of A).

2.4 Eigenvalues and eigenvectors

We have learned above that using matrices we can transform vectors, changing both their size and their direction. It turns out that for each particular matrix there exists a set of special vectors called **eigenvectors**. If you apply the matrix to these special eigenvectors, it will only change their size, but not their direction. Note that this is the same effect as when you would multiply the vector with a scalar, so with these special vectors the matrix in fact behaves as a scalar. The factor by which the eigenvector changes size when the matrix is applied to it (you could say the size of the “scalar”), is called the corresponding **eigenvalue**.

Formally, we can write this as follows

$$A\mathbf{v} = \lambda\mathbf{v} . \quad (2.7)$$

which says that for a certain vector \mathbf{v} , application of the transformation matrix A results only in the scaling of this vector by an amount λ . Thus, \mathbf{v} is an eigenvector and λ the corresponding eigenvalue of transformation matrix A . Note that eigenvectors are not unique, in the sense that you can always multiply them by an arbitrary constant k to get another eigenvector:

$$kA\mathbf{v} = k\lambda\mathbf{v} \quad \text{or} \quad A(k\mathbf{v}) = \lambda(k\mathbf{v}) . \quad (2.8)$$

therefore, we can say that $k\mathbf{v}$ is also an eigenvector of Eq. (2.7), corresponding to eigenvalue λ .

What is the use of knowing eigenvalues and eigenvectors of a matrix and hence a system of equations? It can be shown that eigenvectors give the principal directions of change imposed by a matrix, whereas the eigenvalues give the amount of change in each of these directions. Thus, if we know the eigenvector with the largest eigenvalue, we can to a large extent predict the effect of a matrix on a vector, and hence the behavior of the system: it will be rotated into the direction of this dominant eigenvector (see Fig. 2.4). Finding eigenvalues and eigenvectors is one of the most important problems in applied mathematics. It arises in many biological applications, such

as population dynamics, biostatistics, bioinformatics, image processing and many other fields. In this course we will apply it to the solution of systems of differential equations, which we will consider in Chapter 3.

Let us consider how to solve the **eigenvalue problem** for a 2×2 matrix (i.e. how to find the eigenvalues λ and eigenvectors v):

$$A\mathbf{v} = \begin{pmatrix} a & b \\ c & d \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix} = \lambda \begin{pmatrix} x \\ y \end{pmatrix}. \quad (2.9)$$

We can rewrite this as a system of two equations with three unknowns λ, x, y

$$\begin{cases} ax + by = \lambda x \\ cx + dy = \lambda y \end{cases}, \quad (2.10)$$

which can be further rewritten as:

$$\begin{cases} (a - \lambda)x + by = 0 \\ cx + (d - \lambda)y = 0 \end{cases} \quad \text{or in matrix form} \quad \begin{pmatrix} a - \lambda & b \\ c & d - \lambda \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix}. \quad (2.11)$$

This system always has a solution $x = y = 0$. However, eigenvectors are defined to be non-zero vectors, and the $(0 \ 0)$ solution does not correspond to an eigenvector. In order to find non-zero solutions let us multiply the first equation by $d - \lambda$, the second equation by b , and then subtract them. Multiplication gives:

$$\begin{cases} (d - \lambda)[(a - \lambda)x + by] = 0 \\ b[cx + (d - \lambda)y] = 0 \end{cases} \quad \text{or} \quad \begin{cases} (d - \lambda)(a - \lambda)x + (d - \lambda)by = 0 \\ bcx + b(d - \lambda)y = 0 \end{cases}.$$

Subtracting the second equation from the first then gives:

$$(d - \lambda)(a - \lambda)x - bcx + (d - \lambda)by - b(d - \lambda)y = 0 \quad \text{or} \quad [(d - \lambda)(a - \lambda) - bc]x = 0,$$

and given that $v \neq 0$ we obtain

$$(d - \lambda)(a - \lambda) - bc = \lambda^2 - (a + d)\lambda + (ad - cb) = \lambda^2 - \text{tr}\lambda + \det = 0, \quad (2.12)$$

which is a quadratic equation, with two possible solutions λ_1 and λ_2 found using the classical ‘abc’-formula,

$$\lambda_{1,2} = \frac{\text{tr} \pm \sqrt{\text{tr}^2 - 4\det}}{2}. \quad (2.13)$$

In general, for an $n \times n$ matrix there is a maximum of n solutions for λ . Eq. (2.12), or the equivalent Eq. (2.13), is called the **characteristic equation**.

Let us use this approach to find the eigenvalues of the following matrix

$$\begin{pmatrix} 1 & 2 \\ 2 & 1 \end{pmatrix},$$

with $\text{tr} = 2$ and $\det = 1 - 4 = -3$. Using the characteristic equation we write

$$\lambda_{1,2} = \frac{2 \pm \sqrt{4 + 12}}{2} = \frac{2 \pm \sqrt{16}}{2},$$

giving $\lambda_1 = 3$ and $\lambda_2 = -1$. As a next step we have to find the eigenvectors belonging to these two eigenvalues. We can do this by substituting the eigenvalues into the original equations and

solving the equations for x and y . For the eigenvector corresponding to the eigenvalue $\lambda_1 = 3$ we obtain:

$$\begin{cases} (1-3)x + 2y = 0 \\ 2x + (1-3)y = 0 \end{cases} \quad \text{or} \quad \begin{cases} -2x + 2y = 0 \\ 2x - 2y = 0 \end{cases} \quad \text{or} \quad \begin{cases} -2x = -2y \\ 2x = 2y \end{cases} . \quad (2.14)$$

The two equations give us the same solution: $x = y$. This means that if $y = 1$, then $x = 1$, and that $\mathbf{v}_1 = (1 \ 1)$ is an eigenvector corresponding to the eigenvalue $\lambda_1 = 3$. However, we can use any other value for x and hence y as long as $x = y$ is satisfied, which we can write as

$$\begin{pmatrix} x \\ y \end{pmatrix} = k \begin{pmatrix} 1 \\ 1 \end{pmatrix} , \quad (2.15)$$

where k is an arbitrary number. Eq. (2.15) thus gives us all possible solutions of Eq. (2.14). It also illustrates a general property of eigenvectors which we have already proven in Eq. (2.8), namely that if we multiply an eigenvector by an arbitrary number k , we will get another eigenvector of our matrix.

Similarly we can find the eigenvector corresponding to the other eigenvalue $\lambda_2 = -1$:

$$\begin{cases} (1-(-1))x + 2y = 0 \\ 2x + (1-(-1))y = 0 \end{cases} \quad \text{or} \quad \begin{cases} 2x + 2y = 0 \\ 2x + 2y = 0 \end{cases} \quad \text{or} \quad \begin{cases} 2x = -2y \\ 2x = -2y \end{cases} . \quad (2.16)$$

Hence the relation between x and y obeys $x = -y$, and for the eigenvector we could use $\mathbf{v}_2 = (-1 \ 1)$.

Note, that in both cases we could have used the first equation only to find the eigenvectors. In both cases the second equation did not provide any new information. Therefore we derive a simpler method for finding the eigenvectors of a general system (see Eq. (2.10)). Assume we found eigenvalues λ_1 and λ_2 from the characteristic equation, Eq. (2.12). To find the corresponding eigenvectors, we need to substitute the found eigenvalues into the matrix and solve the following system of linear equations (see Eq. (2.11)):

$$\begin{cases} (a - \lambda_1)x + by = 0 \\ cx + (d - \lambda_1)y = 0 \end{cases} \quad (2.17)$$

It is easy to check that the values $x = -b$ and $y = a - \lambda_1$ give the solution of the first equation

$$(a - \lambda_1)x + by = (a - \lambda_1)(-b) + b(a - \lambda_1) = -b(a - \lambda_1) + b(a - \lambda_1) = 0 ,$$

and substituting these expressions into the second equation provides

$$cx + (d - \lambda_1)y = -cb + (d - \lambda_1)(a - \lambda_1) = 0 .$$

To prove that this expression is also zero, note that $(d - \lambda_1)(a - \lambda_1) - cb$ is zero, in accordance with the characteristic equation, Eq. (2.12). Therefore $x = -b$ and $y = a - \lambda_1$ give a solution of Eq. (2.17), which is an eigenvector corresponding to the eigenvalue λ_1 . Similarly we find the eigenvector corresponding to the the eigenvalue λ_2 . This approach will not work if in Eq. (2.11) both $b = 0$ and $a - \lambda = 0$, and then we can use the second equation $cx + (d - \lambda_1)y = 0$, to find an eigenvector as $x = d - \lambda_1$ and $y = -c$. Summarizing, the final formulas are:

$$\mathbf{v}_1 = \begin{pmatrix} -b \\ a - \lambda_1 \end{pmatrix} \ \& \ \mathbf{v}_2 = \begin{pmatrix} -b \\ a - \lambda_2 \end{pmatrix} \quad \text{or} \quad \mathbf{v}_1 = \begin{pmatrix} d - \lambda_1 \\ -c \end{pmatrix} \ \& \ \mathbf{v}_2 = \begin{pmatrix} d - \lambda_2 \\ -c \end{pmatrix} . \quad (2.18)$$

Let us apply this for the example used above, i.e.,

$$A = \begin{pmatrix} 1 & 2 \\ 2 & 1 \end{pmatrix} \quad \text{with eigenvalues} \quad \lambda_1 = 3 \quad \text{and} \quad \lambda_2 = -1 .$$

The eigenvectors can be found from Eq. (2.18) as:

$$\mathbf{v}_1 = \begin{pmatrix} -b \\ a - \lambda_1 \end{pmatrix} = \begin{pmatrix} -2 \\ 1 - 3 \end{pmatrix} = \begin{pmatrix} -2 \\ -2 \end{pmatrix} \quad \text{and} \quad \mathbf{v}_2 = \begin{pmatrix} -2 \\ 1 - (-1) \end{pmatrix} = \begin{pmatrix} -2 \\ 2 \end{pmatrix},$$

which are equivalent to the eigenvectors, $\mathbf{v}_1 = \begin{pmatrix} 1 \\ 1 \end{pmatrix}$ and $\mathbf{v}_2 = \begin{pmatrix} -1 \\ 1 \end{pmatrix}$, that were obtained above.

2.5 Exercises

1. Write the following linear systems in a matrix form $A\vec{X} = \vec{V}$. Find the determinant of matrix A .
 - a. $\begin{cases} 2x - 4y = 3 \\ x + y = 1 \end{cases}$
 - b. $\begin{cases} ax + by = 0 \\ cx + dy = -b \end{cases}$
2. Find eigenvalues and eigenvectors of the following matrices:
 - a. $\begin{pmatrix} -2 & 1 \\ 1 & -2 \end{pmatrix}$
 - b. $\begin{pmatrix} 1 & 4 \\ 1 & 1 \end{pmatrix}$

Chapter 3

Introduction to systems of two differential equations

The general form of a system of two differential equations is:

$$\begin{cases} dx/dt = f(x, y) \\ dy/dt = g(x, y) \end{cases} , \quad (3.1)$$

where $x(t)$ and $y(t)$ are unknown functions of time t , and f and g are functions of both x and y . A linear example of such a system is

$$\begin{cases} dx/dt = ax + by \\ dy/dt = cx + dy \end{cases} , \quad (3.2)$$

and because the above equations only contain linear terms, this is called a **linear system of differential equations**. Depending on the values and signs of the parameters a, b, c, d these equations can describe a range of different processes. Let us consider the specific case $a = -2, b = 1, c = 1, d = -2$:

$$\begin{cases} dx/dt = -2x + y \\ dy/dt = x - 2y \end{cases} \quad (3.3)$$

in this example x and y both decay with a rate -1 , and are converted into one another at a rate 1 (and, hence, have a total loss rate of -2).

3.1 Solutions of Linear 2D Systems

As for one-dimensional systems, it is possible to find analytical solutions for linear two-dimensional systems Eq. (3.2). Rather than deriving this solution for linear 2D systems here, we will simply provide it and illustrate its analogy with the solution of linear one-dimensional systems. For one-dimensional linear systems of the form

$$\frac{dx}{dt} = ax , \quad \text{we know that } x(t) = Ce^{at} , \quad (3.4)$$

is the general solution, where C is an unknown constant depending on the initial value of x (in this case $C = x(0)$). From this equation it follows that for $a > 0$, x approaches infinity

over time, which means that $x = 0$ is an unstable equilibrium. For $a < 0$, x will approach zero, meaning that $x = 0$ is a stable equilibrium (or attractor) of this equation.

In an analogous manner, a two-dimensional system of the form

$$\begin{cases} dx/dt = ax + by \\ dy/dt = cx + dy \end{cases} ,$$

which in matrix notation can be written as

$$\begin{pmatrix} dx/dt \\ dy/dt \end{pmatrix} = \begin{pmatrix} a & b \\ c & d \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix} = A \begin{pmatrix} x \\ y \end{pmatrix} ,$$

has as a general solution

$$\begin{aligned} x(t) &= C_1 x_1 e^{\lambda_1 t} + C_2 x_2 e^{\lambda_2 t} \\ y(t) &= C_1 y_1 e^{\lambda_1 t} + C_2 y_2 e^{\lambda_2 t} , \end{aligned}$$

which in matrix notation can be written as:

$$\begin{pmatrix} x(t) \\ y(t) \end{pmatrix} = C_1 \begin{pmatrix} x_1 \\ y_1 \end{pmatrix} e^{\lambda_1 t} + C_2 \begin{pmatrix} x_2 \\ y_2 \end{pmatrix} e^{\lambda_2 t} , \quad (3.5)$$

where λ_1, λ_2 are the eigenvalues, and $\mathbf{v}_1 = \begin{pmatrix} x_1 \\ y_1 \end{pmatrix}$ and $\mathbf{v}_2 = \begin{pmatrix} x_2 \\ y_2 \end{pmatrix}$ are the eigenvectors of the matrix A . As we saw in Chapter 2, the eigenvectors indicate the major directions of change of the system described by the matrix, and all solutions can be written as a linear combination of the growth along the two eigenvectors. Finally, note that similar to the single unknown C depending on $x(0)$ in the one-dimensional solution of Eq. (3.4), we here have two unknowns C_1 and C_2 depending on the initial values of x and y , i.e., $x(0) = C_1 x_1 + C_2 x_2$ and $y(0) = C_1 y_1 + C_2 y_2$.

Similar to the single exponent a in the solution of one dimensional linear systems, the sign of the two eigenvalues determine the stability of the equilibrium point $(0, 0)$. Note that for the equilibrium point to be stable both exponential parts of the solution need to converge to zero. From this it follows that both eigenvalues need to be smaller than zero. In case of complex valued eigenvalues (see Chapter 7), which occur for spiral and center point equilibria types, the real part of the two eigenvalues needs to be smaller than zero.

Since $x(t)$ and $y(t)$ grow when $\lambda_{1,2} > 0$ we obtain:

- a stable node when both $\lambda_{1,2} < 0$
- an unstable node when both $\lambda_{1,2} > 0$
- an (unstable) saddle point when $\lambda_1 > 0$ and $\lambda_2 < 0$ (or vice versa).

When $\lambda_{1,2}$ are complex, i.e., $\lambda_{1,2} = \alpha \pm i\beta$, we obtain:

- a stable spiral when the real part $\alpha < 0$
- an unstable spiral when the real part $\alpha > 0$
- a neutrally stable center point when the real part $\alpha = 0$.

For example we derive the general solution of the system in Eq. (3.3) for the matrix

$$A = \begin{pmatrix} -2 & 1 \\ 1 & -2 \end{pmatrix} .$$

Since $\text{tr} = -4$ and $\det = 4 - 1 = 3$ we obtain:

$$\lambda_{1,2} = \frac{-4 \pm \sqrt{16 - 12}}{2} = -2 \pm 1 \quad \text{so} \quad \lambda_1 = -1 \quad \text{and} \quad \lambda_2 = -3 .$$

Hence solutions tend to zero and $(x, y) = (0, 0)$ is a stable node. To find the eigenvector v_1 we can now write

$$\mathbf{v}_1 = \begin{pmatrix} -b \\ a - \lambda_1 \end{pmatrix} = \begin{pmatrix} -1 \\ -1 \end{pmatrix} \quad \text{or} \quad v_1 = \begin{pmatrix} 1 \\ 1 \end{pmatrix}.$$

and for v_2 we can write:

$$\mathbf{v}_2 = \begin{pmatrix} -b \\ a - \lambda_2 \end{pmatrix} = \begin{pmatrix} -1 \\ 1 \end{pmatrix}.$$

We write the general solution as

$$\begin{pmatrix} x(t) \\ y(t) \end{pmatrix} = C_1 \begin{pmatrix} 1 \\ 1 \end{pmatrix} e^{-t} + C_2 \begin{pmatrix} -1 \\ 1 \end{pmatrix} e^{-3t} \quad \text{or} \quad \begin{cases} x(t) = C_1 e^{-t} - C_2 e^{-3t} \\ y(t) = C_1 e^{-t} + C_2 e^{-3t} \end{cases}.$$

Note that the integration constants C_1 and C_2 can subsequently be solved from the initial condition, i.e., $x(0) = C_1 - C_2$ and $y(0) = C_1 + C_2$.

3.2 Exercises

1. Find the solution for the following initial value problem:

$$\begin{pmatrix} dx/dt \\ dy/dt \end{pmatrix} = \begin{pmatrix} 1 & -2 \\ 5 & 8 \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix} \quad \text{with} \quad \begin{pmatrix} x(0) \\ y(0) \end{pmatrix} = \begin{pmatrix} 3 \\ -3 \end{pmatrix}$$

Hint: Proceed by first finding the general solution. After that, substitute $t = 0$ and $x(0) = 3$, $y(0) = -3$ to find the values of constants C_1 and C_2 .

2. Two different concentrations of a solution are separated by a membrane through which the solute can diffuse. The rate at which the solute diffuses is proportional to the difference in concentrations between two solutions. The differential equations governing the process are

$$\begin{cases} dA/dt = -\frac{k}{V_1}(A - B) \\ dB/dt = \frac{k}{V_2}(A - B) \end{cases},$$

where A and B are the two concentrations, V_1 and V_2 are the volumes of the respective compartments, and k is the rate constant at which the chemical exchanges between the two compartments. If $V_1 = 20$ liters, $V_2 = 5$ liters, and $k = 0.2$ liters/min and if initially $A = 3$ moles/liter and $B = 0$, find A and B as functions of time. Hint: this exercise is similar to the previous one!

Chapter 4

Linear approximation of non-linear 2D systems

For non-linear systems we typically do not have an analytical solution. In this chapter we will discuss that such a system can be linearized around its steady state, and that we can solve the linearized system analytically. This can be used to establish the stability of that steady state. Close to an equilibrium point, the analytical solution of the approximate linear system approaches the behavior of the original system closely.

Since the derivative of a function $f(x)$ at point \bar{x} can be written as

$$f'(\bar{x}) = \lim_{x \rightarrow \bar{x}} \frac{f(x) - f(\bar{x})}{x - \bar{x}} ,$$

we can use this expression to write a linear approximation of $f(x)$ for x close to \bar{x} , i.e.,

$$f(x) \simeq \bar{x} + f'(\bar{x}) (x - \bar{x}) .$$

Indeed, a two-dimensional function $f(x) = ax^2 + b$ can be represented as a line in a two-dimensional plot, with the value of x on the x -axis and the value of $f(x)$ on the y -axis (see the curved red line in Fig. 4.1a). By taking the derivative of f in a particular point \bar{x} , i.e., $f'(\bar{x})$, we obtain the slope, or tangent line, of the graph of $f(x)$ in point \bar{x} (see the straight blue line in Fig. 4.1a). To explicitly write that we are taking the derivative with respect to x we can also write $f'(\bar{x})$ as $\partial_x f(\bar{x})$, i.e., for $f(x) = ax^2 + b$ we obtain that $\partial_x f(x) = 2ax$. The derivative can be used to approximate the curved $f(x)$ around a particular value \bar{x} . From Fig. 4.1a we can read that

$$f(x) \simeq f(\bar{x}) + \partial_x f(\bar{x}) (x - \bar{x}) ,$$

where $h_x = x - \bar{x}$ is a small step in the x -direction that we multiply with the local slope, $\partial_x f(\bar{x})$, to approximate the required change in the vertical direction. Note that when $h_x \rightarrow 0$ this linear approximation should become extremely good.

4.1 Partial derivatives

Now consider the three-dimensional function $f(x, y) = 3x - x^2 - 2xy$ plotted in Fig. 4.1b with x on the x -axis, y on the y -axis, and the value of the function $f(x, y)$ on the z -axis. The function

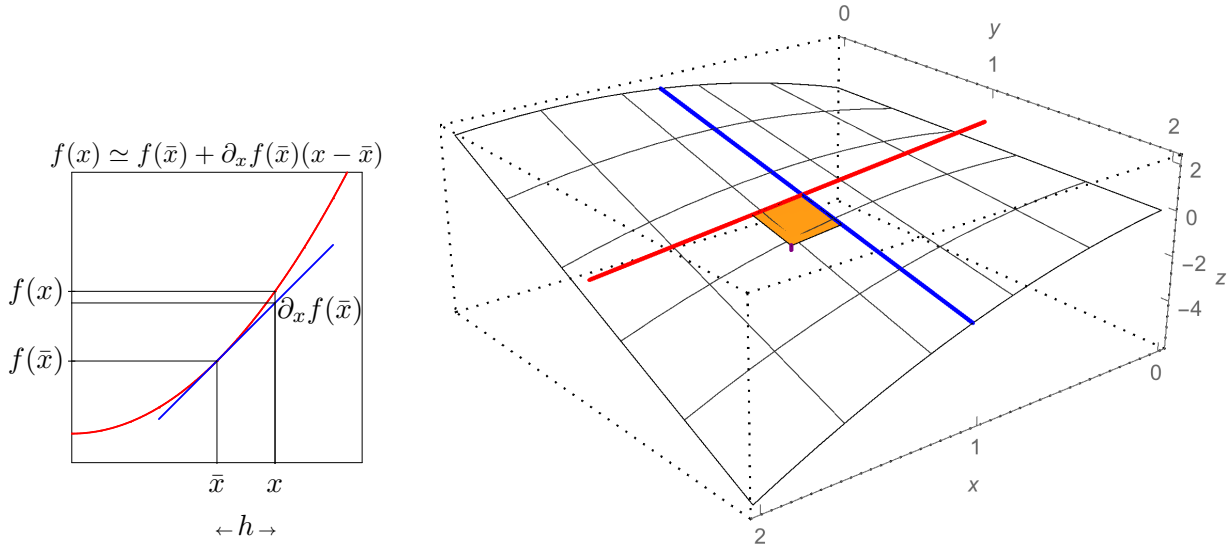


Figure 4.1: On the left we have the function $f(x) = ax^2 + b$ (curved red line) with its local derivative in the point \bar{x} depicted as $\partial_x f(\bar{x}) = 2a\bar{x}$ (straight blue line). On the right we depict the function $f(x, y) = 3x - x^2 - 2xy$, with in the point $(\bar{x}, \bar{y}) = (1, 1)$ its partial derivatives $\partial_x f(x, y) = 3 - 2x - 2y = -1$ and $\partial_y f(x, y) = -2x = -2$, depicted by the heavy red and blue lines, respectively. We approximate the value of $f(1.25, 1.25)$ by these partial derivatives (see the colored small plane), i.e., $f(1.25, 1.25) \simeq f(1, 1) + \partial_x f(1, 1)0.25 + \partial_y f(1, 1)0.25 = -1 \times 0.25 - 2 \times 0.25 = -0.75$. Note that the true value of $f(1.25, 1.25) = -0.9375$, and that the short vertical heavy purple line depicts the distance between the true and the approximated value.

value at the point $(\bar{x}, \bar{y}) = (1, 1)$ is zero, i.e., $f(1, 1) = 3 - 1 - 2 = 0$. We can now linearize the function by differentiating it with respect to x and y , respectively, i.e.,

$$\partial_x f(x, y) = 3 - 2x - 2y \quad \text{and} \quad \partial_y f(x, y) = -2x ,$$

because y is treated as a constant when one differentiates with respect to x , and x is taken as a constant when we take the partial derivative with respect to y . To make this explicit one speaks of **partial derivatives** of the function $f(x, y)$.

These partial derivatives again define the local tangents of the curved function $f(x, y)$. For instance, in the point $(\bar{x} = 1, \bar{y} = 1)$ the slope in the x -direction is $\partial_x f(1, 1) = 3 - 2 \times 1 - 2 \times 1 = -1$ (see the heavy red line in Fig. 4.1b), and the slope in the y -direction is $\partial_y f(1, 1) = -2 \times 1 = -2$ (see the heavy blue line in Fig. 4.1b). We can use these two tangent lines to approximate $f(x, y)$ close to the point (\bar{x}, \bar{y}) , i.e.,

$$f(x, y) \simeq f(\bar{x}, \bar{y}) + \partial_x f(\bar{x}, \bar{y})(x - \bar{x}) + \partial_y f(\bar{x}, \bar{y})(y - \bar{y}) . \quad (4.1)$$

Because $f(\bar{x}, \bar{y}) = f(1, 1) = 0$ the approximation would in this case simplify to

$$f(x, y) \simeq \partial_x f(\bar{x}, \bar{y})(x - \bar{x}) + \partial_y f(\bar{x}, \bar{y})(y - \bar{y}) , \quad (4.2)$$

where again we could write $h_x = x - \bar{x}$ and $h_y = y - \bar{y}$ to define the step sizes in the x -direction and y -direction, respectively. For very small step sizes this should become a very good approximation. For instance, taking a step size $h_x = h_y = 0.25$ we obtain that

$$f(x, y) \simeq -1h_x - 2h_y = -0.25 - 0.5 = -0.75$$

(see the small orange plane in Fig. 4.1). This is close to the true function value $f(1.25, 1.25) = -0.9375$ (the error is depicted by the short vertical purple line in Fig. 4.1).

4.2 Linearization of a system: Jacobian

Consider a general system of two differential equations:

$$\begin{cases} dx/dt = f(x, y) \\ dy/dt = g(x, y) \end{cases}, \quad (4.3)$$

with an equilibrium point at (\bar{x}, \bar{y}) , i.e., $f(\bar{x}, \bar{y}) = 0$ and $g(\bar{x}, \bar{y}) = 0$. Using Eq. (4.2) we find a linear approximation of $f(x, y)$ close to the equilibrium

$$f(x, y) \simeq \partial_x f(\bar{x}, \bar{y})(x - \bar{x}) + \partial_y f(\bar{x}, \bar{y})(y - \bar{y}) = \partial_x f(x - \bar{x}) + \partial_y f(y - \bar{y}), \quad (4.4)$$

where $\partial_x f$ is an abbreviation for the partial derivative at the steady state (\bar{x}, \bar{y}) . A similar approach for $g(x, y)$ yields:

$$g(x, y) \simeq \partial_x g(x - \bar{x}) + \partial_y g(y - \bar{y}). \quad (4.5)$$

If we now replace the right hand sides of Eq. (4.3) by their approximations, Eq. (4.4) and Eq. (4.5), we obtain

$$\begin{cases} dx/dt \simeq \partial_x f(x - \bar{x}) + \partial_y f(y - \bar{y}) \\ dy/dt \simeq \partial_x g(x - \bar{x}) + \partial_y g(y - \bar{y}) \end{cases} \quad (4.6)$$

The system of Eq. (4.6) is simpler than the original system defined by Eq. (4.3), because the partial derivatives in Eq. (4.6) are *real numbers* representing the slope at the equilibrium point (\bar{x}, \bar{y}) . We therefore rewrite Eq. (4.6) into

$$\begin{cases} dx/dt = a(x - \bar{x}) + b(y - \bar{y}) \\ dy/dt = c(x - \bar{x}) + d(y - \bar{y}) \end{cases}, \quad (4.7)$$

where $a = \partial_x f$; $b = \partial_y f$; $c = \partial_x g$ and $d = \partial_y g$. As \bar{x} and \bar{y} are also constants, and hence their derivatives are zero, we can apply a trick and write

$$\frac{dx}{dt} = \frac{dx}{dt} - \frac{d\bar{x}}{dt} = \frac{d(x - \bar{x})}{dt} \quad \text{and} \quad \frac{dy}{dt} = \frac{dy}{dt} - \frac{d\bar{y}}{dt} = \frac{d(y - \bar{y})}{dt}$$

giving

$$\begin{cases} d(x - \bar{x})/dt = a(x - \bar{x}) + b(y - \bar{y}) \\ d(y - \bar{y})/dt = c(x - \bar{x}) + d(y - \bar{y}) \end{cases}. \quad (4.8)$$

Because $x - \bar{x}$ and $y - \bar{y}$ define the distances to the steady state (\bar{x}, \bar{y}) , we can change variables and rewrite this into the distances, $h_x = x - \bar{x}$ and $h_y = y - \bar{y}$, i.e.,

$$\begin{cases} dh_x/dt = ah_x + bh_y \\ dh_y/dt = ch_x + dh_y \end{cases}. \quad (4.9)$$

Since this has the form of a general linear system, we know the solution

$$\begin{pmatrix} h_x(t) \\ h_y(t) \end{pmatrix} = C_1 \begin{pmatrix} x_1 \\ y_1 \end{pmatrix} e^{\lambda_1 t} + C_2 \begin{pmatrix} x_2 \\ y_2 \end{pmatrix} e^{\lambda_2 t},$$

where λ_1 and λ_2 are the eigenvalues of the matrix defined by the four constants in Eq. (4.9), and $\mathbf{v}_1 = \begin{pmatrix} x_1 \\ y_1 \end{pmatrix}$ and $\mathbf{v}_2 = \begin{pmatrix} x_2 \\ y_2 \end{pmatrix}$ are the corresponding eigenvectors. In Chapter 3 we learned that this means that the distances to the steady state decline when $\lambda_{1,2} < 0$. In all other cases small disturbances around the equilibrium will grow.

Summarizing, to determine the behavior of general 2D system Eq. (4.3) around a steady state, we need to determine the values of the partial derivatives in the equilibrium point, which together constitute the matrix defining the linearized system:

$$J = \begin{pmatrix} \partial_x f & \partial_y f \\ \partial_x g & \partial_y g \end{pmatrix} = \begin{pmatrix} a & b \\ c & d \end{pmatrix}. \quad (4.10)$$

This matrix is called **the Jacobian** of system Eq. (4.3) in the point (\bar{x}, \bar{y}) . It allows us to determine the eigenvalues and hence establish the type of the equilibrium type of the original system. The approach we developed here for 2D systems is equally valid for systems composed more than two ODEs. One just obtains a larger Jacobi matrix and computes the dominant eigenvalues of that matrix to establish the stability, and/or type, of the equilibrium point.

4.3 Exercises

1. Find partial derivatives of these functions. After finding derivatives evaluate their value at the given point (if asked).
 - a. $\partial_x z$ and $\partial_y z$ for $z(x, y) = x^2 + y^2 - 4$ at $x = 1; y = 2$
 - b. $\partial_x z$ for $z(x, y) = x(25 - x^2 - y^2)$ at $x = 3; y = 4$
2. Find a linear approximation for the function $f(x, y) = x^2 + y^2$ at $x = 1, y = 1$.
3. Find equilibria of the following non-linear systems, $dx/dt = f(x, y)$ and $dy/dt = g(x, y)$, and find the partial derivatives, $\partial_x f, \partial_y f, \partial_x g$ and $\partial_y g$, at each equilibrium point
 - a. $\begin{cases} dx/dt = -4y \\ dy/dt = 4x - x^2 - 0.5y \end{cases}$
 - b. $\begin{cases} dx/dt = 9x + y^2 \\ dy/dt = x - y \end{cases}$
 - c. $\begin{cases} dx/dt = 2x - xy \\ dy/dt = -y + y^2 x \end{cases}$

Chapter 5

Efficient analysis of 2D ODEs

In the previous chapters we learned how to determine the type and stability of an equilibrium from the original matrix of a linear system, or by determining the Jacobian matrix of a non-linear system in the equilibrium point. From these matrices we computed the eigenvalues to find out which type of equilibrium the system has. In the next section we will demonstrate an efficient method for determining the signs and types of the eigenvalues, and hence the type of equilibrium, from the coefficients of the matrix without actually computing the eigenvalues.

5.1 Determinant-trace method

We have learned in the previous chapters that we can linearize the non-linear functions of any system of differential equations, e.g.,

$$\begin{cases} dx/dt = f(x, y) \\ dy/dt = g(x, y) \end{cases} ,$$

around a steady state (\bar{x}, \bar{y}) into a Jacobian matrix

$$J = \begin{pmatrix} \partial_x f & \partial_y f \\ \partial_x g & \partial_y g \end{pmatrix} = \begin{pmatrix} a & b \\ c & d \end{pmatrix} ,$$

and that the eigenvalues of this matrix are given by

$$\lambda_{1,2} = \frac{\text{tr} \pm \sqrt{D}}{2} \quad \text{where} \quad D = \text{tr}^2 - 4 \det , \quad (5.1)$$

where $\text{tr} = a + b$ and $\det = ad - bc$.

Thus, although the original linearized system depends on four parameters, a, b, c, d , the characteristic equation of Eq. (5.1) depends only on two parameters, $\text{tr}[J]$ and $\det[J]$, and if we know the determinant and the trace of the Jacobian, we can find the eigenvalues, and hence the type of the equilibrium (\bar{x}, \bar{y}) . The solution of Eq. (5.1) are like the roots of any quadratic equation, and can prove that they obey the following expressions

$$\lambda_1 + \lambda_2 = \text{tr}[J] \quad \text{and} \quad \lambda_1 \times \lambda_2 = \det[J] . \quad (5.2)$$

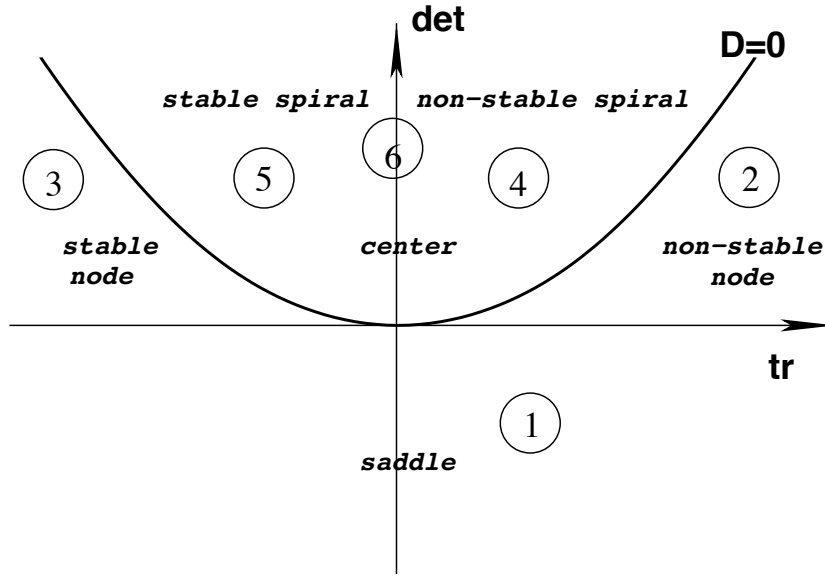


Figure 5.1: The trace and the determinant determine the type of steady state. Plotting the trace, tr , along the horizontal axis and the determinant, det , along the vertical axis, we can plot the parabola where the discriminant $D = 0$. Saddle points (case 1 in the text) corresponds to the lower half of the plane. Stable points (case 3 and 5 in the text) are located in the upper left quadrant, and unstable points (case 2 and 4) in the upper right section. The discriminant depicted by the parabola separates the real from the complex roots. For reasons of completeness we indicate “center points” along the positive part of the vertical axis where $\text{tr}[J] = 0$. Such steady states are neither stable or unstable, i.e., they said to be “neutrally stable”, and occur as bifurcation points (in proper models).

The former is true because $\lambda_1 + \lambda_2 = (\text{tr} + \sqrt{D} + \text{tr} - \sqrt{D})/2$, and the latter can be checked by writing

$$\frac{1}{2}(\text{tr} + \sqrt{D})\frac{1}{2}(\text{tr} - \sqrt{D}) = \frac{1}{4}(\text{tr}^2 - D) = \frac{1}{4}(\text{tr}^2 - \text{tr}^2 + 4\text{det}) = \text{det} .$$

Remember that the steady state is only stable when when both eigenvalues are negative. When $\text{det} > 0$ one knows that either both eigenvalues are negative or that they are both positive (because $\lambda_1 \times \lambda_2 = \text{det}[J]$). Having $\text{det} > 0$ and $\text{tr} < 0$ one knows that they cannot be positive (because $\lambda_1 + \lambda_2 = \text{tr}[J]$), and therefore that they are both negative and the steady state has to be stable. Summarizing a quick test for stability is $\text{tr}[J] < 0$ and $\text{det}[J] > 0$.

Although it is typically sufficient to know whether a steady state is stable or unstable, we can elaborate this somewhat because the signs of the trace, determinant, and discriminant also provide information on the type of the equilibrium (see Fig. 5.1):

1. if $\text{det} < 0$ then $D > 0$, and the eigenvalues are real, with $\lambda_{1,2}$ having an unequal sign: saddle point.
2. if $\text{det} > 0$, $\text{tr} > 0$ and $D > 0$ the eigenvalues are real, with $\lambda_{1,2} > 0$: unstable node.
3. if $\text{det} > 0$, $\text{tr} < 0$ and $D > 0$ the eigenvalues are real, with $\lambda_{1,2} < 0$: stable node.
4. if $\text{det} > 0$, $\text{tr} > 0$ and $D < 0$ the eigenvalues form a complex pair (see Chapter 7),

$$\lambda_{1,2} = \frac{\text{tr}}{2} \pm i \frac{\sqrt{-D}}{2} ,$$

and having a positive trace means that the steady state is an unstable spiral, because the real part of the eigenvalues, $\text{tr}/2$, is positive.

5. if $\det > 0$, $\text{tr} < 0$ and $D < 0$ the eigenvalues form a similar complex pair, but since the real part of the eigenvalues, $-\text{tr}/2$, now is negative, the steady state is a stable spiral point (see Chapter 7).

5.2 Graphical Jacobian

Since the stability of the steady states just depends on the signs of the determinant and the trace of the Jacobi matrix, it is often sufficient to just know the signs of the partial derivatives that make up the Jacobian. Fortunately, the sign of the partial derivatives (+, −, 0) in the equilibrium can be obtained from the vectorfield around the steady state.

The main idea can be seen in Fig. 5.2, where we consider an equilibrium point (\bar{x}, \bar{y}) , at the intersection of the solid $dx/dt = f(x, y) = 0$ nullcline and the dashed $dy/dt = g(x, y) = 0$ nullcline. Since

$$\partial_x f(x, y) \simeq \frac{f(x, y) - f(\bar{x}, y)}{x - \bar{x}} = \frac{f(x + h, y) - f(x, y)}{h},$$

where $h = x - \bar{x}$, is the change in $f(x, y)$ as a consequence of a small increase in x . This is the difference in the $f(x, y)$ value between the original point (\bar{x}, \bar{y}) and a nearby point with a slightly higher x value $(\bar{x} + h, \bar{y})$, divided by the distance $h = x - \bar{x}$ between these two points. Similarly, since $\partial_y f(x, y) \simeq [f(x, y + h) - f(x, y)]/h$, the change in $f(x, y)$ as a function of an increase in y , is the difference in $f(x, y)$ value between the original point (\bar{x}, \bar{y}) and a nearby point with a slightly higher y value $(\bar{x}, \bar{y} + h)$ divided by the distance h between these two points.

In other words

$$J = \begin{pmatrix} \partial_x f \simeq \frac{f(\bar{x} + h, \bar{y}) - f(\bar{x}, \bar{y})}{h} & \partial_y f \simeq \frac{f(\bar{x}, \bar{y} + h) - f(\bar{x}, \bar{y})}{h} \\ \partial_x g \simeq \frac{g(\bar{x} + h, \bar{y}) - g(\bar{x}, \bar{y})}{h} & \partial_y g \simeq \frac{g(\bar{x}, \bar{y} + h) - g(\bar{x}, \bar{y})}{h} \end{pmatrix} = \begin{pmatrix} \alpha & \beta \\ \gamma & \delta \end{pmatrix}, \quad (5.3)$$

with $\text{tr}[J] = \alpha + \delta$ and $\det[J] = \alpha\delta - \beta\gamma$. Obviously, this approximation will be best if the point $(\bar{x} + h, \bar{y})$ and $(\bar{x}, \bar{y} + h)$ is close to the equilibrium point, i.e., if h is small. Since we typically only need to know the signs of the trace and the determinant, it is often sufficient to just obtain the signs of the four elements of the Jacobian. From Eq. (5.3) one can see that the sign of $\partial_x f(x, y)$ is the same as the sign of $f(\bar{x} + h, \bar{y})$, and hence that the sign of the elements of the Jacobi matrix are given by the local vector field around the steady state.

Summarizing, for the steady state (\bar{x}, \bar{y}) we can use the point $(\bar{x} + h, \bar{y})$ (slightly to the right) and the point $(\bar{x}, \bar{y} + h)$ (slightly upward) to determine the partial derivatives (see Fig. 5.2):

- the horizontal vector field, \rightarrow or \leftarrow , gives the sign of $f(x, y)$ in those points, i.e., the horizontal arrow in the point $(\bar{x} + h, \bar{y})$ determines the sign of $\partial_x f(\bar{x}, \bar{y})$, and the horizontal arrow in the point $(\bar{x}, \bar{y} + h)$ determines the sign of $\partial_y f(\bar{x}, \bar{y})$.
- the vertical direction vector, \uparrow or \downarrow , provide the sign of $g(x, y)$, i.e., the vertical arrow in point $(\bar{x} + h, \bar{y})$ determines the sign of $\partial_x g(\bar{x}, \bar{y})$, and the vertical arrow in point $(\bar{x}, \bar{y} + h)$ determines the sign of $\partial_y g(\bar{x}, \bar{y})$.

Indeed in Fig. 5.2a and c we see that the leftward horizontal arrow (\leftarrow) in a point to the right of the equilibrium, $(x + h, y)$, tells us that $\partial_x f(x, y) = \alpha < 0$, and that the horizontal leftward arrow (\leftarrow) in a point above the steady state tells us that $\partial_y f(\bar{x}, \bar{y}) = \beta < 0$. Similarly, the vertical upward arrow (\uparrow) in the point $(\bar{x} + h, \bar{y})$ tells us that $\partial_x g(\bar{x}, \bar{y}) = \gamma > 0$, whereas the downward vertical arrow (\downarrow) in the point $(\bar{x}, \bar{y} + h)$ tells us that $\partial_y g(\bar{x}, \bar{y}) = \delta < 0$.

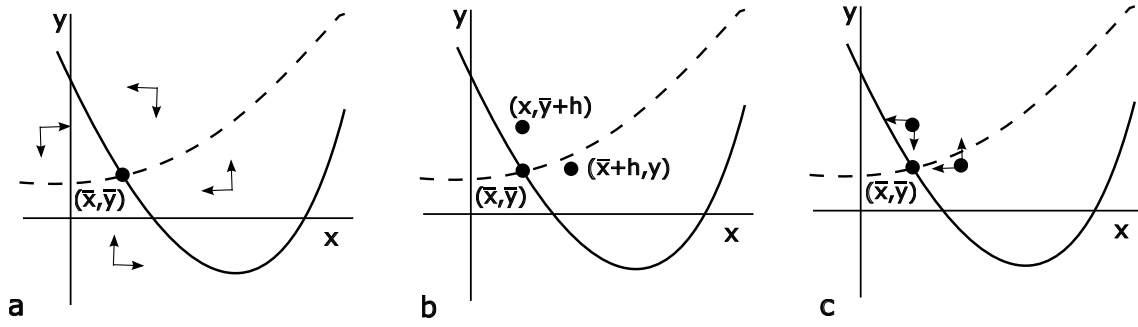


Figure 5.2: The graphical Jacobian method. Panel (a) shows the null-clines, vectorfield, and the location of the equilibrium (\bar{x}, \bar{y}) . Panel (b) shows two reference points, one located slightly to the right $(\bar{x} + h, \bar{y})$, and one located just above $(\bar{x}, \bar{y} + h)$ the equilibrium. These are used to compute the partial derivatives: Panel (c) shows the vector field in these two reference points, i.e., (\leftarrow, \uparrow) and (\leftarrow, \downarrow) , respectively.

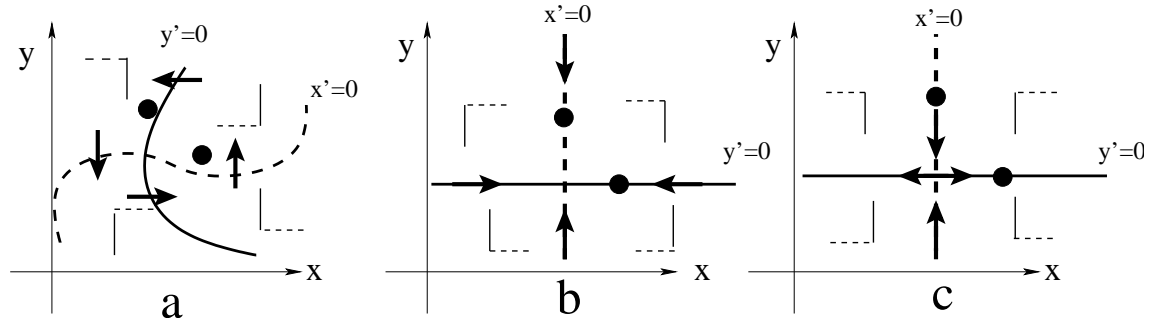


Figure 5.3: A few examples of applying the graphical Jacobian.

Note that a point to the right of the equilibrium will lie on the nullcline if the nullcline is perfectly horizontal, and that $\partial f_x = 0$ (if this were the $dx/dt = f(x, y) = 0$ nullcline) or that $\partial g_x = 0$ (if this would be the $dy/dt = g(x, y) = 0$ nullcline). Similarly, a nullcline is exactly vertical we obtain that either $\partial f_y = 0$ or that $\partial g_y = 0$ (depending on which nullcline one lands).

Consider the examples this graphical approach for the nullclines presented in Fig. 5.3, where the shifted points $(\bar{x} + h, \bar{y})$ and $(\bar{x}, \bar{y} + h)$ are marked by bullets. In Panel

- we find the following Jacobian $J = \begin{pmatrix} -\alpha & -\beta \\ \gamma & -\delta \end{pmatrix}$, with $\text{tr} = -\alpha - \delta < 0$ and $\det = \alpha\delta + \beta\gamma > 0$, implying that this is a stable node or stable spiral. We cannot tell the difference because that depends on the exact values of the partial derivatives,
- we find the Jacobian $J = \begin{pmatrix} -\alpha & 0 \\ 0 & -\delta \end{pmatrix}$, with $\text{tr} = -\alpha - \delta < 0$, $\det = \alpha\delta > 0$, and hence $D = \text{tr}^2 - 4\det = (\alpha + \delta)^2 - 4\alpha\delta = (\alpha - \delta)^2 > 0$. Thus, this is a stable node (which one can also see from the vector field in Fig. 5.3b),
- we find the Jacobian $J = \begin{pmatrix} \alpha & 0 \\ 0 & -\delta \end{pmatrix}$, with $\text{tr} = \alpha - \delta$ having an unknown sign, but because $\det = -\alpha\delta < 0$, we know from Fig. 5.1 that this is a saddle point (which one can also derive from the vector field in Fig. 5.3c).

5.3 Plan of qualitative analysis

We summarize all of the above by formulating a plan to qualitatively study systems of two differential equations:

$$\begin{cases} dx/dt = f(x, y) \\ dy/dt = g(x, y) \end{cases} . \quad (5.4)$$

The main aim is to plot the phase portrait and determine the stability (and possibly the type) of the equilibrium points, such that we can predict the dynamics of the system.

Start with sketching **Nullclines and the vector field**:

1. Decide which variables can most easily be solved from the $f(x, y) = 0$ and $g(x, y) = 0$ expressions, and plot that variable on the vertical axis (and the other on the horizontal axis). Sketch the $f(x, y) = 0$ and $g(x, y) = 0$ nullclines in this phase space (using different colors or line-styles).
2. Choose a point in an “extreme” region (e.g., both variables big, both small, or an asymmetric point) on the x, y plane, and find the local horizontal arrow from $f(x, y)$. Plot the corresponding arrow, i.e., \rightarrow if $f(x, y) > 0$ and \leftarrow if $f(x, y) < 0$, (use the same color or line-style as you used for the $dx/dt = f(x, y) = 0$ nullcline).
3. Check all regions of the phase space and swap the horizontal arrow when crossing this nullcline.
4. Do the same to find the direction of the vertical arrows, i.e., take an extreme point to find the local vertical arrow from $g(x, y)$, and swap this arrow when crossing the $dy/dt = 0$ nullcline.
5. Look at the vector field in the four different regions surrounding each equilibrium point, and see if this provides enough information on stability of the equilibrium.

Should the vector field be insufficient to determine the stability of an equilibrium, we determine the **graphical Jacobian** of the equilibrium point:

1. For each equilibrium point (\bar{x}, \bar{y}) choose two points. One located slightly to the right, $(\bar{x}+h, \bar{y})$, and one slightly above, $(\bar{x}, \bar{y}+h)$, the equilibrium. Find the signs of the Jacobian from the local vector field at these points.
2. Compute the sign of the trace and determinant of this Jacobi matrix, check whether $\text{tr} < 0$ and $\det > 0$, and see if this identifies the type of equilibrium from Fig. 5.1.

Finally, if the stability of the equilibrium can not be determined from the graphical Jacobian, we need to determine the **full Jacobian** by taking the partial derivatives of $f(x, y)$ and $g(x, y)$ at the steady state (\bar{x}, \bar{y})

$$J = \begin{pmatrix} \partial_x f & \partial_y f \\ \partial_x g & \partial_y g \end{pmatrix} = \begin{pmatrix} a & b \\ c & d \end{pmatrix} , \quad (5.5)$$

to solve the eigenvalues of this matrix, i.e.,

$$\lambda_{1,2} = \frac{\text{tr} \pm \sqrt{D}}{2} \quad \text{where} \quad D = \text{tr}^2 - 4 \det , \quad (5.6)$$

and $\text{tr} = a + b$ and $\det = ad - bc$. When both $\lambda_1 < 0$ and $\lambda_2 < 0$ the steady state (\bar{x}, \bar{y}) is stable.

Independent of how we determined the type and stability of the equilibria, we use our knowledge of the type and stability of each equilibrium the vector field and null-clines, to draw a local phase portrait around each equilibrium point. Finally, connecting the different local phase portraits into a global phase portrait we get an idea of the separatrices and the basins of attraction of the attractors.

5.4 Exercises

1. Find the type and stability of the equilibria of the following linear (or linearized) systems using the determinant-trace method:

a. $\begin{cases} dx/dt = 3x + y \\ dy/dt = -20x + 6y \end{cases}$ b. $\begin{cases} dx/dt = 2x + y \\ dy/dt = 2x - 10y \end{cases}$ c. $\begin{cases} dx/dt = 2x + y \\ dy/dt = 5x - 2y \end{cases}$

2. Consider the following model

$$\begin{cases} dx/dt = 2x(1 - y) & x \geq 0; \\ dy/dt = 2 - y - x^2 & y \geq 0. \end{cases}$$

- a. Find all equilibria of the system.
b. Find the general expression for the Jacobian of this system.
c. Determine the type of each equilibrium using the “determinant-trace” method, and sketch the qualitative local phase portraits around each equilibrium point. Try to connect them into a global phase portrait.
3. Study the model of the previous question again using the graphical Jacobian approach:
a. Sketch the vector field for the system using null-clines.
b. Find type and stability of equilibria using the graphical Jacobian.
c. Compare your results to the previous question.

Chapter 6

Lotka Volterra model

Using the famous Lotka Volterra model as an example we review these methods for analyzing systems of non-linear differential equations. The Lotka-Volterra predator prey model can be written as:

$$\frac{dR}{dt} = aR - bR^2 - cRN \quad \text{and} \quad \frac{dN}{dt} = dRN - eN, \quad (6.1)$$

where a, b, c, d , and e are positive constant parameters, and R and N are the prey and predator densities. The derivatives dR/dt and dN/dt define the rate at which the prey and predator densities change in time.

A first step is to sketch nullclines (0-isoclines) in phase space. A nullcline is the set of points (R, N) for which the corresponding population remains constant. Thus, the R -nullcline is the set of points at which $dR/dt = 0$. Setting $dR/dt = 0$ and $dN/dt = 0$ in Eq. (6.1) one finds

$$R = 0, \quad N = \frac{a - bR}{c} \quad \text{and} \quad N = 0, \quad R = \frac{e}{d}, \quad (6.2)$$

for the prey nullclines and the predator nullclines, respectively. These four lines are depicted in Fig. 6.1. For biological reasons we only consider the positive quadrant.

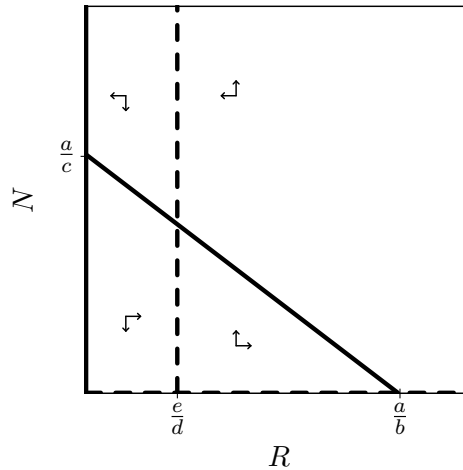


Figure 6.1: The phase space of the Lotka Volterra model with the vector field indicated by the arrows. We here consider the case where the nullclines intersect in a non-trivial equilibrium point, i.e., $e/d < a/b$.

A second step is to determine the vector field. Not knowing the parameter values, one considers extreme points in phase space. In the neighborhood of the point $(R, N) = (0, 0)$, for example, one can neglect the quadratic bR^2 , cRN , and dRN terms, such that

$$\frac{dR}{dt} \simeq aR, \quad \frac{dN}{dt} \simeq -eN. \quad (6.3)$$

Since the former is strictly positive, and the latter strictly negative, we assign $(\rightarrow, \downarrow)$ to the local direction of the vector field (see Fig. 6.1). This means that $dR/dt > 0$ below the R -nullcline, i.e., we sketch arrows to the right, and that at the left hand side of the N -nullclines $dN/dt < 0$, i.e., we sketch arrows pointing to the bottom. At the R and N -nullclines the arrows are vertical and horizontal, respectively. The derivatives switch sign, and the arrows switch their direction, when one passes a nullcline. Nullclines therefore separate the phase space into regions where the derivatives have the same sign.

An important step is to determine the steady states of the system. A steady state, or equilibrium, is defined as $dR/dt = dN/dt = 0$. Graphically steady states are the intersects of the nullclines. Analytically, one finds

$$(R, N) = (0, 0), \quad (R, N) = (a/b, 0) \quad \text{and} \quad (R, N) = \left(\frac{e}{d}, \frac{da - eb}{dc}\right) \quad (6.4)$$

as the three steady states of this system. Note that the non-trivial steady state only exists when $\frac{da - eb}{dc} > 0$. We will further analyze the model for the parameter condition that all three steady states exist, i.e., we consider $da > eb$.

Finally, one has to determine the nature of the steady states. For the steady states $(0, 0)$ and $(a/b, 0)$ one can read from the vector field that they are saddle points. Around $(a/b, 0)$ the vertical component is the unstable direction, and around $(0, 0)$ the horizontal component is the unstable direction. This is not so simple for the non-trivial point. Because there is no stable and unstable direction in the vector field the non-trivial steady state cannot be a saddle point, and it has to be a node or a spiral point. To determine its stability one can check for local feedback. Increasing R in the steady state makes $dR/dt < 0$, and increasing N in the steady state keeps $dN/dt = 0$ because one lands exactly on the $dN/dt = 0$ nullcline (see Fig. 6.1). Because locally there is no positive feedback we expect that the non-trivial steady state is stable.

6.1 Linearization of non-linear ODEs

A more formal technique to determine the stability of steady states is to linearize the differential equations by taking partial derivatives. The linearized system can be solved explicitly, and can be used to predict the long-term behavior in the immediate neighborhood of the steady state. This linearized system is written as a Jacobi matrix, and the local feedback we studied above was basically a trick to obtain the trace elements of the Jacobi matrix; if these are positive the steady state tends to be unstable.

To linearize a 2-dimensional function $f(x, y)$ around an arbitrary point (\bar{x}, \bar{y}) one adopts Eq. (4.1), i.e.,

$$f(x, y) \simeq f(\bar{x}, \bar{y}) + \partial_x f(\bar{x}, \bar{y}) (x - \bar{x}) + \partial_y f(\bar{x}, \bar{y}) (y - \bar{y}). \quad (6.5)$$

or

$$f(x, y) = f(\bar{x} + h_x, \bar{y} + h_y) \simeq f(\bar{x}, \bar{y}) + \partial_x f(\bar{x}, \bar{y}) h_x + \partial_y f(\bar{x}, \bar{y}) h_y, \quad (6.6)$$

where $h_x = x - \bar{x}$ and $h_y = y - \bar{y}$. Thus, for the Lotka Volterra model one defines the functions

$$\frac{dR}{dt} = aR - bR^2 - cRN = f(R, N) \quad \text{and} \quad \frac{dN}{dt} = dRN - eN = g(R, N). \quad (6.7)$$

Next one rewrites the model into two new variables h_R and h_N that define the distance to the steady state (\bar{R}, \bar{N}) . Now one approximates the system $f()$ and $g()$ with

$$\frac{d(\bar{R} + h_R)}{dt} = \frac{dh_R}{dt} = f(\bar{R} + h_R, \bar{N} + h_N) \simeq f(\bar{R}, \bar{N}) + \partial_R f(\bar{R}, \bar{N}) h_R + \partial_N f(\bar{R}, \bar{N}) h_N, \quad (6.8)$$

where $h_R = R - \bar{R}$ and $h_N = N - \bar{N}$. and

$$\frac{d(\bar{N} + h_N)}{dt} = \frac{dh_N}{dt} = g(\bar{R} + h_R, \bar{N} + h_N) \simeq g(\bar{R}, \bar{N}) + \partial_R g(\bar{R}, \bar{N}) h_R + \partial_N g(\bar{R}, \bar{N}) h_N, \quad (6.9)$$

where h_R and h_N define the distance to (\bar{R}, \bar{N}) . Because (\bar{R}, \bar{N}) is an equilibrium point, i.e., $f(\bar{R}, \bar{N}) = 0$ and $g(\bar{R}, \bar{N}) = 0$, this simplifies into

$$\frac{dh_R}{dt} = \partial_R f(\bar{R}, \bar{N}) h_R + \partial_N f(\bar{R}, \bar{N}) h_N, \quad (6.10)$$

and

$$\frac{dh_N}{dt} = \partial_R g(\bar{R}, \bar{N}) h_R + \partial_N g(\bar{R}, \bar{N}) h_N. \quad (6.11)$$

This linearized system describes the growth of a small disturbance (h_R, h_N) around the steady state (\bar{R}, \bar{N}) . If the solutions of this system approach $(h_R, h_N) = (0, 0)$ the steady state is locally stable. The four partial derivatives in the steady state form the so-called Jacobi-matrix,

$$J = \begin{pmatrix} a - 2b\bar{R} - c\bar{N} & -c\bar{R} \\ d\bar{N} & d\bar{R} - e \end{pmatrix}, \quad (6.12)$$

and the general solution of the linear system has the form

$$\begin{pmatrix} h_R(t) \\ h_N(t) \end{pmatrix} = c_1 \begin{pmatrix} R_1 \\ N_1 \end{pmatrix}_1 e^{\lambda_1 t} + c_2 \begin{pmatrix} R_2 \\ N_2 \end{pmatrix}_2 e^{\lambda_2 t}, \quad (6.13)$$

where $\lambda_{1,2}$ are the eigenvalues, and $\mathbf{v}_1 = \begin{pmatrix} R_1 \\ N_1 \end{pmatrix}$ and $\mathbf{v}_2 = \begin{pmatrix} R_2 \\ N_2 \end{pmatrix}$ the corresponding eigenvectors of the Jacobian. One can see that the steady state is stable if, and only if, $\lambda_{1,2} < 0$. Whenever both eigenvalues are negative small disturbances will die out.

To determine the stability of the three steady states, one therefore only needs to know the eigenvalues of the Jacobian (or its trace and determinant). For $(\bar{R}, \bar{N}) = (0, 0)$ one finds

$$J = \begin{pmatrix} a & 0 \\ 0 & -e \end{pmatrix}. \quad (6.14)$$

Because the matrix is in the diagonal form, one can immediately see that the eigenvalues are $\lambda_1 = a$ and $\lambda_2 = -e$. Because $\lambda_1 > 0$ the steady state is unstable, i.e., a saddle point. For $(\bar{R}, \bar{N}) = (a/b, 0)$ one finds

$$J = \begin{pmatrix} -a & -\frac{ac}{b} \\ 0 & \frac{da - eb}{b} \end{pmatrix}. \quad (6.15)$$

The eigenvalues are $\lambda_1 = -a$ and $\lambda_2 = (da - eb)/b$. Because of the requirement $da > eb$ one knows $\lambda_2 > 0$, and hence that the point is not stable. (Note that $(\bar{R}, \bar{N}) = (a/b, 0)$ will

be stable when $da < eb$: to see what happens sketch the nullclines for that situation). For $(\bar{R}, \bar{N}) = (\frac{e}{d}, \frac{da-eb}{dc})$ one obtains

$$J = \begin{pmatrix} -\frac{be}{d} & -\frac{ce}{d} \\ \frac{da-eb}{c} & 0 \end{pmatrix} = \begin{pmatrix} -b\bar{R} & -c\bar{R} \\ d\bar{N} & 0 \end{pmatrix}. \quad (6.16)$$

One finds

$$\text{tr} J = -b\bar{R} < 0 \quad \text{and} \quad \det J = cd\bar{R}\bar{N} > 0, \quad (6.17)$$

which tells us that the steady state is stable. Note that we never filled in numerical values for the parameters in this analysis.

Graphical Jacobian

Consider the vector field around the steady state of some system $dx/dt = f(x, y)$ and $dy/dt = g(x, y)$. Around the steady state (\bar{x}, \bar{y}) in the phase space (x, y) the sign of dx/dt is given by the horizontal arrows, i.e., the horizontal component of the vector field. The sign of $\partial_x f$ can therefore be determined by making a small step to the right, i.e., in the x direction, and reading the sign of dx/dt from the vector field. Similarly, a small step upwards gives the effect of y on dx/dt , i.e., gives $\partial_y f$, and the sign can be read from the vertical arrow of the vector field. Repeating this for $\partial_x g$ and $\partial_y g$, while replacing x, y with R, N , one finds around the steady state $(0, 0)$ in Fig. 6.1:

$$J = \begin{pmatrix} \partial_x f & \partial_y f \\ \partial_x g & \partial_y g \end{pmatrix} = \begin{pmatrix} \alpha & 0 \\ 0 & -\beta \end{pmatrix}, \quad (6.18)$$

where α and β are positive constants. Because $\det(J) = -\alpha\beta < 0$ the steady state is a saddle point (see Fig. 5.1). For the steady state without predators one finds

$$J = \begin{pmatrix} -\alpha & -\beta \\ 0 & \gamma \end{pmatrix}, \quad (6.19)$$

Because $\det(J) = -\alpha\gamma < 0$ the equilibrium is a saddle point. For the non-trivial steady state one finds

$$J = \begin{pmatrix} -\alpha & -\beta \\ \gamma & 0 \end{pmatrix}, \quad (6.20)$$

and because $\text{tr}(J) = -\alpha < 0$ and $\det(J) = \beta\gamma > 0$ the equilibrium is stable. This method is also explained in the book of Hastings (1997).

6.2 Exercises

Determine the stability of the non-trivial equilibrium point of this Lotka Volterra model after setting $b = 0$, i.e., after disallowing for a carrying capacity of the prey.

Chapter 7

Complex Numbers

7.1 Complex numbers

Consider a general quadratic equation

$$a\lambda^2 + b\lambda + c = 0 , \quad (7.1)$$

with roots given by the ‘abc’-formula

$$\lambda_{1,2} = \frac{-b \pm \sqrt{b^2 - 4ac}}{2a} = \frac{-b \pm \sqrt{D}}{2a} \quad \text{where} \quad D = b^2 - 4ac .$$

The value D is called the discriminant. What happens with this equation if $D < 0$? Does the equation still have roots in this case?

You have probably learned that a quadratic equation cannot be solved if $D < 0$. It is indeed true that the equation has no *real* solutions in this case, because the squareroot of a negative number does not exist in any real sense. However, we shall see that even if the solutions are not real numbers, we can still perform calculations with them. In order to do this, so-called complex numbers have been invented, which allow for a solution of Eq. (7.1), even if $D < 0$. Let us define the basic complex number i as:

$$i^2 = -1 \quad \text{or equivalently} \quad i = \sqrt{-1} . \quad (7.2)$$

To see how this works, consider the equation $\lambda^2 = -3$, which does not have a real solution. Given that $i^2 = -1$ we can rewrite this into

$$\lambda^2 = -1 \times 3 = i^2 \times 3 \quad \text{or} \quad \lambda_{1,2} = \pm i\sqrt{3} . \quad (7.3)$$

Here i is the basic complex number, which is similar to ‘1’ for real numbers. In general, the equation $\lambda^2 = -a^2$, has solutions $\lambda_{1,2} = \pm ai$. Although we call ai a complex *number*, it is quite different from the real numbers. Using a complex number ai we cannot count how many books we have in the library, for example. The only meaning of i is that $i^2 = -1$.

A general complex number z can be written as $z = \alpha + i\beta$, where α is called the real part and $i\beta$ is called the imaginary part of the complex number z .

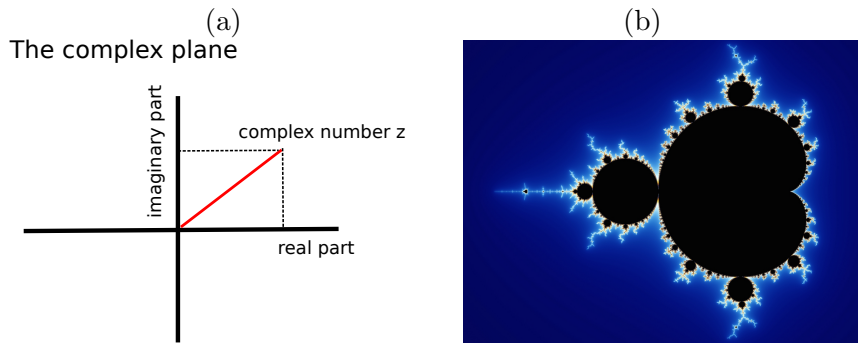


Figure 7.1: Panel (a): complex numbers represented as points or vectors on a complex plane. This is called an Argand diagram. Panel (b): the Mandelbrot set created by the series $z_i = z_{i-1}^2 + z_0$, where z_0 is a point in the Argand diagram, and the color indicates the size of z_n after a fixed number of iterations $i = 1, 2, \dots, n$. This image was taken from Wikipedia.

Now we can solve Eq. (7.1) for the case $D < 0$. If D is negative, then $-D$ must be positive, and we can write $\sqrt{D} = \sqrt{-1} \times \sqrt{-D} = i\sqrt{-D}$, and

$$\lambda_{1,2} = \frac{-b \pm i\sqrt{-D}}{2a} . \quad (7.4)$$

For example, solve the equation $\lambda^2 + 2\lambda + 10 = 0$:

$$\lambda_{1,2} = \frac{-2 \pm \sqrt{4 - 4 \times 10}}{2} = \frac{-2 \pm \sqrt{-36}}{2} = \frac{-2 \pm 6i}{2} . \quad (7.5)$$

In other words, $\lambda_1 = -1 + 3i$ and $\lambda_2 = -1 - 3i$. We see that the solution of this equation forms a complex pair with real part -1 , and imaginary part 3 . Complex numbers that have identical real parts and imaginary parts with opposite signs, are called complex conjugates. The number $z_2 = a - ib$ is called the complex conjugate to the number $z_1 = a + ib$, which it is denoted as $\bar{z}_1 = z_2 = a - ib$. Roots of a quadratic equation with a negative discriminant ($D < 0$) are always complex conjugates to each other.

Complex numbers are often plotted on a complex plane. This is a graph in which the horizontal axis is used for the real part, and the vertical axis is used for the imaginary part of the complex number (see Fig. 7.1a). Note that this is very similar to the depiction of a vector $(x \ y)$, when x and y are real valued numbers on a real plane. In other words, you can think of a complex number $z = \alpha + i\beta$ as a vector $(\alpha \ \beta)$ on a complex plane. Indeed it turns out that scaling, adding and multiplication of complex numbers follow the same rules as for vectors.

Adding two complex numbers is a simple matter of adding their real parts together, and then adding their imaginary parts together. For example, with $z_1 = 3 + 10i$ and $z_2 = -5 + 4i$,

$$z_1 + z_2 = (3 + 10i) + (-5 + 4i) = 3 - 5 + 10i + 4i = -2 + 14i .$$

Note that this is the same as adding two expressions containing a variable (e.g. $(3+10x) + (-5+4x)$). Moreover, if you think of the complex numbers as vectors on a complex plane, addition works the same as it would for normal vectors: $(3 \ 10) + (-5 \ 4) = (-2 \ 14)$. As was already stated, scaling, adding and multiplication of complex numbers follow the same rules as defined for vectors. We only need to remember is that $i^2 = -1$. Thus, multiplication by a real number (a scalar) results in the multiplication of both the real and imaginary parts by this number. For example, if $z_1 = 3 + 10i$ then $10z_1 = 10(3 + 10i) = 30 + 100i$.

Multiplication of two complex numbers is the same as multiplying two expressions that contain a variable (e.g. $(a + bx)(c + dx)$). In the case of complex numbers, the real and imaginary part of the first number should both be multiplied by both the real and imaginary part of the second number. Consider the same examples as before, $z_1 = 3 + 10i$ and $z_2 = -5 + 4i$

$$\begin{aligned} z_1 \times z_2 &= (3 + 10i)(-5 + 4i) = 3(-5) + 3 \times 4i + 10i(-5) + 10i4i = -15 + 12i - 50i + 40i^2 \\ &= -15 - 38i + 40i^2 = -15 - 38i - 40 = -55 - 38i . \end{aligned}$$

Similarly, one can check that $(z_1)^2 = (3 + 10i)^2 = -91 + 60i$. Now that we can do addition and multiplication with complex numbers, we can check that $\lambda_1 = -1 + 3i$ is indeed a solution of the equation in example (7.5). It is just a simple matter of filling in (substituting) λ_1 into the equation

$$\lambda^2 + 2\lambda + 10 = (-1 + 3i)^2 + 2(-1 + 3i) + 10 = 1 - 6i - 9 - 2 + 6i + 10 = 0 .$$

Now that you know how to add and multiply complex numbers, you may be interested to explore the beautiful fractal world of the Mandelbrot set (see Fig. 7.1b and Wikipedia), which contains amazing shapes just created by taking the complex numbers $z_0 = x + yi$ at all positions in a particular area of an Argand diagram, squaring z_0 , and adding the result to the original number, i.e., $z_1 = z_0^2 + z_0$, z_1 is squared again, and added to the original number, and so on i.e., $z_i = z_{i-1}^2 + z_0$ (for $i = 1, 2, \dots, n$).

Dividing two complex numbers is a bit more difficult. For this, we use a little trick to get rid of the imaginary value in the denominator. Remember that you can always multiply both the numerator and the denominator of a fraction with the same expression. The fraction of two complex numbers $\frac{z_1}{z_2}$, can therefore be multiplied with $\frac{\bar{z}_2}{\bar{z}_2} = 1$,

$$\frac{z_1}{z_2} = \frac{z_1 \bar{z}_2}{z_2 \bar{z}_2} , \quad (7.6)$$

which allows us to get rid of the i in the denominator. An example would be

$$\frac{1 + 3i}{1 - 4i} = \frac{1 + 3i}{1 - 4i} \frac{1 + 4i}{1 + 4i} = \frac{(1 + 3i)(1 + 4i)}{1^2 + 4^2} = \frac{1 + 3i + 4i + 12i^2}{17} = \frac{-11 + 7i}{17} = \frac{-11}{17} + \frac{7}{17}i .$$

To see why this works, we can use $|z|$, the absolute value or modulus of a complex number z . If $z = a + ib$, then $|z| = \sqrt{a^2 + b^2}$. Note that this is equal to the length of the vector $(a \ b)$ on the complex plane. You can check for yourself that that $(a + ib)(a - ib) = a^2 + b^2$, which means that $z\bar{z} = |z|^2$. A complex division can therefore also be written as

$$\frac{z_1}{z_2} = \frac{z_1 \bar{z}_2}{z_2 \bar{z}_2} = \frac{z_1 \bar{z}_2}{|z_2|^2} = \frac{(a_1 + b_1 i)(a_2 - b_2 i)}{a_2^2 + b_2^2} .$$

7.2 Complex valued eigenvalues of ODEs

Consider the general linear system of ODEs:

$$\begin{cases} dx/dt = ax + by \\ dy/dt = cx + dy \end{cases} \quad \text{with eigenvalues} \quad \lambda_{1,2} = \frac{\text{tr} \pm \sqrt{D}}{2} ,$$

where $D = \text{tr}^2 - 4\det$, $\text{tr} = a + d$ and $\det = ad - bc$. When the discriminant D is negative we can rewrite the square root as $i\sqrt{-D}$, and hence

$$\lambda_{1,2} = \frac{\text{tr} \pm i\sqrt{-D}}{2} \quad \text{or} \quad \lambda_{1,2} = \alpha \pm i\beta , \quad (7.7)$$

where α and β are the real and the imaginary part of this complex conjugate. The corresponding eigenvectors are also complex,

$$\mathbf{v}_1 = k \begin{pmatrix} -b \\ a - \lambda_1 \end{pmatrix} = k \begin{pmatrix} -b \\ a - (\alpha + i\beta) \end{pmatrix} = k \begin{pmatrix} -b \\ a - \alpha \end{pmatrix} - ik \begin{pmatrix} 0 \\ \beta \end{pmatrix} = k\mathbf{w}_1 - ik\mathbf{w}_2, \quad (7.8)$$

where k is an arbitrary real constant, and $\mathbf{w}_1 = \begin{pmatrix} -b \\ a - \alpha \end{pmatrix}$ and $\mathbf{w}_2 = \begin{pmatrix} 0 \\ \beta \end{pmatrix}$ correspond to the real and imaginary parts of the eigenvector \mathbf{v}_1 . Similarly

$$\mathbf{v}_2 = k \begin{pmatrix} -b \\ a - \lambda_2 \end{pmatrix} = k \begin{pmatrix} -b \\ a - (\alpha - i\beta) \end{pmatrix} = k\mathbf{w}_1 + ik\mathbf{w}_2. \quad (7.9)$$

We can substitute these complex eigenvectors and eigenvalues into the equation for the general solution, i.e.,

$$\begin{pmatrix} x(t) \\ y(t) \end{pmatrix} = C_1(\mathbf{w}_1 - i\mathbf{w}_2)e^{(\alpha+i\beta)t} + C_2(\mathbf{w}_1 + i\mathbf{w}_2)e^{(\alpha-i\beta)t}, \quad (7.10)$$

where the constants k are absorbed into C_1 and C_2 .

It remains quite unclear what this means for the behavior of the solutions. To get an idea about this we need to introduce a new mathematical relationship. Just as we have equations relating trigonometric functions (e.g. $\sin^2 x + \cos^2 x = 1$), or exponential functions (e.g. $e^{a+b} = e^a \times e^b$), there also is a special function relating trigonometric and exponential functions via complex numbers:

$$e^{ix} = \cos x + i \sin x \quad \text{or} \quad e^{-ix} = \cos x - i \sin x. \quad (7.11)$$

This famous equation is called Euler's formula. With this formula we rewrite

$$e^{\alpha+i\beta} = e^\alpha e^{i\beta} = e^\alpha (\cos \beta + i \sin \beta), \quad e^{\alpha-i\beta} = e^\alpha (\cos \beta - i \sin \beta), \quad (7.12)$$

and hence

$$\begin{aligned} \begin{pmatrix} x(t) \\ y(t) \end{pmatrix} &= C_1(\mathbf{w}_1 - i\mathbf{w}_2)e^{\alpha t}(\cos \beta t + i \sin \beta t) + C_2(\mathbf{w}_1 + i\mathbf{w}_2)e^{\alpha t}(\cos \beta t - i \sin \beta t) \\ &= e^{\alpha t} [C_1(\mathbf{w}_1 - i\mathbf{w}_2)(\cos \beta t + i \sin \beta t) + C_2(\mathbf{w}_1 + i\mathbf{w}_2)(\cos \beta t - i \sin \beta t)]. \end{aligned}$$

Note that at this point the general solution would give us both real valued and complex valued x and y values, which is impossible for biological variables. Nevertheless, we can already see that the solutions would tend to zero whenever $\alpha = \text{tr}/2 < 0$, suggesting that a negative trace remains a requirement for stability (see Fig. 5.1). We can learn more about this equation by also considering the initial time point, where $t = 0$, $e^{\alpha t} = 1$, $\cos \beta t = 1$ and $i \sin \beta t = 0$, and where we have the initial condition $(x(0) \ y(0))$, corresponding to two real numbers, i.e.,

$$\begin{aligned} \begin{pmatrix} x(0) \\ y(0) \end{pmatrix} &= C_1(\mathbf{w}_1 - i\mathbf{w}_2) + C_2(\mathbf{w}_1 + i\mathbf{w}_2) \\ &= \mathbf{w}_1(C_1 + C_2) \cos \beta + i\mathbf{w}_2(C_2 - C_1) \cos \beta, \quad \text{or} \end{aligned}$$

$$x(0) = -b(C_1 + C_2) \quad \text{and} \quad y(0) = (a - \alpha)(C_1 + C_2) + i\beta(C_2 - C_1), \quad (7.13)$$

from which one can solve the complex pair C_1 and C_2 satisfying this equation (note that $C_1 + C_2$ should be real, whereas $C_2 - C_1$ should be an imaginary number to cancel the imaginary term in the expression for $y(0)$).

These complex conjugates C_1 and C_2 should also cancel the imaginary parts of the full solution, i.e., the $\mathbf{w}_1 i \sin \beta t$ and the $i\mathbf{w}_2 \cos \beta t$ terms, such that the full solution $(x(t) \ y(t))$ remains real.

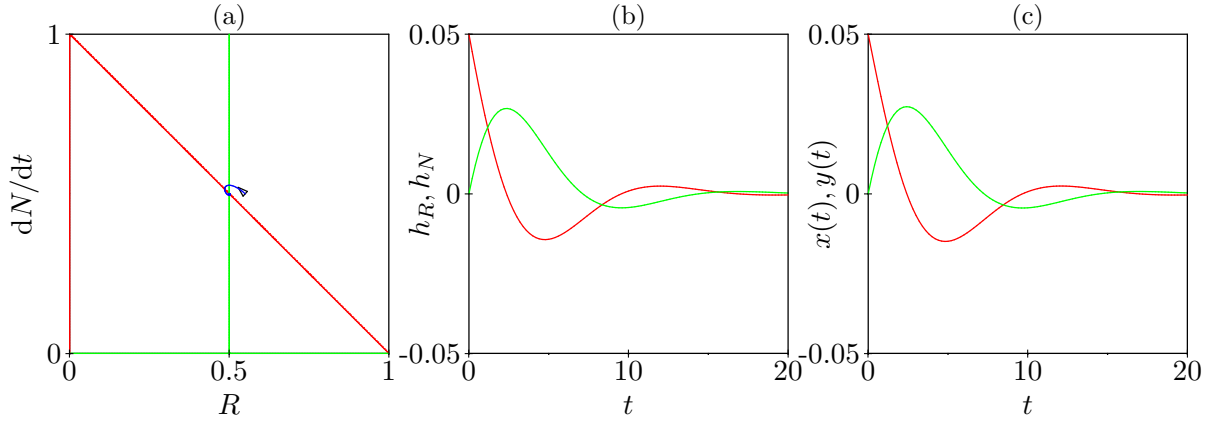


Figure 7.2: The stable spiral point of the Lotka Volterra model. Panel (a) depicts the nullclines with a nontrivial steady state at $\bar{R} = 0.5$ and $\bar{N} = 0.5$. The trajectory starting at $\bar{R} = 0.55$ and $\bar{N} = 0.5$ spirals into the steady state. Panel (b) depicts for this trajectory the distances $h_R = 0.5 - R$ (red) and $h_N = 0.5 - N$ (green) as a function of time. Panel (c) depicts the very similar solution of the linearized model of Eq. (7.14) (red) and Eq. (7.15) (green). Parameters: $a = b = c = d = 1$ and $e = 0.5$.

The remaining $\mathbf{w}_1 \cos \beta t$ and $\mathbf{w}_2 \sin \beta t$ terms define oscillatory behavior of real $x(t)$ and $y(t)$ values, and we see that $1/\beta$ determines the wave length of these oscillations. The real parts of the constants C_1 and C_2 determine their amplitude, and the α parameter in the leading exponential function determines the growth rate of this amplitude. As argued above the oscillations will grow in amplitude when $\alpha > 0$, and will be dampened when $\alpha = \text{tr}/2 < 0$. For complex eigenvalues stability is therefore guaranteed when the trace is negative (see Fig. 5.1).

7.3 Example: the Lotka Volterra model

In Chapter 6 the Lotka-Volterra predator prey model was written as

$$\frac{dR}{dt} = aR - bR^2 - cRN, \quad \frac{dN}{dt} = dRN - eN, \quad \text{with} \quad (\bar{R}, \bar{N}) = \left(\frac{e}{d}, \frac{da - eb}{dc} \right)$$

as the nontrivial steady state, and the Jacobian

$$J = \begin{pmatrix} -\frac{be}{d} & -\frac{ce}{d} \\ \frac{da - eb}{c} & 0 \end{pmatrix} = \begin{pmatrix} -b\bar{R} & -c\bar{R} \\ d\bar{N} & 0 \end{pmatrix}.$$

For $a = b = c = d = 1$ and $e = 0.5$, the nontrivial steady state is at $\bar{R} = 0.5$ and $\bar{N} = 0.5$, and the Jacobian becomes

$$J = \begin{pmatrix} -0.5 & -0.5 \\ 0.5 & 0 \end{pmatrix} \quad \text{with} \quad \text{tr} = -0.5, \quad \det = 0.25, \quad \text{and} \quad D = -0.75,$$

implying that

$$\lambda_{1,2} = \frac{\text{tr} \pm i\sqrt{-D}}{2} \quad \text{or} \quad \lambda_{1,2} = \frac{-0.5 \pm i\sqrt{0.75}}{2} = -0.25 \pm i 0.43.$$

Hence $\alpha = -0.25$ and $\beta = 0.43$, the nontrivial state is stable, has a return time of $-1/\alpha = 4$, and a wave length proportional to $1/\beta$. This is sufficient to classify the steady state as a stable

spiral, which is confirmed in Fig. 7.2 where we start a trajectory at $R(0) = 0.55$ and $N(0) = 0.5$, and observe it spiraling into the steady state $(0.5, 0.5)$.

To illustrate how the solutions become real even if we have complex eigenvalues and eigenvectors, we proceed by studying the linearized solution of this system, starting at the point $R(0) = 0.55$ and $N(0) = 0.5$. Corresponding eigenvectors are

$$\mathbf{v}_1 = \begin{pmatrix} 0.5 \\ -0.5 - \lambda_1 \end{pmatrix} = \begin{pmatrix} 0.5 \\ -0.25 - i0.43 \end{pmatrix} \quad \text{and} \quad \mathbf{v}_2 = \begin{pmatrix} 0.5 \\ -0.5 - \lambda_2 \end{pmatrix} = \begin{pmatrix} 0.5 \\ -0.25 + i0.43 \end{pmatrix} .$$

Hence the general solution for the distance $x = \bar{R} - R(t)$ and $y = \bar{N} - N(t)$ is

$$\begin{pmatrix} x(t) \\ y(t) \end{pmatrix} = e^{-0.25t} [C_1 \mathbf{v}_1 (\cos 0.43t + i \sin 0.43t) + C_2 \mathbf{v}_2 (\cos 0.43t - i \sin 0.43t)] ,$$

or

$$\begin{aligned} x(t) &= e^{-0.25t} [C_1(0.5)(\cos 0.43t + i \sin 0.43t) + C_2(0.5)(\cos 0.43t - i \sin 0.43t)] , \\ &= e^{-0.25t} 0.5[(C_1 + C_2) \cos 0.43t + (C_1 - C_2)i \sin 0.43t] . \end{aligned} \quad (7.14)$$

Similarly, using $i^2 = -1$, we obtain

$$\begin{aligned} y(t) &= e^{-0.25t} [C_1(-0.25 - i0.43)(\cos 0.43t + i \sin 0.43t) + \\ &\quad C_2(-0.25 + i0.43)(\cos 0.43t - i \sin 0.43t)] \\ &= e^{-0.25t} [0.43(C_1 + C_2) \sin 0.43t - 0.25(C_1 + C_2) \cos 0.43t + \\ &\quad i0.25(C_2 - C_1) \sin 0.43t + i0.43(C_2 - C_1) \cos 0.43t] . \end{aligned} \quad (7.15)$$

For the initial condition, where $t = 0$, $e^{-0.25t} = 1$, $\cos 0.43t = 1$, and $\sin 0.43t = 0$, the linearized solution $x(t)$ simplifies into $x(0) = 0.05 = 0.5(C_1 + C_2)$, or $C_1 + C_2 = 0.1$, and $y(t)$ simplifies into $y(0) = 0 = i0.43(C_2 - C_1) - 0.25(C_1 + C_2)$. Together, this delivers $C_1 = 0.05 + i0.029$ and $C_2 = 0.05 - i0.029$. Substituting these two constants into Eq. (7.14) and Eq. (7.15) gives

$$x(t) = e^{-0.25t} [0.05 \cos 0.433t - 0.0289 \sin 0.433t] \quad \text{and} \quad y(t) = e^{-0.25t} 0.0577 \sin 0.433t , \quad (7.16)$$

which is perfectly real, and closely resembles the true approach to the steady state (compare Fig. 7.2b with c).

7.4 Exercises

Find the eigenvalues and eigenvectors of the following matrix $\begin{pmatrix} -1 & 5 \\ -1 & 3 \end{pmatrix}$.

Chapter 8

Answers for exercises

Exercises Chapter 2

1. **a.** $\begin{pmatrix} 2 & -4 \\ 1 & 1 \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix} = \begin{pmatrix} 3 \\ 1 \end{pmatrix}$, $\det = 2 \times 1 - (-4) \times 1 = 2 + 4 = 6$.
b. $\begin{pmatrix} a & b \\ c & d \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix} = \begin{pmatrix} 0 \\ -b \end{pmatrix}$, $\det = ad - bc$.
2. **a.** $\lambda^2 - \text{tr}\lambda + \det = \lambda^2 + 4\lambda + 3 = (\lambda + 3)(\lambda + 1) = 0$
 $\lambda_1 = -1 : \mathbf{v}_1 = k \begin{pmatrix} -1 \\ -2 - (-1) \end{pmatrix} = k \begin{pmatrix} -1 \\ -1 \end{pmatrix}$,
 $\lambda_2 = -3 : \mathbf{v}_2 = k \begin{pmatrix} -1 \\ -2 - (-3) \end{pmatrix} = k \begin{pmatrix} -1 \\ 1 \end{pmatrix}$, where k is an arbitrary number.
b. $\lambda^2 - \text{tr}\lambda + \det = \lambda^2 - 2\lambda - 3$ so $\lambda_{1,2} = \frac{2 \pm \sqrt{2^2 + 4 \times 3}}{2} = \frac{2 \pm \sqrt{16}}{2} = \frac{2 \pm 4}{2} = 1 \pm 2$
 $\lambda_1 = -1 : \mathbf{v}_1 = k \begin{pmatrix} -4 \\ 1 - (-1) \end{pmatrix} = k \begin{pmatrix} -4 \\ 2 \end{pmatrix}$;
 $\lambda_2 = 3 : \mathbf{v}_2 = k \begin{pmatrix} -4 \\ 1 - 3 \end{pmatrix} = k \begin{pmatrix} -4 \\ -2 \end{pmatrix}$, where k is an arbitrary number.

Exercises Chapter 3

1. The eigenvalues of matrix of this system of ODEs are solved from $\lambda^2 - \text{tr}\lambda + \det = \lambda^2 - 9\lambda + 18 = (\lambda - 6)(\lambda - 3) = 0$ so $\lambda_1 = 3$ and $\lambda_2 = 6$. Thus, the eigenvectors are

$$\mathbf{v}_1 = \begin{pmatrix} 2 \\ 1 - 3 \end{pmatrix} = \begin{pmatrix} 2 \\ -2 \end{pmatrix} \text{ and } \mathbf{v}_2 = \begin{pmatrix} 2 \\ 1 - 6 \end{pmatrix} = \begin{pmatrix} 2 \\ -5 \end{pmatrix}.$$

The general solution is

$$\begin{pmatrix} x(t) \\ y(t) \end{pmatrix} = C_1 \begin{pmatrix} 2 \\ -2 \end{pmatrix} e^{3t} + C_2 \begin{pmatrix} 2 \\ -5 \end{pmatrix} e^{6t}.$$

Using the initial condition one substitutes $x(0) = 3$ and $y(0) = -3$ and obtains

$$\begin{pmatrix} 3 \\ -3 \end{pmatrix} = C_1 \begin{pmatrix} 2 \\ -2 \end{pmatrix} e^{3 \times 0} + C_2 \begin{pmatrix} 2 \\ -5 \end{pmatrix} e^{6 \times 0} = \begin{pmatrix} 3 \\ -3 \end{pmatrix} = C_1 \begin{pmatrix} 2 \\ -2 \end{pmatrix} + C_2 \begin{pmatrix} 2 \\ -5 \end{pmatrix}.$$

Writing $3 = C_1 \times 2 + C_2 \times 2$ and $-3 = C_1 \times -2 + C_2 \times -5$, one finds $C_1 = 1.5 - C_2$ from the first equation. Substituting this into the second equation gives

$$-3 = -2(1.5 - C_2) - 5C_2 = -3 + 2C_2 - 5C_2 = -3 - 3C_2 \quad \text{so} \quad C_2 = 0 \quad \text{and} \quad C_1 = 1.5 .$$

Finally we write the solution of the initial value problem as:

$$\begin{pmatrix} x \\ y \end{pmatrix} = 1.5 \begin{pmatrix} 2 \\ -2 \end{pmatrix} e^{3t} .$$

2. We are dealing again with an initial value problem of a linear system here. First write it in the more familiar form

$$\begin{pmatrix} dA/dt \\ dB/dt \end{pmatrix} = \begin{pmatrix} -0.01 & 0.01 \\ 0.04 & -0.04 \end{pmatrix} \begin{pmatrix} A \\ B \end{pmatrix} \quad \text{with} \quad \text{tr} = -0.05 \quad \text{and} \quad \det = 0 .$$

Finding the eigenvalues $\lambda^2 - \text{tr}\lambda + \det = \lambda^2 + 0.05\lambda = \lambda(\lambda + 0.05) = 0$ so $\lambda_1 = 0$ and $\lambda_2 = -0.05$. Thus, the eigenvectors are

$$\mathbf{v}_1 = \begin{pmatrix} -0.01 \\ -0.01 - 0 \end{pmatrix} = \begin{pmatrix} -0.01 \\ -0.01 \end{pmatrix} \quad \text{and} \quad \mathbf{v}_2 = \begin{pmatrix} -0.01 \\ -0.01 - (-0.05) \end{pmatrix} = \begin{pmatrix} -0.01 \\ 0.04 \end{pmatrix} ,$$

and the general solution is

$$\begin{pmatrix} A(t) \\ B(t) \end{pmatrix} = C_1 \begin{pmatrix} -0.01 \\ -0.01 \end{pmatrix} e^{0t} + C_2 \begin{pmatrix} -0.01 \\ 0.04 \end{pmatrix} e^{-0.05t} = C_1 \begin{pmatrix} -0.01 \\ -0.01 \end{pmatrix} + C_2 \begin{pmatrix} -0.01 \\ 0.04 \end{pmatrix} e^{-0.05t} .$$

Using the initial condition by substituting $A(0) = 3$ and $B(0) = 0$ one obtains

$$\begin{pmatrix} 3 \\ 0 \end{pmatrix} = C_1 \begin{pmatrix} -0.01 \\ -0.01 \end{pmatrix} + C_2 \begin{pmatrix} -0.01 \\ 0.04 \end{pmatrix} e^{-0.05 \times 0} = C_1 \begin{pmatrix} -0.01 \\ -0.01 \end{pmatrix} + C_2 \begin{pmatrix} -0.01 \\ 0.04 \end{pmatrix} ,$$

and write $3 = -0.01C_1 - 0.01C_2$ or $300 = -C_1 - C_2$, and $0 = -0.01C_1 + 0.04C_2$ or $0 = -C_1 + 4C_2$. From the first equation we obtain $C_1 = -C_2 - 300$ substituting this into the second equation gives $0 = C_2 + 300 + 4C_2 = 5C_2 + 300$, meaning that $C_2 = -60$ and hence $C_1 = -240$. The solution of the initial value problem is

$$\begin{pmatrix} A(t) \\ B(t) \end{pmatrix} = -240 \begin{pmatrix} -0.01 \\ -0.01 \end{pmatrix} - 60 \begin{pmatrix} -0.01 \\ 0.04 \end{pmatrix} e^{-0.05t}$$

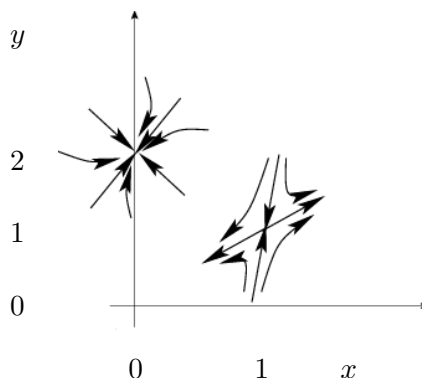
Exercises Chapter 4

- a. $\partial_x z = 2x$ and $\partial_y z = 2y$. At $(x, y) = (1, 2)$ we obtain $\partial_x z = 2$ and $\partial_y z = 4$.
b. $\partial_x z = 25 - 3x^2 - y^2$, which at $(3, 4)$ is -18.
- $f(1, 1) = 2$, $\partial_x f = 2x$ which in $(1, 1)$ also equals 2, $\partial_y f = 2y$ which in $(1, 1)$ also equals 2, hence $f(x, y) \simeq 2 + 2(x - 1) + 2(y - 1) = 2 + 2x - 2 + 2y - 2 = -2 + 2x + 2y$.
- a. $dx/dt = -4y = 0$ gives $y = 0$, and substituting this into dy/dt gives $4x - x^2 = x(4 - x) = 0$, so $x = 0$ or $x = 4$. Thus, the equilibria (\bar{x}, \bar{y}) are $(0, 0)$ and $(4, 0)$. For the Jacobian we take the partial derivatives $\partial_x f = 0$, $\partial_y f = -4$, $\partial_x g = 4 - 2x$, and $\partial_y g = -0.5$. Thus in $(\bar{x}, \bar{y}) = (0, 0)$ we obtain $J = \begin{pmatrix} 0 & -4 \\ 4 & -0.5 \end{pmatrix}$, and in $(\bar{x}, \bar{y}) = (4, 0)$ $J = \begin{pmatrix} 0 & -4 \\ -4 & -0.5 \end{pmatrix}$.

- b. $dy/dt = x - y = 0$ gives $x = y$ substituting this into $dx/dt = 0$ gives us $9x + x^2 = x(9+x) = 0$ so $x = 0$ or $x = -9$. Thus equilibria are $(0, 0)$ and $(-9, -9)$. For the partial derivatives we find $\partial_x f = 9$, $\partial_y = 2y$, $\partial_x g = 1$, and $\partial_y g = -1$. Thus in $(\bar{x}, \bar{y}) = (0, 0)$ we obtain $J = \begin{pmatrix} 9 & 0 \\ 1 & -1 \end{pmatrix}$, and in $(\bar{x}, \bar{y}) = (-9, -9)$ $J = \begin{pmatrix} 9 & -18 \\ 1 & -1 \end{pmatrix}$.
- c. $dx/dt = 2x - xy = x(2 - y) = 0$ gives us $x = 0$ or $y = 2$. Substituting $x = 0$ into $dy/dt = 0$ gives $-y = 0$ or $y = 0$. Substituting $y = 2$ into $dy/dt = 0$ gives us $-2 + 4x = 0$ so $x = 0.5$. So the equilibria are $(0, 0)$ and $(0.5, 2)$. For the partial derivatives we find $\partial_x f = 2 - y$, $\partial_y f = -x$, $\partial_x g = y^2$, $\partial_y g = -1 + 2xy$, meaning that in $(\bar{x}, \bar{y}) = (0, 0)$: $J = \begin{pmatrix} 2 & 0 \\ 0 & -1 \end{pmatrix}$, and in $(\bar{x}, \bar{y}) = (0.5, 2)$ $J = \begin{pmatrix} 0 & -0.5 \\ 4 & 1 \end{pmatrix}$.

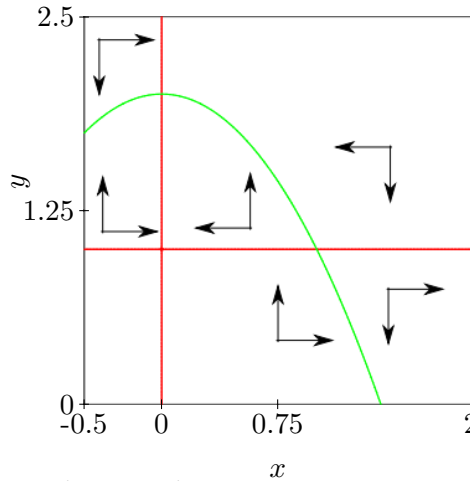
Exercises Chapter 5

- In each system $(\bar{x} = 0, \bar{y} = 0)$ is the steady state. In
 - this is not a saddle point because $\det = 3 \times 6 - 1 \times -20 = 38 > 0$, it is unstable $\text{tr} = 3 + 6 = 9 > 0$, and because $D = \text{tr}^2 - 4\det = 9^2 - 4 \times 38 = 81 - 152 = -71 < 0$, the eigenvalues are complex numbers, and this has to be an unstable spiral.
 - this is a saddle point because $\det = 2 \times -10 - 1 \times 2 = -20 - 2 = -22 < 0$.
 - this is also a saddle point because $\det = 2 \times -2 - 1 \times 5 = -4 - 5 = -9 < 0$.
- $dx/dt = 2x(1 - y) = 0$ gives $x = 0$ or $y = 1$. First substitute $x = 0$ in dy/dt to get $dy/dt = 2 - y = 0$ which gives $y = 2$. Next substitute $y = 1$ in dy/dt to get $dy/dt = 2 - 1 - x^2 = 1 - x^2 = 0$ which gives $x^2 = 1$ and hence $x = 1$ or $x = -1$. Thus, the equilibria are $(0, 2)$, and $(1, 1)$, and note that equilibrium $(-1, 1)$ is not valid as we required $x \geq 0$.
 - Taking $f(x, y) = 2x(1 - y)$ and $g(x, y) = 2 - y - x^2$, the partial derivatives are $\partial_x f = 2(1 - y)$, $\partial_y f = -2x$, $\partial_x g = -2x$ and $\partial_y g = -1$, such that $J = \begin{pmatrix} 2(1 - y) & -2x \\ -2x & -1 \end{pmatrix}$.
 - For $(0, 2)$ we obtain $J = \begin{pmatrix} -2 & 0 \\ 0 & -1 \end{pmatrix}$ with $\det = -2 \times -1 = 2 > 0$ and $\text{tr} = -2 - 1 = -3 < 0$. This point is stable, and because $D = \text{tr}^2 - 4\det = 9 - 4 \times 2 = 9 - 8 = 1 > 0$ it is a stable node. For $(1, 1)$ we obtain $J = \begin{pmatrix} 0 & -2 \\ -2 & -1 \end{pmatrix}$ with $\det = (0 \times -1) - (-2 \times -2) = -4 < 0$, implying that it is a saddle point (which is always unstable):



- $dx/dt = 2x(1 - y) = 0$ gives $x = 0$ or $y = 1$ as the $x' = 0$ nullclines, and

$dy/dt = 2 - y - x^2 = 0$ gives $y = 2 - x^2$ as the $y' = 0$ nullcline. Having no free parameters we can simply fill in numbers here. Let us fill in $x = 2$ and $y = 2$. This gives $dx/dt = 2 \times 2(1 - 2) = 4 \times -1 = -4$ so the vector field points leftward (\leftarrow) and $dy/dt = 2 - 2 - 2^2 = -4$ so the vector field points downward (\downarrow). From this we construct the remainder of the vectorfield:



- b. For $(0, 2)$ we obtain $J = \begin{pmatrix} -\alpha & 0 \\ 0 & -\gamma \end{pmatrix}$ (note that zero in second row occurs because moving to the left for a tiny bit on the horizontal maximum of the parabola lands on the $y' = 0$ nullcline). Hence $\text{tr} = -\alpha - \gamma = -(\alpha + \gamma) < 0$ and $\det = -\alpha \times -\gamma - 0 \times 0 = \alpha \times \gamma > 0$, and the point is stable. We cannot tell whether it is spiral or node. For $(1, 1)$ we obtain $J = \begin{pmatrix} 0 & -\beta \\ -\delta & -\gamma \end{pmatrix}$ with $\det = (0 \times -\gamma) - (-\beta \times -\delta) = -\beta \times \gamma < 0$, implying that this is a saddle (and therefore unstable).
- c. As stated in the text, we find the same answers, except that for the stable equilibrium we can not determine whether it is node or spiral.

Exercises Chapter 6

The model $dR/dt = aR - cRN$ and $dN/dt = dRN - eN$ has the non-trivial steady state $(\bar{R}, \bar{N}) = (e/d, a/c)$. The Jacobian of this steady state is

$$J = \begin{pmatrix} a - c\bar{N} & -c\bar{R} \\ d\bar{N} & d\bar{R} - e \end{pmatrix} = \begin{pmatrix} 0 & -ce/d \\ da/c & 0 \end{pmatrix}, \quad (8.1)$$

with $\text{tr} = 0$ and $\det = ae$ and $D = 0 - 4\det = -4ae$. Because the trace is zero the steady state has a “neutral” stability. The eigenvalues of this matrix are

$$\lambda_{\pm} = \pm \frac{\sqrt{-4ae}}{2} = \pm i \sqrt{ae}. \quad (8.2)$$

Because the eigenvalues have no real part the system is not structurally stable: any small change of the system will either make the equilibrium stable or unstable. The behavior of the model are cycles of neutral stability: any perturbation of the predator or prey densities leads to a new cycle. Because the model is so sensitive to any small change, it is “structurally unstable” and should not be used in a biological context.

Exercises Chapter 7

With $\text{tr} = 2$ and $\det = 2$ we obtain

$$\lambda_{1,2} = \frac{2 \pm \sqrt{2^2 - 4 \times 2}}{2} = \frac{2 \pm i\sqrt{4}}{2} = 1 \pm i$$

For $\lambda_1 = -1 + i$ we obtain

$$\mathbf{v}_1 = k \begin{pmatrix} -b \\ a - \lambda_1 \end{pmatrix} = k \begin{pmatrix} -5 \\ -1 - (1 + i) \end{pmatrix} = k \begin{pmatrix} -5 \\ -2 - i \end{pmatrix} = k \begin{pmatrix} -5 \\ -2 \end{pmatrix} - ik \begin{pmatrix} 0 \\ 1 \end{pmatrix} ,$$

where k is an arbitrary real number. And for $\lambda_2 = -1 - i$ we obtain

$$\mathbf{v}_2 = k \begin{pmatrix} -5 \\ -1 - (1 - i) \end{pmatrix} = k \begin{pmatrix} -5 \\ -2 \end{pmatrix} + ik \begin{pmatrix} 0 \\ 1 \end{pmatrix} ,$$

where k is an arbitrary real number.

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